
Effects of the Environment on the Behaviour of Lowland Gorillas in Zoos

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ABSTRACT

The purpose of this study was to observe as many gorilla groups as possible and to compare their behaviour in different exhibits, social structures and visitor situation. Gorillas were studied in 15 zoos, they lived in 14 groups with male and female adults and immatures, 2 groups of adults without immatures, 3 adult pairs, 2 solitary silverbacks and several groups of immatures. The gorillas lived in 17 indoor and 11 outdoor enclosures with glass (15), moat (11) and bars (2). Data of behaviours were collected by one-zero sampling (locomotion, dominance, display, aggression, positive contact, social play, abnormal behaviours, watching of the visitors, visitor- directed display), the whereabouts of each group member by scan sampling. Visitor number and activity was observed with scan and one-zero sampling.

The number of different movable objects was negatively correlated with watching the visitors. The enclosure's floor space was not correlated with frequencies of the observed behaviours. In spacious enclosures the gorillas did not like to stay in the open but usually spent most time near structures, especially the walls of niches. In enclosures with several compartments they frequently retreated from the group by staying in a separate room, no matter whether it was visible for the public or not. If the compartments were very small and not furnished, only those individuals used them for considerable time, that were pregnant or sought privacy for other reasons. Rest areas above the ground and climbing structures were used particularly in small enclosures without any other privacy, but even in spacious outdoor exhibits.

Solitary silverbacks and adults in pairs showed more interest in visitors than adults in groups. Males in 2-male-groups did not behave differently from males in 1-male-groups. The number of group members was positively correlated with locomotion, aggressive and positive social behaviours (correlation of female aggression with the number of adult females in a group was also observed in free-ranging gorillas).

Frequency of noncompliant behaviour in visitors did not differ with enclosure types and the presence of signs or barriers. In enclosures with a moat barrier the gorillas observed the visitors more frequently, in enclosures with glass they spent more time near the visitors; glass seems to be most effective in reducing the disturbances by visitors, and even more, if an additional space with plantings separates visitors and gorillas.

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" that are mainly dealing with laboratory primates (e. g., Amer. J. Primatol. Suppl. 1, 1989; NOVAK & PETTO, 1991; SEGAL, 1989). But 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. GRIEDE (1989) worked out guidelines for keeping primates in the EEC, and presently the gorilla-EEP-commission is compiling special guidelines for this species. If and how the physical environment affect the apes' "well-being", has been examined in gorillas by several authors (AKERS & SCHILDKRAUT, 1985; BOWEN, 1980; FORD, 1990; GOERKE et al., 1987; GOULD & BRES, 1986; HEDEEN, 1982, 1983; HOMANN, 1986; 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 of housing, of group composition and of visitor presence and activity.

MATERIALS AND METHODS

Subjects

Table 1 [not scanned] shows the compositions of the study groups. 14 groups with immatures were observed (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 [not scanned]).

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 had bars and the rest a moat to separate gorillas and humans. Four indoor enclosures and two outdoor exhibits consisted of several compartments (Table 2 [not scanned]).

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.

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 behaviours 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 by scan sampling 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 sampled 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

Table 3 [not scanned] shows the main was correlated positively with locomotion, dominance, aggression, positive contact, social play and staying in the front part of the enclosure (Spearman, $n=127$). Regarding the behaviour of females only, 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 positive contacts and social play than adults without immatures (Mann-Whitney, $n=73/6$). When comparing the behaviour of silverbacks, I found no significant behavioural differences between two silverbacks, who lived in one group with females and immatures, and single males in such a group (Mann-Whitney, $n=6/17$).

A solitary silverback spent more time above the floor and showed more locomotion 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 area and type

The main results of the statistical analyses are listed in table 4 [not scanned]. 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, $n=55$).

In moat exhibits the gorillas showed more locomotion. In exhibits with glass, aggression was higher; this probably results from the higher mean number of group members in glass enclosures, which is positively correlated with aggression (see above). 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 a barrier were compared to moat enclosures, which always had a barrier, there was no significant difference.

Withdrawal

In glass enclosures the time spent 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, $n=712$). 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 in) and furnished were used more often than those that were small (less than 15 in) 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 the difference was significant (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 spent more time watching humans 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 found no significant correlation.

DISCUSSION

Enclosure structure

KOPFF (1982) and SUCKER (1987) already noticed 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, which 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 observed 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 - 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. During my observations in Seattle for example, the gorillas stayed near the visitor viewing area most time, which was located in a niche and seemed to be 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 the public and thus the animals often stayed out of the visitors' view (Table 5 [not scanned]; 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 shapes and furnishings. If the enclosure provides that kind of enrichment, the gorillas are less interested in visitors, who in deprived enclosures offer 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 and PATERSON (1989) found, that female gorillas reproduced more successfully if their enclosure contained various structures, 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 frequently 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 and boring cages, away from the public, which is not appreciated.

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. One reason for staying in sleeping cages is to avoid visual contact with the rest of the group, which can as well be achieved by providing several enclosure compartments. Another reason can be that those places are more attractive (Table 5 [not scanned]). The way to keep the animals in the exhibit would be, in this case, to make the exhibit more attractive, not to shut the sleeping cages.

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 AMUNDIN, 1991 and 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 humans were positioned higher than the animals, they felt like the higher ranking ones and behaved accordingly. If they stood lower than the animals, they showed respect and were willing to learn more about them.

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 the gorillas are usually positioned lower than the visitors, if they stay near the moat; this may lead the visitors to throw objects into the exhibit, especially, if the gorillas are begging. 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 confirm 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, when many people stand at the exhibit and when they are active. In my study, silverbacks 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) and HOMANN (1986). BOER and 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 and 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). Moreover the pairs in my study (as many others too) had been reared together from infancy on, while in the wild females frequently emigrate from their natal group when they grow up. Even nowadays gorillas in zoos are 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.

If a gorilla harem is established, its composition usually remains stable for several years (YAMAGIWA, 1987a, b); frequent changes in zoo groups therefore do not correspond to the situation in the wild. During the first years in Howletts Zoo females were kept together with different males, but when one male started to attack the offspring of another male, stable groups were established (HALLIDAY, 1983). A change of the leading male resulted in killing of an infant several times 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 male groups in captivity, surplus males can be kept solitary without 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 (BOND, 1990; BOUSSEKEY, 1991; MAGER, 1981).

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 frequently 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 in several rooms or on different sides of the enclosure.

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 practiced 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.). Displays of silverbacks in adjoining cages in Howletts led to aggression against other group members (HALLIDAY, 1983, 1986).

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REFERENCES

- AKERS, J. S. & SCHILDKRAUT, D. S. (1985): Regurgitation/reingestion and coprophagy in captive gorillas. *Zoo Biology* 4: 99-109.
- ALTMANN, J. (1974): Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.
- AMUNDIN, M. (1991): Gorilla studies in Kolmdrdens Djurpark. Unpublished manuscript.
- BECK, B. (1981): A primate passion play at Brookfield. *Brookfield Bison*, June/July: C1-C8.
- BITGOOD, S., CARNES, J., NABORS, A. & PATTERSON, D. (1988): Controlling public feeding of zoo animals. *Visitor behavior* 2 (4): 6.
- BOER, M. & JANKE-GRIMM, G. (1990): Verhaltensuntersuchungen an Flachlandgorillas (*Gorilla g. gorilla*) im Zoologischen Garten. *Zool. Garten* 60: 137-189.
- BOND, M. (1990): Profile: Nikumba. *Gorilla Gazette* 4 (1): 11-13.
- BOUSSEKEY, M. (1991): Behavioural study of a gorilla red-tailed monkey mixed group in the St.- Martin-La-Plaine Zoological Park. Unpublished manuscript.
- BOWEN, R. A. (1980): The behaviour of three hand-reared lowland gorillas, with emphasis on the response to a change in accommodation. *Dodo* 17: 63-79.
- CARO, T. M. (1976): Observations on the ranging behaviour and daily activity of lone silverback mountain gorillas (*G. g. beringei*). *Anim. Behav.* 24: 889-897.
- CARROLL, R. W. (1988): Relative density, range extension, and conservation potential of the lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia* 52: 311-323.
- COE, J. C. (1985): Design and perception: Making the zoo experience real. *Zoo Biol.* 4: 197-208.

FARST, D. D. (1977): Zoo V.I.P. Brownsville Zoo News 6 (2): 1-3.

FOSSEY, D. (1983): Gorillas in the mist. London, Hodder and Stoughton.

FOSSEY, D. (1984): Infanticide in mountain gorillas (*Gorilla gorilla beringei*) with comparative notes on chimpanzees. Pp. 217-235 in: HAUSFATER, G. & HRDY, S. B. (eds.) Infanticide. New York, Aldine.

FORD, J. C. (1990): The effects of a change to a more naturalistic zoo enclosure on the behaviour of western lowland gorillas. Unpublished B.Sc. thesis, University of Melbourne.

GOERKE, B., FLEMING, L. & CREEL, M. (1987): Behavioral changes of a juvenile gorilla after a transfer to a more naturalistic environment. Zoo Biol. 6: 283-295.

GOULD, E. & BRES, M. (1986): Regurgitation and reingestion in captive gorillas: description and intervention. Zoo Biology 5: 241-250.

GRIEDE, T. (1989): Guidelines for adequate housing and care of non-human primates in zoos. Amsterdam, National Foundation for Research in Zoological Gardens.

HALLIDAY, P. (1980): The integration of an adult female gorilla into the Howletts collection. Help 3: 6- 8.

HALLIDAY, P. (1983): Recent changes in the Howletts colony. Help 5: 11-14.

HALLIDAY, P. (1986): Gorilla diary update. Help 8: 12-14.

HARCOURT, A. H. (1978): Strategies of emigration and transfer by primates, with particular reference to gorillas. Z. Tierpsych. 48: 401-420.

HARCOURT, A. H. (1981): Intermale competition and the reproductive behavior of the great apes. Pp. 301-318 in: GRAHAM, C. E. (ed.) Reproductive biology of the great apes. New York, Academic Press.

HARCOURT, A. H. (1988): Bachelor groups of gorillas in captivity: the situation in the wild. Dodo 25: 54-61.

HARCOURT, A. H., FOSSEY, D. & SABATER P, J. (1981): Demography of gorilla gorilla. J. Zool. London 195: 215-233.

HARCOURT, A. H. & STEWART, K. J. (1981): Gorilla male relationships: can differences during immaturity lead to contrasting reproductive tactics in adulthood? Anim. Behav. 29: 206-210.

HARDIN, C. J., DANFORD, D. & SKELDON, P. C. (1969): Notes on the successful breeding by incompatible gorillas at Toledo Zoo. Int. Zoo Yb. 9: 84-88.

HEDEEN, S. E. (1982): Utilization of space by captive groups of lowland gorillas (*Gorilla g. gorilla*). Ohio J. Sci. 82 (1): 27-30.

HEDEEN, S. E. (1983): The use of space by lowland gorillas (*Gorilla g. gorilla*) in an outdoor enclosure. Ohio J. Sci. 83 (4): 183-185.

HESS, J. (1989): Familie 5. Basel, Birkhäuser.

HOMANN, E. (1986): Gorillahaltung in 5 zoologischen Institutionen. Staatsexamensarbeit, Bielefeld.

HUTCHINS, M., HANCOCKS, D. & CROCKETT, C. (1984): Naturalistic solutions to the behavioral problems of captive animals. Zool. Garten 54: 28-42.

JONES, C. & SABATER PI, J. (1971): Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. Basel, Karger.

KIRCHSHOFER, R. (1989): International studbook for the Gorilla, *Gorilla gorilla* (SAVAGE and WYMAN, 1947), 1988. Frankfurt, Zoological Garden.

KOPFF, H.-O. (1982): Vergleichende Studie über die Haltung von Flachlandgorillas (*Gorilla g. gorilla*) in verschiedenen Zoologischen Gärten und ähnlichen Einrichtungen. Diplomarbeit, Heidelberg.

- KOPFF, H.-O. (1989): Transfers of male and female lowland gorillas at Apenheul, Apeldoorn, Holland, and a short note on Zoological Garden Budapest. Proc. 1st Gorilla-EEP-meeting, Frankfurt.
- KOPFF, H.-O. & MAGER, W. B. (1989): Further developments in the breeding population of lowland gorillas at Apenheul. Zoo Biol. 9: 165-170.
- MAGER, W. (1981): Stimulating maternal behaviour in the lowland gorilla at Apeldoorn. Int Zoo Yearbook 21: 138-143.
- MAPLE, T. & Hoff, M. P. (1982): Gorilla behavior. New York, Van Nostrand Reinhold.
- MEDER, A. (1982): Untersuchungen zum sozialen Verhalten in einer Gruppe von Flachlandlandgorillas mit Schwerpunkt auf dem Grad sozialer Integration handaufgezogener Tier. Diplomarbeit, Heidelberg.
- MILLER-SCHROEDER, P. & PATERSON, J. D. (1989): Environmental influences on reproduction and maternal behavior in captive gorillas. Pp. 389-415 in: SEGAL, E. F. (ed.) Housing, care and psychological wellbeing of captive and laboratory primates. Park Ridge, Noyes Publications.
- NOVAK, M. A. & PETTO, A. J. (eds.) (1991): Through the looking glass. Washington, D. C., American Psychological Association.
- OGDEN, J. J., FINLAY, T. W., JACKSON, D. & MAPLE, T. L. (1989a): Gorillas of Cameroon: A post-occupancy evaluation. AAZPA Reg. Conf. Proc. (1989): 557-563.
- OGDEN, J., HORTON, C. & PERKINS, L. (1989b): New facilities open at Zoo Atlanta. Gorilla Gazette 3 (1): 12-14.
- SEGAL, E. F. (ed.) (1989): Housing, care and psychological wellbeing of captive and laboratory primates. Park Ridge, Noyes.
- SIEGEL, S. (1976): Nicht-parametrische statistische Methoden (Non-parametric statistics for the behavioral sciences, deutsch). Frankfurt, Fachbuchhandlung für Psychologie.
- SOKAL, R. R. & ROHLF, F. J. (1981): Biometry. San Francisco, W. H. Freeman.
- SUCKER, K.-J. (1987): Verhaltensstudie über Raumnutzung, Raumverteilung und Raumdynamik einer Gorillagruppe in seminatürlicher Haltungsform. Staatsexamensarbeit, Bielefeld.
- TAIS, E. N. (1982): Untersuchungen von Verhaltensanomalien bei Tieflandgorillas (G. g. g., SAVAGE and WYMAN) in Zoologischen Gärten und deren Beeinflussbarkeit durch Haltungsbedingungen. Dissertation, Berlin (BRD).
- THOMPSON, V. D. (1984): Noncompliant behavior in zoo visitors. Zool. Garten 54: 177-190.
- TUTIN, C. & FERNANDEZ, M. (1987): Sympatric gorillas and chimpanzees in Gabon. Anthroquest 37: 3-6.
- VRANCKEN, A., ELSACKER, L. VAN & VERHEYEN, R. F. (1990): Preliminary study on the influence of the visiting public on the spatial distribution in captive eastern lowland gorillas (Gorilla gorilla graueri, MATSCHIE, 1914). Acta Zoologica et Pathologica Antverpiensia 81: 9-15.
- WATTS, D. P. (1989): Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. Ethology 81: 1-18.
- WATTS, D. P. (1990a): Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. Zoo Biol. 9: 185-200.
- WATTS, D. P. (1990b): Ecology of gorillas and its relation to female transfer in mountain gorillas. Int. J. Primatol. 11: 21-45.
- WILSON, S. F. (1982): Environmental influences on the activity of captive apes. Zoo Biol. 1: 201-209.
- YAMAGIWA, J. (1986): Activity rhythm and the ranging of a solitary male mountain gorilla (Gorilla gorilla beringei). Primates 27: 273-282.
- YAMAGIWA, J. (1987a): Intra- and inter-group interactions of an all-male group of mountain gorillas (Gorilla gorilla beringei). Primates 28: 1-30.

YAMAGIWA, J. (1987b): Male life histories and the social structure of wild mountain gorillas (*Gorilla gorilla beringei*). Pp. 31-51 in: KAWANO, S.,

CONNELL, J. H. & HIDAKA, T. (eds.) Evolution and coadaptation in biotic communities. Tokyo, University of Tokyo Press.

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