The effect of familiarity, age, dominance and rearing on the reproductive success of captive gorillas

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Abstract

Wild gorillas live in stable multi-female groups that are led by a dominant male and frequently include one or several younger males. Females usually transfer to another male as young adults. Gorillas in captivity avoid mating with partners of certain age classes and very familiar individuals. Males mate more readily with similarly aged females than with older ones that they have known since birth. The reason is usually the intervention of the dominant male. Females rarely initiate copulation with the male that already led the group during their infancy. They have the highest reproductive success with males that they were introduced to at the beginning of sexual maturity. Keeping the animals in pairs as well as hand-rearing have negative effects on breeding. However, by the formation of larger groups and the introduction of hand-reared to mother-reared individuals, reproductive success can be increased.

Introduction

In populations that are genetically heterogenous, inbreeding may cause an increase of infant mortality, hereditary diseases and susceptibility to infections (Ralls & Ballou 1982). Fossey (1983) supposed that some morphological abnormalities that she observed in the Virunga mountain gorillas were an indication of inbreeding. Mechanisms for the avoidance of breeding between closely related individuals evolved in many plants and animals. Social animals usually avoid copulating with relatives. The genetic relationship is less important for this behaviour than the familiarity between the partners.
Most primatologists regard the avoidance of mating with relatives or familiar conspecifics as a trigger for leaving the natal group in certain age and sex classes (e. g. Pusey 1990; Pusey & Packer 1987). Incest avoidance is usually accepted as the reason for transfers of young females to other social units, if the leadership of the dominant male in that species lasts until his daughters reach sexual maturity. Such is the case in free ranging mountain gorillas. Females usually transfer, and males are also known to leave their natal group in many cases (Harcourt 1978; Yamagiwa 1987). In order to simulate the situation in the wild, male and female gorillas are often transferred in zoos.
There have only been nine certain and six possible cases of reproduction between relatives in nearly 700 captive births. Among the certain inbreeding cases four are between full and two between half siblings, two between father and daughter and one between mother and son. With one exception, these dyads had not lived together from birth. The present study was conducted to find out whether gorillas avoid copulations resp. reproduction with certain partners and under what conditions this is the case.

Material and methods

Data were collected from the files of the International Gorilla Studbook, from publications and personal communications. In addition, questionnaires were designed and mailed to 159 zoos. 114 zoos replied. The data were analyzed in 2x2 tables with the non-parametric G-test. Two criteria were used for the evaluation: matings (complete copulations) and reproduction (siring/giving birth to offspring). If not noted otherwise, only those dyads that lived together until both partners were at least 10 years old were considered for analysis. "Father-daughter dyads" are classified as dyads of mother-reared females and their fathers that lived in the same groups since the daughters' births. "Mother-son dyads" are dyads of females and their mother-reared male offspring. "Aunts" are females that are at least 6 years older than the respective male.
The gorillas were classified in the following age classes: infant (0 to 3 years), juvenile (3 to 6 years), subadult (6 to 8 years), adult female (more than 8 years), blackback male (8 to 11 years) and silverback male (more than 11 years).
Unless stated otherwise, only dyads living in groups of at least three individuals without an older, dominant male were considered for comparison. When comparing the breeding of animals living in

groups and those living in pairs, there were significant differences in both sexes, irrespective of the age at which the partners had been introduced to each other. In all cases the reproductive success of animals living in groups was higher.

Results

Sexual maturity

The median age at first conception in females was 7 years 9 months (range: 5 years 7 months to 15 years; n=67). Mother-reared females conceived earlier (median: 7 years 4 months) than hand-reared ones (8 years 3 months). Wild mountain gorilla females become fertile at the earliest with a little less than 8 years, that means 2.5 years later than lowland gorillas in zoos, and give birth for the first time at a median age of 10 years (Watts 1991).
Males in zoos produced their first offspring at a median age of 9 years 9 months (range: 7 years to 13 years 5 months; n=30). There was no difference between hand- and mother-reared individuals. If no older male is present, they become fertile about 2 years later than females, when they are still blackbacks. The age of sexual maturity in the wild is not known, as they usually have no opportunity to copulate with fertile females before they are fully grown (at about 15 years).

Blackback males

Generally silverbacks did not disrupt sexual activities between juvenile males and adult females. However, as soon as the males became adult, the group leaders started to interfere.
31 mother-son dyads lived together until the son was at least 7 years old, but only five of them until he became 10 years old. One of the latter dyads, the only one with no older male in the group, sired an offspring. Five of the other dyads copulated, 16 did not and in nine cases no information was available. Two males were removed from their groups after they had copulated with their mothers. In all cases the males initiated the copulations; two of the mothers rejected their sons' approaches, and in one case the leading male interfered.
26 males grew up in a group with their mothers and other females. None of the males reproduced with his mother or an aunt, but some of them with a younger female. However, even this was rare, as in all cases an older male lived in the group. 21% of the males copulated with their mothers, 13% with other older females and 54% with peers. The difference between copulations with the latter and with older females is significant (with mothers $p<0.05$, with aunts $p<0.01$). Blackbacks that lived together with a dominant male only rarely mated with peers whom they had met already in their first year of life. If they were more than 1 year old when they were introduced to them, sexual interest was much higher ($p<0.05$).
In general, males bred more frequently with peers than with older females. Moreover, in groups with no older male they had offspring more frequently than in groups with a dominant male. This difference was significant for males that had been infants when they were introduced to the partner ($p<0.001$) and for males that were more than 6 years old then ($p<0.01$). If males came into a group (without an older male) when more than 6 years old, they reproduced with peers more frequently later ($p<0.05$) than if they were between 3 and 6 years old when joining the group.
Some leading males did not prevent younger males from breeding. Eight males that had grown up in groups with older males took over those groups as blackbacks. Three of them already produced offspring when the dominant male was still in the group, but not with all females; with some females they only started breeding when they had become leaders of the groups. Three other males out of those eight copulated with some females when the older male was still present, and one of them later reproduced with the same females. The two remaining males started to reproduce only after the dominant males were no more in their groups.

Young females

Two infants were born by father-daughter dyads. One of the mothers had grown up without her father and was introduced to him when she was 4 years old, the other one had been hand-reared and intro-

duced to her parents' group at the age of about 1 year. In another case (a mother-reared female that grew up with her father and another male), paternity is still not clarified.
Out of 21 father-daughter dyads that had been together from the daughter's birth until she was at least 7 years old, only three lived together for more than 10 years. Not one of those dyads reproduced with certainty. In four dyads at least one copulation was observed, and two females of these dyads were removed from their groups to avoid inbreeding. 14 dyads did not mate, and for three no information is available. Descriptions of the sexual activity are available for five dyads; in three cases the daughter initiated copulations, and in two cases the father.
Daughters and fathers reproduced much less frequently than females with non-leading males whom they knew since their birth and that were old enough to be their fathers ($p<0.05$). Mating and reproductive success of females with their fathers and with younger males that lived in the same group were not significantly different.

Age at introduction

Females bred most frequently with partners that they met when they were 6 to 8 years old, and males with partners whom they met with 3 to 6 and 6 to 8 years; however, none of these differences were significant. Females and males had less reproductive success with partners to whom they were introduced when more than 8 years old ($p<0.01$ and $p<0.05$). (The reason for this is probably that older individuals with behavioural abnormalities often are introduced to new partners many times without success.)

Age differences between the partners

Similarly aged partners (peers) bred more readily than dyads with older males ($p<0.05$) and older females ($p<0.01$). Females that lived in a group since their first year of life had significantly less frequently offspring with males that were more than 6 years older compared to females that were older when they were introduced to their partners ($p<0.05$). Females that met their partners when they were 3 to 6 years old initiated sexual activities more frequently with males that were 3 or more years older than when they had the same age ($p<0.05$). Moreover, these females reproduced more frequently with 3 to 6 years older males than females that were younger or older at the introduction ($p<0.01$ and $p<0.05$).

Rearing

Hand-reared males sired offspring with significantly less females than mother-reared and wild born males. Most conspicuous was the difference between hand-reared and mother-reared individuals ($p<0.001$). Moreover, mother-reared males reproduced more frequently than wild born ones ($p<0.01$). In females, there was no significant difference. However, when dyads were arranged by rearing, females also showed a clear tendency. Hand-reared males bred significantly less with hand-reared females than with mother-reared ones ($p<0.05$); hand-reared females bred less readily with hand-reared than with wild born ($p<0.01$) and mother-reared males ($p<0.001$). Furthermore, they mated less frequently with wild born than with mother-reared males ($p<0.01$).

New partners

If gorilla females did not produce any offspring, they were frequently introduced to new males or transferred to other zoos. Females were mostly sent to other zoos when they were 6 to 16 years old and males when they were 10 to 17 years old. These transfers were most successful in 7 to 9 year old females. Males that had never reproduced before most frequently impregnated females whom they met when they were 8 to 14 years old. Out of 30 females that were introduced to a new partner at the age of 10 years or more, 50% had an infant within 1 year. They conceived within the first 4 months they spent with the male.

˘Discussion

Rearing

The differences in the reproductive success of differently reared animals shows that experience in early infancy affect their reproductive behaviour considerably. Hand-reared as well as wild born gorillas, who were also reared by humans, have offspring less often than individuals that grew up with their mothers (Meder 1990). For the wild born gorillas the experiences during their first years of life, probably the shock when their family was killed and they themselves were captured, had a lasting effect on their behaviour. Growing up without adult conspecifics also seems to affect reproductive success.
The choice of partners strongly determines whether the animals will breed. Mother-reared females can make hand-reared males reproduce and vice-versa, while hand-reared/hand-reared dyads rarely produce offspring.

Blackback males

As the relationship between mother and son is very close, it can be expected that they have an especially strong incest avoidance. This was found in studies of various primate species like macaques and guenons (Pusey 1990). Chimpanzee mothers and sons mate extremely rarely. Sometimes sons try to initiate copulations with their mothers, but are rejected (Goodall 1986; Pusey 1980). According to Pusey (1990) and Manson & Berry (1993) females generally avoid copulations with relatives more strongly than males in barbary macaques, baboons, chimpanzees and rhesus monkeys.
In wild mountain gorillas, mating was observed in only one mother-son dyad, after the partners had been separated for 6 years (Watts 1990). As young males in zoos are usually kept in groups with dominant males and are removed from their natal group before their silverback has developed, it is very difficult to prove incest avoidance between mothers and sons. Some males, however, copulate with their mothers even if an older male is present. Females usually avoid initiations by their sons, if the dominant male does not interfere.
Copulations with the mothers are about as frequent as copulations with other females that were already adult when the males were born. The males mate in their natal groups significantly more often with peers. The most important reason for this is probably not their lack of interest in older females but the more frequent interventions of the dominant males if they notice that blackbacks try to copulate with "their" partners. Younger females that grew up in the group are watched over less by the leading male during their estrus and therefore are the most likely partners for younger males, as Hess (1989) also noted in the wild. If a feral group contains no suitable females, subordinate males leave it. According to Harcourt (1978) four mountain gorilla males emigrated when 10 to 13.5 years old. Captive gorilla males prefer partners of similar age, even if no older males are present.

Young females

In primates that live in multimale groups, paternity is usually unclear. Daughters do not avoid copulations with their fathers as clearly as mothers with sons, for example in chimpanzees (Goodall 1986). However, even in these dyads there is a certain degree of avoidance. Some females do not mate with males who, with regard to their age, could be their fathers (Pusey 1980). Much stronger do chimpanzee females avoid copulations with partners to whom they had a close relationship during infancy (Pusey 1980). The same was observed by Küster et al. (in press) in barbary macaques, who also live in multimale groups. In this species fathers and daughters show no clear incest avoidance, but this is noticed in young females and males that had cared for them intensively in their first year of life. The degree of familiarity in early infancy, not the age difference in general, obviously reduces sexual attraction within a dyad.
Captive gorilla fathers copulate with their daughters very rarely. The males' rank determines this, besides their age; the females breed significantly more frequently with much older males that did not lead the natal groups of the females. The results from this study do not indicate whether fathers or daughters avoid incest more strongly. Usually, however, the females prefer similarly aged males in their natal

group. Captive females have the highest reproductive success with males that they meet for the first time as soon as they become fertile. Wild mountain gorilla females transfer for the first time when they are 6.5 to 13 years old (Harcourt 1978). The median is 8 to 9.5 years - the age at which they become sexually mature.
In the wild gorilla fathers and daughters copulate very rarely, and so far no offspring has been born to such a dyad (Watts 1990). This could have two reasons: a lack of sexual interest by the leading male in young females, or higher attraction between the young members of the group. Wild gorilla females usually transfer to other groups before they reproduce if the only breeding male was already adult when they were born. If a second male is in the group, the females mate with him. In this case they give birthe to their first infant in their natal group, yet frequently transfer before conceiving their next infant (Harcourt 1978; Watts 1990, 1991). In this study only very few copulations were noted also with young males; perhaps the dominance of the older males prevent matings, or the sexual attraction in those dyads is very low too.

Conclusions

- Females have the best reproductive success with partners that they meet at the beginning of sexual maturity.
- Hand-reared gorillas breed with mother-reared partners much more frequently than with hand-reared ones.
- Females breed very rarely with group leaders that they know from the first year of life. If they were older than 1 year when they met the males for the first time, they do not avoid copulations.
- Maturing males do not clearly avoid mating with their mothers; such sexual activities are, however, usually prevented by the dominant males or the mothers themselves. Males reproduce less frequently with females that were already adult in their infancy than with younger females.

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