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The effect of new enclosure and group split on daily activities and social interactions in western lowland gorillas in Prague Zoo

MASTER'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled "The effect of new enclosure on daily activities and social interactions in western lowland gorillas in Prague Zoo" independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague **DATE**

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Marie Žabková

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Abstract

Primates in general and great apes in particular face a threat of extinction in the wild, which is caused by a variety of anthropogenic factors, including poaching, habitat loss and global climate change. Keeping primates in zoos informs the public about these complicated issues and gives insight into behaviour of these remarkable animals in controlled conditions. To ensure that the best possible care is given to these animals, it is important to recognize normal behaviour as well as behaviour indicative of stress. The main aim of this thesis was thus to investigate the effect of translocation to new zoo enclosure and group split on daily activities, individual and social behaviour in western lowland gorillas (*Gorilla gorilla gorilla*) living in a group in Prague zoo (Prague, Czech Republic). To reach this aim, a scientific literature review was conducted, and behavioural observations were completed under daily life conditions on seven gorillas (three males, four females). We combined focal instantaneous sampling and focal continuous sampling whereby every focal observation lasted for 20 minutes and was done twice a day per individual, for a total of 897 observations, i.e. 299 hours. Subsequently, behavioural responses were transcribed into Excel and statistically processed in R. Results indicate that moving to a different enclosure and group split affected gorillas' daily activities and social interactions, namely their locomotion, time spent in contact, time spent in proximity and the rate of approaches. The effect was particularly visible in the period immediately after the changes when the proportions or rates of these aforementioned behaviours increased. These results indicate that individuals coped well with the changes and were able to overcome this event by using social support and comfort each other. Studies like this one represent a valuable source of information for zoos and are instrumental for future managerial interventions in captive care.

Keywords: western lowland gorilla; *Gorilla gorilla gorilla;* captivity; zoo; stress; social behaviour

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List of the abbreviations used in the thesis

Aja	Ajabu
Kam	Kamba
Kibu	Kiburi
Kiji	Kijivu
Nur	Nuru
Rich	Richard
Shin	Shinda
IUCN	International Union of Conservation of Nature
AZA	Association of Zoos and Aquariums
EAZA	European Association of Zoos and Aquariums

1. Introduction

The popularity of great apes with biologists and primatologists is indisputable mainly because of their genetic and phenotypic similarities to humans, their high intelligence, formation of strong social and family bonds, communication with conspecifics, use of tools and much more. They also raise special interest in zoo visitors. However, keeping animals like great apes in human care requires vast knowledge and experience; even with these, there are inevitable situations where animals may naturally feel stressed and thus alter their behaviour.

According to the International Union for Conservation of Nature (IUCN) Red List (2018), the conservation status of all great ape species ranges from endangered to critically endangered. As part of the conservation programmes, apes have been kept in zoos for decades. In zoos they receive appropriate care, but there are some routine practices that can naturally make the animals feel uneasy, ranging from cleaning of the enclosures and simple veterinarian checkups to more challenging ones, like moving to different enclosures or changes in group composition. These situations may eventually lead to changes in daily activities, increased stress levels and alterations of their self–directed and/or social behaviour.

Abnormal behaviour, including coprophagy, regurgitation and reingestion, hair plucking, body rocking or exaggerated grooming or scratching, is usually considered to be a stress-coping mechanism (Walsh et al. 1982; Nash et al. 1999; Birkett & Newton-Fisher 2011). When animals are stressed, social behaviours may be altered as well, resulting in inappropriate aggression, distancing or excessive grooming (Morgan & Tromborg 2006). To be able to successfully protect and keep apes in captivity while meeting all their needs, it is crucial to understand how the changes in keeping or housing alter their behaviour.

This thesis is in the form of a case study conducted in Prague Zoo, where we closely studied the behaviour of a group of western lowland gorillas (*Gorilla gorilla gorilla*), formerly living together in the same enclosure. Due to construction of a new enclosure, part of the group was moved into this enclosure to form a new breeding group, and part of the group stayed in the old enclosure as a bachelor group. This case study aims to investigate if and how managerial changes alter gorillas' social behaviour and daily activity, and provides a valuable insight into keeping great apes in captivity.

2. Aims of the Thesis

The present thesis aimed to investigate if and how moving to a new enclosure and changes in social composition affect the individual and social behaviour of captive western lowland gorillas (*Gorilla gorilla gorilla*) kept in Prague Zoo. To do so, we observed individuals in four periods: before the move, immediately after the move and group split, later after the move and three months after these changes when the new enclosure opened to public.

We aimed to answer following questions:

1) Are there any behavioural changes in terms of daily budget and activities of gorillas when comparing the four above mentioned time periods.
2) Are there any changes in social behaviour of gorillas when comparing the four above mentioned time periods?

3. Methodology

3.1. Individuals and housing conditions

Prague Zoo has been keeping western lowland gorillas since 1963 (Gorillas Land 2022) and it is also the only Czech zoo keeping these animals. The zoo currently houses nine individuals – one silverback male (Richard), three adult females (Kamba, Kijivu, Shinda) that have been living together since 2003, and three juvenile males (their offspring – Kiburi, Nuru, Ajabu). In October 2022, they were joined by two unfamiliar adult individuals (Kisumu, Duni), but these gorillas were not part of the group in times of data collection. More detailed information about individuals, their European studbook number, sex, year of birth, age, rearing management and the year since they have been in Prague Zoo, can be seen in **Chyba! Chybný odkaz na záložku.** and Gorillas Land (2022).

Table 1: Subject information (Gorillas Land 2022)

Subject	European studbook #	Sex	Birth year	Age	Birth type	In zoo since
Kamba	532	F	1972	50	wild	2005
Richard	1169	M	1991	31	captive	2003
Shinda	1168	F	1991	31	captive	2003
Kijivu	1281	F	1993	29	captive	2003
Kiburi	2043	M	2010	12	captive	2010
Nuru	2127	M	2012	9	captive	2012
Ajabu	2277	M	2016	6	captive	2016
Kisumu*	1430	M	1997	25	captive	2022
Duni*	2151	F	2013	9	captive	2022

The gorillas used to be housed in an old enclosure (inside area 238 m^2 and outside area 811 m^2) located in the southern part of the zoo, which is also the lowest part and with a high risk of flooding. Prague Zoo has experienced flooding several times, but the most destructive flood happened in 2002 when almost half of the area was underwater and more than 100 animals passed away, including one gorilla male. In times of floods, gorillas could be moved to a flood control tower located near their enclosure, however, such emergency relocation was stressful for both the animals and the keepers. For those reasons, Prague Zoo has decided to build a new enclosure in a safer location, in the northern and upper part of the zoo.

3.2. New enclosure and group changes

The new gorilla enclosure, built in 2022, is a part of the Dja reservation, inspired by the Cameroonian Dja reserve, where Prague Zoo is actively participating in an *in-situ* conservation programme. Both the inside enclosure (466 m^2) and the outside area (2570 m^2) are well equipped with climbing and resting structures and enrichment tools that are stimulating for gorillas. With a total area of 3036 m^2, it can accommodate more animals than the previous enclosure and is more adequate for gorillas' needs.

Initially, the whole group was supposed to be moved to the new enclosure. It was later decided by the management that the silverback male and two of his sons will stay and form a new bachelor group in the old enclosure, while three females and the youngest male will move to the new enclosure and form a new breeding group there.

The move took place on the morning of 8th June 2022, taking about two hours with no complications. Roughly a month later, on 14th July 2022, the freshly moved gorilla group started to share their enclosure with mantled guereza monkeys (*Colobus guereza*) to form a mixed species exhibition. In September, two new gorillas, female gorilla Duni, formerly living in Spain (granddaughter of Kijivu, adult female presently living in Prague Zoo) and silverback male Kisumu, formerly living in Austria, arrived to Prague Zoo and quarantined together for month and a half. On 18th October 2022 the groups started having regular visual contact through bars. The Dja reservation, as well as the new gorilla enclosure was opened for public on 28th September 2022.

Following dates are purely informative as they are not analysed in this thesis. On 1st November 2022, Kisumu and Duni were allowed to explore their future enclosure while the gorilla group was having a snack in the back, and on 7th November 2022, the two groups were finally connected.

3.3. Behavioural observations

Data were collected on seven individuals formerly living in one group – one silverback male, three adult females and three juvenile males (see Table **1**). Data collection took place from May to October 2022, from 10 am to 6 pm each day, in four periods; “before” (i.e. period before the move) that was between 11th May and 7th June, “after1” (i.e. period immediately after the move) that was between 14th June and 27th July, “after2” (i.e. period later after the move) that was between 28th July and 2nd September, and “open” (i.e. period after the enclosure was opened to public) that was between 1st October to 28th October. The order of behavioural observations for each individual was chosen randomly on a given day. Each individual was observed twice a day. Behavioural observations of 20 minutes each were done with a combination of focal instantaneous sampling and focal continuous sampling, totalling 897 focal observations, i.e. 299 hours. The number of visitors in front of the enclosure was also recorded at the beginning and the end of each observation. More details on focal observations, namely the number of focal observations per individual, before the move (“before”), after the move (“after1”, “after2”) and after opening the enclosure to public (“open”) can be found in Table 2.

The ethogram for this study included two types of behavioural categories: instantaneous and continuous. Instantaneous samples (e.g. feeding, resting, grooming, locomotion, play, enrichment manipulation) were taken every two minutes and focused on “longer” lasting behaviours, or so called states, with the information on focal animal activity, ID of social partner and the direction of social activity (if relevant), and area of presence (see Appendix 1). Continuous samples (e.g. scratching, yawning, approach, departure, coprophagy, aggression) were made whenever the behaviour occurred in the focal individual and included “short” lasting behaviours, or so called acts. Social behaviours were not mutually exclusive and indicated both the recipient and/or initiator of the behaviour (see Appendix 2).

Only several behaviours were chosen to be analysed in this study. Among daily activities we analysed locomotion, feeding and resting, and among social interactions we analysed time spent in contact, time spent in proximity and number of approaches.

There were two observers in total who both contributed the data to obtain a larger sample. Each observer collected data on a different day. Inter-observer reliability tests were conducted on a subset of focal observations with intra-class correlation (ICC). The agreement between two observers in scoring continuous behavioural variables was found to be excellent (ICC (3, 1) = 0.917, 95% confidence interval [CI] lower, upper = 0.721, 0.977, $F = 21.1$, $p < 0.001$). The agreement between two observers in scoring instantaneous behavioural variables was also found to be excellent (ICC (3, 1) = 0.967, 95% confidence interval [CI] lower, upper = 0.889, 0.991, $F = 62.5$, $p < 0.001$).

Table 2: Total number of focal observations per subject throughout the periods

Subject	before	after1	after2	open
Kamba	34	47	28	30
Richard	34	29	26	25
Shinda	34	45	28	31
Kijivu	33	45	28	31
Kiburi	35	31	26	25
Nuru	34	30	24	25
Ajabu	33	47	28	31

3.4. Data analysis

All statistical analysis were run in R 4.0.5 (R Core Team 2022). The effect of time period on the time budget (locomotion, rest, feeding) and social interactions (contact, proximity, approach initiated, approach received) was tested with general linear mixed models (GLMM) using the 'glmmTMB' package (Brooks et al. 2017). The level of significance was set to 0.05.

For the assessment of nearest neighbours, the porportion of time spent as a nearest neighbour (i.e. in contact, proximity, or nearest individual above the proximity level) was calculated for each individual. The two nearest neighbours were compared among the study period for each individual.

The locomotion, rest, feeding, contact and proximity were analysed using GLMMs with beta family and logit link. The approaches were analysed using GLMMs. The individual identity was set as a random effect and time period ("before", "after1", "after2", "opening") as a fixed effect. Significance of each predictor was tested using the likelihood ratio tests using the drop1 function. Then, if results were significant, Tukey's range test was performed. For social interactions, statistics were adjusted for the new number of individuals, since after the group split, there were fewer individuals in each group.

4. Theoretical background

4.1. Primate taxonomy

Modern taxonomy of primates reflects their evolutionary relationships based on molecular data. The current taxonomy divides primates into two suborders: Strepsirrhines (lemurs, lorises, and galagos) and Haplorrhines (tarsiers, monkeys, great apes, and humans; Perelman et al. 2011). Strepsirrhines, also called prosimians, have characteristics such as a wet nose, claw-like digits, and a smaller brain size relative to Haplorrhines. Haplorrhines are anthropoids that have characteristics such as a dry nose, flattened nail-like digits, and a larger brain size relative to Strepsirrhines.

Anthropoids are further divided into two infraorders: Platyrrhines (New World monkeys) and Catarrhines (Old World monkeys, apes, and humans). Platyrrhines have nostrils that are widely spaced and face outwards, while Catarrhines have nostrils that are closely spaced and face downwards. All great apes and monkeys possess prehensile hands and feet with which they can manipulate objects well and, in some cases, use tools due to their fine motor skills (MacDonald 1984).

Catarrhines are further divided into two superfamilies: Cercopithecoidea (Old World monkeys) and Hominoidea (great apes). Hominoidea are further divided into two families: Hylobatidae (gibbons and siamangs) and Hominidae (orangutans, gorillas, chimpanzees, bonobos, and humans; Perelman et al. 2011). A noticeable characteristic of great apes and gibbons is the absence of tail (MacDonald 1984).

All great apes belong to the Hominidae family, which is divided into four genera – *Pan*, *Gorilla*, *Pongo* and *Homo*. Genus *Pan* is divided into two species and four subspecies; genus *Gorilla* is divided into two species and four subspecies; genus *Pongo* is divided into three species (ITIS 2021). *Homo* has only one living member and that member is human (*Homo sapiens*).

4.1.1. Genus *Gorilla*

Genus *Gorilla* includes two species, the eastern gorilla (*Gorilla beringei*) and the western gorilla (*Gorilla gorilla*), and four subspecies, eastern lowland gorilla (*G. b. graueri*), mountain gorilla (*G. b. beringei*), western lowland gorilla (*G. g. gorilla*) and cross-river gorilla (*G. g. diehli*). Gorillas are the largest primates native to central and western Africa (Figure 1). Their natural habitats cover tropical or subtropical forests in Sub-Saharan Africa and a wide range of elevations, but their populations have been declining due to habitat destruction and hunting. Both eastern and western lowland gorillas, as well as cross-river gorillas, live in dense forests, lowland swamps and marshes as low as sea level. Mountain gorillas usually inhabit montane cloud forests of the Virunga Volcanoes (altitudes from 2200 to 4300 metres). Gorillas are primarily herbivores and feed on a variety of plants and fruits, and opportunistically feed on insects. These animals share 98% of their DNA with humans and exhibit complex social behaviour and cognition (Puschmann et al. 2009).

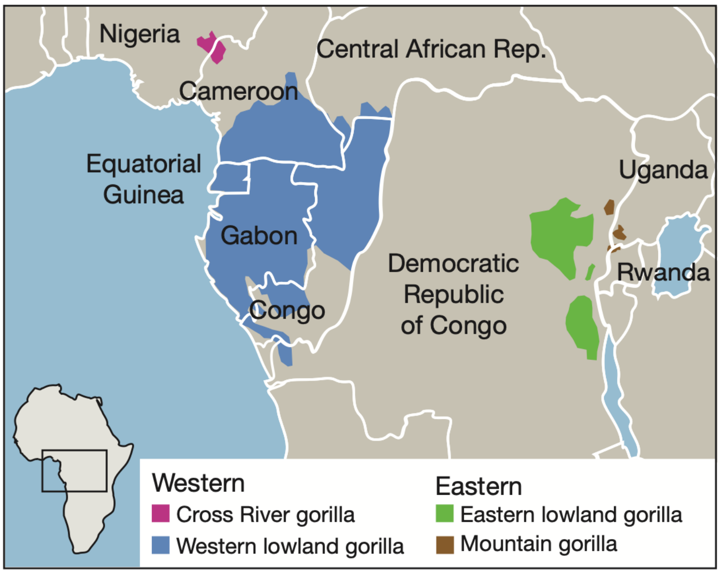

Figure 1: Distribution of gorilla subspecies (Scally et al. 2010)

4.2. Socioecology of great apes

The smallest living species of Hominidae is bonobo (*Pan paniscus*), weighing 30–40 kilograms, and the largest is the eastern gorilla (*Gorilla beringei*), whose males weigh 140–180 kilograms. Degree of sexual dimorphism is species-specific, but males are usually larger and stronger than females (MacDonald 1984). Compared to other primates, their brain volume is higher in relation to their body weight, and volume and structure of the brain are prerequisites for the versatile abilities that these animals possess (Puschmann et al. 2009). The surface of the cerebral cortex is extensive and they have excellent memory skills and learning ability (Many Primates et al. 2022). All of the great ape species are omnivorous, but most of their diet consists of plant material. As orangutans

(*Pongo*) and chimpanzees (*Pan troglodytes*) spend notable time arboreally, fruit makes an abundant part of their diet. Gorillas restore to eating leaves, barks and shoots during fruit shortages, and their digestive tract is well adapted to nutritionally poor diet (MacDonald 1984). Gestation period ranges from eight to nine months and the youngs are born precocial, however, they are very dependent on parental care for long periods of time (Puschmann et al. 2009).

There are several structures of great ape social groupings. Having a single female and her offspring is rare in primates but common in other mammals. Female spends time with her offspring until it reaches sexual maturity and they split. The adult males lead their lives mostly alone. This type of social structure is among apes found only in orangutans (Boekhorst et al. 1990).

One-male, multi-females is a social structure consisting of one (or rarely two) mating males, several females and their offspring with polygynous mating pattern (Maestripieri et al. 2007). This social structure is among apes found only in gorillas. As females reach sexual maturity, they leave their families and disperse, either joining a single male to form a new family, or they join an already existing family (Puschmann et al. 2009). When gorilla males reach sexual maturity, they are usually expelled by the dominant male, and later either form their own groups, or join other solitary males in a bachelor group made up of at least three males of similar age or with a biological bond. In captivity, bachelor groups are created based on factors like genetics, age or housing availability (Puschmann et al. 2009).

Last but not least is a fission – fusion social structure, where size and composition of the social group are dynamic and change as time passes, sometimes throughout the day, sometimes over night. Animals can split from the group (fission, e.g. foraging in smaller groups) and merge back (fusion, e.g. sleeping in one place). This structure is among apes found only in chimpanzees (Ramos-Fernandéz & Morales 2014; Aureli et al. 2008).

4.3. Conservation status

All great apes (except genus Pan and Homo) are currently listed as critically endangered in the wild ("CR", see Table 3) by IUCN (2018). There are several factors that have contributed to their conservation status. One of the biggest threats to apes is habitat loss. The forests in which they live are being destroyed or are fragmented by logging, mining, and agriculture. Great apes are also hunted and killed for their meat, which is considered a delicacy in some parts of the world. They are also captured and sold as pets or for use in the entertainment industry. Great apes are also vulnerable to diseases, especially zoonotic ones, in the same way as humans. In fact, humans can transmit many diseases to the great apes, to which they have no immunity. Climate change might be a slow, but equally important factor, as it is causing changes in rainfall patterns, which is affecting the availability of food for great apes (IUCN 2018).

Table 3: Conservation status of great apes (IUCN 2023)

Species	**Scientific name**	**Status**	**Last revised**
Western gorilla	*Gorilla gorilla*	CR	2016
Eastern gorilla	*Gorilla beringei*	CR	2018
Chimpanzee	*Pan troglodytes*	EN	2016
Bonobo	*Pan paniscus*	EN	2016
Sumatran orangutan	*Pongo abelii*	CR	2017
Bornean orangutan	*Pongo pygmaeus*	CR	2016
Tapanuli orangutan	*Pongo tapanuliensis*	CR	2017

4.4. Great apes in zoos

With situation progressively worsening, zoos and other institutions are becoming crucial facilities in the successful conservation of great ape species. Opinions differ on whether to keep, not only nonhuman primates, but also other animals in captivity, but scientific merit in the light of conservation of such species is indisputable. Most facilities and zoos strive to provide the best possible care and a good quality of life to captive animals. These institutions ought to exist as they often serve as rehabilitation centres, aid in repairing ecosystems or help us in educating the next generations in animal biology (Stokes et al. 2017). Captive animals can serve as ambassadors for their wild counterparts, raising awareness about the threats they face and the importance of saving their habitats. Captive breeding programs can help to increase the population of great apes, to be later released in the wild. These programs can help with maintaining genetic diversity, which is important for the long-term survival of the species (Prado-Martinez et al. 2013). Studying great apes in captivity can also provide valuable information about their behaviour, biology, and socio-ecology, which can inform conservation efforts in the wild (Bettinger et al. 2021). Zoos and other institutions that house great apes often have educational programs that teach visitors about the species and the conservation efforts underway to protect them.

Studying great apes in captivity can provide valuable insights and better understanding of their (social) life. Studying their behaviour can help us understand their social dynamics, communication and cooperation. This knowledge can then be applied to conservation efforts in the wild, such as improving social dynamics in reintroduced groups or identifying and mitigating social stressors in wild populations (Staes et al. 2015). Research in captivity can also be helpful in understading their physiology, reproductive cycles and developing medical treatments. In captivity, copulation is usually initiated by females. Cycle length of great apes is around 32 days on average (orangutan 28 days; gorilla 30 days; chimpanzee 36 days; bonobo 34 days). Gestation period of great apes is around 237 days on average (orangutan 245 days; gorilla 267 days; chimpanzee 229 days; bonobo 245 days). Primiparous females usually need several cycles to successfully conceive. With age and number of offspring that females had, the number of cycles decreases. Diagnosis of pregnancy is difficult in the initial stages, as missing a period is a possible, but not very reliable indicator. Combination of missing a period, swelling of genitalia and changes in behaviour can be observed to diagnose the pregnancy (Puschmann et al. 2009). Understanding their reproduction characteristics can inform us about differences between wild and captive populations, and therefore aid in conservation planning. Keeping great apes in captivity can also help us understand the diseases that affect them in captivity and can thus help us develop treatments for wild populations, such as vaccinations or medications to treat specific illnesses (D'arc et al. 2015). By studying apes in captivity, we can identify and develop better ways to care for them, including improving nutrition, housing and enrichment. This is especially useful for captive breeding programs and sanctuaries, where great apes are often kept before being reintroduced to the wild (Lambeth et al. 2006).

All institutions of the Association of Zoos and Aquariums (AZA) and the European Association of Zoos and Aquariums (EAZA) are committed to improving the welfare of primates in captivity, however, due to ever-changing findings and technologies, acceptable standards and best practices are continuously changing and face debate (Maple 2012). Many factors, like space, activity opportunities, staff availability, housing design, social organization, training or behavioural enrichment need to be considered when keeping any animal, including great apes (Hill 2018). Even when all these requirements are met, captive environments inevitably bring some stressful situations for animals.

4.5. Stressors in captive environments

Any significant change, like that in the diet, enclosure, social group or staff, number of visitors and/or veterinary check-ups, can be stressful for animals in captivity, make them feel uneasy and result in changes in social behaviour and increase in some self-directed/abnormal or in extreme cases even pathological behaviour (Hill 2018). For example, gorillas have shown more relaxed behaviours during periods of low visitor density, and higher rates of aggression, self-grooming and abnormal behaviours during periods of high visitor density (Wells 2005). As discussed in Collins and Marples (2016), changes in group structure, such as the birth of an infant or splitting of the group, may also have an effect on how gorillas react to visitors.

Coping with stressful situation might be highly individual with some animals coping with challenges better than others. This individual variation can be affected by captive group management (in terms of group structure and size, presence of infants in the group). Murray (1998) investigated the effects of different types of rearing conditions on personality in chimpanzees and found that individuals in larger groups with more than seven individuals scored higher on positive personality traits (e.g. playful) than those reared in smaller groups with less than three individuals. The latter ones were also rated as more irritable.

Although it was mentioned earlier that any change can be a potential source of stress, study on innovation in great apes show they might not be so conservative. Manrique et al. (2013) presented captive great apes with different types of puzzle boxes with rewards in form of snacks. The main finding of the study is that captive great apes exhibit high degrees of behavioural flexibility, are capable of abandoning old strategies that no longer work and adapting to new challenges. This suggests that great apes have the ability to cope with changes, despite their initial reluctance to accept them.

4.5.1. Effect of visitors on the behaviour of captive apes

Most of the studies examining relationship between the number of visitors and the behaviour of captive animals in response to them were conducted between 1985 and 2005, but based on the nature of our study, some of their findings are still relevant and applicable, and can serve well for comparisons. It is important to note that, as great apes have different personalities, their responses to crowds may differ significantly on an individual scale.

Study by Wells (2005) showed that high visitor density had negative effect on western lowland gorillas. Individuals spent significantly more time nesting when visitor density was low, and there was significantly more intragroup aggression, stereotypical behaviour and self-grooming when visitor density was high. Carder & Semple (2008) investigated an impact of visitor numbers and possible mediating effect of feeding enrichment on anxiety among western lowland gorillas in two UK zoos, Port Lympne and Chessington. Analyses revealed no evidence for a visitor effect at Chessington, with durations of self-scratching and visual monitoring unrelated to visitor number, either during or outside of periods of enrichment. At Port Lympne, visitor number correlated with anxious behaviours when no feeding enrichment was taking place; no such relationships were seen during periods of feeding enrichment. In contrary, Vrancken et al. (1990) found no significant difference in behaviour when visitor density was high in eastern lowland gorillas.

Three studies on Bornean orangutans showed contrasting results. While Mather (1999) and Boekhorst et al. (1990; 2002) found no difference in behaviour as a response to visitor density, Birke (2002) found a negative effect of high visitor density, resulting in infants holding onto adults more, and adults using paper sacks (initially as an enrichment) to cover their heads more during these periods.

In chimpanzees kept in research medical centre, Lambeth et al. (1998) looked at a database of wounding incidents to see if the presence of humans affects the frequency of these incidents. It was found that there were more wounding episodes on weekdays when there was more human activity, suggesting that the presence of humans is associated with increased aggression in chimpanzees. Increase in aggressive behaviours, affiliative behaviours, mother–child contact and locomotion as a result of presence of active visitor groups were also present in a study by Cook & Hosey (1995).

In other primate species, including lemurs (*Lemur catta*) and Diana monkeys (*Cercopithecus diana*), there was a significant increase in aggression and activity, and decrease in affiliative behaviour when visitor number was high (Chamove et al. 1998). In two groups of cotton-top tamarins (*Saguinus oedipus*), one housed in a public exhibit and one with no visitor contact, there was less affiliative behaviour of publicly housed tamarins when compared to conspecifics housed off-exhibit (Glaston et al. 1984). Although the results of these studies are not uniform, they suggest that the behaviour of primates is changing, mainly in a negative way, with a higher number of visitors.

4.5.2. Effect of transfers on the behaviour of captive apes

Transfers, or moves between or within different facilities, can have significant effects on the behaviour of captive apes, that can be both positive and negative. On the positive side, transfers can provide access to new social groups and enrichment opportunities, such as different toys, climbing structures and new challenges, that can stimulate natural behaviours and prevent boredom and other negative behaviours. However, transfers can also be stressful, particularly if apes are moved to an unfamiliar environment or separated from their familiar social group. Stress can manifest in a variety of negative behaviours, including aggression, self-injury and/or decreased appetite.

Ross et al. (2011) examined the effects of transfer of chimpanzees and western lowland gorillas into new, more naturalistic, environment. After the move both species exhibited lower levels of abnormal and attention-seeking behaviours, and higher rates of inactivity. Higher rates of scratching were observed, but only in the first year after the transfer, indicating a period of acclimatization. Seasonal effects on feeding behaviour and activity levels were evident, whereby both species were more active in the winter.

Shapiro et al. (2012) analysed physiological and welfare consequences of transport to a different facility of 72 captive chimpanzees. Blood samples were collected immediately prior to departure, immediately upon arrival, and at additional time points (three to 12 weeks) after arrival. Comparison of these three periods showed significant changes in the haematological, clinical chemistry of the blood and its immunological parameters immediately upon arrival at the new facility, indicating stress and welfare changes. Some values returned to normal, but others remained altered for up to 12 weeks after transport. Chimpanzees also lost an average of 2.5 kg during the transport.

Goerke et al. (1987) observed the behaviour of a captive juvenile gorilla before and after being transferred to a larger and more naturalistic environment. While some stress-associated behaviours decreased after the transfer, the gorilla's play behaviour decreased dramatically during the first month in the new environment and never fully recovered to the levels observed in the old environment. Self-clasping behaviour increased initially and remained high for one year but decreased four years after the move. These results indicate that a larger and more naturalistic environment does not always lead to increased play and a reduction in all stress-associated behaviours.

To minimize negative effects of transfers on captive apes, it is important to carefully plan and manage the transfer process, including ensuring that the new environment is well-suited to the needs of the individual apes and to provide adequate time for training, as well as acclimation and socialization. Veterinary care and support should be provided throughout the process, and ongoing monitoring of behaviour and welfare should be conducted after the transfer.

4.5.3. Effect of enrichment on the behaviour of captive apes

Enrichment enhances the physical and mental well-being of animals in captivity. In captivity, apes may experience limited opportunities to engage in these natural behaviours, which can lead to boredom, frustration and other negative behaviours. Providing enrichment can help to address these issues by providing a more stimulating environment, which is important for their welfare.

Chamroy et al. (2015) examined the effects of various forms of environmental enrichment on gorillas' activity and foraging levels at Brookfield Zoo. Results indicated that automatic belt feeders had the greatest impact on behaviour, and they increased gorillas' activity levels, but there were individual differences between animals. Padrell et al. (2021) investigated whether providing an artificial termite-fishing task for sanctuary-housed chimpanzees would change their behaviour. This task led to no significant changes in abnormal or self-directed behaviours, nor in affiliation- or aggression-related behaviours, but there was a decrease in inactivity and an increase in tool use, feeding behaviour and social proximity especially in chimpanzees that participated more. Overall, the results suggest that this type of enrichment can promote species-typical behaviours in captive chimpanzees without major effects on social activities.

4.6. Social structure of gorillas in wild and captivity

Knowledge about the group structure and social behaviour of wild gorillas is mostly based on field observations of mountain gorillas. Reproductive units are harem-like groups consisting of one adult male referred to as a silverback (usually older than 13 years), several females and their offspring. There is a clear hierarchy in the group – the silverback serves as the protector and leader of the group, and he is responsible for settling disputes and making decisions about the group's activities, while younger males, referred to as blackbacks, obey him. The mothers with offspring (Puschmann et al. 2009) have the highest position among females.

Most of gorilla males (i.e. blackbacks), with exception of the silverback, are leaving the group when they reach sexual maturity, between the age of 6 and 9. If they fail in finding a new harem group, they can live a solitary life (however, that applies for only 10% of whole gorilla population), or they can find another solitary males and create a bachelor group. Females also leave their home group when they reach sexual maturity at the age of 6 to 8, to find a new group or a solitary male (Puschmann *et al.* 2009).

Social structure of captive gorillas should resemble the natural setting as much as possible. However, there are some variables that can make the group structure in captivity different. Captive gorillas, especially the blackbacks, are not able to leave the group when reaching sexual maturity, so the keepers need to monitor their interactions closely to know when they should be separated (Puschmann et al. 2009). Also, the ecological, ontogenetic and social variables such as food availability, predation pressure or inter-group aggression are lifted in a captive environment (Parnell 2002). Gorilla Species Survival Plan (SSP) and AZA monitors the population of gorillas and makes recommendations for social groupings. Most of captive gorillas are thus found in groups resembling the natural harem structure, however, this leads to a surplus of males, and these might be housed in bachelor groups or as solitary males.

4.7. Social behaviour of gorillas in wild and captivity

Behaviour within and between gorilla groups is very complex. They express affection (grooming, playing, time in proximity to each other) as well as aggression. Their bonds are strong and should not be intervened by humans. The bond between the silverback and his females is the core of their social life. By bonding with the male, females gain mating opportunities and protection from predators or infanticide (Watts 1989). Aggressive behaviour between sexes can occur, but rarely leads to a serious injury. Relationships between females may vary. Maternally related females in a troop tend to be friendly towards each other and associate closely, otherwise, females have few friendly encounters and act aggressively towards each other, i.e. may fight for social access to males (Watts 2010; 1989).

Male non-kin gorillas have weak social bonds, particularly in groups with apparent hierarchies and strong competition. Males in bachelor groups tend to have friendly interactions and socialise regularly through play, grooming, contact, and they occasionally engage in homosexual interactions (Yamagiwa 1987). Severe aggression is rare in stable groups, but if two groups meet, the two silverbacks can fight to the death.

Social interactions with other neighbouring groups and even other species are much more complex than scientists previously thought (Sanz et al. 2022). In a long-term study of western lowland gorillas by Forcina et al. (2019), it was discovered that families have a dynamic social structure and there are frequent exchanges among family groups. Young individuals can enter temporarily into other family groups without any close relatives. This social behaviour is perhaps linked to the lack of infanticide records in this subspecies. Adults show peaceful interactions even among different groups. Cooksey et al. (2020) showed that intraspecific interactions and social exchanges were more frequent and varied than expected, seemingly driven more by defence of mates rather than food resources. While members of different groups were observed engaging in direct competition, they also engaged in friendly interactions such as play. In terms of inter-specific interactions, Sanz et al. (2022) showed that gorillas inhabiting Nouabalé-Ngoki national park in Congo were frequently and regularly seen interacting with groups of chimpanzees. These interactions ranged from playful behaviours to lethal aggression, possibly serving as protection against predators, facilitation during foraging, information dispersal and social skills enhancement. These new insights have changed the views on the gorilla behaviour.

In captivity, gorillas exhibit a range of social behaviours that are similar to those observed in their natural habitats. They form hierarchical harem groups. Silverbacks in captivity are little less responsible for the group decisions, since some of the activities, like feeding, waking up or going to sleep, are controlled by their keepers. They communicate using a variety of vocalizations, body language, and grooming behaviours to establish and maintain social bonds. They may also engage in play behaviour, especially with young gorillas. However, their social behaviour may be impacted by the captive environment; confinement in small, artificial environments with limited space and opportunities for social interaction can lead to altered behaviours such as self-harm, aggression towards others, and/or reduced levels of social activity (Morgan & Tromborg 2006). It is thus crucial to provide captive gorillas in zoos and other institutions with environments that mimic their natural habitats as closely as possible, and to give them opportunities for socialization, physical activity and foraging.

4.8. Daily time budget

In the wild, gorillas spend a majority of their day (more than ~40%) on foraging and feeding. They also spend about ~40% time resting, and up to 15% time traveling (Table 4; Ostrofsky & Robbins, 2020). They also engage in social behaviours such as grooming and playing.

Table 4: Time budget of wild mountain gorillas (%) (according to Ostrofsky & Robbins 2020)

	silverback	blackback	adult female	juvenile
feeding	44.2	44.2	48.2	41.4
resting	43.2	40.4	39.0	40.8
locomotion	12.5	15.4	12.7	17.7

In captivity, the daily time budget of gorillas can be quite different (Table 5). They typically have access to a more predictable and nutrient-dense diet, which can reduce the time spent foraging (up to ~30%). As a result, they may spend more time resting or engaging in other behaviours such as playing with enrichment items provided by caretakers, which can take up to 71.98% of their time.

Table 5: Time budget of captive western lowland gorillas (%) (according to Cheang & Wigman 2020)

	silverback	mother	adult female	juvenile
feeding	20.52	28.44	30.8	31.56
resting	71.98	60.15	53.56	51.80
locomotion	3.57	8.21	13.97	13.06
other	3.93	3.20	1.67	3.58

5. Results

5.1. Changes in time budget

Time period had a significant effect on the proportion of time individuals spent moving (i.e. on locomotion) (Chi square test, $\chi2 = 12.27$, DF = 3, p = 0.007) (Figure 2: Differences among the study periods in proportion of time spent moving Symbols = estimate from GLMM; error bars = 95% confidence intervals). In particular, individuals spent significantly less time moving in the first period before the move (i.e. "before") in comparison to all following periods ("after1", "after2", "open"), and there was no significant difference in between these following periods (Table 6).

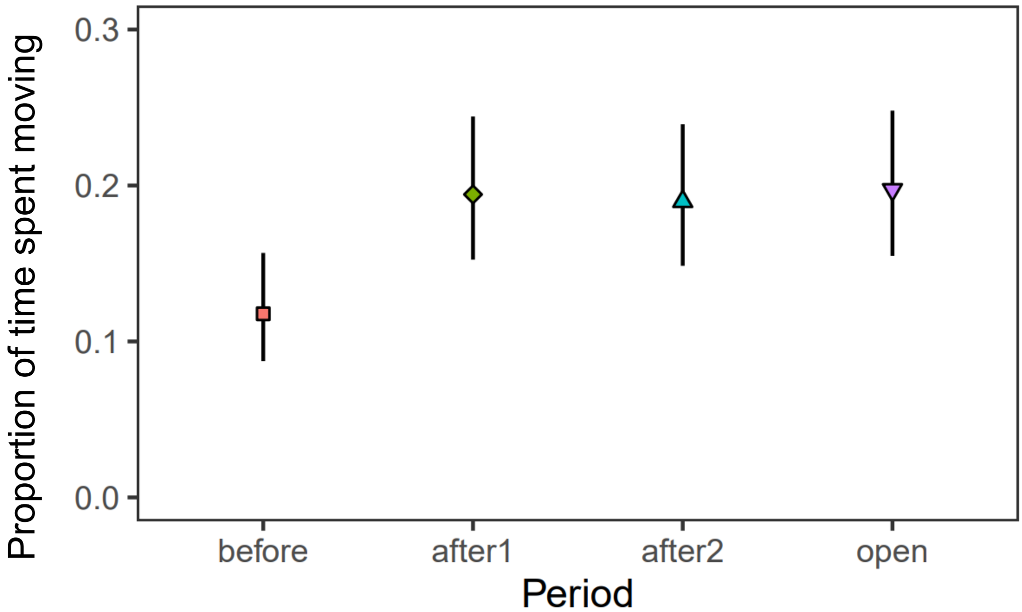

Figure 2: Differences among the study periods in proportion of time spent moving
Symbols = estimate from GLMM; error bars = 95% confidence intervals

Table 6: Results of the post-hoc Tukey's range tests analysing the differences between periods for locomotion. Period "before" marked in red, period "after1" marked in green, period "after2" marked in blue, period "open" marked in purple to correspond with depiction in Figure 2

	estimate	SE	z	p
after1 – **before**	0.5916	0.1852	3.146	**0.008**
after2 – **before**	0.5626	0.1855	3.032	**0.013**
open – **before**	0.6108	0.1849	3.303	**0.006**
after2 – **after1**	-0.0290	0.1679	-0.173	0.998
open – **after1**	0.0192	0.1676	0.115	0.999
open – **after2**	0.00482	0.1677	0.287	0.992

There were some individual differences in the proportion of time spent in each activity. As seen in Figure 3, there was a general increase of the time spent moving in the first period after the move ("after1") compared to the period before the move ("before"), except for Nuru (adult male). Kijivu (adult female; mother of Kiburi and Nuru) showed the most substantial increase in locomotion compared to every other individual in this period. Lastly, in period after opening the enclosure to public ("open"), there was an increase of time spent moving in the bachelor group and decrease of time in locomotion in the breeding group.

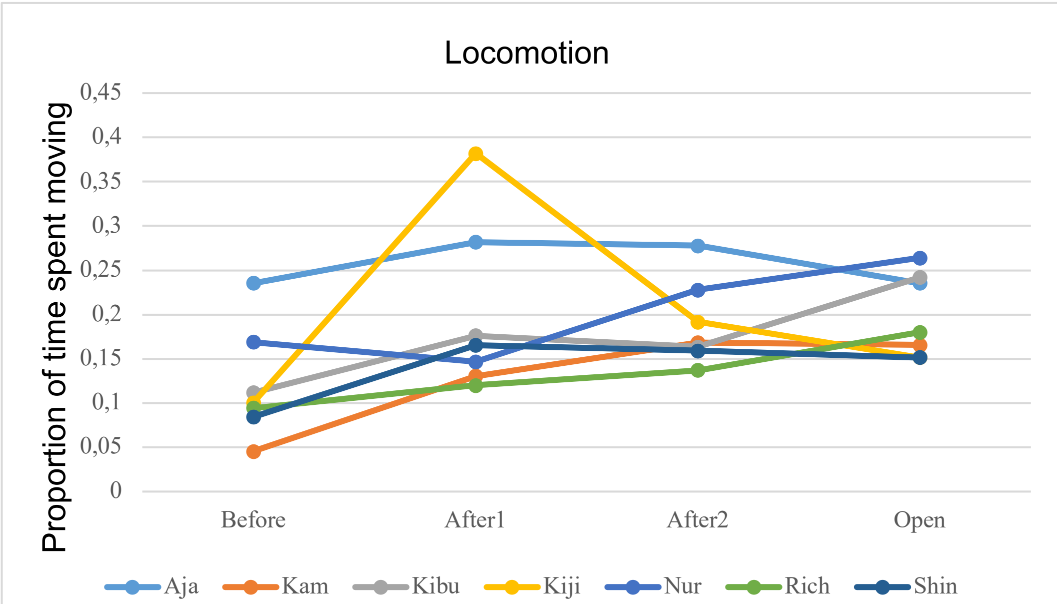

Figure 3: Individual changes in locomotion throughout different periods. Different individuals are depicted in different colours.

Time period had no significant effect on the proportion of time individuals spent resting (Chi square test, $\chi2 = 6.74$, DF = 3, p = 0.081) (Figure 4). Individuals tended to rest less in the last period when the new enclosure was open to public ("open"). The biggest, however not statistically significant, difference in resting was observed between the first period after the move ("after1") and period after the opening of the new enclosure ("open"). The results were not, however, enclosure-dependent – the proportion of time spent resting by individuals in the old enclosure and by individuals in the new enclosure was approximately the same.

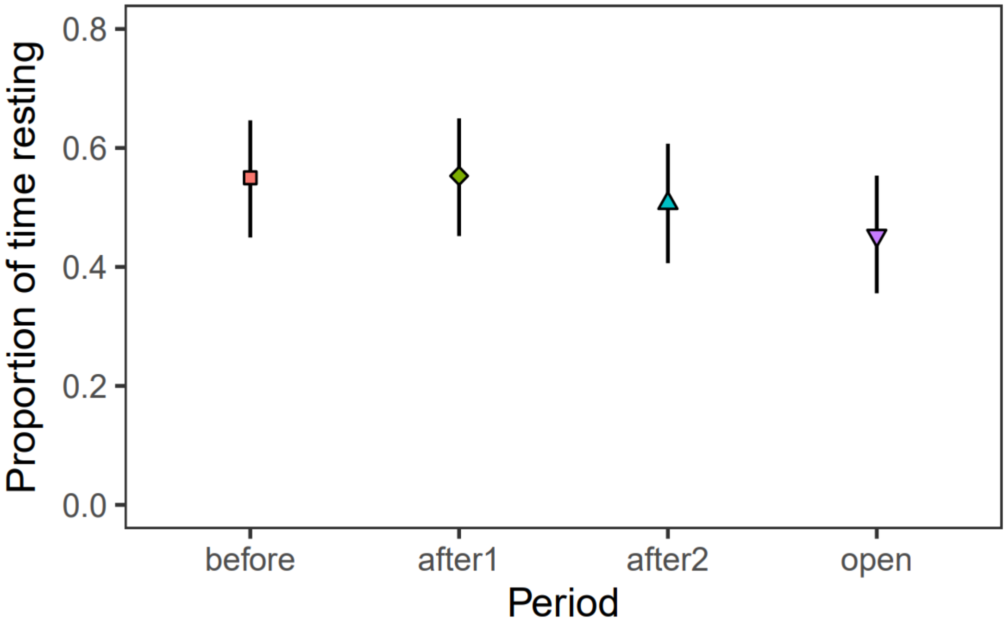

Figure 4: Differences among the study periods in proportion of time spent resting.
Symbols = estimate from GLMM; error bars = 95% confidence intervals

Kijivu had a substantial increase in resting in the first period after the move (Figure 5). In the period after the move, resting time generally decreased, except for Ajabu (juvenile male) and Shinda (adult female; mother of Ajabu). Nuru's resting time substantially decreased in the last period in comparison to all other periods. Similar trend in terms of resting throughout all four periods can be observed in Kamba and Richard.

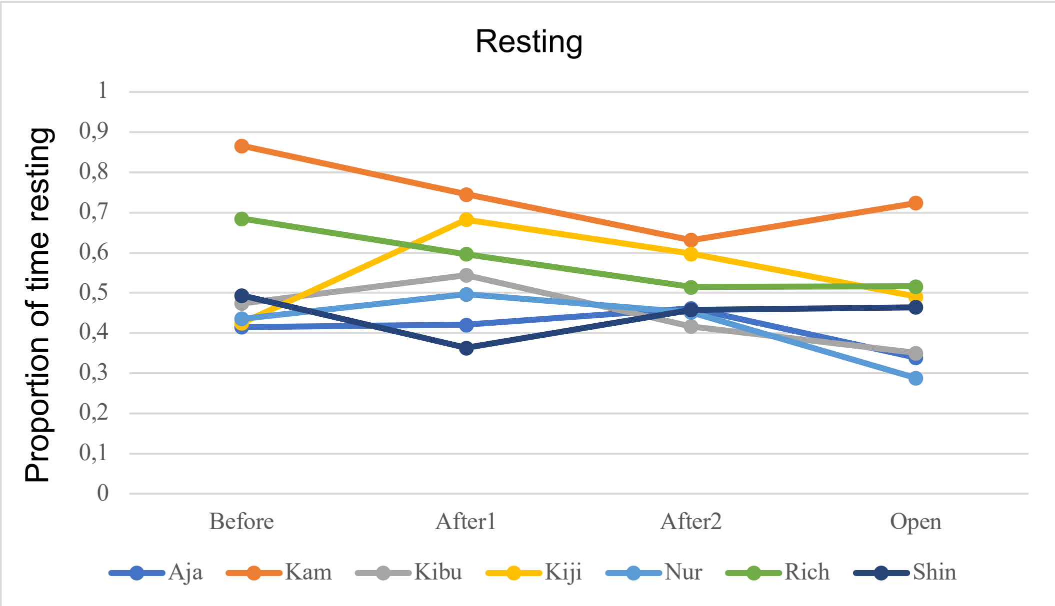

Figure 5: Individual changes in resting throughout different periods.
Different individuals are depicted in different colours.

Time period had no significant effect on the proportion of time individuals spent feeding (Chi square test, $\chi2 = 5.33$, DF = 3, p = 0.149) (Figure 6). Individuals tended to spend on average less time feeding in the first period after the move (“after1”) in comparison to other periods (“before”, “after2”, “open”), however this difference was not statistically significant.

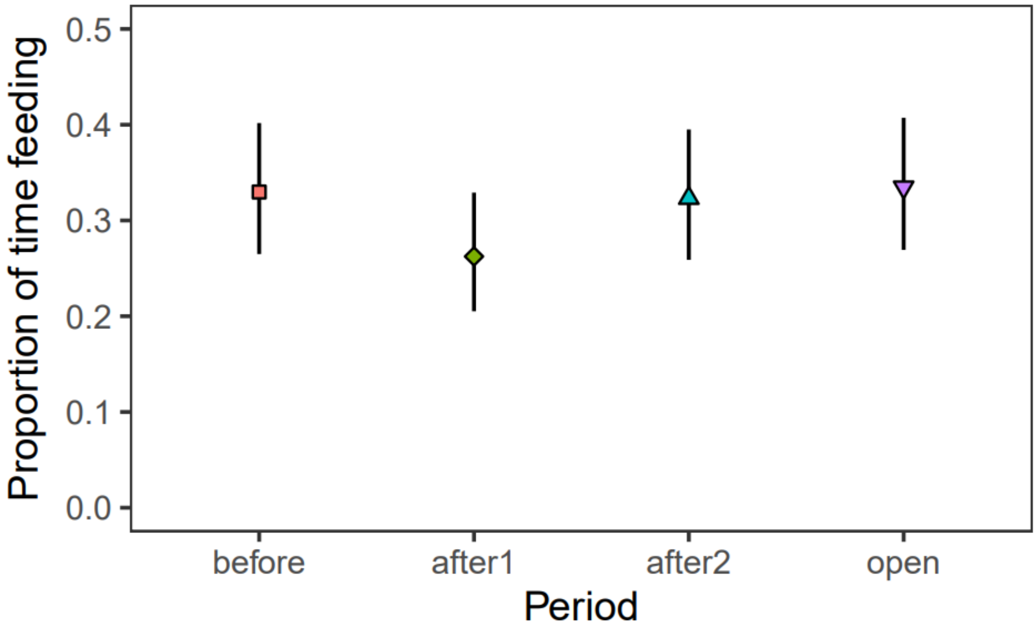

Figure 6: Differences among the study periods in proportion of time spent feeding. Symbols = estimate from GLMM; error bars = 95% confidence intervals

As seen in Figure 7, Kijivu's feeding time decreased substantially in the first period after the move compared to the period before the move. In the period later after the move, Kiburi's (adult male) feeding time increased substantially. Similar trend in terms of feeding throughout all four periods can be observed in Kijivu and Ajabu.

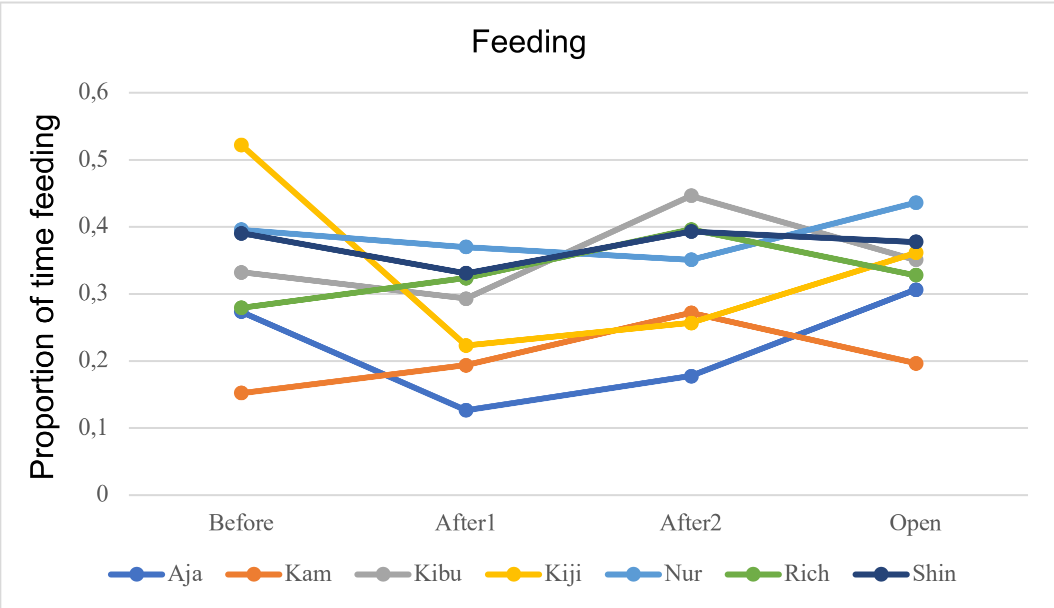

Figure 7: Individual changes in feeding throughout different periods.
Different individuals are depicted in different colours.

5.2. Changes in social spacing and interactions

Time period had a significant effect on the proportion of time individuals spent in contact with their social partners (Chi square test, $\chi2 = 22.45$, DF = 3, $p < 0.001$) (Figure 8). Specifically, they spent more time in contact with each other in the period after the move ("after1") in comparison to every other period ("before", "after2", "open") (Table 7).

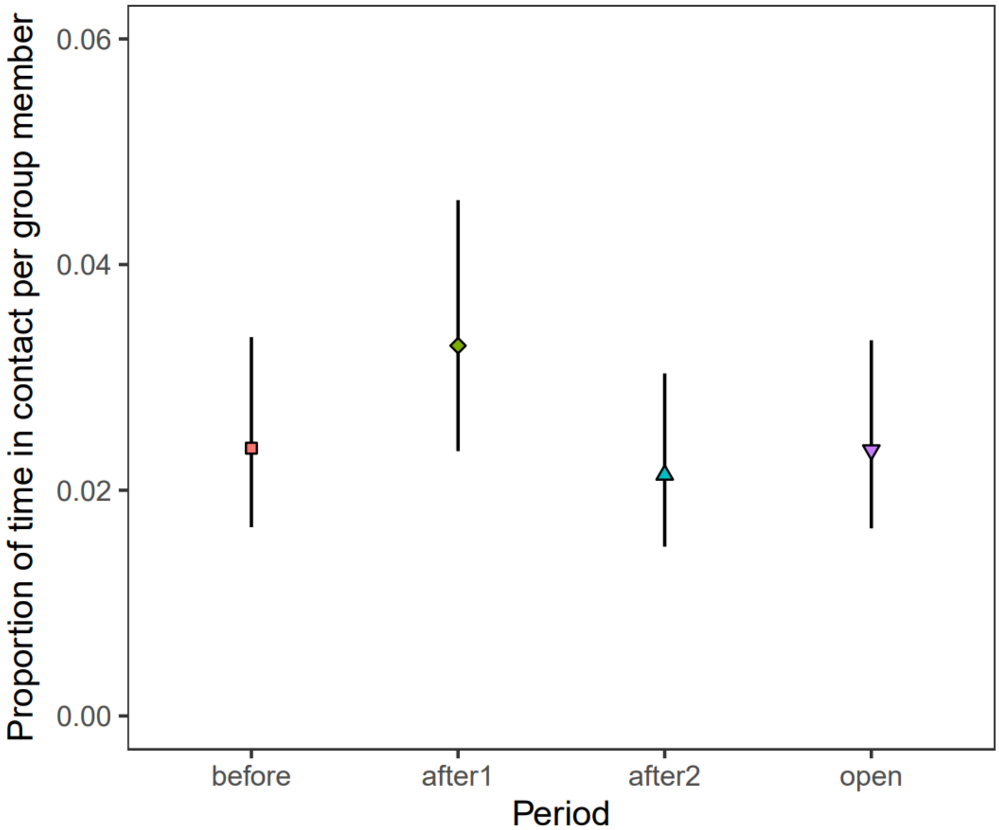

Figure 8: Differences among the study periods in proportion of time spent in contact. Symbols = estimate from GLMM; error bars = 95% confidence intervals

Table 7: Results of the post-hoc Tukey's range tests analysing the differences between periods for contact. Period "before" marked in red, period "after1" marked in green, period "after2" marked in blue, period "open" marked in purple to correspond with depiction in Figure 8

	estimate	SE	z	p
after1 – before	0.333517	0.106026	3.146	**0.009**
after2 – before	-0.107355	0.115483	-0.930	0.789
open – before	-0.007457	0.112864	-0.066	0.999
after2 – after1	-0.440872	0.108897	-4.049	**0.001**
open – after1	-0.340974	0.105379	-3.236	**0.007**
open – after2	0.099898	0.115630	0.864	0.823

Time period had a significant effect on the time spent in proximity to group members (Chi square test, $\chi 2 = 34.82$, DF = 3, $p < 0.001$) (Figure 9). Individuals spent more time in proximity in the first period after the move (“after1”) in comparison to periods “before” and “open”. In the last period (“open”) individuals spent less time in proximity in comparison to all previous periods (see Table 8).

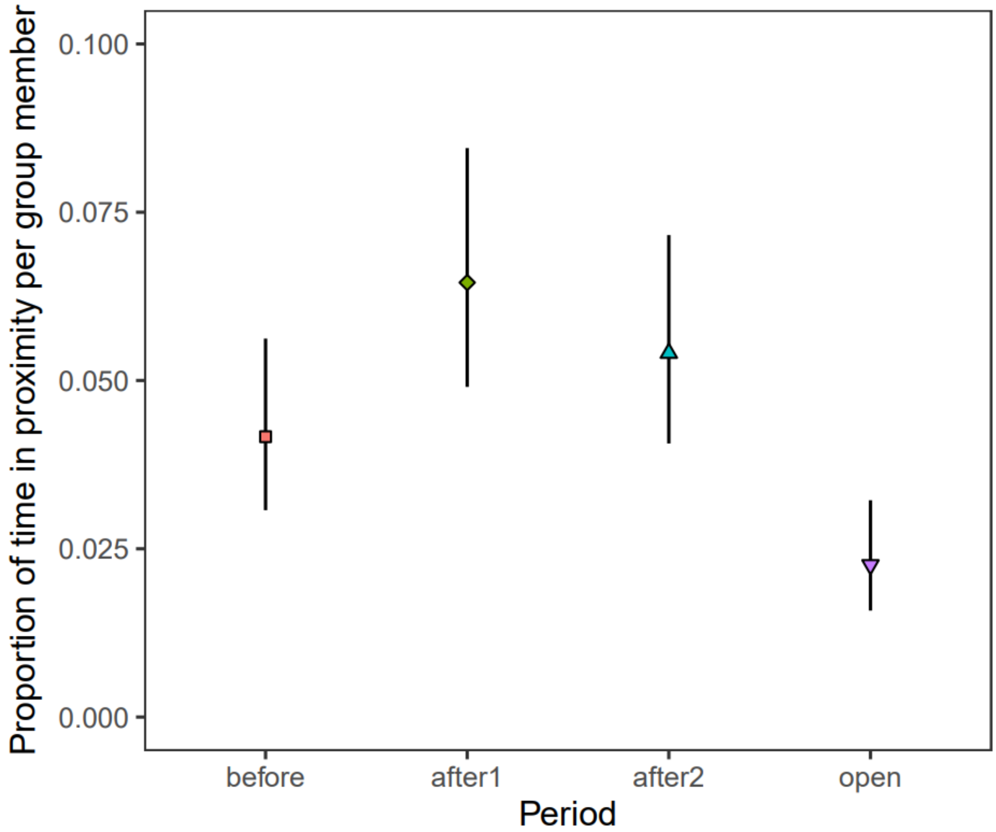

Figure 9: Differences among the study periods in proportion of time spent in proximity. Symbols = estimate from GLMM; error bars = 95% confidence intervals

Table 8: Results of the post-hoc Tukey’s range tests analysing the differences between periods for proximity. Period “before” marked in red, period “after1” marked in green, period “after2” marked in blue, period “open” marked in purple to correspond with depiction in Figure 9

	estimate	SE	z	p
after1 – **before**	0.4624	0.1374	3.366	**0.004**
after2 – **before**	0.2740	0.1414	1.939	0.209
open – **before**	-0.6308	0.1762	-3.580	**0.002**
after2 – **after1**	-0.1884	0.1281	-1.471	0.451
open – **after1**	-1.0932	0.1656	-6.601	**0.001**
open – **after2**	-0.9048	0.1693	-5.344	**0.001**

Time period had a significant effect on the rate of approaches (Chi square test, $\chi2 = 18.30$, DF = 3, p = 0.001) (Figure 10). Individuals approached each other more often in the first period after the move ("after1") in comparison to periods "before" and "open" (see Table 9).

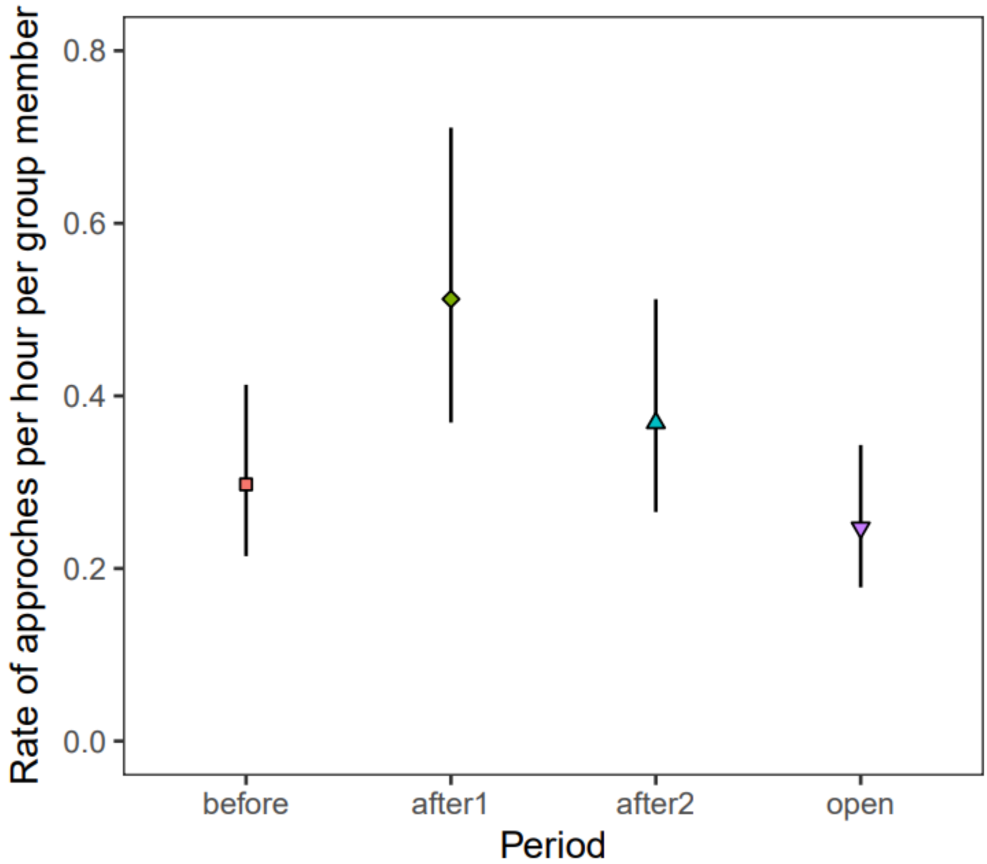

Figure 10: Differences among the study periods in rate of approaches.
Symbols = estimate from GLMM; error bars = 95% confidence intervals

Table 9: Results of the post-hoc Tukey's range tests analysing the differences between periods for approaches. Period "before" marked in red, period "after1" marked in green, period "after2" marked in blue, period "open" marked in purple to correspond with depiction in Figure 10

	estimate	SE	z	p
after1 – before	0.5435	0.1817	2.991	**0.015**
after2 – before	0.2146	0.1807	1.187	0.635
open – before	-0.1853	0.1822	-1.017	0.740
after2 – after1	-0.3289	0.1814	-1.813	0.267
open – after1	-0.7287	0.1821	-4.003	**0.001**
open – after2	-0.3998	0.1824	-2.192	0.125

Not surprisingly, the social dynamics of the gorillas measured by nearest neighbour characteristics changed immediately after the move, resulting in a change in at least one nearest neighbour of each individual. This can be seen when comparing the time period before the move ("before") to the period immediately after the move to the new enclosure ("after1"). These "new" nearest neighbours then remained relatively stable for the remainder of the study (see Table 10). For instance, Kamba's nearest neighbour in the period before the move ("before") used to be Richard (the silverback) and Kiburi (adult male). However, after the move to the new enclosure, her nearest neighbours changed to Kijivu (adult female) and Ajabu (juvenile male) and stayed the same until the end of the observation.

Table 10: Top two nearest neighbours of each individual throughout different periods. Individuals marked with asterisk (*) are males that stayed in the original "old" enclosure.

	before		after1		after2		open	
	1st	**2nd**	**1st**	**2nd**	**1st**	**2nd**	**1st**	**2nd**
Aja	Shin	Nur	Shin	Kiji	Shin	Kiji	Shin	Kiji
Kam	Rich	Kibu	Kiji	Aja	Kiji	Aja	Kiji	Aja
Kibu*	Nur	Kam	Nur	Rich	Nur	Rich	Nur	Rich
Kiji	Nur	Shin	Kam	Shin	Kam	Aja	Kam	Aja
Nur*	Kiji	Kibu	Kibu	Rich	Kibu	Rich	Kibu	Rich
Rich*	Kam	Nur	Nur	Kibu	Nur	Kibu	Nur	Kibu
Shin	Aja	Rich	Aja	Kiji	Aja	Kam	Aja	Kiji

6. Discussion

Results of this study show that implemented changes had a significant effect on daily activities and social interactions of the western lowland gorillas in Prague zoo. Among daily activities, there was a significant increase in time spent in locomotion. That change was most notable immediately after the move and remained relatively constant during all following periods. Among social interactions, there was a significant increase in time spent in contact, time spent in proximity and the rate of approaches. Those changes were most notable in the period immediately after the move and group split and were slowly getting to their initial levels in the following periods.

The apparent change in behaviour (that happened predominantly immediately after the move) of the studied gorillas could be caused by the stressful nature of the managerial changes, which in our case was the move to a new enclosure and the associated group split. It could be therefore suggested that the observed behavioural changes were reactions of the individuals to these events and their strategies on how to cope with the situation. A recent study in some great ape species (bonobos, gorillas, and orangutans) focusing on measuring stress hormone cortisol during three different occasions (normal days, enrichment days and days after moving to a new enclosure) clearly showed that moving represents a major stressor for the individuals. Namely, cortisol levels were the highest after moving to the new enclosure (Behringer et al. 2022). Shapiro et al. (2012) focused on the effect of chimpanzee transfer to a different environment and came to a similar conclusion that transport can be a stressor for animals, resulting in physiological and behavioural changes. Additionally, most of the changed physiological values (including clinical chemistry and immunological parameters) slowly returned to normal pre-transfer levels, which resembles the same pattern as the behavioural changes seen in our results. Likewise, Skurski (2016) was observing behavioural changes and changes in cortisol levels of western lowland gorillas during a potentially stressful situation (i.e. short-term space restriction to indoor housing facilities), and found no significant differences in social interactions, but increased cortisol levels, indicating stress. Although the mentioned study in contrast to ours found no significant differences in behaviour, the levels of cortisol were higher than during normal days, identifying confinement as a possible stressor. Gorillas in our case study were also confined for few weeks to indoor facility only, and thus the exhibited stress-related changes in behaviours could be associated with the confinement to indoor facility.

However, as we had two major stressors in our case study (moving to a new enclosure and a group split), it is difficult to distinguish which of these effects (or perhaps both) was responsible for the observed changes. Nonetheless, based on the behavioural changes and the events that gorillas went through, we could state that individuals went through a stressful period. Higher stress levels can result in stress-related behaviours, including aggression, avoidance, increased contact with other individuals, excessive grooming or changes in sleeping and feeding patterns (i.e. sleeping more and feeding less) (Morgan & Tromborg 2006; Eckardt et al. 2019). However, we did not observe increased aggression among individuals; in fact, aggressive behaviours were so low it was not possible to analyse them.

Visitors can have an effect on the behaviour of gorillas (Miller et al. 2021). Miller and colleagues (2021) focused on behavioural changes of zoo-housed gorillas in times of complete visitor absence (due to the global pandemic). Majority of gorillas was observed foraging less and being more inactive in the 18 weeks when visitors were absent, whereas the adult male silverback showed the opposite pattern. Decreased activity was also reported in a study by Wells (2005), where gorillas spent more time resting when visitor density was low. The high inactivity of our focal group in the last period corroborates the results from these studies. Although our results did not show any significant changes between different periods, we can still see that gorillas rested the least in the last period where the new enclosure was opened to the public. Opening the new enclosure to the public after a two-month long acclimatization period resulted in a sudden increase in the number of visitors, therefore, one of the possible explanations of the changes in the last period could be the number of visitors present. However, in our case, no notable differences were observed in between two different gorilla groups/enclosures, because the group in the “old” enclosure continued having visitors during the whole study time (apart from a two-week period immediately after the move).

Individuals had their “favourite” conspecific to be around of, which we referred to as the nearest neighbour. With group split, there was a high chance of them not being able to spend time around their conspecific of choice, and as indicated by the results, the nearest neighbour changed immediately after the group split. However, the new social situation remained relatively constant for all the following periods. Therefore, it seems that the group split was the major factor responsible for the change in social dynamics and nearest neighbour dynamic.

When looking at individual differences in behaviour, more apparent changes were seen in females rather than males. Similar results were found by Edes et al. (2016). In their study, allostatic load (i.e. estimate of stress-induced physiological dysregulation based on an index of multiple biomarkers) was positively associated with age in gorillas at the Columbus Zoo and Aquarium, and was higher in females than in males. Although this might be a possible explanation, in our case the males and females experienced these events under different conditions, thus the results might not be driven purely by sex, but also by the fact that all females experienced the translocation which was not the case for all males.

Additionally, there was a dramatic change in daily activities especially in one of the adult female gorillas, Kijivu. Kijivu, as we also confirmed with the keepers, is a nervous individual by nature, so going through a stressful event may affect her behaviour more than other individuals. In this study, Kijivu has shown changes in daily activities (increase in time spent in locomotion and decrease in time spent resting and feeding), and it could be suggested that these changes are a form of a stress-coping mechanism. Increased locomotion as a result of stress has been reported in some studies (Chamove et al. 1988; Collins & Marples 2016); however, the overall significance of this increase is unclear. Dramatic changes were also expected to be seen in the silverback, Richard, because, according to the information from keepers, Richard is very nervous, anxious, and does not like changes. For these reasons, Richard was given a small dose of sedatives for an extended period of time in period after the changes ("after1"), therefore, changes in his individual behaviour were not that pronounced.

More individual differences and behavioural indicators of stress can be seen in a study by the second observer (Čížková 2023). She found the biggest rates of behaviours indicating stress in the period before the move ("before"). In contrast to our results for daily activities and social interactions, most individuals experienced a decrease in behavioural indicators of stress and stereotypical manifestations after the changes (as well seen in Ross et al. 2011 and Goerke et al. 1987). Over time, there was no significant increase in observed manifestations of these behaviours.

As indicated by the results, even though individuals went through a potentially stressful event of the group split and move to a new enclosure, they were able to cope with changes well, presumably because of the social support and comfort they found in each other. Social support expressed through affiliative interactions was found to reduce stress in primates in several studies (Boccia et al. 1995; Cheney & Seyfarth 2009; Judge & Mullen 2005).

This case study has several limitations. Unexpectedly and contrary to the original plan, this study deals with two big changes, i.e. move to a new enclosure and a group split, instead of just the move to a new enclosure. This makes the interpretation of the behavioural changes difficult in relation to the importance of the two changes. Moreover, the sample size of seven individuals is rather small, which makes it difficult to make generalized assumptions for the whole population, but increasing sample size in future studies could be a difficult task and a multi-zoo effort. The gorilla group in Prague Zoo with seven individuals falls within the range of average gorilla group size that are held in zoos, and the highest number of individuals in one group is currently eleven (Burger's Zoo, Arnhem, Netherlands; Port Lympne Reserve, Lympne, UK; Zooparc de Beauval, Saint-Aignan, France), with exception of some African primate sanctuaries or rehabilitation centres, that house more individuals (Gorillas Land 2022). The last limitation of this work is the fluctuating presence of visitors throughout different periods. Namely, visitors had access to the "old" enclosure in periods before the move ("before") and after the opening of the new enclosure ("open") but had no access to the new enclosure in the period immediately ("after1") and some time after the move ("after2"). Most of the studies show negative effect of high number of visitors on behaviour of captive apes (Carder & Semple 2008; Birke 2002; Cook & Hosey 1995). On the other hand, some studies show no effect of visitors on the behaviour of captive apes, as seen for example in Vrancken et al. (1990). Not only there is no definitive pattern among those studies, but also in our case, due to many factors changing at the same time, it is difficult to distinguish which factor is causing the changes.

For future studies, it would be beneficial to conduct the same research in multiple zoos, compare the results and create guidelines for future managerial interventions. Additionally, more research on changes of social interactions in great apes as a response to stress could be beneficial, as majority of the literature is focused on self-directed behaviours only.

7. Conclusions

The aims of this thesis were to investigate whether there are any changes in daily activities and social interactions among group of western lowland gorillas after going through a group split and a move to a different enclosure. By conducting focal observations, we concluded that there were changes both in daily activities and social interactions throughout different periods of the study. The results showed that these changes were the most prominent immediately after the move. In conclusion, results indicate that gorillas went through a potentially stressful event but that they managed to overcome it quite well by using mutual social support and comfort. Studies of this nature represent a valuable resource for zoos and their future managerial interventions and provide an insight into keeping great apes in captivity, which is crucial for future conservation of these species. By understanding their life in captivity and in the wild (including their behaviour, biology, and socio-ecology), we can focus on raising awareness about the threats they face, create conservation programs that aid in improving genetic diversity, and ensure them a better life.

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List of the Appendices:

Appendix 1: Ethogram of instantaneous behaviours

Instantaneous behaviours were noted down every two minutes, on designated focal points, and focused on longer lasting behaviours with the information on focal animal activity, ID of social partner, the direction of social activity (if relevant), area of presence in the enclosure and moments where animal was not visible to the observer (out of sight).

Name	Definition
feeding	An animal is consuming food (and/or enrichment, branches, leaves), including chewing and food manipulation
resting	An animal is sitting or laying, eyes are closed for most of the time, no obvious activity
grooming	An animal is going through hair of the other, while watching the groomed place on the other‘s body, using its fingers or mouth, may or may not pick up some particles
grooming-self	An animal is going through hair of its own body, is watching the groomed place, may or may not pick up some particles
vigilance	Animal is stationary in any posture while paying attention (i.e. monitoring) its environment or actively scanning the environment, can also watch a particular stimulus
locomotion	Any kind of movement resulting in changing its position, and which is not defined as part of another behaviour, including walking/running/climbing/jumping for a distance longer than 3 meters, or which results in changing the substrate (e.g. coming from tree log to the ground)
social play	Physical play with a partner, includes chase, mock bite, poke/hit, throw at, object tug, wrestle, etc, and excluding any aggressive events. Does not necessitate continuously maintained proximity with a play partner
solitary play	Physical play without a partner, includes locomotory play and object play

contact	An animal is in direct physical contact with another conspecific, i.e. touching with any part of the body, but not grooming with the conspecific, or doing any other defined behaviour
proximity	An animal is out of direct contact but within an arm's reach of another conspecific
coprophagy	An animal feeds on faeces (its own or of another conspecific)
enrichment	An animal attends to any type of enrichment provided by the keepers, includes object manipulation, play and exploration

Appendix 2: Ethogram of continuous behaviours

Continuous samples were recorded whenever they occurred in the focal individual between the two focal points, and they consisted of short-lasting behaviours.

Name	Definition
scratching	Animal is going fast through its fur and body surface with its arm/hand, leg/foot, or is rubbing self against another surface, no visible attention to the scratched part
grooming-self	An animal is going through hair of its own body, is watching the groomed place, may or may not pick up some particles
yawning	An animal clearly opens its mouth in automatic manner
approach	An animal comes into proximity (an arm's reach) of the other or others
departure	An animal goes out of proximity (an arm's reach) of the other or others
contact aggression	Charge another individual with bite, push, grab/pull hair, hit/slap, poke, wrestle
non-contact aggression	Charge another individual with hitting or throwing object(s), chase, roar
social play	Physical play with a partner, includes chase, mock bite, poke/hit, throw at, object tug, wrestle, etc. Does not necessitate continuously maintained proximity with another play partner
solitary play	Physical play without a partner, includes locomotory play and object play
hair plucking	A single (or multiple) hair is plucked with a rapid jerking-away motion, may be accompanied by inspection and consumption of the hair shaft and follicle, can be self-directed or done to another individual
regurgitation	An animal voluntarily brings up partially digested food and then reingests it; considered as abnormal behaviour
coprophagy	An animal feeds on faeces; considered as abnormal behaviour

enrichment	An animal attends to any type of enrichment provided by the keepers, includes object manipulation and exploration
out of sight	An animal is not visible to the observer