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Research article

Hierarchical position of individual captive western lowland gorillas *Gorilla gorilla gorilla* and its impact on neighbour associations and behaviour

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Abstract

This study investigated the social relationships observed within a captive breeding group of western lowland gorillas *Gorilla gorilla gorilla* at a European Association of Zoos and Aquaria (EAZA) accredited facility: Blackpool Zoo, UK. Gorillas are complex and intelligent primates, and the western lowland subspecies is popular in zoo collections. Captivity can raise issues for gorillas which, in the wild, live in large family groups with a distinct hierarchy forming the basis of group stability. Studying captive groups can help facilities make informed decisions for gorilla captive management. This study considered if and how captive gorilla behaviour could be influenced by social positioning. It was carried out in May–July 2018 and focused on social behaviour, nearest neighbour and position in the enclosure recorded for focal individuals with notes on enclosure design taken. Interval focal sampling was used to record gorilla (n=6; two adult females, one adult male, two juvenile females and one infant male) social behaviour, their nearest neighbour (the animal physically closest to the focal individual) and position in the enclosure simultaneously every 10 min, during six-hour observation periods over two months. A different individual was observed daily. Data on independent and social behaviours were collected to determine activity budgets using an ethogram. Data on independent behaviours can demonstrate if there are variations in behaviour when gorillas are in social proximity. Mann-Whitney U tests were conducted on mean frequencies of independent (n=10) and social (n=5) behavioural categories for each individual. Independent inactive behaviours were most common (n=53.6) with adult gorillas displaying increased levels of sitting and lying in comparison with younger individuals. There is a difference among the gorillas in their social behaviour. Nearest neighbour data were analysed using cluster analysis. The silverback was most closely associated to his youngest offspring and lactating female. The sub-adult female has the weakest associations in comparison to the rest of the group. The results suggest individual preferences for social associations, with younger individuals associating closely with their mothers, and a mother and infant associating closely with the silverback. A sub-adult female was less associated with all individuals, which could suggest her readiness to transfer. This study emphasises the influence that hierarchical social organisation within a captive setting has on captive gorilla behaviour monitoring in general, relating to how individual gorillas manage their position in a hierarchical group. This study also provides specific suggestions for gorilla management within the centre and in conjunction with BIAZA guidelines, including a suggestion to relocate the sub-adult female to a new group and considerations for aggression mitigation.

Introduction

Social cohesion is a fundamental component of group living. Tactility is a utilised mode of relationship development in many species (Jablonski 2021). Gorillas are observed to be less socially tactile than other ape species (Fay et al. 1995). Instead, researchers use social proximity patterns to determine closeness amongst conspecifics (Nakamichi and Kato 2001). After conflict, western lowland gorillas *Gorilla gorilla gorilla* have been observed closely associating themselves with their opponent in an attempt to reconcile and re-establish a connection (Cordoni et al. 2006). Grooming is used in social species to establish and maintain bonds between individuals (Sparks 2011). This behaviour is not commonly displayed as an affiliative behaviour in gorillas: whilst allogrooming does occur, it is almost exclusively between a mother and her infant,

and breeding pairs (Fay et al. 1995). The silverback–female social bond is crucial in gorilla society; the stronger this bond, the higher the level of protection that the female is likely to receive from the silverback (Maryanski 1987). Female–female bonds tend to be weaker; this is because females are more likely to transfer between groups throughout their life, therefore do not have as many opportunities to build bonds with unrelated females (Stokes et al. 2003).

Social interactions are heavily influenced by hierarchical structure in many species (Tibbets et al. 2022). Hierarchical structures within gorilla populations are complex, and may be linked to their evolutionary relationship with humans Homo sapiens (Morrison et al. 2019) and are generally defined as systems of social organisation in which some individuals enjoy a higher social status than others. Gorillas have a harem social system which means there is a dominant individual with all other individuals being submissive (Magliocca et al. 1999). The dominant male at the top of the hierarchy uses intragroup aggression to retain privileges of first access to food, mates and other resources. Dominance is usually determined with a combination of asserting agonistic behaviour on other group members, and the amount of time that the dominant individual spends in the group (Yahner 2012). In gorilla society, dominance can also be inherited, i.e. if the dominant silverback dies of natural causes, a younger son remaining in the group can become head of the hierarchy (Less et al. 2010). Silverbacks act as a mediator of intragroup conflicts (Klailova 2011). The dominant male also provides protection for the group, and in turn has access to all breeding females within the group as well as first access to food and other resources (Sapolsky 2005). The level of protection varies depending on the social positioning of the individual—females with infants sired by the silverback tend to have the highest level of protection, as well as longer access to food. First-time mothers tend to invest more energy, often carrying their infant for longer than experienced mothers (Brown and Dixson 2000). Family groups usually consist of one dominant adult silverback male, his harem of two to three adult females and their offspring. Gorillas have a matriarchal social structure where females and sometimes males leave their natal group by ten years old when they reach sexual maturity; this is linked to competition for females (Douadi et al. 2007). If males do not leave their natal group, they will remain subordinate to the silverback (Robbins 2001).

A captive environment alters the natural behaviour of animals (Fischer and Romero 2019; Sherwen and Hemsworth 2019; Sueur and Pelé 2019). Studies by Bonnie et al. (2016) and Ogden et al. (1990) suggest abnormal behaviours are more common in captive gorillas, which could impact the conventional social associations expected in western lowland gorillas. In addition, captive environments remove the spatial freedom experienced in the wild, meaning social proximities may not reflect those of wild counterparts and may 'force' social proximity in some instances. The complex nature of gorilla groups, with the added factor of captivity, presents areas for research. This study aimed to explore the social associations observed in a captive group of western lowland gorillas in relation to the hierarchal structure of the group by noting social and independent behaviour of the individuals, through analysis of social proximity (measured as nearest neighbour) and displayed behaviours. It was hypothesised that closely related gorillas (notably mother and offspring) would be in social proximity (measured as physical distance observed during observation window) to each other more than to non-related gorillas. It was also hypothesised that individuals lower in the hierarchy would have fewer close associations with others and that the total number of social behaviours would be lower for lower ranked gorillas.

Methods

Subjects and hierarchy

The gorillas at Blackpool Zoo are a breeding family consisting of six individuals. All gorillas were captive-born with the three offspring born on-site. The group consists of adult male Bukavu (aged 20 years), adult females and half-sisters N'Jema (24) and Miliki (23), sub-adult female Meisie (8), juvenile female Moanda (5) and infant male Makari (10 months). There is a hierarchy in this group: as the silverback, Bukavu is the most dominant followed by Miliki (and Makari) due to her having an infant in the study period, then Moanda and Meisie and finally N'Jema who is the least dominant. Dominance within the group was determined through ad libitum sampling of behaviours and social proximities, access to priority resources and qualitative interviews with keepers. Feeding of the group routinely took place in the mid-morning and mid-afternoon and consisted of distance provision from outside of the enclosure. Daily visual health checks by Blackpool Zoo staff took place away from public view, usually between 1500 and 1600.

Data collection

The study was conducted between May and July 2018, during the hours of 0800 to 1500, with a one-hour lunch break taken each day at alternating times to ensure all hours were observed during the data collection period. Observations occurred six days per week, using focal sampling on a different individual each day. The 'day off' from observations was taken on a rotating schedule to remove bias relating to visitor numbers (the zoo received many more visitors at weekends). Observations were conducted on all days of the week, rotating the day off to ensure all days were represented evenly. The gorilla observed daily was randomly assigned to ensure each gorilla was observed on different days each week. Data collection comprised of six-hour focal sampling sessions with data recorded every 10 minutes, resulting in 288 hours of data collection or 48 hours per gorilla. The sampling interval ensured that behaviours were independent from one another (Altmann 1974). All dependent gorillas (n=5) were observed separately. However, Miliki and Makari were observed at the same time due to Makari's age during data collection (8–10 months), but behaviours of both gorillas were analysed separately as the infant became gradually more independent from his mother Miliki and displayed independent behaviours during the study. Social data were collected, including recording the identity and distance of nearest neighbour to the focal individual: distances were then categorised as: 0 m, 1–5 m, 6–10 m and >10 m. With reference to an ethogram adapted from Ogden and Schildkraut (1991) (see Appendix 1), state behaviours including social interactions were recorded using interval sampling during the observation period (36 data points/gorilla/day). The gorillas had access to three distinct but connected enclosures (connected by doors): an indoor room, the paddock and Gorilla Mountain. The gorillas were observed in all three enclosures to avoid 'out of sight' instances, as keeper schedules and visitor numbers may have impacted behaviours.

Statistical analysis

Mean daily frequencies of all observed behaviours (n=47, see Appendix 1) were calculated for each gorilla. Data on both social and independent behaviours were then compared using Mann-Whitney U tests between individuals, focusing on sex (male n=3, female n=3), age (adult=3, juvenile=3) and place in the hierarchy. Additionally, a point system based on observed distance between individuals (1=0 m, 2=1–5 m, 3=6–10 m, 4=11–20 m) was used to calculate distance to nearest neighbour. Statistical analysis was conducted using SPSS v.22 (IBM Corporation, Armonk, NY). Behaviours were pooled into separate categories: social and independent and their frequencies analysed for individual gorillas

using a Mann-Whitney U test. The physical distance between individuals was analysed using one-way analysis of variance (ANOVA). To visually understand the intragroup relationships and associations, a cluster analysis model using neighbour association data (dendrogram) was created using UCINET (see Borgatti et al. 2002).

Results

Independent behaviours

A one-way Mann-Whitney U test was conducted to assess the relationship during the study period between individual gorillas and the frequency with which they exhibited different independent behaviour types: feeding (E), sitting (S), lying (L), playing (P) and foraging (F). N'Jema, Bukavu, Moanda and Meisie were all equally likely to exhibit any of the independent behaviours (Mann–Whitney U=6.5, P>0.05; U=10.5, P>0.05; U=3.65, P>0.05; U=7.1, P>0.05, respectively). Miliki and Makari were more likely to exhibit certain independent behaviours (Mann–Whitney U=7.3, P<0.05; U=8.2, P<0.05). Total independent behaviour frequencies per individual gorilla were compared using one-way ANOVA. In total, 25 expected cell frequencies were less than 5, showing a statistically significant moderate association between different independent behaviours and individual gorillas ($F_{(2,5)}$=2.76, P<0.05; Pearson's correlation r=0.54, P<0.05). This statistically significant result allows acceptance of the alternative hypothesis and rejection of the null hypothesis (that there is no variable association between individuals and independent behaviours).

Independent behaviour frequencies differ descriptively per individual (Figure 1). The most frequent independent behaviour for all gorillas is sitting (mean across all individuals=31.4%). Makari has the highest frequency of sitting (30.8%) in contrast with Moanda with the lowest (25.3%). Makari's high frequency of sitting is categorised as individual behaviour due to sitting with or on Miliki. Lying is the second most common individual behaviour, with Bukavu displaying the highest observed values (33.9%). This behaviour occurs at relatively high frequencies for all individuals (22%). The older individuals including Meisie had very low frequencies of independent play behaviour (independent playing not observed in Meisie), with 4.8% for Moanda and 5.4% for Makari. Meisie has the highest level of foraging (23.9%). Comparatively Makari's foraging behaviour is very low at 1.9%. Feeding is also a common behaviour across all individuals (24.7%); except for Makari (2.2%). Bukavu grooms considerably more than other individuals (97.7% of all self-grooming across individuals).

Social behaviours

A Mann-Whitney U test was conducted to assess the relationship between individual gorillas and the frequency with which they exhibit different social behaviour types: RN (rest near), AGG/R (allogrooming giving/receiving), GP (group play) and A (aggression). N'Jema and Miliki are both equally likely to exhibit any of the social behaviours (Mann–Whitney U=6.6, P>0.05; U=5.65, P>0.05). Bukavu's social interactions were infrequent (Mann–Whitney U=4.6, P>0.05). Cumulative frequencies for social behaviours in all individuals were analysed. Twenty cells had expected counts less than five. Thus, there is a statistically significant association between the individual and the social behaviours exhibited ($F_{(2,5)}$=2.71, P<0.001).

The results for social behaviours show a pattern for the young gorillas. Moanda (83.9%) and Meisie (51.4%) played together considerably more than any other individuals, with the adults N'Jema (4.2%), Bukavu (2.9%) and Miliki (1.4%) playing considerably less. Aggressive behaviour was only exhibited by N'Jema (4.2%) and Bukavu (12.5%). Allogrooming was not common with the exception of Miliki (allogroom give=46.7%) and Makari (allogroom receive=35.3%). Rest near behaviour was most commonly observed in N'Jema (83.3%) and Moanda (48.6%). There appears to be no general trend across all gorillas, with individuals exhibiting different behaviours most frequently. Bukavu has the lowest overall frequency of social behaviours (4.8% of total social behaviours), with Moanda displaying the highest frequency of social behaviours (42.4% of total social behaviours) (Figure 2).

A chi-squared test of independence was conducted between individual and nearest neighbour category (1=0 m, 2=1–5 m, 3=6–10 m, 4=11–20 m).

There is no relationship with nearest neighbour category for N'Jema ($\chi^2_{(21)}$=17.804, P>0.05), Meisie ($\chi^2_{(21)}$=16.405, P>0.05),

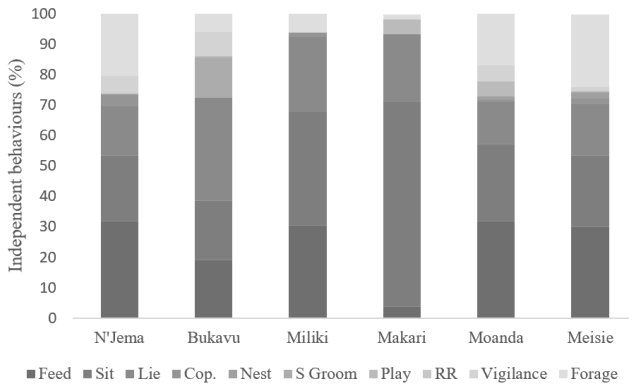

Figure 1. Independent behaviours of gorilla individuals expressed as a percentage of total time observed. (cop = coprophagy, S Groom = self-groom, RR = regurgitation and reingestion).

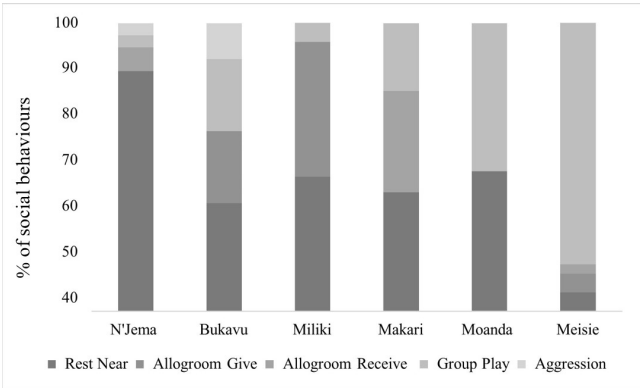

Figure 2. Social behaviour percentage for each individual.

Miliki ($\chi^2_{(21)}$=21.073, P>0.05) and Makari ($\chi^2_{(21)}$=19.129, P>0.05). There is a significant relationship with nearest neighbour category for Bukavu ($\chi^2_{(21)}$=57.989, P<0.001) and Moanda ($\chi^2_{(21)}$=54.458, P<0.001). All individuals' frequencies for nearest neighbour categories were analysed using ANOVA. All expected cell counts were less than five. Thus, there is a statistically significant association between individual gorillas and nearest neighbour distance category ($\chi^2_{(15)}$=142.290, P<0.001).

On visual inspection, the gorillas appear to have a clear pattern of nearest neighbour proximity. Gorillas spent much of their time (44%) in the second level (1–5 m). Makari has the highest number of observations in the second level (19.5%) with N'Jema having the lowest (13.4%). The least common level of contact between individuals is level 1 (direct contact) with 11.8% of cases. Miliki has the lowest frequency of direct contact with others (6.0%), and Makari has similar results (6.6%). Moanda has considerably more observations in level 1 than other individuals (44.5%). The highest level (>10 m) is less commonly observed (12% across all individuals) but is fairly consistent across all individuals (14.0–15.6%) with the exception of N'Jema (22.6%) and Meisie (18.3%; Figure 3). Makari and Miliki were not compared with each other in this analysis, as it was assumed they were always in direct contact with each other.

Cluster analysis

The cluster analysis dendrogram shows average linkage cluster analysis of the six gorillas based on social proximity and social behaviours (Figure 4). Each gorilla is represented by a horizontal line at the left of the diagram. Pairs or clusters of gorillas are joined by vertical lines. The further left the vertical line appears, the closer the two gorillas are linked. The cluster diagram shows that Bukavu is most closely linked to Miliki and Makari. Bukavu is least linked to N'Jema. N'Jema is most closely linked to her daughter Moanda. Makari and Miliki are closely associated with each other. Meisie appears not to be closely linked to any other individuals (based on her branch on the dendrogram), but is most linked to Miliki, Makari and Bukavu. The common connection at the end shows that all individuals share some relationship or connection.

Discussion

Cluster and nearest neighbour analysis

The cluster analysis largely reflects the family makeup of the gorilla troop based on hierarchy and genetic relationships. Social associations in gorillas reveal much about group stability. Blackpool Zoo is a member of the European Association of Zoos and Aquaria (EAZA), who advise that captive western lowland gorillas should be treated as an 'ex-situ conservation programme' as they are part of the European Endangered Species Programme (EEP; EAZA 2021). By using cluster analysis and reference to the international studbook, facilities may be able to make informed decisions regarding individuals that may benefit from moving to a new establishment for breeding purposes or positive enrichment for individuals with low affiliative behaviours with others in the group (e.g. in this study, Meisie with N'Jema and N'Jema with Miliki). Watts (1994) suggests related females show little affiliative behaviour, instead preserving this behaviour for males, as was observed in the study group. Before breeding occurs, the male and female will engage in affiliative grooming and spend more time in close proximity to one another. Tetley and O'Hara (2012) suggest that studying aspects of gorilla sociality including social associations that reflect wild counterparts should influence captive behaviour management.

In this study, the silverback was most closely associated with lactating mother and infant. This is likely linked to the silverback's function of protection (Harcourt and Greenberg 2001). Cheney

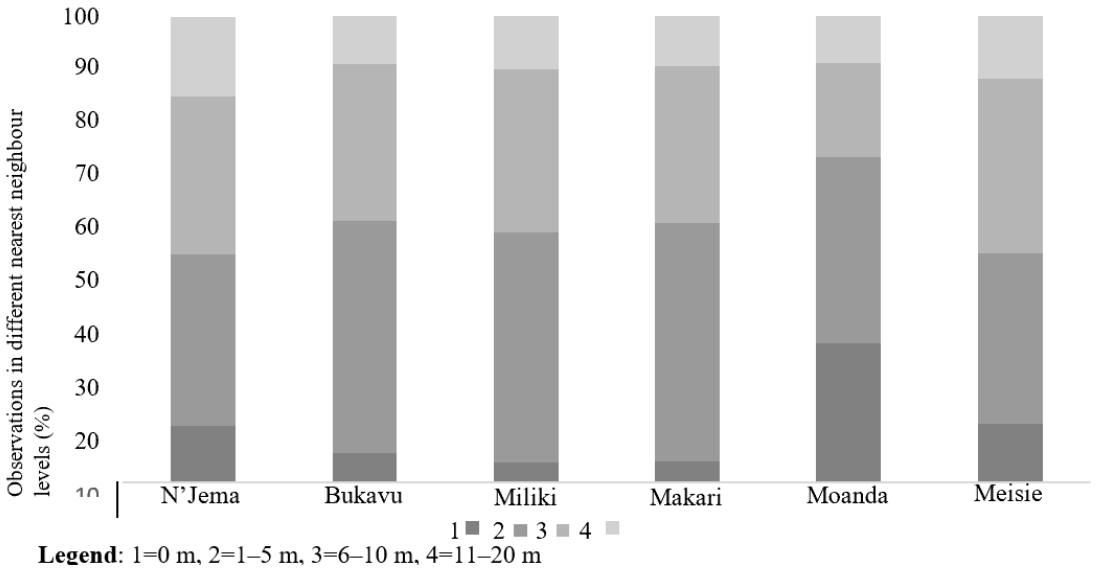

Figure 3. Percentage of nearest neighbour levels observed per individual.

and Wrangham (1987) suggest that silverbacks provide protection for the infant against potential predators. The more protection provided by a male, the less likely a female is to transfer to a new group (Yamagiwa et al. 2009). Harcourt (1979) suggests that the closeness of the male towards the mother and infant is actually a closeness to the infant, to whom the mother is close. This suggests that the male and female relationship is weak and instead the relationship strength lies between the silverback and the infant (Palombit 2000). Females usually initiate their proximity to the silverback (Nakamichi et al. 2014). This was observed during this study. Another mechanism for this close association could be to prevent infanticide (Manguette et al. 2020), despite no other silverbacks being present in this captive setting. Bukavu spent 56.2% of time less than five metres from a neighbour—this is higher than for gorillas observed in all-male groups (Stoinski et al. 2004) and can be linked to Bukavu's protection of the infant. In addition, Miliki and Makari are closely associated due to Makari's reliance on his mother at this age (Hoff et al. 1981).

All gorillas in this troop are captive-born yet adults display behaviour to protect their offspring through close association. Whether this behaviour is instinctive or learned is unclear, however it is also observed in wild counterparts. This captive-wild mirrored behaviour could suggest that although the environment is artificial, these behaviours have evolved in the natural gorilla environment (McPhee and Carlstead 2010). It is also important to consider that these behaviours may have been learned from other individuals; like humans, gorillas develop unique cultures within groups (Robbins et al. 2016). Moanda was observed frequently seeking proximity to her mother. The median age for proximity seeking by young is 30 months. At 5 years old, Moanda is considerably older than this. The average weaning age is 4.6 years (Nowell and Fletcher 2007) and this is consistent with Moanda, who finished suckling a few months before this study began. Moanda rested near to her mother N'Jema more than expected; other studies of mother and daughter social associations show lower frequencies of this behaviour (Maestripieri et al. 2002). The frequency of Moanda resting close to N'Jema could be due to N'Jema's position in the hierarchy (the bottom). Those at the bottom of the hierarchy are often comforted by other subordinate individuals, which aids stress prevention amongst the two individuals (de Waal 2012).

Meisie appears to not be closely clustered to any individual. At eight years old, she is of the age where, in the wild, she may transfer into a new group (Yamagiwa and Kahekwa 2001). This is also reflected in the nearest neighbour results, as Meisie was observed 11–20 metres away from others 34 times. In the wild, female transfer is voluntary and done by moving into a new group when a suitable one is in the vicinity (Sicotte 2001). Meisie will not encounter another gorilla troop in her current captive environment, but her willingness to be further away from her natal group could suggest her readiness to transfer. Harcourt et al. (1976) suggest that female transfer can occur in response to group size. Their study found that females tend to prefer smaller groups. The mean harem number in western lowland gorillas is five (Meder 1992). Despite this naturalistic grouping, abnormal behaviours were still observed in individuals, particularly the lower ranking female N'Jema. Bukavu displayed agonistic behaviour such as charging towards and hitting N'Jema. She was observed to follow this interaction with abnormal behaviours such as rocking and head rolling in a crouched position.

Exhibited behaviours

Play in gorillas is a complex communication with a large repertoire of behaviours (Weigel and Berman 2018). Group play was highest between the two youngest individuals Moanda and Makari but was also observed in eight-year-old Meisie. For infants, play is the

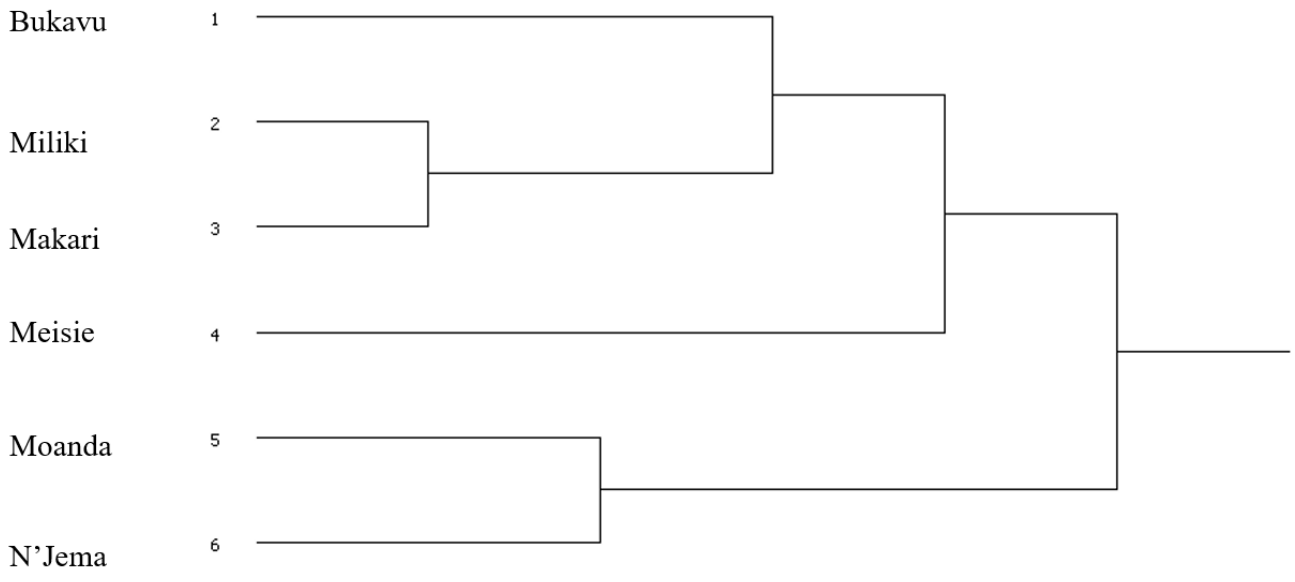

Figure 4. Cluster analysis dendrogram showing individual relationships within the group

most common social behaviour not linked to their mother (Parnell 2002). During play bouts with Moanda, Miliki was observed retrieving Makari from the situation, which is a common behaviour when the infant is approximately 8–10 months old (Kurtycz et al. 2014). Play behaviour is rarely seen in gorillas over 20 years old (Cordoni et al. 2022) and this was reflected in this study, with only Bukavu exhibiting one bout of solitary play behaviour. Group play behaviour was rarely exhibited in adults, and was always initiated by younger gorillas. Play behaviour is commonly observed in young gorillas, and in chimpanzees has been shown to help youngsters achieve motor and social milestones earlier than individuals with lower levels of play (Heintz et al. 2017). Weigel and Berman (2018) found that gorillas must have a suitable play partner to exhibit play, and so the high level of group play in Moanda and Meisie is likely due to their sibling relationship and similar age. During observation periods, Meisie and Moanda frequently played together. However, independent play in Meisie was not observed. Parnell (2002) notes that play behaviour can be hard to recognise in sub-adult gorillas.

Behaviours such as chest beating can be interpreted as an adult behaviour or as a play behaviour. Play behaviour has an important function for behavioural development (Hoff et al. 1981). Animals that were prevented from exhibiting play behaviour as infants tend to have a less advanced social repertoire in adult life (Heintz et al. 2017). The Early Surplus Energy theory proposes that gorillas use play to spend excess energy, often after feeding (Spencer 1977). Play can have many functions: social communication, integration and development, as well as physical development. Most crucially, play is useful in establishing dominance (Cordoni et al. 2018). For example, play between Moanda and Meisie was initiated by Moanda, but finished by Meisie as she is older and therefore stronger.

Pullen (2008) reported that mixed-sex groups of captive gorillas exhibit higher levels of aggression than single-sex groups. In captivity, aggressive behaviour can be considered a stress-related behaviour. Bukavu, at the top of the hierarchy, displayed aggressive behaviour. Brady et al. (1958) argue that being at the top of a hierarchy results in higher stress levels. Fuller et al. (2018) recommend that the addition of manipulable objects may result in fewer physical blows from the silverback to others as objects may allow males to display efficiently. The current enclosure has very few manipulable objects and the addition of items such as barrels may reduce observed instances of intraspecific aggression, particularly towards lower ranking individuals. Dominant individuals within a despotic hierarchy maintain their dominance by exhibiting mild aggressive behaviour to their subordinates (Sapolsky 2005). However, those lower in the hierarchy may be more likely to display stressful behaviour, which is reflected in the current study data as N'Jema (at the bottom of the hierarchy) also displayed aggressive behaviour: this is referred to as 'resource inequity' (Thierry et al. 2008). High levels of aggression in captivity can be interpreted as abnormal behaviour responses (Kummrow 2021); group suitability should be reconsidered in housing facilities where abnormal behaviour levels (associated in this case with aggressive instances) are high.

Grooming in gorillas is minimal in comparison to other social primate species (Simonds 1974). The most common social grooming is maternal (Hedeen 1980). In the current study, allogrooming was most common between mother and offspring and was not observed at all between adults; this is similar to other captive populations (Halliday 1980). Further, virtually no affiliative behaviour was observed between adults. This excluded copulation between N'Jema and Bukavu. N'Jema and Miliki did not groom each other at all despite related female gorillas tending to groom each other more than unrelated females (Watts 2009). Bukavu self-groomed more than any other individual, namely his finger hairs, which could be considered a stereotypic behaviour. Hair-plucking is common in captive western lowland gorillas (Less et al. 2013) and has been linked to stress (O'Malley et al. 2021). Bukavu also had a lower frequency of foraging which can be linked to hair-plucking—Hill (2004) found a correlation between increased foraging opportunities and a decreased rate of hair-plucking. As no other gorillas in the group showed frequent self-grooming, it is possible that Bukavu learnt this behaviour from his natal group in Germany; this is considered the most likely way gorillas develop this behaviour in captivity (Less et al. 2013).

Miliki and N'Jema spent the most time feeding of all individuals, which is consistent with Clutton-Brock (1977) who found that adult females spent more time feeding than their male counterparts. Harcourt and Stewart (1984) found that males fed more than females, which is not supported by our research. Lactation is costly in energy and therefore more food is required to sustain this biological function (Leeds 2019) which could explain Miliki's greater frequency of feeding.

Conclusion

The nearest neighbour levels and cluster analysis show that the gorillas at Blackpool Zoo have preferences over how they orientate themselves and how close they get to other individuals, although this may also be influenced by space availability within the enclosure. The two youngest individuals, Moanda and Makari, are still closely associated with their mothers and Meisie has no strong relationships in the cluster analysis. Bukavu is closely linked to Miliki and Makari as he provides protection and security for the mother and her infant. There appears to be a relationship between nearest neighbour levels and social behaviours, with individuals who most commonly occupy levels 1 and 2 of neighbour closeness exhibiting more social behaviours. Sapolsky (2005) states that dominance and hierarchical structures are not only species-specific, they are also unique to each group. The gorillas at Blackpool have a social makeup and living situation unique to any other group of gorillas due to their husbandry routines and surroundings. Additionally, their personalities and social relationships will influence group structure and atmosphere, which will undoubtedly have an impact on stress levels and behaviours. This study emphasises how relationships within the group influence the associations and behaviours of individuals, and highlights the need to monitor this as group dynamics can change over time following births, deaths and introductions. The results suggest that zoos should take time to consider how these relationships can impact both group dynamics and individual wellbeing. For example, it is recommended that Blackpool Zoo provides more access to the off-show room to give the gorillas a place to avoid others, both gorillas and humans. This was highlighted in a study on the same gorilla troop which indicated higher levels of stereotypic behaviour could be linked to lack of off-show access (Hashmi and Sullivan 2020). The current study shows that N'Jema and Meisie spent the most amount of time further from others which could suggest they were seeking separation from the group. Further research should be conducted to determine how an animal's hiearchical position influences individual psychological health and wellbeing. Currently there are conflicting theories (Thierry et al. 2008; Whitehead 1997) on this topic. This information could help to ascertain when individuals should be transferred to other collections (which should be completed as part of the EEP). For example, Meisie has few close associations and therefore lacks a close bond with the other individuals; this suggests her readiness to transfer. It is recommended that females should transfer at the age of 6–8 years old (Stokes et al. 2003). Meisie has now surpassed this age (at the time of observations, she was 8 years old) and has shown elements of appropriate sibling care, which is identified as a key experience required by female gorillas destined for breeding

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and rearing offspring.

Initially, the multi-sex and age grouping of the gorillas reflects a natural wild troop. The silverback has the recommended number of females (n=2; EAZA 2021), however agonistic behaviours were still observed which triggered abnormal behaviours in individuals. To mitigate this, sightscreens or selective barriers could be added to the enclosure to allow visual and physical separation. At the time of research, visual barriers were largely absent from the indoor enclosure where the gorillas spend the majority of their time. Guidelines recommend that where silverback–female aggression is present within the group, slightly smaller enclosures may be beneficial to prevent chasing, and allow aggressive situations to diffuse more quickly. The size of the gorilla indoor enclosure is suitable in this context.

Blackpool Zoo follows EAZA guidelines, which means that welfare standards within the zoo are high. This study demonstrates that the gorillas housed in the zoo exhibit behaviours also observed in wild counterparts, and behaviours routinely observed in other captive populations. Providing Blackpool Zoo with information on social associations from the current study will aid their husbandry practices, particularly during cleaning when connections between the rooms are temporarily removed. This study also demonstrates the useful nature of cluster analysis for captive populations: to better understand the social makeup of groups and help zoos make informed management decisions. Social interactions should be monitored on a regular basis to identify changes in the social structure of the group. This approach can easily be applied in other institutions that house gorillas.

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References

Altmann J. (1974) Observational study of behaviour: Sampling methods. *Behaviour* 49(3–4): 227–266. doi:10.1163/156853974X00534

Bonnie K.E., Ang M.Y.L., Ross S.R. (2016) Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla*) at a zoo. *Applied Animal Behaviour Science* 178: 102–110. doi:10.1016/j.applanim.2016.03.003

Borgatti S.P., Everett M.G., Freeman L.C. (2002) *Ucinet 6 for Windows: Software for Social Network Analysis.* Harvard, Massachusetts: Analytic Technologies Inc.

Brady J.V., Porter R.W., Conrad D.G., Mason J.W. (1958) Avoidance behavior and the development of duodenal ulcers. *Journal of the Experimental Analysis of Behavior* 1(1): 69–72. doi:10.1901/jeab.1958.1-69

Brown G.R., Dixson A.F. (2000) The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). *Primates* 41: 63–77. doi:10.1007/BF02557462

Cheney D.L., Wrangham R.W. (1987) Predation. In: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W., Struhsaker T.T. (eds.). *Primate Societies.* Chicago, Illinois: University of Chicago Press, 227–239.

Clutton-Brock T.H. (1977) *Primate Ecology*. London, UK: Academic Press, 539–556.

Cohen J. (1988). *Statistical Power Analysis for the Social Sciences* (2nd edition). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Cordoni G., Palagi E., Tarli S.B. (2006) Reconciliation and consolation in captive western gorillas. *International Journal of Primatology* 27: 1365–1382. doi:10.1007/s10764-006-9078-4

Cordoni G., Norscia I., Bobbio M., Palagi E. (2018) Differences in play can illuminate differences in affiliation: A comparative study on chimpanzees and gorillas. *PLoS One* 13(3): e0193096.

Cordoni G., Pirarba L., Elies S., Demuru E., Guéry J.P., Norscia I. (2022) Adult–adult play in captive lowland gorillas (*Gorilla gorilla gorilla*). *Primates* 63: 225–235. doi:10.1007/s10329-022-00973-7

de Waal F.B.M. (2012) The antiquity of empathy. *Science* 336(6083): 874–876. doi:10.1126/science.1220999

Douadi M.I., Gatti S., Levrero F., Duhamel G., Bermejo M., Vallet D., Menard N., Petit E.J. (2007) Sex-biased dispersal in western lowland gorillas (*Gorilla gorilla gorilla*). *Molecular Ecology* 16(11): 2247–2259. doi:10.1111/j.1365-294X.2007.03286.x

EAZA (2021) E*AZA Statement on Gorilla Management* [press release], 24 November 2021. Available online: https://www.eaza.net/assets/Uploads/2021-11-24-Press-statement-gorillas4.pdf

Fay J.M., Carroll R., KerbisPeterhans J.C., Harris D. (1995) Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29(1): 93–99. doi:10.1006/jhev.1995.1048

Fischer C.P., Romero L.M. (2019) Chronic captivity stress in wild animals is highly species-specific. *Conservation Physiology* 7(1): coz093. doi:10.1093/conphys/coz093

Fuller G., Murray A., Thueme M., McGuire M., Vonk J., Allard S. (2018) Behavioral and hormonal responses to the availability of forage material in Western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology* 37(1): 23–34. doi:10.1002/zoo.21393

Halliday P. (1980) The integration of an adult female gorilla into the Howletts collection. *Help* 3: 6–8.

Harcourt A.H., Greenberg J. (2001) Do gorilla females join males to avoid infanticide? A quantitative model. *Animal Behaviour* 62(5): 905–915.

Harcourt A.H. (1979) Social relationships between adult male and female mountain gorillas in the wild. *Animal Behaviour* 27(2): 325–342. doi:10.1016/0003-3472(79)90166-0

Harcourt A.H., Stewart K.J. (1984) Gorillas' time feeding: aspects of methodology, body size, competition and diet. *African Journal of Ecology* 22: 207-215.

Harcourt A.H., Stewart K.S., Fossey D. (1976) Male Emigrations and Female Transfer in Wild Mountain Gorillas. *Nature* 263: 226–227.

Hashmi A., Sullivan M. (2020) The visitor effect in zoo-housed apes: The variable effect on behaviour of visitor number and noise. *Journal of Zoo and Aquarium Research* 8(4): 268–282. doi:10.19227/jzar.v8i4.523

Hedeen S.E. (1980) Mother-infant interactions of a captive lowland gorilla. *The Ohio Journal of Science* 80(4): 137.

Heintz M.R., Murray C.M., Markham A.C., Pusey A.E., Lonsdorf E.V. (2017) The relationship between social play and developmental milestones in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American Journal of Primatology* 79(12): e22716. doi:10.1002/ajp.22716

Hill S.P. (2004) Reduction of abnormal behaviour in two captive western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Research News* 5: 2–3.

Hoff M.P., Nadler R.D., Maple T.L. (1981) The development of infant play in a captive group of lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology* 1(1): 65–72. doi:10.1002/ajp.1350010108

Jablonski N.G. (2021) Social and affective touch in primates and its role in the evolution of social cohesion. *Neuroscience* 464: 117–125. doi:10.1016/j.neuroscience.2020.11.024

Klailova M. (2011) *Interunit, Environmental and Interspecific Influences on Silverback-Group Dynamics in Western Lowland Gorillas (*Gorilla gorilla gorilla*).* PhD Thesis. University of Stirling, UK.

Kummrow M. (2021) Diagnostic and therapeutic guidelines to abnormal behavior in captive nonhuman primates. *Veterinary Clinics of North America: Exotic Animal Practice* 24(1): 253–266.

Kurtycz L.M., Shender M.A., Ross S.R. (2014) The birth of an infant decreases group spacing in a zoo-housed lowland gorilla group *(Gorilla gorilla gorilla*). *Zoo Biology* 33(5): 471–474. doi:10.1002/zoo.21156

Leeds C.A. (2019) *A Physiological Evaluation of Social Bonding in Western Lowland Gorillas (*Gorilla gorilla gorilla*).* PhD Thesis. Case Western Reserve University, USA.

Less E.H., Lukas K.E., Kuhar C.W., Stoinski T.S. (2010) Behavioral response of captive western lowland gorillas (*Gorilla gorilla gorilla*) to the death of silverbacks in multi-male groups. *Zoo Biology* 29(1): 16–29. doi:10.1002/zoo.20246

Less E.H., Kuhar, C.W., Lukas, K.E. (2012) Assessing the prevalence and characteristics of hair-plucking behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare* 22(2); 1–11.

Maestripieri D., Ross S.K., Megna N.L. (2002) Mother-infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): Spatial relationships, communication, and opportunities for social learning. *Journal of Comparative Psychology* 116(3): 219–227. doi:10.1037/0735-7036.116.3.219

Magliocca F., Querouil S., Gautier-Hion A. (1999) Population structure and group composition of western lowland gorillas in North-Western Republic of Congo. *American Journal of Primatology* 48(1): 1–14. doi:10.1002/(SICI)1098-2345(1999)48:1<1::AID-AJP1>3.0.CO;2-2

Manguette M.L., Breuer T., Robeyst J., Kandza V.H., Robbins M.M. (2020) Infant survival in western lowland gorillas after voluntary dispersal by pregnant females. *Primates* 61: 743–749.

Maryanski A.R. (1987) African ape social structure: Is there strength in weak ties? *Social Networks* 9(3): 191–215. doi:10.1016/0378-8733(87)90020-7

McPhee M.E., Carlstead K. (2010) The importance of maintaining natural behaviors in captive mammals. In: Kleiman D.G., Thompson K.V., Baer C.K. (eds.). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edition). Chicago, Illinois: University of Chicago Press, 303–313.

Meder A. (1992) Effects of the environment on the behaviour of lowland gorillas in zoos. *Primate Report* 32: 167–183.

Morrison R.E., Groenenberg M., Breuer T., Manguette M.L., Walsh P.D. (2019) Hierarchical social modularity in gorillas. *Proceedings of the Royal Society B* 286(1906): 20190681. doi:10.1098/rspb.2019.0681

Nakamichi M., Onishi K., Silldorf A., Sexton P. (2014) Twelve-year proximity relationships in a captive group of western lowland gorillas (*Gorilla gorilla gorilla) at the San Diego Wild Animal Park, California, USA*. Zoo Biology 33(3): 173–183. doi:10.1002/zoo.21131

Nakamichi M., Kato E. (2001) Long-term proximity relationships in a captive social group of western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology* 20(3): 197–209. doi:10.1002/zoo.1020

Nowell A.A., Fletcher A.W. (2007) Development of independence from the mother in *Gorilla gorilla gorilla. International Journal of Primatology* 28: 441–455. doi:10.1007/s10764-007-9128-6

Ogden J.J., Finlay T.W., Maple T.L. (1990) Gorilla adaptations to naturalistic environments. *Zoo Biology* 9(2): 107–121. doi:10.1002/zoo.1430090205

Ogden J., Schildkraut D. (1991) *Compilation of Gorilla Ethograms.* Atlanta, Georgia: Gorilla Behavior Advisory Group.

O'Malley M., Woods J.M., Byrant J., Miller L.J. (2021) How is western lowland gorilla (*Gorilla gorilla gorilla*) behavior and physiology impacted by 360° visitor viewing access? *Animal Behaviour and Cognition* 8(4): 468–480. doi:10.26451/abc.08.04.02.2021

Palombit R.A. (2000) Infanticide and the evolution of male-female bonds in animals. In: van Schaik C.P., Janson C.H. (eds.). *Infanticide by Males and its Implications.* Cambridge, UK: Cambridge University Press, 239–268. doi:10.1017/CBO9780511542312.013

Parnell R. (2002) *The Social Structure and Behaviour of Western Lowland Gorillas* (Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo*. PhD Thesis. University of Stirling, UK.

Pullen K. (2005) Preliminary comparisons of male/male interactions within bachelor and breeding groups of western lowland gorillas (*Gorilla gorilla gorilla*), *Applied Animal Behaviour Science* 90(2): 142-153.

Robbins M.M., Ando C., Fawcett K.A., Grueter C.C., Hedwig D., Iwata Y., Lodwick J.L., Masi S., Salmi R., Stoinski T., Todd A., Vercellio V., Yamagiwa J. (2016) Behavioral variation in gorillas: Evidence of potential cultural traits. *PLoS One* 11(9): e0160483. doi:10.1371/journal.pone.0160483

Robbins M.M., Sicotte P. Stewart K.J. (2001) *Mountain Gorillas: Three Decades of Research at Karisoke*. Cambridge: Cambridge University Press.

Sapolsky R.M. (2005) The influence of social hierarchy on primate health. Science 308(5722): 648–652. doi:10.1126/science.1106477

Sherwen S.L., Hemsworth P.H. (2019) The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals* 9(6): 366. doi:10.3390/ani9060366

Sicotte P. (2001) Female mate choice in mountain gorillas. In: Robbins M.M., Sicotte P., Stewart K.J. (eds.). *Mountain Gorillas: Three Decades of Research at Karisoke.* Cambridge, UK: Cambridge University Press, 59–87.

Simonds P.E. (1974) *The Social Primates.* New York, New York: Harper and Row.

Sparks J. (2011) Allogrooming in Primates: A Review. In: Morris D. (ed.). *Primate Ethology.* Transaction Publishers, 148–175.

Spencer H. (1977) The Principles of Psychology. Boston, Massachusetts: Longwood Press.

Stoinski T., Lukas K., Kuhar C.W., Maple T.L. (2004) Factors influencing the formation and maintenance of all-male gorilla groups in captivity, *Zoo Biology* 23(3): 198–203.

Stokes E.J., Parnell R.J., Olejniczak C. (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology* 54: 329–339. doi:10.1007/s00265-003-0630-3

Sueur C., Pelé M. (2019) Importance of living environment for the welfare of captive animals: Behaviours and enrichment. In: Hild S., Schweitzer L. (eds.). A*nimal Welfare: From Science to Law*. UNESCO, Paris: Fondation Droit Animal, Éthique et Sciences, 175–188.

Tetley C.L., O'Hara S.J. (2012) Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals. *Animal Welfare* 21: 463–476.

Thierry B., Aureli F., Nunn C.L., Petit O., Abegg C., de Waal F.B.M. (2008) A comparative study of conflict resolution in macaques: Insights into the nature of trait covariation. *Animal Behaviour* 75(3): 847–860. doi:10.1016/j.anbehav.2007.07.006

Tibbets E.A., Pardo-Sanchez J., Weise C. (2022) The establishment and maintenance of dominance hierarchies. *Philosophical Transactions of The Royal Society B* 377(1845): 20200450. doi:10.1098/rstb.2020.0450

Watts D.P. (2009) Gorilla social relationships: A comparative overview. In: Taylor A., Goldsmith M.L. (eds.). *Gorilla Biology: A Multidisciplinary Perspective.* Cambridge, UK: Cambridge University Press, 302–327. doi:10.1017/CBO9780511542558.014

Watts D.P. (1994) Social relationships of immigrant and resident female mountain gorillas, II: Relatedness, residence, and relationships between females. *American Journal of Primatology* 32(1): 13–30. doi:10.1002/ajp.1350320103

Weigel E.A., Berman C.M. (2018) Body signals used during social play in captive immature western lowland gorillas. *Primates* 59: 253–265. doi:10.1007/s10329-017-0646-3

Whitehead H. (1997) Analysing animal social structure. *Animal Behaviour* 53(5): 1053–1067. doi:10.1006/anbe.1996.0358

Yahner R.H. (2012) *Wildlife Behavior and Conservation*. New York, New York: Springer. doi:10.1007/978-1-4614-1518-3

Yamagiwa J., Kahekwa J. (2001) Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins M.M., Sicotte P., Stewart K.J. (eds.). *Mountain Gorillas: Three Decades of Research at Karisoke*. Cambridge, UK: Cambridge University Press, 89–122.

Yamagiwa J., Kahekwa J., Basabose A.K. (2009) Infanticide and social flexibility in the genus *Gorilla. Primates* 50: 293–303. doi:10.1007/s10329-009-0163-0