Effects of the environment on the behaviour of lowland gorillas in zoos

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PRIMATE REPORT 32, 167–183. 1992.

Introduction

During the last years the physical environment of primates in captivity has become a subject of considerable interest. There is a great number of publications on "psychological well-being" (e. g. Amer. J. Primatol. Suppl. 1, 1989; Novak & Petto 1991; Segal 1989). The reasons for primate keeping in zoos are different from those in laboratories. Besides keeping them healthy and breeding them, the presentation of the animals to the visitors is most important, and the physical environment usually is designed for this purpose. Studies on this subject in zoos are rare; not only because primate housing mostly is not as deprived there as in laboratories, but also because significant results are obtained with much more difficulties under such complex conditions.
Gorillas seem to be extremely sensitive to environmental conditions, and a discussion of their needs is one prerequisite for establishing a self-sustaining population in captivity. The gorilla-EEP-commission is presently compiling respective guidelines. If and how the physical environment affect the apes' "well-being", has been examined in this species by several authors (Akers & Schildkraut 1985; Bowen 1980; Ford 1990; Goerke et al. 1987; Gould & Bres 1986; Hedeen 1982, 1983; Kopff 1982; Maple & Hoff 1982; Miller-Schroeder & Paterson 1989; Sucker 1987; Tais 1982; Wilson 1982). The purpose of my study was to compare the behaviour of gorillas in various places and under different conditions, regarding the housing, the group composition and the presence and activity of visitors.

Materials and methods

Subjects

Table 1 shows the compositions of the study groups. I observed 14 groups with immatures (three of them included two silverbacks), two groups without immatures, three pairs of adults and two solitary silverbacks. Besides, I studied three pairs and one group of three hand-reared immatures and two solitary infants. One of the groups with two silverbacks was studied with one male also, and one silverback alone and with a female (Tab. 1).

Table 1. Group compositions

F=female, M=male; A=adult, S=subadult (6–8 years), J=juvenile (3–6 years), BB=blackback, I=infant (1–3 years), B=baby (less than 1 year); Stuttgart i./o.=inside/outside

	MA	FA	BB	SM	SF	MJ	FJ	MI	FI	B
Basel	2	3	0	0	1	0	0	0	0	1
West Berlin	2	3	0	0	0	0	1	0	0	0
Seattle	2	2	0	0	0	1	1	0	0	0
Seattle	1	2	0	0	0	1	1	0	0	0
Frankfurt	1	5	1	0	0	0	0	1	0	1
San Diego WAP	1	2	1	0	0	2	0	0	0	1
Stuttgart i./a.	1	3	1	0	1	0	0	1	0	0
Stuttgart Sommer	1	3	0	1	1	0	0	0	0	1
Stuttgart Winter	1	3	0	1	1	0	0	1	0	0
Krefeld	1	2	0	1	1	0	2	0	0	1
Hannover	1	2	0	0	1	0	0	0	0	0

Atlanta	1	2	0	1	0	0	0	0	0	0
Rotterdam	1	3	0	0	0	1	0	0	1	0
Zürich	1	3	0	0	0	0	0	0	1	0
Cologne	1	3	0	0	0	0	0	0	0	2
Columbus	1	2	0	0	0	2	0	1	0	0
Columbus	1	2	0	0	0	0	0	1	0	0
Atlanta	1	2	0	0	0	0	0	0	0	0
Leipzig	1	2	0	0	0	0	0	0	0	0
Leipzig	1	1	0	0	0	0	0	0	0	0
East Berlin	1	1	0	0	0	0	0	0	0	0
Heidelberg	1	1	0	0	0	0	0	0	0	0
Heidelberg	1	0	0	0	0	0	0	0	0	0
Atlanta	1	0	0	0	0	0	0	0	0	0
Heidelberg	0	1	0	0	0	1	1	0	0	0
Heidelberg	0	0	0	0	0	1	1	0	0	0
Stuttgart Aufz.	0	0	0	0	0	1	1	0	0	0
Stuttgart Aufz.	0	0	0	0	0	0	1	0	1	0
Stuttgart Aufz.	0	0	0	0	0	0	0	0	1	0
Stuttgart Aufz.	0	0	0	0	0	0	0	0	1	0
Stuttgart Aufz.	0	0	0	0	0	0	0	1	2	0

Physical environment

The gorillas were observed in 17 indoor enclosures, in three cases a moat separated gorillas and visitors and in the others they were separated by glass. One of the eleven outdoor enclosures had glass, two bars and the rest a moat to separate gorillas and humans. Four indoor enclosures and two outdoor exhibits consisted of several compartments (Table 2).
All enclosures besides two outdoor and one indoor exhibit had climbing structures and 18 enclosures had ropes. Objects for manipulation were provided in 14 indoor and three outdoor enclosures, bedding materials in 14 indoor and in one outdoor exhibits. In eight indoor and three outdoor enclosures the gorillas had opportunities to withdraw into sleeping cages or similar facilities, and in five outdoor enclosures the surface structure provided visual barriers. Areas for resting above the ground were provided in 14 indoor and four outdoor enclosures.

Table 2. Physical environment

comp.=number of rooms or compartments; space=floor area that the gorillas could use, excluding moats; Shelves=rest areas above the ground; *=hills provide sight barriers for visitors; +=present; –=not present; m=moat; g=glass; b=bars; l=several floor levels; r=ropes; t=tree trunks; p=part of the exhibit with bars; c=climbing apparatus; O=plastic objects; C=cardboard; T=textiles, clothes; J=burlap; P=paper; N=natural vegetation; B=bedding material; W=water

	Exhibit		Places for privacy			moat
	comp.	space	comp.	space	furnishing	space
Atlanta (outdoors)						
Rann's group	1	1916 m^2	*	445 m^2		– 1)
Calabar	1	1293 m^2	*	889 m^2		– 1)
Willie B.	1	272 m^2	*	47 m^2		– 1)
Basel						
indoors	4	139 m^2	7	18 m^2	–	
East Berlin						
indoors	2	24 m^2	–			

West Berlin							
indoors	3	118 m²	–				
Columbus (outdoors)							
cage	1	22 m²	1	34 m²	+	–	
new exhibit	1	1821 m²	–				–
moat exhibit	1	787 m²	–				208 m²
Frankfurt							
indoors	1	93 m²	4	12 m²	–		
Hannover							
outdoors	1	200 m²	1	36 m²	+	45 m²	
indoors	1	85 m²	2	50 m²	+	31 m²	
Heidelberg							
indoors	1	69 m²	–				18 m²
outdoors	2	167 m²	–				36 m²
Cologne							
indoors	1	180 m²	4	85 m²	+		
Krefeld							
indoors	1	109 m²	3	39 m²	+	52 m²	
Leipzig (per group)							
indoors	1	37 m²	–				
Rotterdam							
indoors	4	68 m²	2	4 m²	–		
San Diego WAP							
outdoors	1	836 m²	4	<10 m²	–	?	
Seattle							
outdoors	1	1161 m²	*	354 m²			139 m²
Stuttgart							
indoors	1	110 m²	3 3)	7 m²	–		
outdoors 2)	2	62 m²	–				
Zürich							
indoors	1	105 m²	6	37 m²	+		

Table 2 (continued)

	Barrier	Shelves	Climbing structures	Manipulable objects
Atlanta (outdoors)				
Rann's group	m	–	t	N,W
Calabar	m	–	t	N,W
Willie B.	m	–	t	N,W
Basel				
indoors	g	4 4),l	r,t,p,c	O,C,J,B,W
East Berlin				
indoors	b + g	–	r,c,p	–
West Berlin				
indoors	g	18	r,c,p	O
Columbus (outdoors)				
cage	b	2	r,p	O,W
new exhibit	b	many	r,p,c	N,sticks
moat exhibit	m	2	r,c	N,W
Frankfurt				
indoors	g	9 4),l	r,p,c	O,C,B,W
Hannover				
outdoors	m	–	t	N
indoors	m	2	t	B

Heidelberg				
indoors	m	3	t	–
outdoors	m	–	t	N
Cologne				
indoors	g	1 4)	r,t,p	J,B
Krefeld				
indoors	m	–	t	C,T,B,W
Leipzig (per group)				
indoors	g	5–6,l	r,p,c	C,B,W
Rotterdam				
indoors	g	30,l	r,p,c	J,O,C,P,B,W
San Diego WAP				
outdoors	m	–	t	N
Seattle				
outdoors	g + m	–	–	N,sticks,B,W
Stuttgart				
indoors	g	bars,l	r,p,c	O,T,B,W
outdoors 2)	g	8	r,p,c	–
Zürich				
indoors	g	2 4),l	t,r,p	J,C,P,B,W...

1) moat not accessible because of electric fence; 2) free access to the indoor enclosure; 3) sleeping dens not accessible for the silverback; 4) additionally hammocks

Data collection

The groups were observed for several days when all group members were together under constant conditions. I collected the data with the one/zero method (Altmann 1974) between 9.00 a. m. and 5.00 p. m. The following behaviors were sampled: locomotion, dominance (supplanting of another group member), display, aggression, positive social contact, social play, stereotypies and other abnormal behaviours, watching the visitors, display directed at visitors.
These behaviours were observed for one minute in adult males, one minute in adult females and one minute in immatures. Additionally the number and activity of the visitors in front of the enclosure was noted (no visitors, 1 to 5, 6 to 20, more than 20 visitors; and for each number category: active or passive).
In 5-minute intervals I noted in which part of the enclosure each animal was situated (in the front half, in the back, above the ground, not visible, in the moat). The last minute of each 5-minute observation block concerned the behaviour of the visitors, I noted the following behaviours: screaming, knocking on the glass or other objects, exaggerated movements, throwing of objects.

Analysis

The data were analyzed with non-parametric tests. For 2 x 2 tables I used the G test (Sokal & Rohlf 1981), for the comparison of two independent samples the Mann-Whitney U test and for correlations of two independent variables Spearman's rank correlation coefficient (Siegel 1976).

Results

Effects of social factors

The number of group members was correlated positively with locomotion, dominance, aggression, positive contact, social play and staying in the front part of the enclosure (Spearman, n=127). In the behaviour of females, the number of females was correlated with aggression, positive contacts and social play (Spearman, n=58). In groups with adults and immatures the number of immatures was only correlated significantly with dominance (Spearman, n=111). Adults in groups with immatures showed more posi-

tive contacts and social play than adults without immatures (Mann-Whitney, n=73/6). Two silverbacks in one group and single males in a group showed no significant behavioural differences (Mann-Whitney, n=6/17).
A solitary silverback spent more time above the floor and showed more locomotion than than when he was together with a female (G test). Hand-reared infants who were kept as a pair spent less time with abnormal behaviours and observing the visitors than the same infants, if they were kept singly (G test).

Enclosure space and type

For none of the observed behaviours I found a significant correlation with the enclosures' floor area (Spearman, n=127). In moat enclosures, watching the visitors was negatively correlated with the floor area (Spearman, n=40). The larger an enclosure with glass, the more frequently stayed the apes near the visitors. This was not found in moat enclosures. In indoor exhibits with glass the number of various manipulable objects was correlated negatively with watching the visitors (Spearman, n=55).
The gorillas observed visitors more often in moat enclosures than in enclosures with glass barriers, in glass enclosures they spent more time near the visitors (Mann-Whitney, n=40/73). In exhibits with bars they displayed more frequently to the visitors than in those with glass (Mann-Whitney, n=14/66).
Staying in the front part of the enclosure was correlated with watching the visitors in glass enclosures, but not in moat enclosures. In glass enclosures with an effective barrier (e. g. plants), the animals rested less frequently near the visitors than without such a barrier (Mann-Whitney, n=21/52). But if glass enclosures with barrier were compared to moat enclosures, which always had a barrier, there was no significant difference.

Table 3. Times with no gorillas visible

place	n (m^2)	visible (m^2)	invisible	no gorilla present (% of time)
Basel	508	139	18	0
Columbus cage	117	22	34	0
Frankfurt	294	93	12	0
Rotterdam	355	68	4	0
Seattle	258	807	354	0
Stuttgart	1126	110	7	0
Hannover outdoors	223	200	36	0.4
Hannover indoors	196	85	50	0.5
San Diego WAP	278	836	<10	0.7
Krefeld	361	109	39	3.0
Zürich	340	105	6	3.2
Atlanta Willie B.	146	225	47	4.7
Atlanta Calabar	187	404	889	18.2
Atlanta Rann	231	1471	445	34.2
Cologne	266	180	85	41.0
Stuttgart outdoors	265	62	117	55.8

Withdrawal

Ih glass enclosures the stay in compartments, that were not visible for the public, was correlated with their floor area and with their portion of the whole enclosure's floor space (Spearman, n=72). But the effect of the enclosure structure was even more important (Table 3). In moat enclosures with areas hidden from the visitors' view by the surface structure of the exhibit, staying in those areas was correlated with their floor area, but not with their portion of the whole floor area (Spearman, n=18).
In indoor exhibits which had only one compartment, the gorillas spent more time observing the visitors and staying near them than in exhibits with several compartments (Mann-Whitney, n=35/27).

The animals used sleeping cages more frequently in exhibits with one room than in those with two or more rooms (Mann-Whitney, n=28/18). The number of sleeping cages was correlated with the time spent there (more cages gave privacy to more individuals (Spearman, n=46). Sleeping cages that were large (more than 30 m^2) and furnished were used more often than those that were small (less than 15 m^2) and not furnished (Mann-Whitney, n=19/29).
The time spent in a moat did not differ in enclosures with further opportunities for withdrawal and in enclosures without such structures (Mann-Whitney, n=32/12).

Visitor behaviour and its effect on the gorillas

Some gorillas threw objects at visitors, others begged for food if they were occasionally fed by visitors. Non-compliant behaviour in visitors ranged from 5 % of the observations (Frankfurt) to 31 % (Seattle). There was no significant difference of non-compliant behaviour in enclosures with an additional barrier for the visitors and those with none. In enclosures with glass, visitors showed the same mean level of activity as in those with a moat (Mann-Whitney, n=10/13). Signs with instructions for the public in general had no significant effect on their behaviour; only in moat enclosures it reached significance (Mann-Whitney, n=12/13).
In glass fronted enclosures and in moat enclosures I found a correlation of non-compliant visitor behaviour and frequency of display to the visitors, in enclosures with a moat the apes watched humans more, if they were active (Spearman, n=66, 40).
But the visitors were affected by the gorillas' behaviour too: Certainly humans spent more time at enclosures with active gorillas, and the gorillas' activity increased the visitors' activity. In Seattle and Zürich the activity of the visitors was positively correlated with the number of gorillas who stayed in the front part of the enclosure (Spearman). In the other zoos (Stuttgart, Frankfurt, Rotterdam, West Berlin, Basel) I noted no significant correlation.

Discussion

Enclosure structure

Kopff (1982) and Sucker (1987) already noted that gorillas do not like to stay in the open; this should be expected, because they are rain forest primates. If the enclosure furnishings are not attractive to them, they spend most time near the walls. This was found by Kopff (1982) especially for Krefeld, when the gorillas could not retreat into the sleeping cages. During my observations in this zoo they spent most time in those sleeping cages, that were obviously more attractive to them.
The floor area of an enclosure has no significant effect on the gorillas' behaviour. This was also found by Goerke et al. (1987) and Bowen (1981), who recorded the behaviour of gorillas before and after the move to a new, larger enclosure. In a comparison of many gorilla groups, Wilson (1982) also found no significant effect of the enclosures' floor area on gorilla locomotor activity.
Much more important for the animals than the mere floor space of a gorilla exhibit is its structure. This means facilities that provide shelter and an opportunity to lean against them, for example trees, walls, niches and sleeping cages. Even a glass barrier is a "wall" and therefore used as a place for rest. In Seattle, the gorillas stayed at the visitor viewing area most time, this place was located in a niche and the most attractive part of the whole enclosure. Some group members spent more than 90% of their time there. In Atlanta the gorillas frequently leaned against trees (Ogden, pers. comm.), but the walls and niches at the holding area were the preferred place for rest; this part of the enclosure was not visible for visitors and thus the animals often stayed out of their view (Table 3; see also Ogden et al. 1989a, b).
An important enrichment is the access to various compartments within the enclosure. This may be indoor and outdoor exhibits or several rooms with different furnishings. If the enclosure provides that kind of enrichment, the gorillas are less interested in visitors, who offer in deprived enclosures the main diversion for them. The same is the case, if the apes are given different kinds of manipulable objects, and in outdoor enclosures with a moat, if the exhibit is very spacious.

Withdrawal

Gorillas need places to withdraw from the sun, from visitors and from conspecifics. Miller-Schroeder & Paterson (1989) found, that female gorillas reproduced mor successfully if their enclosure contained various structures, and especially privacy refuges like sight barriers and cages. The opportunity to stay out of sight from the rest of the group is in accordance with the natural environment of gorillas and used for example by pregnant females or adolescent males, who frequently spend their time at the periphery of the group (Harcourt & Stewart 1981).
If no separate compartments, moats or enclosure areas behind sight barriers are available, staying above the ground is the only way of withdrawal. In small enclosures, furnishings for this purpose are especially important; but even in large exhibits the floor area can not be a substitute for vertical space, and suitable climbing structures are freuqently used by the gorillas. Sucker (1987) noted in the outdoor enclosure of Apeldoorn (2 ha), that the gorillas spent a mean of 8 % of the time above the ground.
The staying above the ground decreases, if the gorillas can withdraw into sleeping cages. Especially insecure individuals, who avoid contact with others (for example during an integration; Meder 1982) prefer this kind of retreat. If the sleeping cages are large and furnished, the gorillas spend more time there than in small, boring cages.
Exhibits with more than one room provide more opportunities for withdrawal and staying in the sleeping cages is less frequent. Thus gorillas do not withdraw to avoid the visitors, but on the one hand to avoid visual contact with the rest of the group, and on the other hand, because those places may be more attractive.

Gorillas and visitors

Gorillas accept glass (and bars also) as more efficient to separate them from the visitors than moats; the close proximity to humans in enclosures with glass does not drive them away, but attracts them (see also Vrancken et al. 1990). However, frequently the gorillas do not face the public, when they sit leaned against the glass.
Coe (1985) analyzed the positions of visitors and zoo animals and discussed the resulting behaviours. He found that if the human was positioned higher than the animal, he was noted as the higher ranking one and behaved accordingly. If he stood lower than the animal, he showed respect and was willing to learn more about it.
Indoor enclosures usually are positioned about half a meter above the floor of the public area to make the visitors shorter. In outdoor enclosures with moats, in general the gorillas are positioned lower than the visitors, when they stay near the moat; this may lead the visitors to throw of objects into the exhibit, especially if the gorillas are begging (Hannover, Krefeld, Radi in Calabar's group).
The feeding of zoo animals frequently is a problem (Thompson 1984). Signs that tell the people not to feed are not always effective. Bitgood et al. (1988) noted less feeding only if the signs explained, why this was not allowed. In my study signs did not have a consistent effect on non-compliant behaviour. Furthermore I found no difference in non-compliant behaviours when comparing enclosures with and without additional barriers for the visitors. Hutchins et al. (1984) state that the improvement of gorilla facilities and the naturalistic enclosure in Seattle resulted in more discipline in visitors; my study does not comfirm this.
In enclosures with moats, not only visual, but also acoustic and olfactory stimuli as well as thrown objects reach the gorillas, therefore the visitors' influence is stronger. The gorillas react in those exhibits more to visitors, especially in small enclosures; this is obvious, if many people stand at the exhibit and if they are active. In my study, adult males in particular showed great interest in visitors, more than females. This corresponds to the behaviour of free ranging gorillas: Males have to be more alert to approaching conspecifics, because females may transfer during an interaction with another group or a lone male (Yamagiwa 1987a, b). Besides, they have to save the group from predators (Fossey 1983).
I observed more frequent watching of visitors and more display to them in moat enclosures than in glass enclosures, the same saw Kopff (1982). He observed even more display, if more visitors were present. Böer & Janke-Grimm (1990), however, saw more display in a small enclosure with bars and glass, than in an enclosure with moat.

Visitors provide diversion for captive gorillas, but they may also produce stress. As it is difficult to lead visitors to appropriate behaviour, the most effective way of reducing the disturbance caused by the public is to protect the gorillas by glass barriers. Miller-Schroeder & Paterson (1989) found, that females who lived behind completely closed barriers showed greater reproductive success.

Group composition

Gorillas in the wild mostly live in stable groups that consist of one leading silverback and several adult females with their offspring (Fossey 1983). In lowland gorilla harems the mean number of group members is 5 (Carroll 1988; Harcourt et al. 1981; Jones & Sabater Pi 1971; Tutin & Fernandez 1987). In 11 out of the 16 harem groups observed in my study, the number was higher than 5; those groups were "established" (Yamagiwa 1987a, b), and in the wild adolescent offspring would leave them. This could explain the increased agonistic contacts that I noted especially in females, if the number of group members was high. Watts (1990b) observed a positive correlation of number of females with aggression and also with emigration in mountain gorilla groups.
Attacks of males against females are not usual in the wild, but frequently observed in captivity, especially in incompatible pairs (Beck 1981; Farst 1977; Hardin et al. 1969; Maple & Hoff 1982). These pairs had been reared together from infancy on, while in the wild females frequently emigrate from their natal group when they grow up. In zoos the animals are still frequently kept in pairs, although in the wild they do not live in pairs but in larger groups (Watts 1990b). The three pairs that I observed in this study hardly had any contact. In one pair the male attacked the female frequently, in the other pair the reaction to humans was extremely high.
In Howletts zoo females were kept together with different males in the beginning, but when one male started to attack the offspring of another male, stable groups were established (Halliday 1983). Killing of an infant by a new group leader has been observed in the wild (Fossey 1984; Watts 1989) and in captivity (e. g. Kirchshofer 1989).

Solitary silverbacks

Gorilla males in the wild frequently leave their natal group when becoming silverbacks and join all-male groups or live solitary, frequently for many years (Caro 1976; Fossey 1983; Yamagiwa 1986). Besides a little more locomotion they show no obvious behavioural differences from males in harems (Yamagiwa 1986). Groups of males have been observed in the wild, but only in mountain gorillas so far (Harcourt 1988; Yamagiwa 1987a, b), and in captivity there are no long-term experiences with all-male groups. As long as we do not know if it is possible to keep males in groups, surplus males can be kept solitary withour problems, because this corresponds to the behaviour of gorillas in the wild and the public should accept it. For enrichment other primates have already successfully been kept together with gorillas (Anon. 1991; Bond 1990).

More than one adult male in a group

In wild gorilla groups an adult male usually does not tolerate another male if he is not his son (Fossey 1983; Harcourt & Stewart 1981; Watts 1990a). The emigration of males starts already when they are blackbacks by their moving to the periphery of the group. Fights between group leaders are not rare and may be lethal (Harcourt 1978, 1981; Hess 1989).
In captivity males also mostly do not tolerate other adolescent males, who then have to be removed from the group. Three of the groups observed in this study included two silverbacks, however, and none of the pairs was father and son. In Seattle and West Berlin they had grown up together, and in Basel the younger one had been born when the older one was already the group leader (they are not related). The behaviour of these males did not differ from the behaviour of other silverbacks in groups. In all cases the males tolerated each other, but kept apart. Several rooms were accessible in all enclosures, and frequently the males stayed on different sides of the enclosure and did not see each other.

Keeping more than one group

An advantage of keeping several gorilla groups in one place is the ease of transfers from one group to another, which is successfully practised in some zoos (Halliday 1980; Kopff 1989; Kopff & Mager 1989). The silverbacks of two groups that can hear, see and smell each other, can display to each other and defend their groups (Kopff and Mager, pers. comm.).
But several groups living in one building and separated only by bars can be a cause of stress for the silverbacks too. In Columbus three groups spent the night in the same house and had permanent visual and acoustic contact and could smell each other. One of the silverbacks permanently ground his teeth, a behaviour which indicates stress and which he had not shown in his natal zoo (Martinez, pers. comm.). In Howletts for example the displays of silverbacks in adjoining cages led to aggression against other group members (Halliday 1983, 1986). Even only visual contact can lead to stress.

Acknowledgements

I want to thank all zoo directors for their support and all curators for additional informations. The cooperation with gorilla keepers was especially important and useful: They helped with measuring enclosures, giving informations about the apes and sometimes even tried to adjust their managemant procedures according to my plans. Free accomodation during the observations was provided by many zoos and by several persons, to whom I am very grateful. The Frankfurt Zoo provided materials. Thanks also to my parents, who made my travels possible by their financial support, and to Benjamin B. Beck, who arranged my invitation into the USA and therefore made the studies in some American zoos possible.

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