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Male-male social relationships in a semi-free ranging group of Japanese macaques (Macaca fuscata)

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Abstract

Male non-human primates compete for access to food resources and mating partners. To reduce intensive agonistic interactions dominance hierarchies are often established. Dominance relationships are however not the only relationships male non-human primates form. Males often engage in affiliative interactions with other males as well. While the benefits of male-male affiliative relationships are often questioned they are found in many primate species including Japanese macaques.

The present study compared male dominance hierarchies across several years of a semi-free ranging group of Japanese macaques (*Macaca fuscata*) at the Affenberg Landskron, Austria especially in respect to a fission in March 2020 that split the group and consequently the male hierarchy apart. While social rank and age always correlated in the years before and two years after the fission no correlation was found a year after the fission, indicating that this unique event facilitated the acquisition of a high social rank for some young males.

Furthermore, this study described male-male affiliative relationships by calculating a Composite Sociality Index using proximity and grooming behaviour collected through focal animal sampling and scan sampling. Adult male Japanese macaques of the Affenberg population showed differentiated affiliative relationships with one another. A link between the quantity of affiliative relationships and social rank, but not between the quality of affiliative relationships and current social rank was found.

With assessing both the dominance hierarchy as well as affiliative relationships between males this study sets a base for future long-term studies to investigate how these two factors might influence each other.

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Introduction

Social animals living in groups engage in a series of social interactions with their group members and out-group members. These interactions may vary in content (what they are doing) and quality (how they are doing it) but if they are patterned in time we can refer to them as social relationships (Hinde, 1976). Building and maintaining those social relationships are argued to serve the purpose of increasing an individual's fitness either directly through increasing its own reproductive success or indirectly through increasing a close relative's reproductive success (inclusive fitness) (Cheney et al., 1986; Hamilton, 1964). Through social relationships animals can structure and organize themselves into and within groups.

One way most social-living species structure their group life is by establishing some sort of dominance hierarchy (Strauss et al., 2022). A hierarchy within a group is based on dominance relationships between conspecifics. They were first described by Schjelderup-Ebbe (1922) a hundred years ago (Strauss and Shizuka, 2022). Based on the amount and direction of aggressive encounters (pecking behaviour) between different individuals of domestic chicken he created a "pecking order" which today is more broadly known as a dominance hierarchy (Strauss & Shizuka, 2022). Ever since a growing body of literature regarding this topic has emerged with researchers using different definitions for the same terms. To tackle this issue Drews has published an extensive review and proposed a definition that is applicable to all species based on Schjelderup-Ebbe's initial definition for the pecking order. Therefore, "Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate" (Drews, 1993, p. 308). By sorting the individuals of a group based on dominance relationships an individual's relative position in the hierarchy can be assessed. This relative position is called "rank" or "rank position" (Drews, 1993).

Benefits of high-ranking individuals are argued to be priority of access to food resources and mating partners and therefore increase their fitness (Collias, 1944). In these instances individuals do not have to fight for food and mate access every time anew and consequently reduce intensive agonistic interactions. While dominance is defined through agonism, Schjelderup-Ebbe himself thought of dominance hierarchies as a conflict regulation among members of a group (cited in Strauss and Shizuka, 2022). Studies in rhesus macaques (*Macaca mulatta*) (Bernstein & Mason, 1963), domesticated pigs (*Sus domesticus*) (Meese & Ewbank, 1973) and mice (*Mus Musculus*) (Lee et al., 2019) could show that the amount as well as the intensity of aggression declined after a dominance hierarchy has been established between previously unacquainted individuals showing support for Schjelderup-Ebbe's hypothesis. However, some contradicting studies showed that aggression, access to food and mating success did not correlate

(Gartlan, 1968) and some argued against the above mentioned functions of a dominance hierarchy (Rowell, 1974).

While looking into ultimate explanations like the function of dominance hierarchies and how they evolved is crucial, investigating proximate explanations of dominance hierarchies like the mechanism of acquiring and maintaining one's position in the hierarchy is just as important and complex.

In non-human animals rank acquisition and maintenance can be partially based on individual attributes such as the fighting ability which mainly relates to morphological characteristics but also to physiological and behavioural traits. Another way to acquire and maintain social rank in some non-human animals is through conventions such as maternal rank inheritance, age or tenure within a group (= time an individual spends in a group) (Strauss & Holekamp, 2019). Here the question arises why low-ranking individuals with high fighting ability do not challenge high-ranking individuals with lower fighting ability and therefore ignore the conventions to climb the hierarchy, given that high dominance rank is often argued to be linked with these benefits. A reason why convention based dominance hierarchy formation preserves is that in some social systems the costs of conflict might outweigh the benefits of a high rank (Tibbetts et al., 2022).

Another way social-living species structure their group life is by establishing affiliative relationships. Affiliative behaviour may include grooming, spatial proximity, body contact, social play and food sharing (Jasso del Toro & Nekaris, 2019). While social relationships and therefore affiliative relationships have to be patterned in time as described by Hinde (1976) it is still of interest to further distinguish how social interactions are patterned in time and for how long they persist. We should therefore differentiate between short-term and long-term relationships. For instance, the relationship between sexual partners could last only for the time of courtship and copulation or might be more stable and last for a lifetime as found in monogamous species (Dunbar & Shultz, 2010).

Long-term affiliative relationships (in different contexts) are broadly referred to as social bonds in literature. The most common form of social bonds in mammals are established between a mother and her offspring, followed by a reproductive pair (Curley & Keverne, 2005). However, the lack of biological definitions and conceptual framework for terms like social bonds and even friendships between non-human animals makes it hard to distinguish between these terms (Silk, 2002). In primatology some researchers use the terms social relationships, social bonds and even friendships synonymously while others differentiate between them (reviewed in Silk, 2002). With the argument that "behaving close" and "feeling close" are two distinct concepts, there were attempts to add an individual's internal emotional state into perspective for both social bonds and friendships (Dunbar & Shultz, 2010) or to distinguish between them and ascribe them to friendships only (Silk, 2002). Since measuring internal emotional states in animals presents various challenges and limitations, behavioural indicators are typically used

instead. To keep it comparable with recent literature on this topic, the following definition will be used henceforth: social bonds are differentiated and enduring affiliative relationships that are stable over (different periods in) time (Silk, 2002).

Male-male social bonds were argued to be rare in non-human primates since males not only compete for food resources but also for estruses females, but they were nonetheless found in many species and not just between kin (van Hooff and van Schaik, 1994). Especially in macaque species that live in big multi-male multi-female groups and where therefore male competition seems high, male-male social bonds have been described broadly. The benefits of male-male social bonds have been argued to lie in the formation of coalitions. For Tibetan macaques (*Macaca thibetana*) coalitions among group males helped maintain an allies' rank (Berman et al., 2007). Coalitions among group males even increased an allies' rank in Assamese macaques (*Macaca assamensis*) (Schülke et al., 2010). Yamagiwa (1985) argued that male Japanese macaques (*Macaca fuscata*) formed coalitions to prevent extra-group males from copulating with females. However, critique arose that such results could be a byproduct of the effects of male dominance hierarchy instead (Watts, 2002). More recent findings showed that the formation of coalition is rather predicted by a male's rank than by male-male social bonds in Japanese macaques (Kawazoe, 2020). Male-male social bonds however predicted tolerance instead in Japanese macaques (Kawazoe, 2020).

In macaques much focus has been put on the causes and consequences of either social bonds or of a dominance hierarchy. Only little attempts were made to link them with each other.

Schülke et al. (2010) could show that the quality of a male's social bonds was linked to his future dominance success but did not correlate to his current dominance success in Assamese macaques. Furthermore, they could show that a male's current dominance success did not correlate with his future social bonds. They concluded that there is a causal link between social bonds and dominance rank and not the other way around.

The dominance style of male Assamese macaques has been described as moderately tolerant (Cooper & Bernstein, 2008) along the scale of categories for social styles in macaques (Thierry, 2000, 2022). Tolerant macaque species are characterized by high social tolerance, less bias towards kin and low dominance asymmetries. The most tolerant macaque species are also referred to as "egalitarian". Macaque species on the other side of the scale show low social tolerance, nepotism and high dominance asymmetries. These intolerant macaque species are also referred to as "despotic". Since it was shown that there is a causal link between male social bonds and male dominance rank in a tolerant macaque species like the Assamese macaques it is of interest whether the same holds true in a despotic species.

To gain insight into this question the present study investigated male-male social relationships in Japanese macaques as one of the most despotic species among the

genus *Macaca* alongside the rhesus macaques (Thierry, 2000). Like other macaque species Japanese macaques live in big multi-male multi-female groups with males being the dispersing sex (Fooden & Aimi, 2005). They are promiscuous and their reproduction is strongly seasonal with the mating season being restricted to autumn and winter. For males the mating season is characterised by high competition and reduced grooming between each other in comparison to the non-mating season (Furuichi, 1985; Horiuchi, 2005). Additionally, during the mating season out-group males frequently visit groups to get access to mating partners. Some out-group males succeed in immigrating into a group once the mating season ends especially those that shared affiliation with group males before (Furuichi, 1985; Kawazoe & Sosa, 2019).

The present study investigated a semi-free ranging group of Japanese macaques housed at the "Affenberg Landskron" in Carinthia, Austria. The Affenberg population was of special interest since it underwent a fission in March 2020 resulting in a separation of a previously unified group into two groups (Hammer et al., 2023). This resulted in social instability through the death of several high-ranking females including the alpha female as well the separation of the top-ranking males across the two groups and therefore changes in the male dominance hierarchy. While social instability can be caused by changes in the dominance hierarchy, it can also lead to such (Strauss & Shizuka, 2022). When the group composition changes, either by gain or loss of several individuals or by a separation of one group into two it can come to a destabilization of the dominance hierarchy. Previously taken positions are opened, and entirely new positions emerge. In the wild several cases were reported where out-group males joined fissioning groups at the alpha position (Sprague et al., 1996, 1998). This is rather unusual since the male dominance hierarchy is primarily based on succession in Japanese macaques and changes in the alpha position mostly occur due to death or emigration of the previous alpha male (Sprague et al., 1996). Following male hierarchy formation under these rare circumstances can enable us to investigate male rank acquisition and maintenance and how these mechanisms might be linked to male social bonds.

In the present study the male dominance hierarchy was determined approximately two years after the fission and compared to dominance hierarchies of years before and one year after the fission. It was hypothesized that the group split enabled younger adult males to enter the dominance hierarchy at higher ranking positions similarly to out-group males joining fissioning groups at the top rank (Sprague et al., 1998).

Furthermore, the occurrence and pattern of male-male affiliative interactions were recorded and analysed. It was expected that adult male Japanese macaques of the "Affenberg Landskron" population show proximity and grooming among each other like found in other populations (Furuichi, 1985; Gartland, 2021; Hill, 1994; Horiuchi, 2005; Kawazoe, 2020). Affiliative relationships between males were therefore assessed by calculating a Composite Sociality Index (CSI) (Kawazoe, 2020; Silk et al., 2006, 2013) for all possible male-male dyads using duration of grooming and frequency of proximity. By

doing so this study is the first to describe male-male (short-term) affiliative relationships in the group under investigation. In addition, it was hypothesized that if affiliative relationships between males were found that they would be differentiated and remain across different periods in time such as the mating and non-mating season (Kawazoe, 2020). Due to time constraints during data collection this study refrained from labelling the here described (short-term) affiliative relationships as (long-term) social bonds. Nonetheless, this thesis sets the base for future studies aiming to disentangle the link between social bonds and social rank in male Japanese macaques.

Methods

Study site and subjects

The present study was conducted on a provisioned semi-free ranging population of Japanese macaques (*Macaca fuscata*) living in a 4-hectare natural forest outdoor enclosure at the "Affenberg Landskron" in Carinthia, Austria. The group derived from 38 individuals from the free-ranging Minoh H group in Minoh, Japan who were translocated to Austria in 1996.

The animals are provisioned on a daily basis with a diet consisting of fruits, vegetables and wheat grains in addition to the natural vegetation of the forest they can forage on. Water is available *ad libitum* through a natural stream which runs through the enclosure. The monkeys of the Affenberg Landskron are habituated to the presence of humans since the park is a tourist attraction allowing visitors to enter the enclosure on predefined visitor pathways in the scope of guided tours only. The park is open to visitors annually from April 1st till November 2nd and data was collected both within and outside that period.

The animals are identifiable via individual facial and body features and detailed records of all births and deaths are kept (see Pflüger et al. (2021) for further demographics). As of February 2022 the group consisted of 169 individuals and was composed of 73 sexually matured females (≥ 3.5 years) and 57 sexually matured males (≥ 4.5 years) of which 42 were socio-sexually matured (≥ 8.5 years (Fooden & Aimi, 2005)) and therefore considered adult males. This resulted in a sex ratio of males to females of 1:1.28.

Behavioural observations

Data was collected on adult males between February 1st and May 2nd of 2022 covering parts of both the mating and the non-mating season. The end of the mating season was marked with February 28th (Pflüger et al., 2021). The male's age ranged between 8.5 years and 25.5 years (14.2 ± 4.5 years, mean ± SD). Focal animal sampling (Martin & Bateson, 2007) was used on 30 out of 42 adult males present in the group. Data collected on one of the focal animals was excluded due to severe injury and later isolation for medical treatment of the individual. A focal animal was followed for the duration of 20 minutes a day, counterbalancing between mornings and afternoons to avoid daytime effects. Each individual was followed every third to fourth day. Observation effort was 260 minutes per individual resulting in a total observation time of 125.6 hours. All instances of behaviours listed in the ethogram (see appendix) including agonistic and affiliative behaviours were continuously recorded. Agonistic behaviours included chasing, lunging, physically attacking (grabbing, hitting, biting), threating, staring, displacing, avoiding, fleeing and fear grinning (see Ethogram for detailed definitions for the listed behaviours). The direction and frequency of these aggressive and submissive behaviours as well as the direction and duration of grooming (affiliative behaviour) was recorded.

In addition to the focal sampling, scan sampling (Martin & Bateson, 2007) was used to instantaneously record the proximity of other males within 5 meters to the focal animal in 5 minute intervals during the 20-min focal protocol.

Additionally, all male-male agonistic interactions outside of focal sampling were recorded *ad libitum*.

On ten randomly selected days across the study period "peanut tests" (Koyama, 1973) were conducted and agonistic interactions were recorded during this artificial food-related competition to ensure sufficient amount of agonistic data for calculating a dominance hierarchy.

Data Analysis

Social rank

To assess male social rank the frequency and direction of dyadic agonistic encounters (n = 1005) between all 41 adult males was used. A dominance hierarchy using the approach of Singh et al., (2003) was calculated. This method was created based on data on Japanese macaques and corrects for the possibility of some dyads never encountering each other in an agonistic way. First, for each individual the proportion of wins per partner was calculated by dividing the number of won interactions over one partner by the total amount of interactions with this partner. A value of zero for the proportion of wins means no interactions were won while a value of one means all interactions were won. Secondly, all proportion of wins were summed up per individual resulting in a preliminary so-called "da score" per individual. In a next step, empty cells of dyads that never encountered each other were estimated based on the preliminary da scores of the involved individuals. The probability of A winning over B if they encountered each other was calculated by dividing the preliminary da score of A by the sum of the preliminary da scores of A and B. Lastly, after filling in the empty cells of dyads that never encountered each other all proportion of wins were summed up per individual again resulting in an individual's final da score. The higher the da score of an individual the higher the rank. The scores were later converted into consecutive numbers, with 1 representing the highest rank and the largest number representing the lowest rank. The dominance hierarchy of 2022 was compared to the dominance hierarchies assessed in the years of 2012/2013, 2015, 2016, 2018 and 2021. Dominance hierarchies of those years were provided by the Affenberg Research Station. Furthermore, a linearity index *h* according to Singh et al., (2003) was calculated to assess the strength of the dominance hierarchy of 2022.

Affiliative relationships

To asses male affiliative relationships in 2022 the Composite Sociality Index (CSI) (Kawazoe, 2020; Silk et al., 2006, 2013) was calculated using duration and direction of grooming as well as frequency of proximity for each possible dyad as follows:

$$CSI_{i\to j} = \frac{\left(\frac{GR_{i\to j}}{\bar{G}} + \frac{PR_{ij}}{\bar{P}}\right)}{2} \quad with \quad GR_{i\to j} = \frac{G_{i\to j}}{O_i + O_j} \quad and \quad PR_{ij} = \frac{P_{ij}}{S_i + S_j}$$

The term $GR_{i\to j}$ is the grooming rate for the dyad between the individuals i and j. It is computed by dividing the duration of individual i grooming individual j ($G_{i\to j}$) by the sum of the observation time per individual (O_i, O_j). The term PR_{ij} is the proximity rate for the dyad between the individuals i and j. It is computed by dividing the number of times a dyad was in proximity (within 5 meters) of each other (P_{ij}) by the sum of the number of scans per individual (S_i, S_j). The terms $\bar{G}$ and $\bar{P}$ are the mean rates of grooming and proximity respectively across all possible dyads. The higher the CSI value the stronger the relationship of a dyad. For 754 pairs 1508 $CSI_{i\to j}$ scores were calculated with taking the direction of the interaction into account. Dyads between two focal animals (n = 812) and dyads between a focal animal and a non-focal animal (n = 696) were considered while dyads between two non-focal animals (n = 132) had to be excluded. CSI scores were calculated once for the entire study period and once for the mating and non-mating season separately to see whether there are pairs that form enduring relationships across different periods. The number of male partners across the entire study period for each focal male was assessed. Furthermore, for each focal male the number of enduring male partners was assessed as well.

Statistics

All statistical analyses were performed using R (Version 4.3.3; R Core Team, 2024) and the significance value was set at 0.05. Figures were created using the package “ggplot2” (Wickham, 2016). Descriptive analysis was primarily used to determine the status quo of the dominance hierarchy and male affiliative relationships. Because of the ordinal nature of social rank non-parametric tests were used for further analysis. Spearman correlations were used for analysing the relation between age and social rank across different years, social rank and number of partners, and social rank and strength of the relationship to an individual’s closest partner. Lastly, spearman correlation was used for analysing the relation between social rank and the number of enduring partners over the mating and non-mating season.

Results

Social rank

Agonistic encounters were observed for 51.5% of all dyads (422 out of 820 dyads). The da scores ranged between zero and 38.19 (Table 1). The individual with the highest da score was assigned with rank 1 while the individual with the lowest da score was assigned rank 39. For three individuals no wins were observed resulting in them sharing the same rank. Only 2.6% of 422 observed dyads did not have a constant winner across multiple interactions. The analysis for dominance hierarchy strength showed a linear distribution of ranks across the 41 males with a linearity index of h = 0.77 (Figure 1).

Table 1 Overview of the male dominance hierarchy of 2022 including rank, da score and age at time (February 2022) of all males (n = 41).

Rank	Name	Da score	Age at time	Rank	Name	Da score	Age at time
1	Spooky	38.19	9.5	22	Holgerson	18.75	13.5
2	Wicky	37.47	9.5	23	Swen	18.08	13.5
3	Marco	34.44	19.5	24	Werner	17.65	13.5
4	Augustin	34.16	20.5	25	Funki	17.56	14.5
5	Pauli	33.05	21.5	26	Leo	16.62	12.5
6	Ferdinand	32.33	21.5	27	Heiko	16.56	14.5
7	Double U	31.98	23.5	28	Silvio	15.44	10.5
8	Adrian	31.42	22.5	29	Finn	15.12	8.5
9	Thomas	29.85	13.5	30	Ludwig	14.74	18.5
10	Mickey	28.83	25.5	31	Manfred	14.12	12.5
11	Heinz	28.52	11.5	32	Lupo	13.84	12.5
12	Kuddl Muddl	26.55	10.5	33	Bernhard	11.45	9.5
13	Nico	26.15	13.5	34	Coco	11.25	12.5
14	Aaron	25.99	11.5	35	Karl	7.57	13.5
15	Jackson	25.20	12.5	36	Lorenz	6.12	8.5
16	Franziskus	24.62	11.5	37	Siegfried	5.93	11.5
17	Rupi	22.91	10.5	38	Momo	3.83	12.5
18	William	21.70	10.5	39	Aiko	0.00	10.5
19	Karl-Vinzenz	20.84	21.5	39	Chris Cross	0.00	8.5
20	Gustav	19.33	19.5	39	Toby	0.00	14.5
21	Dieter	18.83	13.5				

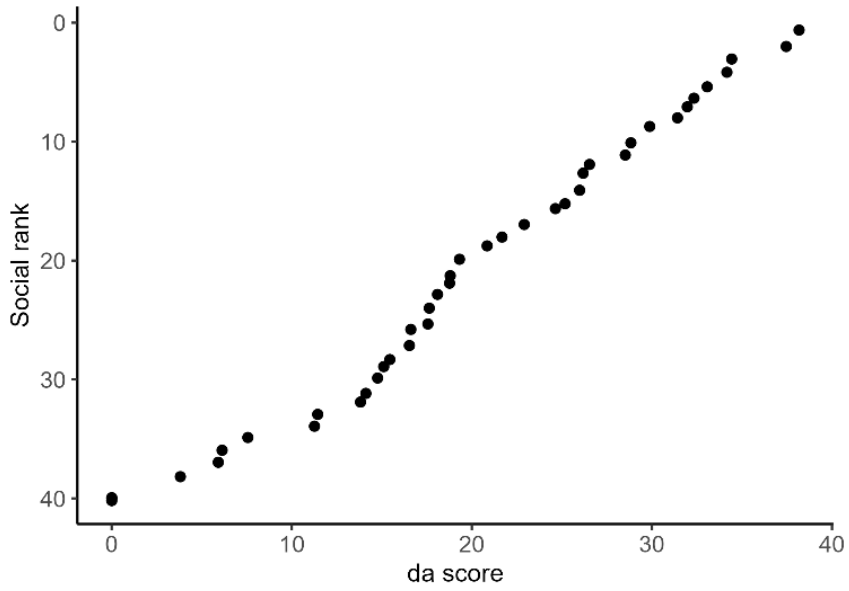

Figure 1 Linear distribution of social ranks (n = 41; 1= highest rank position, 39 = lowest rank position) based on da scores of dyadic agonistic encounters in 2022.

Across the years age correlated with rank except for the year 2021, one year after the group split occurred (Table 2). In general, the older the male the higher was his rank (Figure 2.a). In contrast to the years before, in 2021 two out of three 8.5-year-old males ("Spooky" and "Wicky") joined the hierarchy at the top, namely at the first and second position (Figure 2.b). In this year, no correlation between rank and age was found. A year after that, in 2022, three 8.5-year-old males entered the hierarchy rather at the bottom while Spooky and Wicky could hold their positions (Figure 2.c). No dominance data was collected a year before the group split occurred as well as during and shortly after the group split, therefore no dominance hierarchies are available for these periods. In 2021 one third of the top 10 highest ranking males were former members of the sub-group that split from the main-group in March 2020. In 2022 half of the top 10 positions were filled by former sub-group members (Figure 2.c). This was the year when a significant positive correlation between rank and age was reestablished.

Table 2 Correlation between age and social rank across different years for n males.

Year	**Month**	***n***	r_s	***p***
2012/2013	Nov - Feb	30	-0.55	0.002
2015	Dec	30	-0.46	0.011
2016	Sep - Dec	29	-0.49	0.006
2018	Sep - Dec	36	-0.75	< 0.001
2021	Jan - Mar	39	-0.26	0.109
2022	Jan - May	41	-0.34	0.031

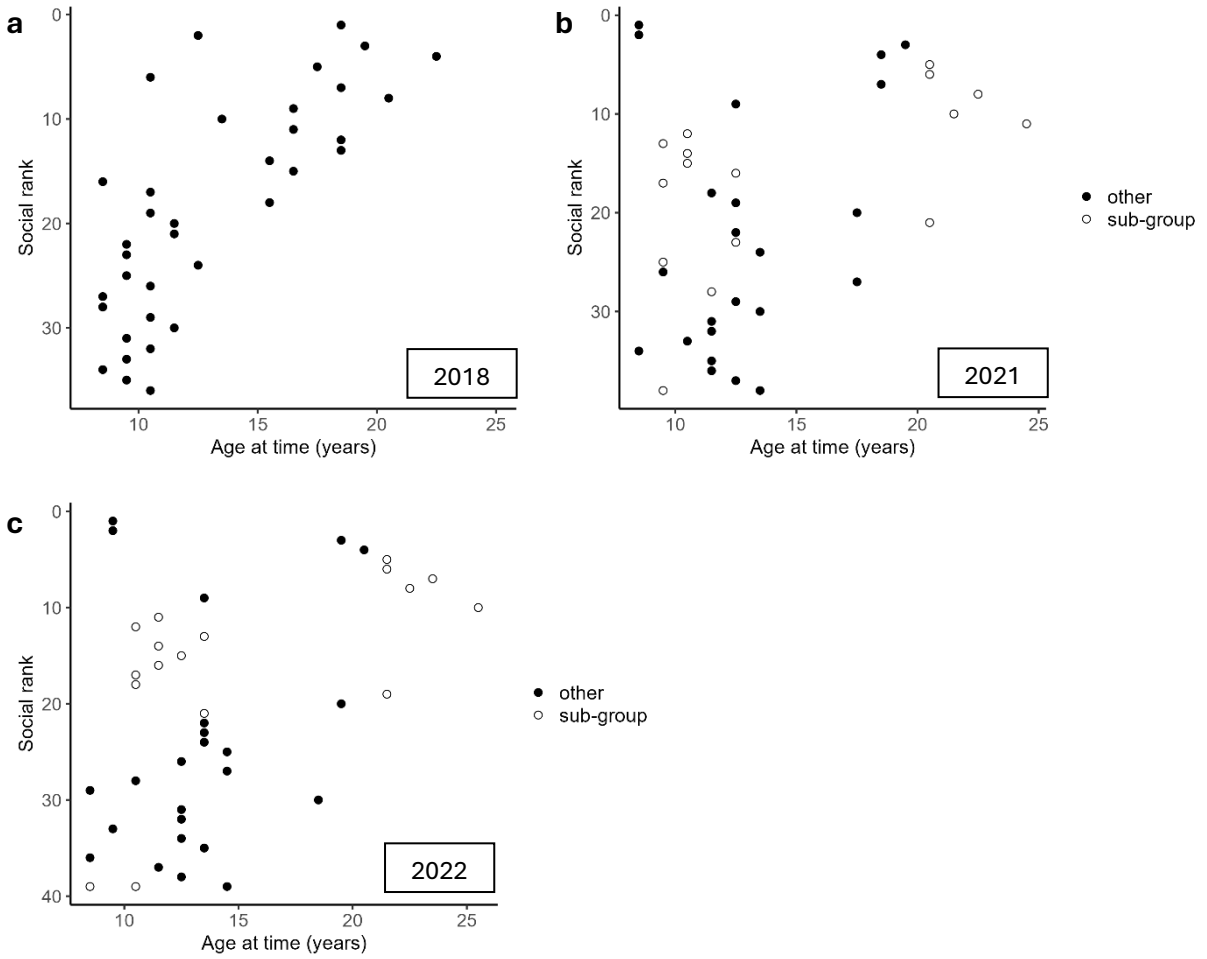

*Figure 2 Correlation between age (in years) at time and male social rank **a)** before (2018, n = 36), **b)** one year after (2021, n = 39) and **c)** two years after the group split (2022, n = 41). 1 = highest rank position,36/38/39 = lowest rank position (in respective years). A discrimination between former members of the sub-group that split from the main-group in March 2020 and other (main-group members and undetermined individuals) was made for **b)** and **c)**. For **a)** no such discrimination was made since the group split occurred after the dominance hierarchy was assessed.*

Affiliative relationships

The CSI scores in 2022 varied highly across all dyads ranging between zero and 98.4 with a mean and SD of 1.0 ± 5.4. Out of 1508 dyads 57.9% had a CSI score of zero and therefore never shared affiliative interactions (Figure 3). However, each individual had at least one male partner with whom he had an affiliative relationship with (CSI value above zero). The number of male partners for the 29 focal individuals ranged from 9 to 29 (mean ± SD = 18.3 ± 4.9) and the higher a male's rank the more male partners he had in general (r_s = -0.59, $p < 0.001$, Figure 4). The newly established alpha male Spooky stood out with only 13 male partners.

The majority of dyads with a CSI score above zero had values between 0.3 and 1.5. The CSI exceeded 1.5 only for 10% of all dyads and 22 dyads showed very high CSI values greater than 10 irrespective of age and social rank.

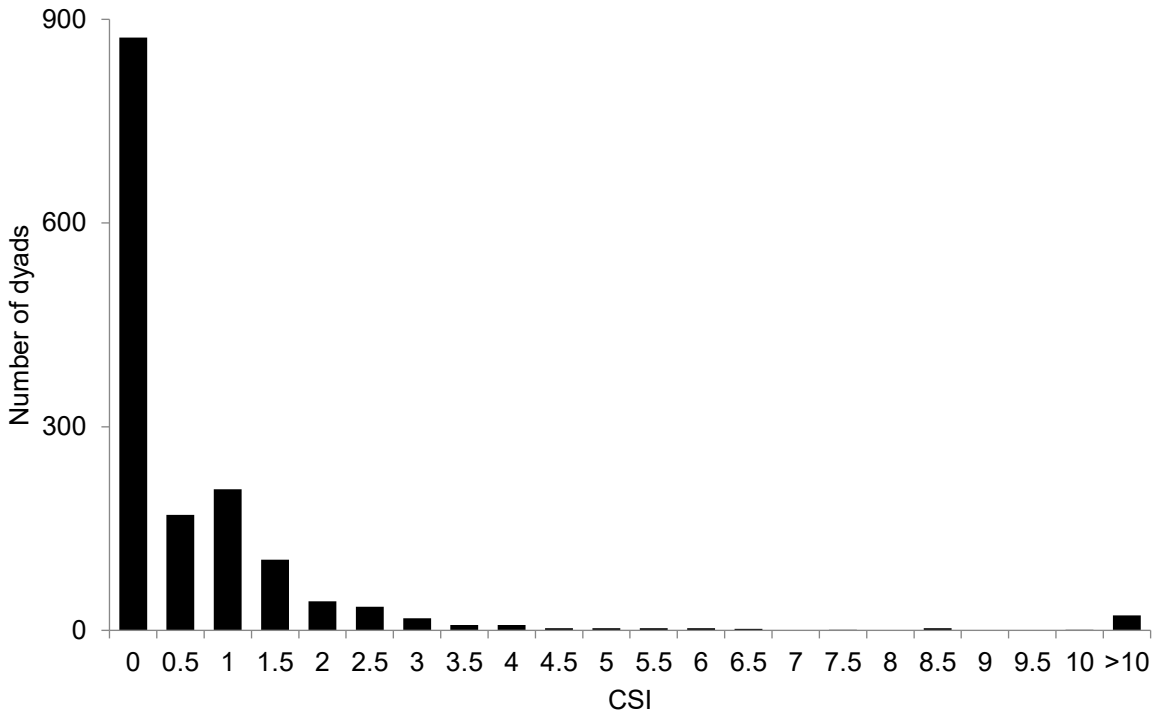

Figure 3 Distribution of CSI scores (n = 1508) for male-male dyads using frequency of proximity and duration of grooming.

Social rank did not correlate with the strength of the relationship an individual invested the most into (r_s = 0.17, p = 0.36, n = 29) nor with the strength of the relationship an individual received the most investment from (r_s = -0.08, p = 0.69, n = 29).

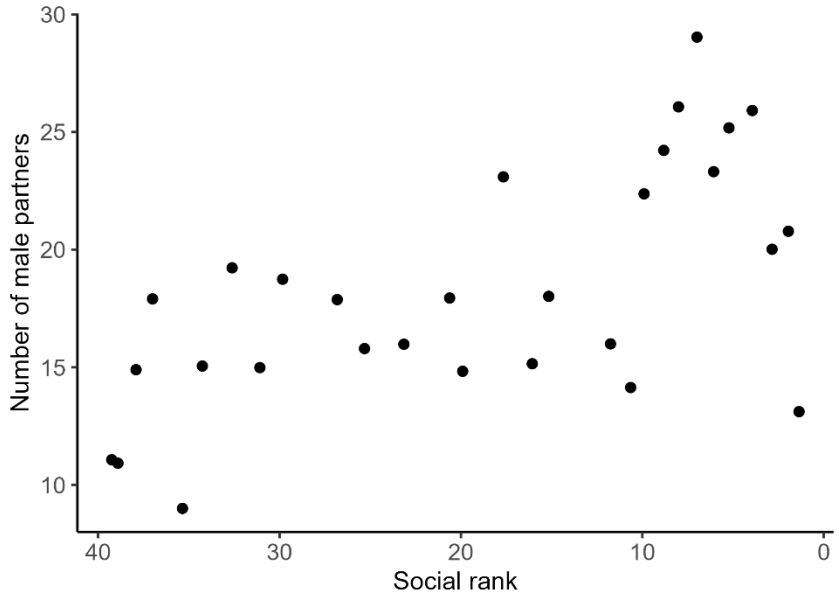

Figure 4 Correlation between male social rank (n = 29; 1= highest rank position, 39 = lowest rank position) and number of male partners he shared an affiliative relationship with.

When dividing the study period into mating and non-mating season and calculating CSI scores for each period 132 dyads shared affiliative relationships across both mating and non-mating season. All focal individuals had at least one enduring affiliative relationship that persisted over both periods. The number of partners for enduring affiliative relationships ranged between 1 and 10 (mean ± SD = 3.9 ± 2.1, n = 29) and the higher a male's rank the more male partners across both mating and non-mating season he had in general (r_s = -0.42, p = 0.02, n = 29, Figure 5).

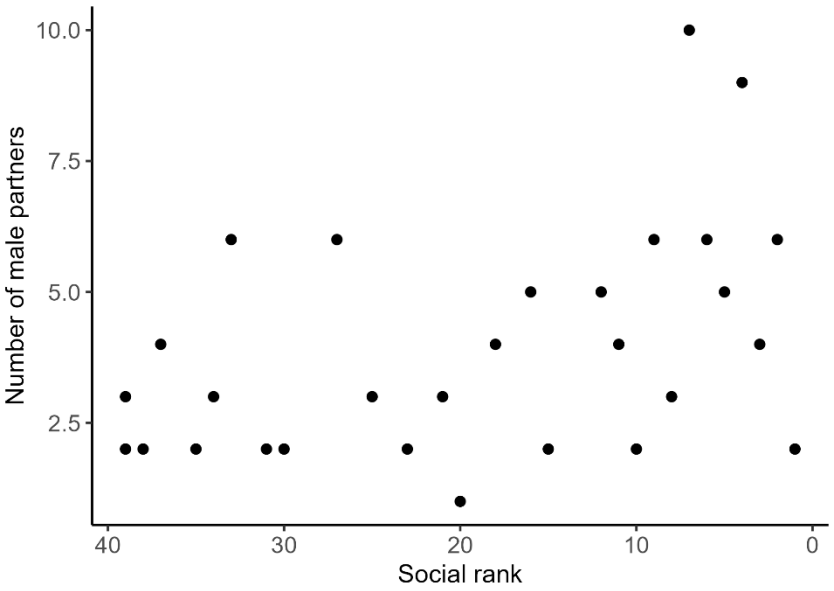

Figure 5 Correlation between male social rank (n = 29, 1= highest rank position, 39 = lowest rank position) and number of (enduring) male partners he shared an affiliative relationship with across both mating and non-mating season.

Discussion

The present study describes changes in the male dominance hierarchy of a semi-free ranging group of Japanese macaques two years after the occurrence of a group split. Furthermore, it investigates the presence and extend of male-male affiliative relationships using a Composite Sociality Index.

The males of the Affenberg population form a linear dominance hierarchy, placing them on the despotic side of the despotic-egalitarian spectrum of social organization (Thierry, 2000). The dominance hierarchy is not as strong as the one found by Singh et al., (2003) in another captive group of Japanese macaques. This might be explained by gaps in the dominance matrix, due to some dyads never encountering each other, which reduces the linearity index (Singh et al., 2003). This study's sample size is four times larger than the one used in Singh et al., (2003) which leads to 18 times more dyads that could have interacted. Due to the large sample size a lot of dyads were never observed to encounter each other in an agonistic way and the outcome of a possible encounter had to be estimated for the dominance hierarchy calculation. The moderate value for the linearity index therefore might not be a product of a weak dominance hierarchy but more of empty cells in the dominance matrix due to missing agonistic dyadic interactions. However, differences within a group across time are possible as well. In another study of male Japanese macaques different linearity indexes across different periods for the same group were reported (Kawazoe, 2020). Kawazoe (2020) reported stronger dominance hierarchies during certain periods but also observed strengths comparable to those found in the present study during other periods.

Comparisons of social rank data across the years before the group split in March 2020 revealed that the older the individuals the higher in rank they were in general. While there is no male data available shortly before, during and after the group spilt the consequences of the fission are notable in the dominance hierarchy of the year 2021 regardless. It was the first time since collecting male dominance data at the Affenberg Landskron that social rank did not correlate with age and therefore tenure length. This did not only pose a novelty for the Affenberg population but is also a rarity when it comes to populations in the wild (Sprague, 1992). After dispersing from their natal group male Japanese macaques usually join new groups at the bottom of the hierarchy (Sprague et al., 1998; Takahashi, 2002). The dominance hierarchy is relatively stable but most commonly changes due to death or emigration of individuals (Sprague et al., 1998; Suzuki et al., 1998; Takahashi, 2002). While aggressive dominance turnover can occur they are rather rare (Hayakawa & Soltis, 2011; Horiuchi, 2005; Kutsukake & Hasegawa, 2005; Nakamichi et al., 1995) and the acquisition of a higher rank is usually based on succession and therefore influenced by the length of the tenure within a group (Sprague et al., 1996). Since the males of the Affenberg population cannot depart from their natal group due to the keeping conditions the length of the tenure within a group is equivalent to their age.

While no dominance hierarchies are available for the time around the group split, anecdotal data of the top-ranking males were communicated by animal care staff and researchers. When the fission occurred the prior alpha ("Pauli") and gamma ("Adrian") males of the previously united group were part of the sub-group while the beta male ("Lucky") stayed in the main-group (Hammer et al., 2023). Lucky was proclaimed the new alpha male of the main-group, however, he passed away shortly after due to a cardiac defect in late December 2020. A young male of 8.5 years ("Spooky") then rose to the alpha position, followed by another 8.5-year-old male ("Wicky") at the beta position (Herzele, unpublished data). Spooky and Wicky did not only occupy the highest-ranking positions of the main-group but were dominant over all males of the Affenberg population. The dominance hierarchy was assessed across all males and was not split into sub- and main-group. Two main reasons were that firstly, the sub-group could not move away and therefore could not separate their nomadic range completely from the main-group. Consequently, individuals with different group affiliations could still encounter each other. Secondly, at the time of data collection the state of the fission as well as the group affiliation of the individuals was uncertain. Recent analyses revealed that only half a year after the fission the groups fused back together and no more discrimination between a sub-group and a main-group could be made (Hammer et al., in prep). This further supports the assessment of a dominance hierarchy across all males. No group determination was made in the year 2022 either because data was only available for males but not for females. In the assessment of group affiliation the lack of data on females could create an immense bias considering the matrilineal organisation of Japanese macaques and the impact of females on the formation of social relationships in macaque species in general (Sosa, 2016; Thierry et al., 2004).

After the groups fused back together the former alpha male Pauli, alongside other priorly high-ranking males that belonged to the sub-group, managed to occupy parts of the top 10 highest ranking positions in the male dominance hierarchy. Although they seemingly have not lost their standing in the group completely, they could not reclaim their old positions as Spooky and Wicky remained the alpha and beta male. However, the comeback of the previously established, old males with long tenures might have inhibited other young males to further climb the hierarchy ladder. In 2022, in alignment with the years prior the group split but in contrast to the year 2021, three 8.5-year-old males obtained their social ranks in the bottom third of the dominance hierarchy. Considering these results, the fission may have served as a stepping stone to attain a high social rank for some young males.

As found in other groups of Japanese macaques both in captivity (Gartland, 2021) as well as in the wild (Hill, 1994; Horiuchi, 2005; Kawazoe, 2020) males at the Affenberg Landskron form affiliative relationships with other males of their group. While they engage in both proximity and grooming with other males, proximity was observed more frequently. Even though grooming was not so common it is possible that it was

underrepresented due to the sampling method. Three times as many grooming bouts were additionally observed *ad libitum* in comparison to the grooming bouts recorded through focal sampling. The *ad libitum* data did not enter the analysis of the present study. Future studies need to take this into consideration and potentially adapt their methods, especially when trying to capture rather rare behaviours.

Affiliative relationships between males were highly differentiated. The majority of dyads did not share any affiliative interactions but within those who did, a large variety could be observed. The strongest relationships were all driven by long or repeated grooming bouts. Since grooming interactions were observed rather little overall they had a large impact on the CSI once observed in a dyad. However, high CSI values and therefore strong relationships could have also been established without grooming and solely based on spatial proximity. Proximity is not to be underestimated in Japanese macaques given their low social tolerance level (Thierry, 2000) reflected in big inter-individual social distances (Wada & Ogawa, 2009).

All males had at least one male partner with whom they shared an affiliative relation with. In general, the higher-ranked a male was the more partners he had. The alpha male Spooky however was one of the monkeys with the fewest male-affiliative relationships.

While rank correlated with the quantity of male affiliative relationships it did not correlate with the quality. High-ranking males did not receive more investment, nor did they invest more into their closest partner (strongest relationship) compared to lower ranking males. The quality of social bonds to other males did not correlate with a male's current social rank in Assamese macaques either but it did correlate with a male's future social rank (Schülke et al., 2010). Furthermore, the current social rank and future social bonds did not correlate either in Assamese macaques. Schülke et al., (2010) therefore concluded that social bonds predict dominance success and not contrariwise. Not only did they find an effect of social bonds on social rank but they could also show that social bonds predict reproductive success showing direct fitness benefits of male-male affiliative relationships.

To test whether (short term) affiliative relationships turn into (long term) social bonds and whether these social bonds predict social rank and reproductive success in Japanese macaques requires longitudinal data over both the mating and non-mating season as well as over several mating seasons and several non-mating seasons. The present study divided the study period by a "mating season" period and a "non-mating season" period to test whether affiliative relationships between males persist over different time periods. While only a low number of dyads showed affiliative relationships over both periods these enduring affiliative relationships between males were nonetheless found in the Affenberg population.

In this case however, one should be careful labelling these affiliative relationships as social bonds. Even though the CSI calculation corrects for the observation effort, it

differed for the two periods alongside the length of the periods. The “mating season” period only covered one month while the “non-mating season” period covered two. Furthermore, the “mating season” period was directly followed by the “non-mating season” period suggesting a clear cut between them. However, it is more of a transition from the one to the other with the sexual activity slowly but steadily decreasing. The onset and duration of the mating season in Japanese macaques varies between populations (Enomoto, 1974). At the Affenberg most conceptions occur between October and December (Pflüger et al., 2021) but sexual activity has been observed from September until May in 2024/2025 (Böhm, unpublished data) with a peak in November and December (Böhm, 2021). Therefore, the “mating season” period of this study is represented by the end of the mating season when sexual activity already declined. Furthermore, no group-wide monitoring of the sexual activity was conducted in the winter of 2021/2022 and a possibility of the presence of sexual activity in the “non-mating season” period of this study cannot be ruled out. Future studies aiming to compare different time periods such as the mating and non-mating season should consider an ecologically relevant cut in the data collection windows to ensure the distinct presence and absence of sexual behaviour for a clear differentiation. This is of importance since mating activity and male competition have an impact on male behaviour such as reduced grooming activity between males during the mating season in comparison to the non-mating season (Furuichi, 1985; Horiuchi, 2005).

Nonetheless, when the study period was divided every focal individual had at least one enduring affiliative relationship. These findings point towards the formation of social bonds between male Japanese macaques in the Affenberg population. Moreover, the more enduring affiliative relationships a male had the higher in rank he was. Whether those enduring affiliative relationships turn into social bonds and whether not only the quantity of these social bonds but also their quality lead to benefits in Japanese macaques needs to be investigated in future studies. It is of further interest whether these benefits are expressed through increased tolerance through reduced aggression just as found in the wild (Kawazoe, 2020) or even through increased dominance and reproductive success as found in other macaque species (Schülke et al., 2010).

Affiliative relationships might not only be relevant for males within a group but could also be important for out-group males trying to immigrate into a new group. A study showed that integration success of a male was predicted by his central position within the male-male grooming network (Kawazoe & Sosa, 2019). While males at the Affenberg cannot migrate between different groups due to the keeping conditions they show differences in the areas of the enclosure they occupy (Table S1). Their use of central and peripheral areas might reflect in their standing in the group’s social network. Therefore, paying more attention to affiliative relationships is worth pursuing in the frame of animal welfare aspects when it comes to introducing new males into a group in captive and semi-free ranging keeping conditions.

When further exploring how male Japanese macaques integrate into new groups, obtain their social rank and how they can maintain it, it is of importance to investigate different male strategies in general. The current alpha male Spooky had neither many nor strong male affiliative relationships. He might have invested more in females, either in sexual partners or non-sexual associations and formed so called peculiar proximate relationships (Huffman & Takahata, 2012; Takahata, 1982) that might have supported him to stay at the top.

To conclude, this study showed the changes in the male dominance hierarchy due to a group fission in Japanese macaques and how such unique events might enable young males to gain a high social rank and bypass the typical succession-based rank acquisition. Further, it described the occurrence and pattern of male-male affiliative relationships and with that sets important groundwork for future long-term studies to link male social rank and male social bonds in a despotic species like the Japanese macaques. Future studies are needed to understand how male social bonds might increase a male's social rank and how they might help males to integrate into new groups and navigate within the male social network.

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Appendix

Deutsches Abstract

Männliche nicht-menschliche Primaten konkurrieren um den Zugang zu Nahrungsressourcen und Paarungspartnerinnen. Um intensive agonistische Interaktionen zu reduzieren, werden oft Dominanzhierarchien etabliert. Dominanzbeziehungen sind jedoch nicht die einzigen Beziehungen, die männliche nicht-menschliche Primaten bilden. Männchen tauschen oft auch affiliative Interaktionen untereinander aus. Obwohl die Vorteile von affiliativen Beziehungen zwischen Männchen oft in Frage gestellt werden, sind sie bei vielen Primatenarten, einschließlich Japanmakaken, zu finden.

Diese Studie verglich in einer semi-freilebenden Gruppe von Japanmakaken (*Macaca fuscata*) am Affenberg Landskron, Österreich, männliche Dominanzhierarchien über mehrere Jahre hinweg. Besonderes Augenmerk lag auf der Gruppentrennung, welche im März 2020 stattfand und die Gruppe und infolgedessen, die männliche Dominanzhierarchie spaltete. Während sozialer Rang und Alter in den Jahren vor und zwei Jahre nach der Gruppentrennung immer korrelierten, war das ein Jahr nach der Gruppentrennung nicht der Fall. Dies deutet darauf hin, dass dieses einzigartige Ereignis das Erlangen eines hohen sozialen Ranges für einige junge Männchen möglich machte.

Darüber hinaus beschrieb diese Studie affiliative Beziehungen zwischen Männchen, indem sie einen Composite Sociality Index (CSI) berechnete. Verhaltensweisen, die zur Berechnung des CSI herangezogen wurden, waren die Nähe zwischen zwei Männchen, sowie das Lausen. Erwachsene männliche Japanmakaken der Affenberg-Population zeigten differenzierte affiliative Beziehungen zueinander. Es wurde ein Zusammenhang zwischen der Anzahl der affiliativen Beziehungen und dem sozialen Rang, jedoch nicht zwischen der Qualität der affiliativen Beziehungen und dem aktuellen sozialen Rang festgestellt.

Diese Studie dient als Grundstein, für zukünftige Langzeitstudien, die sich mit dem Zusammenhang zwischen dem sozialen Rang eines Männchens und seinen affiliativen Beziehungen zu anderen Männchen beschäftigen.

Ethogram

Spatial information

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

Behavioural variables

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

Approach: This behavioural variable occurs in the following contexts:
Focal enters a 3-meter radius with clear focus towards another individual. Focal might stay within the 3-meter radius or leave it in one movement;
Focal enters a 1-meter radius without focus on another individual and remains within a 1-meter radius;
Focal gets closer to another individual while already being in proximity to this individual;
Focal enters and leaves 1 meter radius in one movement while displaying other social behaviours towards the individual it enters proximity with (e.g.: face to face; grab; touch). Leave (see below) must be noted as well.

Approach conflict: Focal approaches a conflict within 3 meters of one involved individual. Focal does not enter the centre of the conflict and shows no involvement.

Attempted mount: Focal tries to mount (see Mount) without being successful.

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

Autogroom: Focal grooms oneself.

Avoid: 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 spatial proximity with the other individual before.

Avoid conflict: Focal focuses its attention on a conflict without approaching the conflict and moves away in the opposite direction.

Avoid in proximity: Focal animal avoids an individual within a one meter radius, while having focus on that individual, without leaving the proximity radius. This is done by changing position. (Added to the Ethogram on 07.03.2022)

Bipedal walk: Focal walks standing up on both hindlegs.

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

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

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

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

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

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

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

Consort sit:

Close consort sit: 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: 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: 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: Focal interrupts consort without showing aggressive behaviour but displacing one or both consorting partners or make them split their proximity.

Copulation call: Focal vocalizes towards a (potential) sexual partner. Can be continuous when pauses between copulation calls are shorter than 10 seconds.

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

Change position: 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.

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

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

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

Displace: Focal approaches another individual who then leaves, after which the focal remains within 1m radius where the other animal used to stay.

Drink: Focal takes in water from a water source that is not food.

Eat sperm: Focal takes repeated bites of its own sperm after ejaculating.

Embrace: Focal holds another individual in its arms.

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

Forage: Focal is sitting or standing while looking for food on the ground

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

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

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

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

Grab food: Focal takes an item of food from a feeding spot to carry it to another place and eat it there.

Groom: 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: Focal hits or wipes the floor with the hand.

Groom displace: 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: 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: Focal slaps another individual by hand.

Intervention:

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

Leave: This behavioural variable occurs in the following contexts:
Focal stops being in proximity with another individual by moving away;
Focal walks away after having displayed aggressive or dominance behaviours (e.g.: face to face; grab; threat) to another individual;
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.

Jump: Focal propels itself upward or over a distance in a single quick motion.

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

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

Lunge: Focal jumps a maximum of two body lengths forwards towards another individual.

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

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

Mock leave: Focal walks away from another individual while turning around at least once

to lunge/scream/threat the other individual.

Mock flee: 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: Focal climbs on another individual with its hands on the receivers back or rump. Note whether it involves thrusts.

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

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

Pass by: 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 (see above)).

Pass by body contact: Focal enters a radius of 1 meter around another individual and leaves this radius within the same movement without displaying any other social behaviours. While walking through the 1 meter radius of another individual the bodies of the focal and its partner brush against each other.

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

Pick up food: Focal picks up small food items while walking.

Play face: Focal opens mouth with open jaws without retracting lips towards another individual. Focal makes no vocalisations.

Present: 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: Focal is within 1 meter of another individual and is not passing by.

Push: Focal makes rough and short body contact with another individual.

Redirection: 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).

Refusal: 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: 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).

Scratch: Focal uses finger(s) or foot to rake across own skin.

Scream: Focal utters high pitched, intense vocalization. Can be continuous when focal screams every 10 seconds.

Self manipulation: All self-directed behaviours that did not include groom and scratch (e.g. wipe face, rub face, lick self (mostly hands), rub nose, rub eyes)

Sit: Focal rests in a posture supported by the buttocks or thighs.

Social play: 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.

Stand: Focal stands on four legs.

Stand up: Focal gets up on his hindlegs (usually in combination of attention or vigilance).

Stare: Focal looks intensively at another individual with a straight back and raised eyebrows.

Startle: Focal jerks or twitches in response to an event or another individual that has approached while the focal individual was occupied with another activity.

Sunbathe: Focal sits upright with chest turned towards the sun.

Support: 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: Focal moves its head with an O-shaped mouth and raised eyebrows towards another individual.

Travel: Focal walks or runs around.

Touch: Focal makes gentle and short body contact with another individual.

Travel together: Focal travels parallel to another individual. Distance between the individuals is less than 3 meters.

Tree shake: Focal holds a tree or object and shakes its body intensively.

Vigilance: 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.

Vocalization: Focal utters a vocalization that is not a copulation call, grunt or scream. Can be continuous when focal vocalizes every 10 seconds.

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

Area use

The enclosure of the Affenberg Landskron can be divided into several central and peripheral sections (see Figure 1 in Hammer et al., 2023) based on differences in vegetation and availability of food resources. *Scan sampling* (Martin & Bateson, 2007) was used on n = 33 afternoons to record in which areas males were located following the approach of Hammer et al., (2023).

Table S1 Area use of n = 41 males. Proportion of time spent in centre and periphery in percentage.

Name	Centre	Periphery
Aaron	73	27
Adrian	68	32
Aiko	32	68
Augustin	81	19
Bernhard	88	12
Chris Cross	15	85
Coco	53	47
Dieter	38	63
Double U	66	34
Ferdinand	79	21
Finn	68	32
Franziskus	68	32
Funki	48	52
Gustav	43	57
Heiko	17	83
Heinz	67	33
Holgerson	44	56
Jackson	67	33
Karl	45	55
Karl-Vinzenz	30	70
Kuddl Muddl	74	26
Leo	56	44
Lorenz	30	70
Ludwig	52	48
Lupo	22	78
Manfred	54	46
Marco	78	22
Mickey	50	50
Momo	57	43
Nico	77	23
Pauli	81	19
Rupi	57	43
Siegfried	29	71
Silvio	62	38
Spooky	78	22
Swen	71	29
Thomas	48	52
Toby	43	57
Werner	50	50
Wicky	50	50
William	67	33