UNIVERSITÉ DE NEUCHÂTEL

ZOO BASEL

Master in Cognitive Sciences

Investigating the social well-being of 5 castrated Gorillas (*Gorilla gorilla gorilla*) living in European zoos.

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Contents

1. Abstract

In polygynous species, the social housing of male in captivity is a challenge for managers. With gorillas, the main solution adopted until now, in both American and European institutions, was the creation of bachelor (all-male) group. Although it was accepted as the best solution worldwide, recent results reported elevated levels of injuries in bachelor compared to breeding groups (Vermeer et al. 2014; Leeds et al. 2015). EEP (European breeding program) thus started thinking and testing castration as a new solution for housing the surplus of male in their native breeding group. In 2015, 10 castrated gorillas, from 3 to 13 years old were living in European zoos. This study aimed to investigate the well-being of the oldest castrated individuals, living in Basel zoo, Gaia Park and la Vallée des Singes. We focused our analysis on three social parameters; activity budget (as a proxy of social disorder), positive and negative interactions, and proximity patterns, in order to investigate if castration affected the gorillas' social well-being. For four out of five individuals, we found castration had no effect on the three parameters. It appeared that they socialized well with the silverback. Rates of positive and negative behaviours, as well as proximity patterns were similar to previous studies in bachelor and breeding groups. For the fifth castrated male, we found five times more negative interaction and zero positive interaction with the dominant male. He also seemed to avoid the silverback, as they shared the same room during only 5.6% of the total time, and because he was often outside of the group. We did conclude that the first four castrated individuals had a satisfying social well-being, but we could not make a clear statement for the last individual. Indeed, although his social well-being did not seemed to be satisfactory and this might be related to his position as a castrated male, it could also be a consequence of the silverback inexperience and recent integration, and thus being a temporary situation. This study offered an initial overview of the European castrated gorillas' situation, but further investigations are necessary before expecting using castration as a solution for housing the surplus of males. In particular workshops should be organised to discuss the factors that are important to the successful integration and maintenance of castrated gorilla in breeding groups. Castrated gorillas also need to be studied on the long term, in order to follow their personal and social evolution. We identified two critical period that could be essential to focus on: childhood and early adulthood.

2. Introduction

1. Group structure in free-ranging Gorillas.

Gorillas are the largest existing primates, and they are well known for their gentle, human-like behaviour (Fossey 1985). Like many other primate species, gorillas are social animals that spend almost their entire life as members of a group. Breeding groups can reach up to thirty individuals, but the average size is ten weaned individuals, with a non-significant variation between the different subspecies of gorillas (Parnell 2002; Harcourt & Stewart 2007). Gorillas live in harem social structure. A breeding group is usually composed with one adult dominant male, also called silverback and several females with their offsprings. Gorilla families are highly cohesive and often permanent, with long-time male-female association and a dispersion limited to the births (Harcourt & Stewart 2007).

A gorilla group have a clear and strong hierarchy which is determined by the sex and age of the individuals. The silverback has the higher-rank, and adult females are dominant over young individuals (Abelló et al. 2017). Individuals are considered as infants (I) until 3-4 years old, which is usually the time they are weaned. During this time, they almost never leave their mother, who dedicates her entire time to them, and consequently, a mother would not give birth during the next three years. Juveniles (J), between 3-4 and 7 years old, are weaned individuals that feed independently, but still keep a lot of contact with their mother; they are not mature or fertile. By 8-10 years old, juveniles usually reach puberty and become sub-adults (SA), they are fertile and a sexual dimorphism appears. Offsprings commonly leave their natal group once they reach maturity. Young adult females either join an existing group or associate with a solitary adult male, while young adult males often stay alone before challenging the leadership of an existing group or attracting females around them to create a new group (Parnell 2002; Harcourt & Stewart 2007). From 10 years, female gorillas are considered as adults (A), they are fully mature and usually reach their adult size a few years later. Maturation of males is longer and has more steps than females. We mainly differentiate adult male gorillas as blackbacks (BB, <14 years) and silverbacks (SB, >14 years). When maturing, the hairs on the back of males gorillas progressively shorten and turn silvery, giving the name of fully mature silverbacks (Harcourt & Stewart 2007; Breuer et al. 2009). It has also been proposed to divide the silverback category in young silverback (YSB, 14-20 years) and old silverback (OSB, >20 years), with YSB being more aggressive than OSB, suggesting a non-dominant position regarding OSB (Stoinski et al. 2013; Leeds et al. 2015).

Silverbacks thus have a leadership role. They protect against intruders and conciliate within the group, especially when fights happen between females, to maintain a strong cohesion. They also initiate and lead travels to find food patches and sleeping areas (Harcourt & Stewart 2007). Silverbacks often have a central position in the group due to females trying to stay close to them (Harcourt & Stewart 2007). Male attractiveness to female is a strong component of group cohesion (Yamagiwa et al. 2003). A hierarchy also exists among females, and ranks are determined according to several factors such as seniority. Amongst the young, ranks are usually determined by the individual age and their mother's rank (Harcourt & Stewart 2007; Abelló et al. 2017). Free-ranging gorillas display far less social interactions than the other great apes, especially adults. Social interactions represent only 0.5% of the gorillas activity budget (Masi et al. 2009). Instead, adult gorillas daily activities are shared between eating (60%) resting (30%) and travelling (10%), with small variation due to environmental factors (Masi et al. 2009). Positive social interaction of gorillas mainly consist in close proximity, social grooming, and supportive intervention (Harcourt & Stewart 2007). Occasionally, adults play, but only infants and juveniles spend long session playing with age-related partners or close relatives (Brown 1988). Positive interaction between females are regulated by individual relatedness. Unrelated females rarely interact with each other while related females (mother/daughters, full sisters) engage in more positive social behaviours, spend more time in close proximity and support each other during conflicts. Females without relatives in the group maintain a close proximity to the silverback, following and initiating more friendly contact with him (Watts 1997; Harcourt & Stewart 2007). Due to their dominant position, silverbacks receive more positive social behaviours than they initiate. For the same reason, they also initiate more aggressive behaviours. In the wild, most of gorillas' aggressions are non-physical, they use a large repertoire of displays and vocalisations. Physical aggressions occur less frequently but they often cause strong injuries, because gorillas use their canines as a weapon. Within the group, feeding competition is the main reason of aggressions between members. Silverbacks also use agonistic behaviours for group policing and to reinforce their dominance (Watts 1994; Watts 1997). In addition, male aggression towards females can be considered as a courtship strategy, which end up after the female submission (Breuer et al. 2016).

2. <u>Group structure and behaviour in captivity.</u>

In 2014, 861 captive Western lowland gorillas (*Gorilla gorilla gorilla*) were housed in 145 worldwide institutions, 405 males and 456 females (Niekisch 2015), usually in one-male breeding groups. Species with harem social structures naturally produces males not required for breeding, which is a challenge for housing in captivity (Vermeer et al. 2014). For the surplus males, the solution adopted by American (Gorilla SSP (Species Survival Plan)) and European breeding programmes (Gorilla EEP (European Endangered species Programme)) was the creation of bachelor groups. The definition of a bachelor group is the "coalition of two or more males in the absence of any females" (Abelló et al.

2017). In the wild, bachelor groups have been observed in Mountain gorillas (*Gorilla beringei beringei*), usually with young male dispersing from their natal group to avoid aggressions from their father, or after group loss, instead of remaining solitary (Robbins 1996; Harcourt & Stewart 2007). However, there are no reports of bachelor groups in the three other subspecies. In Western lowland gorillas, several solitary males have been studied in the wild, and none ever join a bachelor group, suggesting that this social structure is not usual for the subspecies (Parnell 2002; Gatti et al. 2004; T. S. Stoinski et al. 2004). Nevertheless, in captivity, Western lowland gorillas were successfully housed in bachelor groups and this housing has been considered as a viable long term solution for the surplus of males (Stoinski et al. 2001; Stoinski et al. 2004). Captive bachelor groups are usually created with young males which are accompanied by, at least, one silverback. Age between 6 and 9 years has been considered as the optimum for young males as it is similar to emigrating males in the wild and also because gorillas at this age are adaptable to change and thus the most likely to develop social bonds (T.S. Stoinski et al. 2004; Abelló et al. 2017). However, the stability of bachelor groups mainly seems to depend on the individuals character and personality (Kuhar et al. 2006), but also on the enclosure quality and skills of the keepers (Vermeer et al. 2014). Indeed, bachelor groups are not always stable and thus require flexible facilities with several enclosures that allow to temporarily separate individuals (Coe et al. 2009; Abelló et al. 2017). Moreover, although it was accepted as the best solution worldwide, recent results and anecdotal reports from zoos, revealed elevated levels of injuries in bachelors compared to breeding groups, leading to scepticism on the feasibility of bachelor groups through long term period (Vermeer et al. 2014; Leeds et al. 2015). In Europe, Gorilla EEP, thus starting considering castration as an alternative solution to bachelor groups.

3. <u>Welfare issues related to castration.</u>

To date, no study has been conducted on the effect of castration in gorillas, and only a few in other primate species. In marmosets (*Callithrix jacchus*), castration at an early age reduces testosterone levels during development, with long-term effects on aggressiveness and dominance (Dixson 1993). A study in Javan langur (*Trachypithecus auratus*) found that castrated males displayed more submissive behaviours while non-castrated male exhibited more dominant behaviours (Dröscher & Waitt 2012). They also reported that castrated males were not considered as rivals by intact males and thus not extensively aggressed (Dröscher & Waitt 2012). In Gorillas, castration of males at early ages is expected to decrease the individual aggressiveness, especially when reaching age of maturity. Researchers expected castrated males to not challenge their father when they grow up and, in return, silverback are expected to tolerate their sons in the long-term. Consequently, castrated males could remain in their natal group, in a social group they know from birth, with a low risk of negative interaction with other members. However, this solution is on its early stages and needs a full investigation on a range of points before being considered as a viable solution for housing the surplus of male gorillas. Moreover, besides it efficiency, castration of captive Gorillas raises controversy as it is a physical and irreversible act on a species close to human beings in which people use to identify in zoos.

4. Research question and hypotheses.

In 2015, there were 10 castrated gorillas in captivity, ranging from 3 years old to 13 years old, and living in six different European zoos. Our study wanted to investigate how the well-being of these castrated individuals is satisfactory or not, especially those reaching the normal age of maturity. One important consideration was about how the castrated individuals socialized with their group, especially with the silverback. Indeed, male-male interaction is a key factor to solve the surplus problem, because in both solutions (all-male group and castration), several male gorillas have to cohabit with each other. To this end, we aimed to investigate the social relations between the castrated males and the dominant male in breeding groups, which would help to get information about the castrated individuals' social well-being. Our hypothesis was that, if a castrated male was negatively affected by castration, he should have a low social well-being.

Well-being is a broad term, and can be defined as "the status of full physical and mental health in which the individual is in harmony with and adapted to the environment in which it lives and it specific physical and psychological needs are met" (Carrasco et al. 2009). In this specific study, we decided to focus on three parameters to investigate the individuals' social well-being. The first parameter was activity budget. Although it is not a social parameter strictly speaking, we used activity budget as a proxy to reveal social disorders. We predicted to find similar values for castrated males and non-castrated males living in captive breeding groups under satisfying well-being and atypical values for castrated males under low well-being. Especially we predicted a decrease in resting time and social behaviour, and an increase in eating time (food access) and travelling (escape pattern) under low well-being condition. The second parameter investigated was social behaviours, both positive and negative. Our predictions were to find more aggressive, and less positive interactions under low well-being condition than under high well-being conditions. The third parameter investigated was proximity pattern. Gorillas, as a social species, usually display a strong group cohesion and the group is organised around the dominant male. We predicted that, under low well-being condition, castrated males should avoid the dominant male, and should stand outside of the group.

3. Methods

1. Subjects

This study was conducted with Western lowland gorillas (*Gorilla gorilla gorilla*) living in three European zoos: Basel Zoo, Switzerland (BZ), Gaia Park, The Netherlands (GP), and La Vallée des Singes, France (VS). All groups were breeding groups constituted by one silverback male, several adult females, and their youth (juveniles and/or infants). Also, in each group, there was one (BZ) or two (GP and VS) castrated male gorillas, and they represented juvenile, subadult and blackback age categories (Table1).

Table 1: List of Gorillas in the observed groups. Sex: M (male), F (female), C (castrated). Infants were not investigated, only interaction (i.e. social behaviour) with other individuals were reported.

Zoo	Name	Code	Age (years)	Sex	Category	Relationship with SB (mother)
Basel Zoo (BZ)	M'Tongé	SB1	16.6	M	Young Silverback	
	Zungu	C1	13.2	MC	Blackback	Unrelated (Joas)
	Joas		26.3	F	Adult	
	Faddama		32.7	F	Adult	
	Quarta		47.3	F	Adult	
	Goma		56.1	F	Adult	
	Mobali		0.4	M	Infant	
	Makala		0.2	F	Infant	
Gaia Park (GP)	Makula	SB2	26.0	M	Old Silverback	
	Loango	C2	11.1	MC	Blackback	Brother
	Mosi	C3	6.0	MC	Juvenile	Son (Sangha)
	Sangha		15.9	F	Adult	
	Tamidol		17.1	F	Adult	
	Dalila		43.2	F	Adult	
	Ayo		3.1	M	Infant	
	Nala		1.0	F	Infant	
	Zola		1.7	F	Infant	
La Vallée des Singes (VS)	Yaoundé	SB3	32.3	M	Old Silverback	
	D'Jomo	C4	7.5	M©	Subadult	Son (Moseka)
	Mawete	C5	4.3	M©	Juvenile	Son (Moseka)
	MahMah		13.2	F	Adult	
	Hakuna		20.1	F	Adult	
	Moseka		32.2	F	Adult	
	Virunga		45.2	F	Adult	
	Wefa		4.7	F	Juvenile	

2. <u>Sites and facilities</u>

In all three zoos, the gorillas were housed in both indoor and outdoor facilities. Indoor facilities consisted of several rooms with synthetic or bark chips floors, equipped with fake and real trunks, ropes and hammocks. The rooms were connected together by traps, organised so the gorillas had different paths to change rooms and not be trapped other individuals. Outdoor facilities were large areas with grass and trees bordered by a wall of windows (BS) or a river (GP and VS) (Appendix A). Gorillas spent the night locked in the inside facilities, and had a free access outside during the keepers working times, also depending on the weather (the harsh winter condition limited the outside access in GP and VS). Despite the free access, the gorillas did not spent much time outside out of the feeding time in this area, and seemed to prefer remaining inside in BZ. Only in VS, some individuals spent long sessions outside to feed with the natural resources of the island when the weather allowed it.

Keepers' daily management mainly consisted in feeding and checking on the individuals, and cleaning the facilities. These tasks were consequently influencing the gorillas' daily activity. Feeding occurred four to six times each day, every one to two hours. The meals could be provided individually, especially for the main ones (first and last in the day), or the food could be spread in the enclosure and accessible for the entire group. To avoid fights and make sure all individuals got food in the day, gorillas could be separated from each other during feeding time. For the largest part, the food consisted of vegetables and branches, and a smaller part was fruits and pellets. Keepers cleaned the rooms daily, in the early morning in BZ and VS, and spread over the day in GP. Room cleaning lasted between one and three hours and consisted of washing synthetic floors and windows, removing dirt (feces, leftover food), providing missing straw and barks chips, fixing damages and spreading food. During room cleaning, the gorillas were locked in the other rooms and thus had a restricted area access. They were separated in small groups (GP and VS) or all together (BZ and GP). Individual check-up consisted of observing the gorillas close to the enclosure, often during individual feeding (teeth, breath, and wounds) and did not interfere with gorilla activities.

In GP, gorillas were sharing their indoor and outdoor facilities with Mangabeys (*Lophocebus albigena aterrimus)* during the day, but were separated at night. In VS, gorillas were sharing outdoor facilities with Mantled Guereza (*Colobus guereza*). This sharing led to a few interspecies interactions; positive as well as negative.

3. Data collection

We developed and adapted a specific ethogram for this study (Table 2), based on previous research that investigated the behaviour of gorillas in captivity (Stoinski et al. 2001; Stoinski et al. 2004; Kuhar et al. 2006; Carrasco et al. 2009; Less et al. 2012; Stoinski et al. 2012; Stoinski et al. 2013) and in the wild (Eckardt et al. 2015). Data collection was conducted between August 2015 and March 2016 during 4 weeks in BZ (August 31th to September 23th), 4 weeks in GP (January 14th to February 11th) and 4 weeks in VS (February 17th to March 15th). Data was collected 4 days per week, randomly chosen, either in the morning or in the afternoon, with an equal number of both. Morning observations were conducted from 8am to 1pm in BZ, 8am to 12am in BZ, and 8.30am to 1pm in VS. Afternoon observations were conducted from 1pm to 6pm in BZ, 12am to 4pm in GP, 1pm to 5.30pm in VS. Session duration and time were chosen in order to cover the entire gorilla daytime, corresponding to zoo opening time and/or keeper working time. We obtained an amount of 16 sessions of observations per month (8 in the morning, 8 in the afternoon, randomly chosen). Data was collected from the visitor area with an Apple iPad1 v5.1.1, and using the software Pendragon Forms Universal v7.2. As a stranger, my presence in the keeper area tended to annoy the gorillas, so we decided that collecting the data from the visitor area was the best way not to disturb them or influence their behaviour.

The choice to follow all the individuals at the same time was motivated by the species' behaviour, because gorillas are relatively inactive animals, spending most of their time resting and eating, with few social interactions. Groups were relatively small, with 6, 6 and 8 weaned individuals in BZ, GP, and VS, respectively. Also, the facilities offered a good visibility on the entire enclosure, allowing to seeing all the individuals at the same time (except those in remote areas). Finally, to avoid missing important data, we ensured to maximise the observation of the key individuals, with focusing on the castrated first, and then on the silverback when the castrated were not visible. Similar group observations have already been used in other gorilla studies (Stoinski et al. 2001; Stoinski et al. 2004), and the short schedule of the study also justified this choice.

Table 2: Ethogram with behaviour, description, and sampling method.

Category	Behaviour	Description
Activity Budget (5min interval scan sampling)	Rest	Individual is inactive, at rest, not engaged in any obvious or otherwise defined behaviour.
	Displacement	Individual is moving on the ground or climbing.
	Eat	Individual actively eating, carrying, searching for or processing food, including drinking water.
	Care infant	Individual (mother or other) is actively carrying and taking care of an infant.
	Self-directed	Individual is actively grooming (touching, licking, inspecting hair), scratching, self-mouthing, playing alone or display deficit behaviours (self-stimulation, regurgitation/reingestion, or coprophagy).
	Other	Individual is engaged in another solitary behaviour that is not identified in the ethogram.
	Social	Individual is having a social interaction with another individual (next sections for details).
	No Idea	Individual is not visible.
Positive Social Behaviour (All occurrences sampling)	Allogrooming	Individual is initiating or receiving allogrooming.
	Social play	Two or more individuals are actively playing together during at least 15 seconds (wrestling, chasing, sparring)
	Sexual behaviour	Individual is initiating or receiving sexual behaviour.
	Approach	Individual moves to within 2 meters of another individual and remains at least 15 seconds or engage in another affiliative behaviour.
	Contact	Individual is having contact (touching) or siting/lying within 1 meter of another individual during at least 5 seconds.
	Brief contact	Contact that last less than 5 seconds.
	Follow	Individual follow another individual in a significant displacement (at least 5m) for another reason than food (keeper feeding) or escaping the arrival of another individual (escape).
Negative Social Behaviour (All occurrences sampling)	Non-contact aggression	Individual initiates charging, pursuit or display (quadrupedal, tighted-lip, chest beating, cough grunts, ground slapping, vocalisations, throwing objects, arm gesture), without contact aggression following.
	Contact aggression	Individual successfully strikes, drag, shoves or bite another individual
	Intervention	A third party individual which was not previously involved engage in an agonistic interaction. He intervenes to support one individual or to be neutral.
	Retreat	Individual moves away from another individual approaching. The retreat is in direct response to the approaching individual.
Proximity (5min interval scan sampling)		Indicate the room in which the individual is located. If the observer has no idea of the location of an individual, or if he is outside, indicate "No Idea".

4. Data analysis

The statistical analyses were performed using Microsoft Excel 2013 and R Studio version 1.0.1367, with a significance value of $p<0.05$ (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). All values were reported as the mean standard error (SE). Considering the small sample size (5 castrated individuals), and the amount of variable parameters (environment, group size and composition, age of the individual), data analysis was mainly descriptive and tests were non-parametric.

a. Activity Budget

Activity budgets were obtained for each individual by calculating the mean percentage of visible time the individual spent in each categories. The percent was calculated by dividing the total number of scans an individual was recorded in a category by the total number of scans the individual was visible. Categories (rest, eat, displace, self-directed, social) were summed-up from the ethogram (Table 2). We used Mann-Whitney U-tests to evaluate differences in activity budget between the castrated and the non-castrated males. We also tested a possible effect of age on activity budget.

b. Social behaviour

Social behaviour was divided into two categories: positive and negative. For each male dyad (SB-© and ©-©), we calculated the number of interactions per visible hour. The amount of visible time was estimated from the scan data. Kruskal-Wallis tests for non-parametrical data were used to analyse the differences between dyads, with Steel-Dwass post hoc test for multiple comparisons.

c. Proximity

Proximity was evaluated only during time with free access to the entire indoor enclosure, excluding cleaning time and individual feeding time, because, during these periods, gorillas were moving in restricted areas. Proximity was scan-sampled every 5 five minutes as room location for each individual (see ethogram Table 2). Then, we coded the association between each individual as “same room”, “different room”, or “no idea”. We got the proximity values (% of time spent in the same room) between individuals A and B using the following formula:

$$\%\, Time\ A\ with\ B = \frac{Nb\ Scan\ A\ and\ B\ \text{"}same\ room\text{"}}{Nb\ scan\ total - Nb\ scan\ A\ and\ B\ \text{"}no\ idea\text{"}} * 100$$

We calculated the proximity values between each individual to obtain triangular matrices of similarities (Table 3) and repeated the same procedure for the three groups. The three matrices were then separately subjected to the metric MDS procedure, creating a proximity graphical representation. The closer the points are, the more the individuals spent time in the same room (Nakamichi & Kato 2001).

Table 3: triangular matrices of similarities, based on proximity values (%) between gorillas at Basel Zoo (BZ).

	C	SB	F-1	F-2	F-3	F-4
C						
SB	4.6					
F-1	25.7	47.3				
F-2	16.4	58.0	52.0			
F-3	14.6	62.9	48.1	76.2		
F-4	20.0	47.2	37.9	40.8	42.3	

Proximity between males was also calculated as the percentage of scans a male (castrated or not) was observed in the same room as another male during each session of observation. We used a Kruskal-Wallis test, plus a Steel-Dwass post hoc test, to assess differences between individuals in male proximity.

4. Results

1. Activity Budget

There were a few differences in activity budget between castrated males and silverbacks (Figure 1). Castrated individuals (C) spent significantly more time eating ($U(5,3)=15$, $p=0.04$) and less time resting ($U(5,3)=15$, $p=0.04$) than silverbacks (SB). There were no significant differences for the other behaviours: displace ($U(5,3)=13$, $p=0.14$), self-directed ($U(5,3)=7$, $p=1$) and social ($U(5,3)=12$, $p=0.25$). However, these results might be influenced by the castrated individuals' age variability, with the younger individuals (C3, C4, and C5) spending more time having social interaction ($U(3,5)=15$, $p=0.04$), and less time resting ($U(3,5)=15$, $p=0.04$) than the adults males (C1, C2, SB1, SB2 and SB3).

Our sampling was not large enough to make further classic statistical analysis. Nevertheless, Kuhar (2006) suggested an analysis based on means and SE bars for studies with small sample. With this consideration, the graphical analysis did not revealed significant differences in any behaviour between the adult castrated (C1 and C2) and adult non-castrated males (SB1, SB2, and SB3).

Together, this results suggested that there were no main differences in activity budget between castrated male and non-castrated male, and that the few differences reported might account for age differences rather than a direct effect of castration. Overall, we could conclude that in term of activity budget, the well-being of the five castrated individuals was satisfactory.

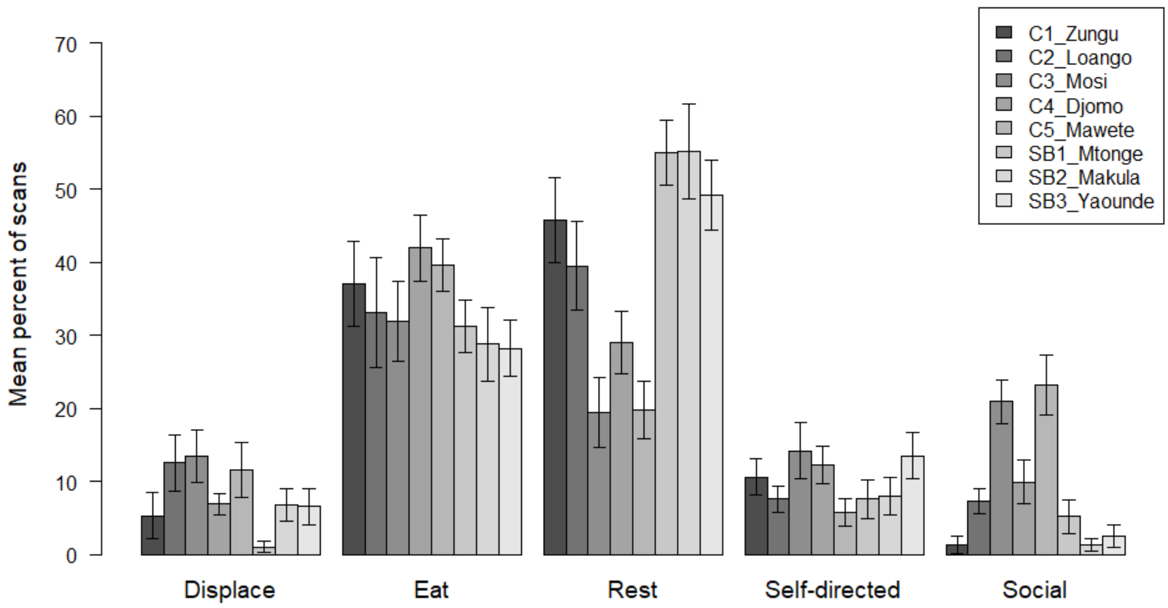

Figure 1: Mean percentage of visible time spent in each behaviour category. C = castrated; SB = silverback.

2. Social Behaviours

We found significant dyad variation in both positive (Kruskal-Wallis chi-squared = 26.081, df = 2, p-value <0.001) and negative behaviours (Kruskal-Wallis chi-squared = 35.151, df = 6, p-value <0.001) (Figure 2 and 3). Our data revealed an effect of the type of dyad on positive behaviours, with castrated individuals having significantly more positive interactions together (C_C: 1.4 occurrences per hour) than they had with silverbacks (SB_C: 0.4 occurrences per hour) (Steel Dwass t > 2.9, p-value < 0.05 for all). However, there was no similar difference in negative behaviours without BZ dyad (SB1_C1) (0.28 occurrences per hour for both) (Steel Dwass t < 1, p-value > 0.97 for all). Indeed, in BZ, the castrated male and the silverback had five times more negative interaction than the other dyads (1.39 occurrences per hour) (Steel Dwass t > 4.3, p-value < 0.001). There was also an effect of zoo institutions (silverback) on the rate of positive behaviours between the castrated individuals and the silverbacks. Indeed, GP dyads (SB2_C: 0.6 occurrences per hour) had three times more interactions than VS dyads (SB3_C: 0.2 occurrences per hour), while there were no positive interactions between the castrated male and the silverback in BZ (SB1_C1: 0 occurrence per hour). (Kruskal-Wallis chi-squared = 26.081, df = 2, p-value < 0.001; Steel Dwass: t > 4, p-value < 0.001).

To sum up, in GP (C2 and C3) and VS (C4 and C5), the four castrated males showed similar social profiles with more positive interactions than negative interactions with the silverback. In BZ (C1), it was the opposite, with more negative interactions than positive between the castrated male and the silverback. These results suggested that the castrated individuals living in GP and VS socialized well with the silverback in their respective zoos, while the castrated male in BZ did not, which might negatively impact his well-being. Nevertheless, all rate of social interaction between males were low, under 2 occurrences per hour for both positive and negative behaviours.

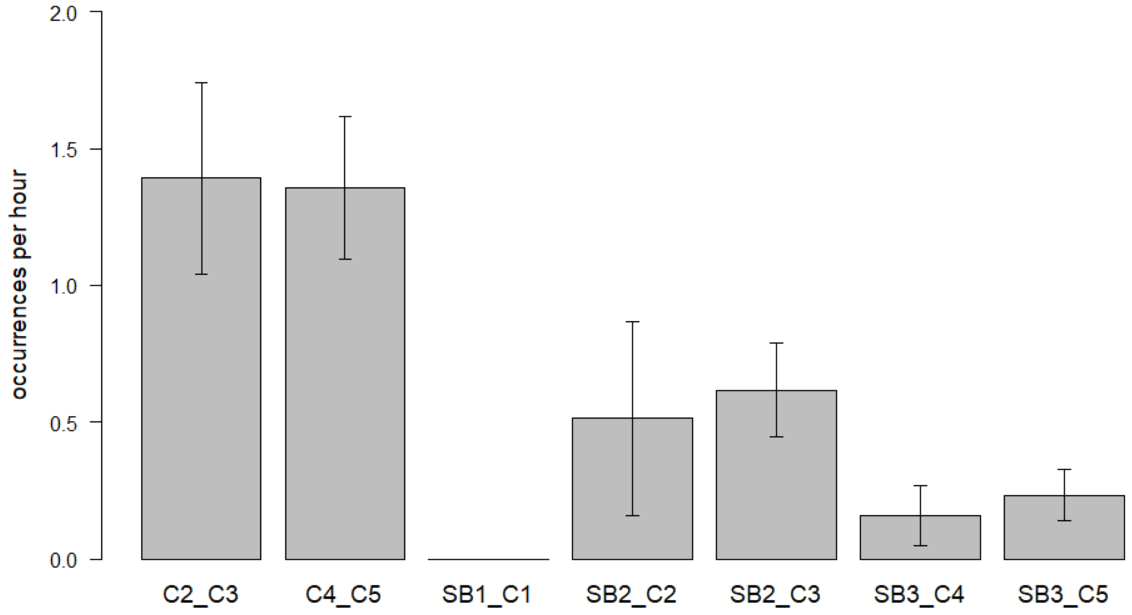

Figure 2: Mean rate per visible hour of positive social interaction in male dyads: C = castrated, SB= silverback.

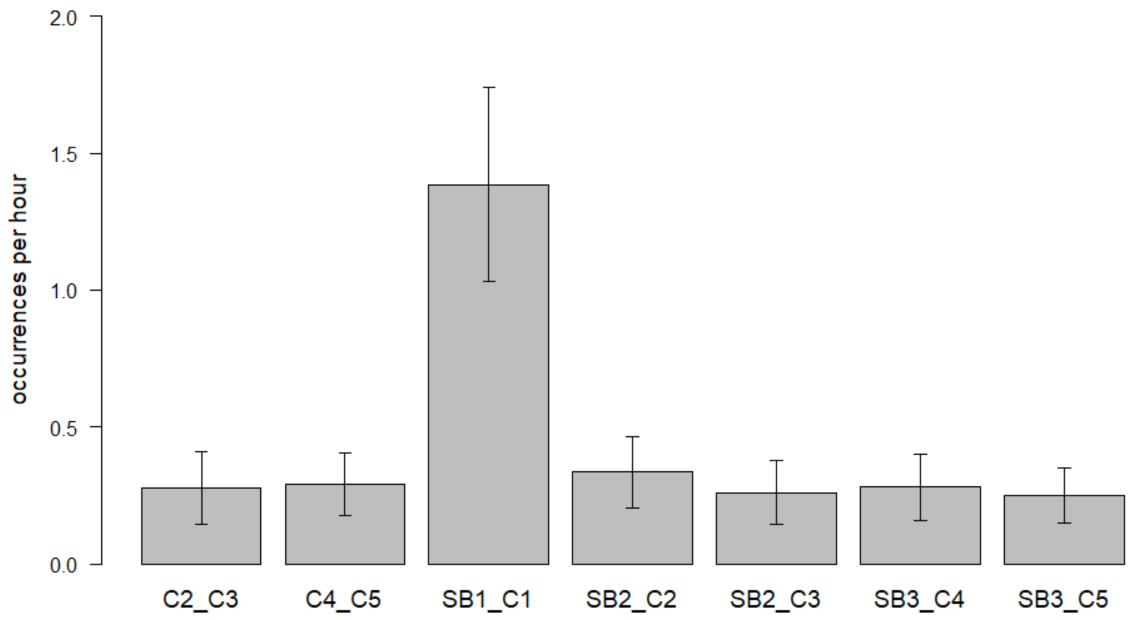

Figure 3: Mean rate per visible hour of negative social interaction in male dyads: C = castrated, SB= silverback.

3. Proximity

In the two dimensional MDS analysis of proximity, we found the castrated individuals (C) were plotted close to the other members of the group in GP and VS, but not in BZ (Figure 4). This result indicated that the castrated gorillas living in VS and GP spent most of their time in close proximity to the group, while the castrated gorilla living in BZ spent most of his time outside of the group. Also, in VS and GP, we reported that the castrated individuals were plotted close to silverback (SB), while in BZ, the castrated gorilla was at the extreme opposite of him. Indeed, in BZ, Zungu and M'Tongé spent only 5.6% of their time in the same room (Figure 5). In contrast, the other castrated gorillas spent significantly more time with the silverback, between 39.6% and 48.1% of the total visible time (Kruskal-Wallis chi-squared = 34.341, df = 6, p-value = 6.343e-07) (Steel Dwass, $p<0.001$). In GP and VS, there was no difference between the time the two castrated individuals spent together, and the time they respectively spent with the silverback (GP: Kruskal-Wallis chi-squared = 0.077161, df = 2, p-value = 0.9622; VS: Kruskal-Wallis chi-squared = 2.7624, df = 2, p-value = 0.2513) (Figure5).

Together, these results suggested that in BZ, the castrated individual avoided the silverback and was not well-integrated in the group. On the contrary, in GP and VS, the castrated individuals were well-integrated and spent about 50% of their time with the silverback. We could thus conclude that in term of proximity, the social well-being of the castrated male in BZ was not satisfactory, while it was satisfactory for the four other castrated individuals.

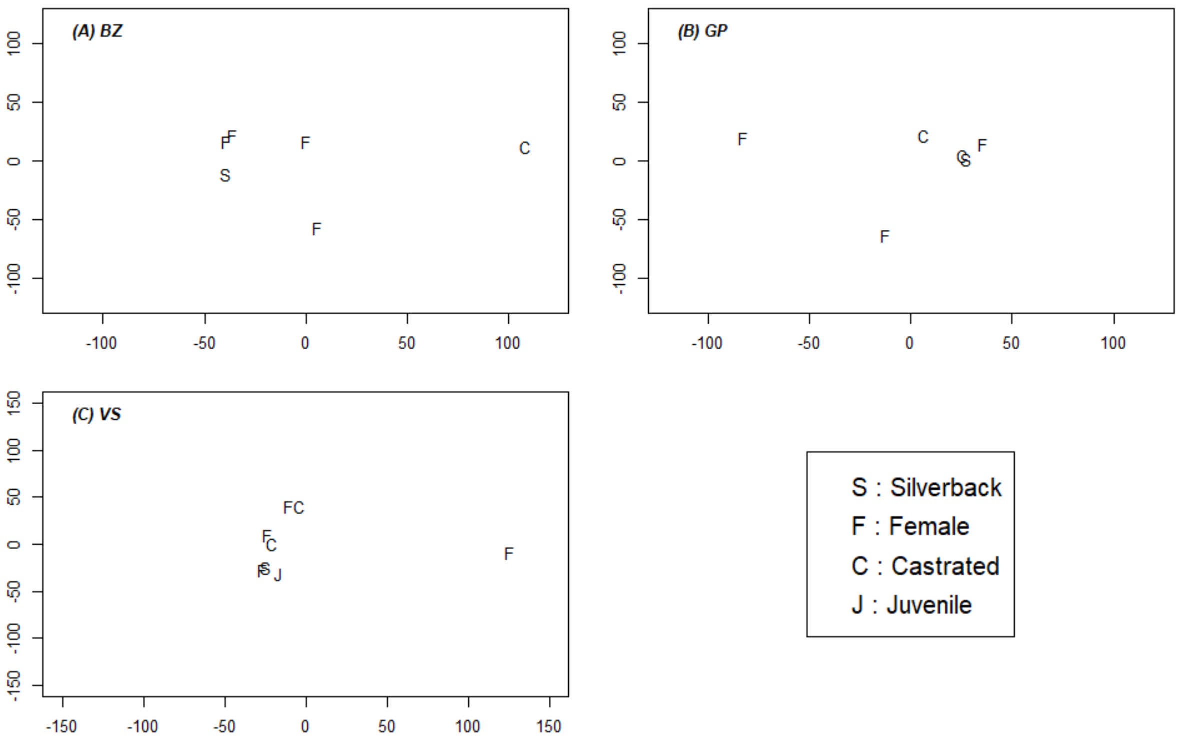

Figure 4: Two-dimensional MDS representing proximity between gorillas in their respective group.

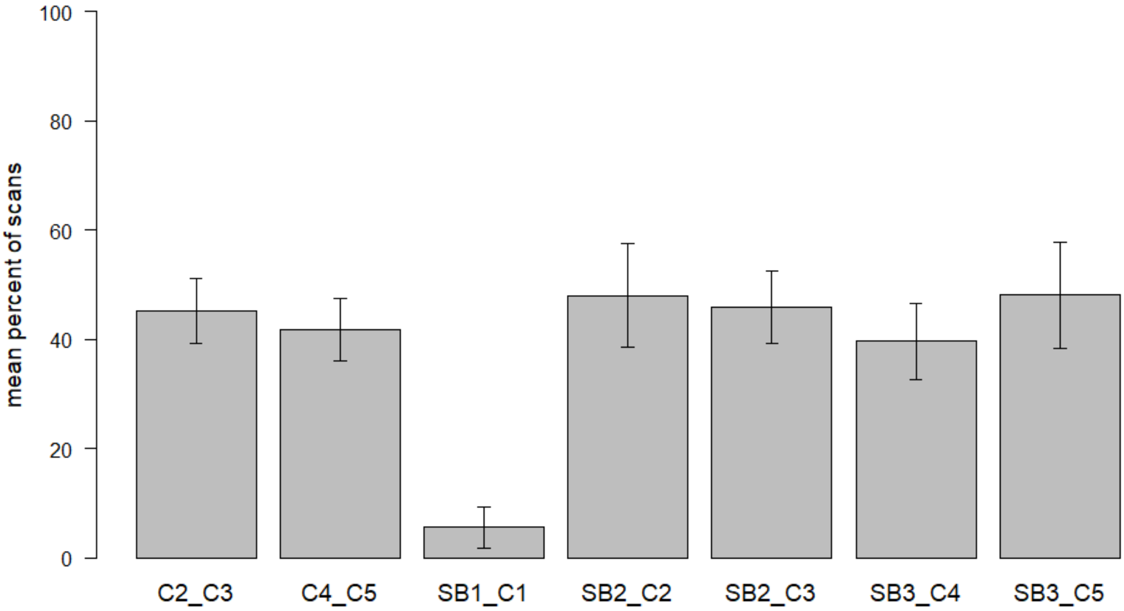

Figure 5: Percentage of time spent in the same room. C1: Zungu, C2: Loango, C3: Mosi, C4: D'Jomo, C5: Mawete, SB1: M'Tongé, SB2: Makula, SB3: Yaoundé.

5. Discussion

1. Castrated gorillas' social well-being.

This study was the first to investigate the social well-being of the captive population of castrated gorillas. Although our results were restricted by the small sample size (5 individuals), and the individuals' age and environment variability, our dataset still represented half of the European population of castrated gorillas. Moreover, we managed to include the oldest individuals, who were the most likely to have well-being issues. Our findings indicated that four out of five castrated gorillas had a satisfactory well-being, while the last individual appeared to not socialize with the silverback and potentially with the rest of his group. None of the castrated gorillas showed an atypical activity budget, which could reasonably let us think that castration did not affected the overall activities of these individuals. All individuals spent around 30% of their time eating, 10% displacing and 10% having self-directed behaviours. Adults spent 40% to 50% resting and less than 5% in social interaction, while youth spent 20% resting and the same percentage having social behaviours. These values were consistent with previous research from captive gorillas in both breeding and bachelor groups (Lukas 1999; Stoinski et al. 2001; Less et al. 2012; Stoinski et al. 2012). In particular, the young castrated males had significantly more social behaviour than the adults, and slightly more self-directed behaviours. This is typical for young gorillas, which spend long sessions playing alone or with partners of their age (Brown 1988). Although we did not compare castrated with non-castrated young gorillas, we could still suggest that they had a normal social development so far.

Social behaviours and proximity patterns were complementary with each other for all castrated individuals. For the four castrated males living in GP and VS, we found a higher rate of positive than negative social interactions with the silverback, as well as a close proximity with him and the rest of the group. It is largely acknowledged that silverbacks are the core of gorilla's groups, and it was thus not surprising to see that the castrated males who socialized the most with him were also those being well integrated in the entire groups (Abelló et al. 2017). We could thus reasonably conclude that, based on the information available, the social well-being of these four castrated individuals was satisfactory. On the contrary, for the castrated individual living in BZ, we found more negative than positive social interactions with the silverback, as well as a very low proximity with him and the rest of the group. With the same reasoning, we concluded that this castrated individual did not socialize with the silverback and was thus outside of the group. This could have a negative impact on his social well-being and thus on his overall well-being. However, the gorilla group in BZ went through many changes in the previous year, and these changes might explain the current position of the castrated male, more than his castration.

2. <u>Zungu situation as a study case.</u>

When we collected data in BZ, Zungu (castrated) and M'Tongé (silverback) had been living together for one year only. Indeed, M'Tongé took the lead of the group in August 2014 after the former silverback died (more details in Appendix B). After M'Tongé's introduction, the two individuals did not socialize, and several factors might explain why. First, M'Tongé was a young inexperienced silverback, and Stoinski et al. (2013) found this age was directly related to aggressive level in male gorillas, with young silverbacks (14-20 years old) initiating more displacements, contact and non-contact aggressions than any other age category. Leeds et al. (2015) found a similar pattern with a predominance of male age rather than group housing on wounding rates. Our results were consistent with these results as we found M'Tongé initiated 2.5 and 1.5 more agonistic interactions than the silverback in GP and VS respectively, and both were old silverbacks (>20 years old) (Appendix C). Second, closely linked to his young age, we suggested that M'Tongé inexperience as a group leader could have played a role in deteriorating the situation. In GP and VS, both silverbacks had been leading their respective group for more than a decade; their dominant position was clearly established and the group cohesion was strong. On the contrary, in BZ, the situation was precarious after the former silverback died, which probably impacted the entire group cohesion and increased the rate of agonistic behaviours (Less et al. 2010). Third, the introduction of a new gorilla in a group usually involves changes of social structure that can create stress (Jacobs et al. 2014), and also increases the rate of agonistic behaviours (Fischer 1984; Hoff et al. 1996). And this is probably more important with a silverback introduction, who would have to establish his dominancy (Breuer et al. 2016). Altogether, these arguments suggested that Zungu low social well-being could be a consequence of M'Tongé's aggressive behaviour, and probably not a direct effect of his castration.

However, other findings suggested that Zungu's personality could also explain this situation. Indeed, a range of studies have focused on the correlations between personality and behavioural profile in gorillas (Kuhar et al. 2006; Eckardt et al. 2015; Schaefer & Steklis 2014). We did not include these elements in our investigation because we only wanted objective parameters, and personality tests require subjective assessments. However, anecdotal reports indicated that Zungu was not always behaving fairly, especially during the former silverback's end of life, as well as during the transition period without a silverback. Keepers also indicated that Zungu sometimes produced agonistic vocalizations during fights between females, which could possibly stimulate the other individuals. However, as we recorded the data from the visitor area, we could not hear these behaviours. Also, we noticed that most of the agonistic interactions between Zungu and M'Tongé were initiated by M'Tongé, but in some infrequent and unpredictable cases, we observed Zungu responding or challenging him. Zungu was castrated at 7 years old, while the other individuals studied were castrated around 3 years old, and he probably already started developing aggressive behaviours. As a consequence, M'Tongé could have considered him as a challenger, and that would explain why they did not socialize well. To conclude, while Zungu's social well-being did not seem to be satisfactory at the moment, we could hope the situation is temporary and his well-being will improve with time.

3. Further investigations and welfare recommendations.

This study, and specifically the situation in BZ raised some questions that need to be answered in future investigations and workshops. Indeed, Zungu's unsatisfactory well-being could be related to his social environment, more than to his castration. Studies revealed that all male group are more successful if they are built carefully, selecting young individuals at similar age and accompanied with an easy-going silverback (T. S. Stoinski et al. 2004; Abelló et al. 2017). Castration should follow the same rules. Unnecessary males for the breeding program should be castrated only if the social environment is ideal for their growth. Investigations are thus necessary to identify the factors which would enhance the successful integration and development of the castrated gorillas. We suggest to give a lot of importance to the group cohesion and experience of the silverback. Indeed, stable groups would always be better for an individual to integrate. Also, individual personality and temperament should be greatly considered. Aggressive silverbacks might not tolerate castrated individuals as well as flexible ones. Also, regarding enclosures, researchers recommend specific designs for bachelor group facilities, including the possibility to isolate one or more individual during periods of tensions (Coe et al. 2009; Abelló et al. 2017). Similar accommodations may be necessary for zoos wanting to keep a castrated male in their breeding group.

Nevertheless, four out of five castrated gorillas investigated appeared to have a satisfactory social well-being. We found values of activity budget, social behaviours and proximity patterns that were consistent with previous studies investigating gorillas in breeding and bachelor groups (Stoinski et al. 2001; T.S. Stoinski et al. 2004; Stoinski et al. 2013). Although this was reassuring on their current social status, it still does not indicate that castration can be feasible on the long term. Indeed, three out of four individuals were young, while only one had reach adulthood. As silverbacks usually tolerate their sons until they reach maturity (Harcourt & Stewart 2007), we might expect problems to start happening after the castrated individual reach adulthood, although castration is expected to prevent aggressive behaviour. Further studies on castrated males should thus focus on the early adulthood period, to investigate if the castrated individuals are still tolerated after this time. Childhood is another critical stage that should be intensively investigated, and ongoing studies are focusing on the effect of castration on the cognitive and social development of young castrated gorillas (personal communication). Additionally, physiological data on stress level would be helpful to get a clearer view of the castrated males' well-being. In human, allostatic load was used to assess stress levels, and this technique was recently applied to gorillas with effective results (Edes et al. 2016a; Edes et al. 2016b). We might also think about positive reinforcement training (PRT) to try improving the individuals' well-being (Carrasco et al. 2009).

Finally, outside scientific considerations, castration also raises moral problems. For many people, castration is considered as a physical mutilation that affects the animal integrity. Over the years, castration has been accepted for domestic animals, usually to reduce unwanted births, and also to decrease aggressiveness and undesired behaviours. However, the use of castration as a birth control for captive animals was highly debated, especially when it concerned great apes, our closest relatives. Indeed, castration could be considered as a failure to manage the captive population of Gorillas (Vermeer & Carroll 2012). Castration should thus be used with parsimony, until we obtain better information on it efficiency and more experience. Nevertheless, castration and bachelor groups might be complementary solutions to the surplus of male gorillas in the future.

6. Conclusion

1. Four out of five investigated castrated gorillas had a satisfactory well-being. We observed typical gorillas' activity budgets, and rates of social behaviours and proximity patterns were consistent with previous studies investigating male-male relationships.

2. The fifth castrated male had a lower social well-being. His activity budget was normal, but he did not socialized well with the silverback. He had zero positive interaction with him and five times more negative interactions than the other castrated males. Also, the castrated seemed to avoid the silverback, as they shared the same room during only 5.6% of the total time, against 40% to 50% for the other castrated males.

3. The low well-being of this individuals might not be a direct effect of his castration. We suggested that it was a consequence of the silverback's young age and inexperience, and the castrated male personality.

4. Overall, castration did not seem to worsen the investigated individuals' well-being, but further investigations are needed before we can confirm this strongly. We suggested childhood and early adulthood are the critical stage at which the effects of castration should be investigated in priority.

5. Workshops should be initiated to address the main point raised by castration. A list of recommendations for gorilla castration should be created, similarly to what has been done with bachelor groups.

6. Castration should remain extraordinary until we have a better knowledge of the effects. Zoos and researchers should work cooperatively to improve our knowledge with more efficiency.

7. Acknowledgments

I first want to thank Klaus Zuberbühler (UniNe) and Adrian Baumeyer (Zoo Basel) for launching and supervising this study. I also want to thank people from the collaborating zoos; the curators, Tjerk ter Meulen (Gaia Park) and Jean-Pascal Guéry (La Vallée des Singes) for facilitating my venue, and the keepers in the three zoos for their nice welcome and discussions. Finally I would like to express my thanks to the University of Neuchâtel for supporting and funding this project.

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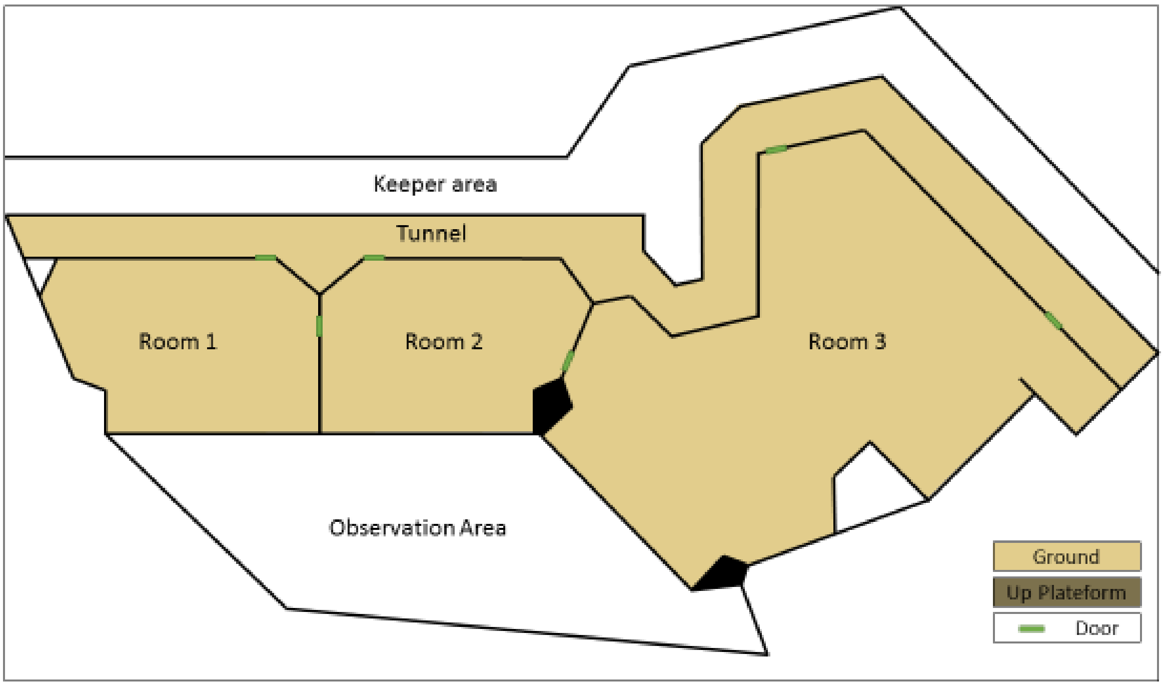
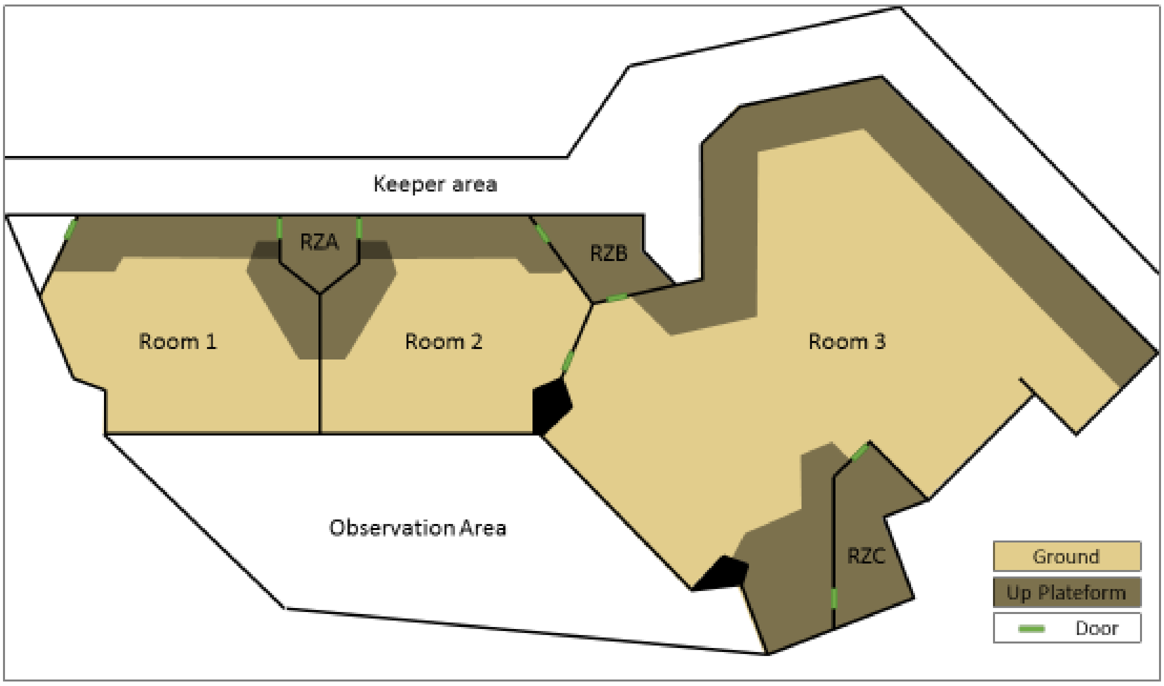
9. Appendices

1. Appendix A: Facilities maps.

a. Basel Zoo

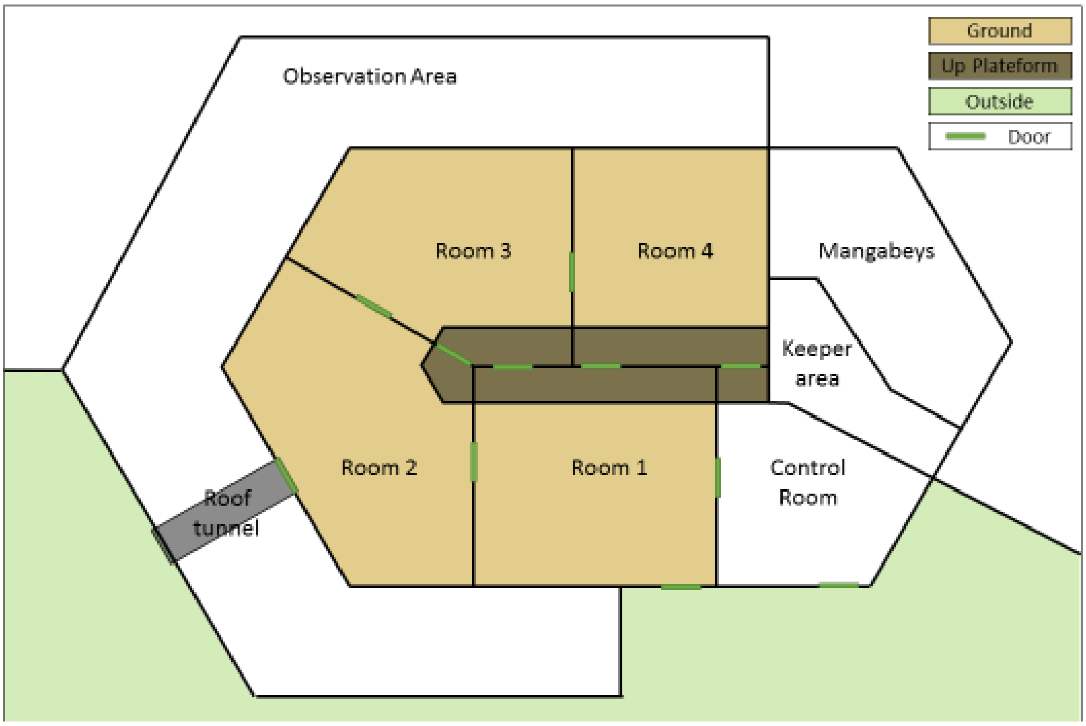


Ground level

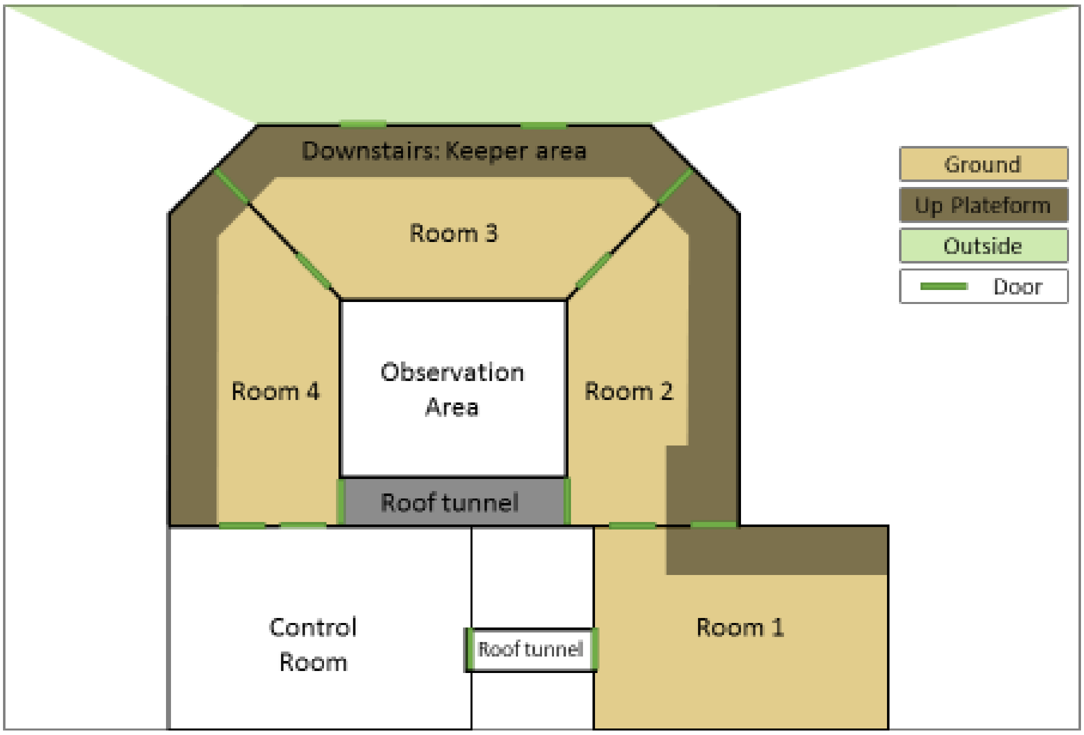


Upper level

b. Gaia Park



c. La Vallée de Singes



2. Appendix B: Basel gorillas' history.

The group of gorillas housed in Basel Zoo went through many changes after the former silverback male (Kisoro) died in May 2014 because of a fox tapeworm disease diagnosed in 2010. The group was first left without a silverback male for 3 months before M'Tongé (the actual silverback male) was introduced in August 2014. Kisoro's son, Zungu, was also diagnosed with a fox tapeworm disease in 2010 and was castrated in the following time. He was a good candidate for castration, because, due to his health problem, he would likely not be transferred to a breeding group in the future. Castration was thus a possibility for him to remain in his natal group with his family. At M'Tongé's arrival, they had agonistic encounters and Zungu got bitten for the first time. M'Tongé progressively took the lead of the group and integrated well with a successful breeding with the two reproductive females of the group, in late 2014 (births in May 2015 and July 2015). However, incidents between M'Tongé and Zungu continued to happen frequently, and occasionally became more intense resulting in impressive, but superficial wounds for Zungu. As the situation tended to drag on, we were wondering if it was creating an animal welfare problem for Zungu, in order to help taking decisions about his future.

3. Appendix C: Silverback agonistic initiations.

We did find a significant effect in the rate of initiating agonistic behaviours against all group members between the silverbacks in the three zoos (Kruskal-Wallis chi-squared = 10.053, df = 2, p-value = 0.007) (Figure 6). The silverback in BZ was significantly more aggressive than the silverback in GP (Steel Dwass: t = 2.973, p-value = 0.008), initiating two times more agonistic behaviours (BZ: 3.9 occurrences per hour, GP: 1.9 occurrences per hour). His rate was also 1.5 higher than the silverback in VS (VS: 2.5 occurrences per hour), but the difference was not significant (Steel Dwass: t = 1.871, p-value = 0.147). There was also no significant difference between GP and VS (Steel Dwass: t = 1.677, p-value = 0.214).

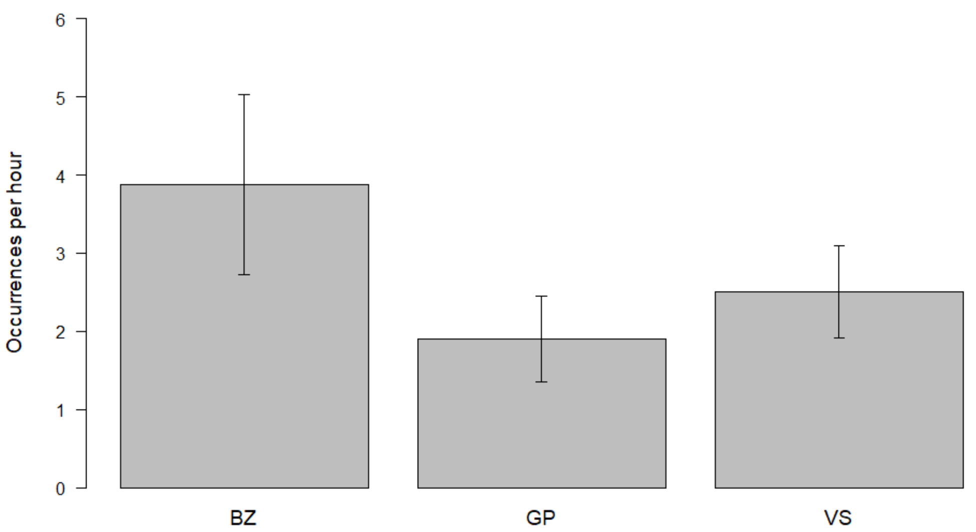


Figure 6: Mean rate per visible hour of agonistic initiations by the silverback in the three zoos.