Contrasts Between Male Relationships
in Wild Gorilla Groups

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Summary. This paper examines proximate and ontogenetic causes of differences between the relationships of wild gorilla males. Two pairs belonging to different reproductive groups were observed. In both, the mature male was dominant over the younger one. However, in one, the males interacted extremely rarely, while in the other, affinitive behaviour, largely initiated by the younger male, was frequent. Three factors that could have influenced the nature of the relationships are discussed. These are their ontogeny, payoffs to the partners from each other's presence, and the ability of at least one partner to alter any imbalance in payoffs. The importance of understanding such proximate causes of variation within species to consideration of differences between species is emphasised.

Introduction

Correlations of parameters of primate population structure, such as group size and composition, or the number of adult males in a group, with various aspects of the environment have been made by a number of authors (Crook, 1970; Crook and Gartlan, 1966; Denham, 1971; Eisenberg et al., 1972; Jolly, 1972). However, a detailed examination of the associations between ecology and social organisation suggested by the above authors brings to light a number of discrepancies (Clutton-Brock, 1974). Though these do not negate the value of the broad generalisations (which provide a framework from which to search for more intricate relations), they do indicate that it is necessary to search beyond mere ecological control of group organisation: investigation of historical and social factors is needed as well. An area in which groups of different size and composition live in the same habitat is a fruitful place to start such an investigation.

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Mountain gorilla groups of various sizes can be found not only in overlapping home ranges, but as stable one-male and multi-male units in the Virunga Volcanoes of Rwanda and Zaire (e.g. Fossey, 1972; Fossey and Harcourt, 1977; Schaller, 1963). For two years from September 1972, the author worked with two main study groups of gorilla in that region. Each contained a fully mature male (silverback), who was the obvious leader of the group, and a younger male of around 9 years of age (blackback), who had not yet assumed full adult morphology. Between the two groups, there was a marked difference in the relationships of these males. One pair was "friendly," while between the other males, interactions of any kind were extremely rare.

The nature of the differences between the pairs, and a discussion of their causes and consequences, are the concerns of this paper. It should be understood that the intention is not to make broad statements about the relationships of male gorillas in general – a study of two pairs is clearly far too small a sample for that. Rather, the contrast between the described relationships is to be used as a paradigm with which to examine results of other studies, and from which to formulate principles for further research.

The development of multi-male groups in some species but not in others "remains one of the most striking enigmas in primate social behaviour" according to Clutton-Brock and Harvey (1976). "Any explanation of differences in social organisation between species must be based on adequate understanding of the causation of intraspecific variation. Indeed a satisfactory account at this level would go a long way to explain differences at the species level." (Crook, 1970, p. 123). Perhaps the following account of variation within a species in relationships between males will go some way towards providing a solution to the problem.

Material and Methods

The study area lay at around 10,000′ in the Parc des Volcans of Rwanda and Zaire. It has been described in detail by Fossey (1974) and Fossey and Harcourt (1977). The two main study groups (groups 4 and 5 in the Karisoke Research Centre nomenclature) each contained the two males already mentioned plus a number of females with their offspring, and other immatures. Particulars of the groups' compositions and their changes through time are given by Harcourt (1978 b and c), as are details of field and recording methods and of procedures of analysis. The quantitative measures of the behavioural parameters used are described as they arise in presentation of the results.

When Fossey first began studies in 1967, the present leader of group 4 was then the beta male, with another male subordinate to him. Early in 1968, the old leader died and the present one then took over. At that time, the young male of this study was 3 years old and an orphan. Like other young gorillas who lose their mother, he developed a strong association with the old leading male (Fossey, 1978). On the latter's death, no similar affiliative relationship was established with the new leader, and the two have almost ignored each other since then. Camp records, collected predominantly by Dian Fossey, show that the early relationship of the two males in group 5 was very different from the above one. When the young male was an infant, the present dominant male was already an established leader of the group and seemed to have a normal friendly relationship with the immature male. While the present leading male of group 4 was very probably not the father of the blackback, it is not impossible that the two males in group 5 were father and son.

Results

Through this section, the interactions, and so the relationships (see Hinde, 1976) between the males of group 4 are compared with those of the group 5 males. Where there are enough data, results for the two years of the study are presented separately so that the stability of the differences between the relationships can be judged. The years are combined when the pattern of interactions was similar in each, but in one or both there were too few data for separate presentation.

I. Affinitive Interactions

A. Proximity

1. Time in Proximity. Times that animals spent within 2 m and 5 m of one another were calculated for each day as the percent of their combined time in sight, with times within 5 m being recorded only in the second year of the study. Only days on which the males were seen for more than 1 h (hereafter termed 'observation days') were used in analysis.

In both years, the males of group 5 spent more time near each other (i.e. within 2 m or 5 m) than did the group 4 males (Fig. 1). Such a result could arise in two ways: the males of group 5 might have been in proximity more frequently, or stayed together for longer when they were in proximity. In the first year, both factors operated; in the second, only the first did so. Thus in year 1, the group 5 males were seen within 2 m of each other on a greater proportion of observation days (33% vs. 16% for group 4; total $n=18$ and 25 respectively), and for a greater proportion of each day that they were in proximity (median of 3.4% vs. 0.9% for group 4; $n=6$ vs. 4; $U=1.5$; $P<0.04$). In year 2, the proportion of each day that the males were in proximity was not significantly different, though the group 5 medians were roughly twice as high as those of group 4. The males of group 5 were, however, in proximity more often: they were seen within 5 m of each other on 60% of observation days (total $n=47$) versus 18% for group 4 ($n=38$), and within 2 m on 49% of days versus only 5% for group 4.

In addition to continuous recording of animals' times in close proximity, scan samples were made at quarter hourly intervals of the spacing of group members. Gorilla groups divide their day into rest periods and travel–feed periods (Harcourt, 1978 a), and scan records taken during each activity period were analysed separately. To ensure independence of records, I used only those taken at intervals of more than $1^{1}/_{4}$ h during rest periods and of more than $^{1}/_{2}$ h during travel–feed periods. (The different intervals are due to the fact that individuals stayed the same distance apart for far longer during rest periods than when travelling and feeding.)

It was found that the males of group 5 were closer together during rest periods than during travel–feed periods ($P<0.001$; Fig. 2), as were most group members (Fossey and Harcourt, 1977; Harcourt, 1978 c). The group 4 males,
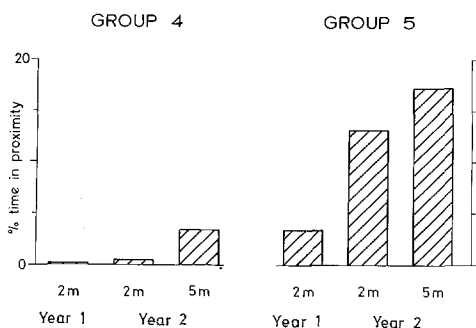
Fig. 1. Comparison between the study groups of the times the males in each spent within 2 m or 5 m of each other in the first year (year 1) and the second year (year 2) of the study (5-m data not recorded in year 1.) The ordinate shows the mean of the daily percents of time the partners were in sight that they spent in proximity. For group 4, $n = 25$ (year 1) and 38 (year 2); for group 5, $n = 18$ (year 1) and 47 (year 2)
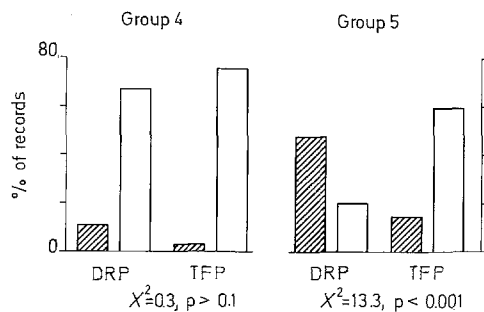

Fig. 2. Comparisons between the groups of the distances between males during day–rest periods (DRP) and travel–feed periods (TFP) in the second year of the study. Hatched histograms = proportion of scan records showing males to be within 5 m of each other; open histograms = proportion showing the males to be more than 15 m apart. For group 4, total $n = 18$ (DRP) and 33 (TFP); for group 5, total $n = 40$ (DRP) and 42 (TFP)

however, stayed far apart when resting, as well as during travel–feed periods (Fig. 2; $P > 0.1$; χ^2 test corrected for continuity). Thus most of the differences between the groups in the males' times within 5 m of each other occurred during day–rest periods.

2. Responsibility for Proximity. A measure of which partner was more responsible for maintenance of proximity is provided by Hinde's responsibility index (see e.g. Hinde, 1969). This index is the percent of approaches between partners made by one of them, minus the percent of leaves performed by the same one. If the subject's index is positive, he was more responsible than was his partner for proximity, and if negative, he was less responsible. In this study, an index was counted as reliable only if more than 30 movements (i.e. approaches and leaves) between partners had been recorded and if each partner had made more than 10 movements.

Because the group 5 males spent the majority of their time in close proximity during day–rest rather than travel–feed periods (see Fig. 2), only data from rest periods were used to calculate which partner was more responsible for most of the time in proximity. This is because factors that influenced responsibility for the relatively small time in proximity during travel–feed periods might have had little bearing on responsibility for the far longer amount of time during rest periods (Harcourt, 1978a; Simpson, in preparation).

Using the criteria given above, only the group 5 males in the second year of study had enough records for their responsibility indices to be calculated. It was found that at neither the 5-m nor the 2-m distances were the indices more than 10% (This was the case during travel–feed periods also.) Thus the males were counted as being about equally responsible for maintenance of proximity at the two distances.

That the younger male of group 5 at least sought some proximity with the leading male is, however, indicated by comparison of the frequency with which each male followed the other's departure. An animal was recorded as 'following' if within 2–3 s of its partner leaving beyond 2 m, it went in the same direction that the partner took. It was found that the group 5 leading male followed not one of the blackback's 20 departures, but the younger male followed after 27% of the leader's 30. With the assumption that the probability of following was not affected by previous reactions to departures, this difference was significant ($P < 0.001$, $\chi^2 = 11.4$; χ^2 test, corrected for continuity).

B. Occurrence of Body Contact

To calculate the rate with which partners touched (excluding contact that was only to groom), the number of bouts that they spent within 2 m of each other that lasted more than $^1/_2$ min was counted. The percentage of such bouts during which the partners were in body contact at least once for more than 5 s is the value expressed as the rate of body contact. Reasons for use of this measure and for the criteria of $^1/_2$ min and 5 s are given in Harcourt (1978b).

It was found that the group 5 males, although they rarely touched, were more often in contact than those of group 4: the latter were never seen touching, while the males of group 5 touched in 1 of 11 bouts within 2 m in year 1 and 6 of 41 in year 2. The younger male initiated slightly more bouts of contact (6 of 7) than he ended (4 of 7) over the two years.

C. Occurrence of Grooming

The measure of grooming rate used is the same as that for body contact described above.

Not only were the males of group 5 more often close together and in contact with one another than were the group 4 males, but they groomed more frequently too: in the 8 bouts that the group 4 males were seen within 2 m of each other, they never groomed, yet grooming between the group 5 males occurred in 2

of 7 bouts in year 1 and 10 of 30 bouts in the second year. The younger male did all the grooming in both years, and since the leading male was never seen to solicit grooming, the younger was counted as having initiated all bouts. The silverback ended some of them, however (2 of 6 in the first year and 3 of 30 in the second).

It was found that the blackback of group 5 was far more likely to groom during long bouts in proximity (i.e. > 10 min) than he was during short ones ($\leq$ 10 min): he groomed in 84.6% of the longer (n = 13), but only 4.2% of the shorter (n = 30) bouts (χ^2 = 28.7, P < 0.001, df = 1; χ^2 test corrected for continuity). This finding becomes relevant to consideration of the predictability of the males' behaviours when the latencies between starts of bouts within 2 m and the initiation of grooming are considered. The median latency for the two years combined was 1 min (n = 10), while the minimum bout length during which grooming occurred was 5 min in the first year and 12 min in the second. In other words, when the young male began to groom the silverback, the observer and presumably the males knew that they would probably stay together for at least the next 10 min or so. It seems likely that such predictability would increase the stability of the males' relationship: a relationship in which there is little uncertainty about future movements is surely more likely to continue than one in which there is much (Altmann, 1962; Wickler, 1976).

II. Agonistic Interactions

Non-aggressive approach–retreat interactions are considered first, and then aggressive interactions. An individual was counted as 'avoiding' its partner's approaches if it at once moved away from the partner but did not go beyond 2 m, or if within 5 s it moved beyond 2 m. Aggressive incidents were classified as 'undirected' 'directed' and 'attacks,' these categories being, essentially, in order of increasing intensity of aggression. Undirected aggression was any component of the chest-beating or strut-walking sequence (Schaller, 1963, pp. 221–236) performed within 5 m of the partner, but which was not seemingly directed specifically at him. Directed aggression was hostility clearly aimed at a particular recipient, and included attacks, i.e. hits, kicks, and bites.

Neither leading male was ever seen to avoid any of the young males' non-aggressive approaches, but the latter occasionally avoided the leading males'. In the two years combined, the group 4 blackback avoided 6 of 9 approaches, and the group 5 blackback, 8 of 31. The other reaction, besides avoidance, was almost to ignore the approach.

Turning to aggressive interactions between the males, they were very infrequent, with a rate of less than one incident every 8 h that the pairs were in sight (see Fig. 3). In group 4, all the aggression was from the leading male, but in group 5, the animals were about equally frequently aggressive to each other (Fig. 3). This is counting all incidents of aggression. When only 'directed' aggression is scored, the silverback had about twice the blackback's rate, although the differences between them in their frequencies of directed as against undirected aggression was not significant (P > 0.05; Fisher Exact Probability Test).
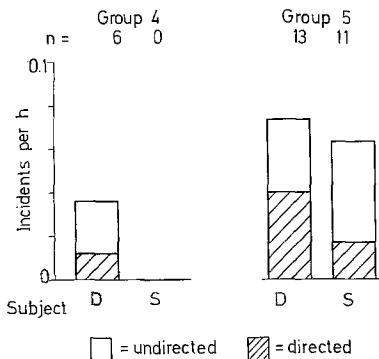
Fig. 3. Comparison between the males within each group of their frequency of aggression to each other. *D*=Dominant male; *S*=younger male. Ordinate=number of incidents of aggression per hour the partners were in sight. 'Directed' and 'undirected' aggression defined in text

Since the young male of group 4 was never seen to be aggressive towards the leading male, only the group 5 leading male's reactions to the younger male's aggression can be commented on: he usually ignored it and was never seen to avoid it. The blackbacks, on the other hand, commonly avoided the silverbacks' aggression. The contrast in the two relationships is evident here also: whereas the group 4 blackback avoided 5 of the silverback's 6 aggressive acts, the young male of group 5 avoided only 7 of 13. His reactions to the other six ranged from grooming the silverback to being aggressive in return.

No specific context could be attached to the group 4 silverback's aggression towards the young male, but competition over females seemed often to be the cause of hostility between the males of group 5 (see below).

III. Competition Between Males for Females

In a number of primate species, it has been found that dominant males are likely to monopolise females around the time of ovulation, but to allow subordinate males to copulate before and after that peak of fertility (baboon – DeVore, 1965; Hausfater, 1975; macaque sp. – Kaufmann, 1965; Stephenson, 1975; chimpanzee – Tutin, 1975). In the study groups, the young males were allowed to copulate without hindrance with juvenile and subadult females, but were not allowed access to fertile females. The young male of group 5 did, in fact, mate with two adult females, but in one instance the female was pregnant (as was the case for one, possibly both, of Schaller's (1963, p. 283) observations of a subordinate male mating in full view of the dominant male) and in the other the female was a nullipara in her first oestrus and so almost certainly still sterile.

In group 4, no aggression over females was ever observed: as far as the leading male was concerned, the blackback was apparently not a competitor for females. This was not the case in group 5. There, overt hostility over females was recorded. The silverback aggressively terminated three of the nine copulations between the nulliparous female mentioned above and the young male,

although he himself mated with her only infrequently and apparently half-heartedly. Moreover, the single observed attack by the leading male on this blackback occurred during one of these instances. In addition, the silverback was seen to stop play between the young male and an adult female who came into oestrus two days later, and he twice aggressively halted affinitive interactions between the young male and the other two females in the group at times when they were not in oestrus.

Discussion

The males of the two study groups had very different relationships: whereas the group 4 males interacted extremely rarely, affinitive interactions between the males of group 5 were common. Furthermore, the younger male of group 4 apparently posed no threat to the dominant male's monopoly of fertile females, yet overt aggression between the group 5 males over females was observed. The clear dominance of the mature males over the younger ones was the only similarity between the two relationships.

Because the two groups live in adjacent and ecologically very similar ranges (see Fossey and Harcourt, 1977), differences in the habitat cannot account for the observed dissimilarities in the form and frequency of interaction between the males: historical and social parameters need to be examined instead. Such parameters, which are known to have differed between the two pairs, are the developmental histories of the young males, the extent of competition for females, and, possibly, their degree of consanguinity. These factors and postulates linking them to the contrasting natures of the males' relationships are considered here.

I. Past Histories of the Males and Their Relationships

The differences between the males in their past histories and relationships are, essentially, contrasts between, on the one hand, an infant and an established dominant male (group 5) and, on the other, an infant and a subordinate male (group 4) (see p. 40). It is known that females with young infants spend more time near the dominant male than they do near subordinate males (Harcourt, 1978 c), and that as the offspring mature, they come to spend as much time near the dominant male (who is probably their father) as they do near their mother (Harcourt, 1978 c; Stewart, in preparation). If familiarity can lead to affinity (Cairns, 1966; Zajonc, 1971), and affinity in immaturity to friendly relationships in adulthood, immatures that associated with the dominant male in their infancy (e.g. group 5) are more likely to be friendly with him in their adulthood than are immatures that did not so associate (e.g. the blackback of group 4).

Although contrasts in past histories of relationships can undoubtedly influence present contrasts (Simpson, 1973), relationships are not immutable. Therefore, other controlling factors, effective at the time of study, must be

important in reinforcing the dissimilarities. Those to be discussed here are costs and benefits to each male in the presence of the other.

II. Payoffs to the Males

Whereas the young male of group 4 did not compete with the leading male for females (nor, probably, for food, since he was usually so peripheral), the blackback of group 5 did so compete. Given only minimal benefits to the silverbacks in the young males' presence (such as slight aid in defence of the group), this means that whereas the leading male of group 4 neither lost nor gained from the young male's residence in the group, the group 5 leading male lost. In addition, both blackbacks were too young to have acquired females outside of the group. Thus, by comparison with the other options available to them, the group 4 blackback lost nothing by remaining in the group, while the young male of group 5, who managed to mate occasionally, clearly gained by his continued presence. It is argued, therefore, that in group 5 there were immediate costs to the leading male, but benefits to the young male, in the latter's remaining in the group, whereas in group 4 payoffs were balanced.

III. Payoffs and the Nature of Relationships

The hypothesis presented here is that balanced payoffs, or inability to alter any imbalance, lead to a stable relationship (excepting the case when both partners lose from the association), while asymmetry plus the ability to redress it leads to an unstable one. In the first instance, neither partner needs to, or can, terminate the association, and the result is a stable relationship with little social interaction, either affinitive or antagonistic, between the partners. In the second situation, the relationship is in danger of breaking down, since the partner at a disadvantage can either leave or expel the other. One extra alternative, besides cessation of such a relationship, is behaviour by the partner that benefits from the association to increase the stability of the relationship.

Group 4 is obviously an example of the first case, and group 5 of the second, because the group 5 silverback was in his prime and capable of expelling the young male. The latter's initiation of affinitive interactions with the silverback can be seen as his working to increase the stability of the relationship. Had the leading male been incapable of ousting the blackback, this 'friendly' behaviour would have been unnecessary: even with imbalance in the payoffs, the relationship would have been stable.

IV. Conclusion

Through the ten years the Karisoke Research Centre has been in existence, the number of adult males in the main study groups has changed as individuals matured, emigrated, or died, so turning the groups from one-male to multi-male

and back again. Thus, independently of the nature of the habitat, these simple demographic processes have altered the structure of the groups over time (cf. Dunbar and Dunbar, 1976). An integral component of group structure is the nature of the group members' relationships (Hinde, 1976). The balance of payoffs to partners, their ability to alter the balance, and the past history of their relationships are, it has been argued, related to the observed nature of the relationships. Greater appreciation of these more proximate factors, as well as speculation on functional considerations, is necessary if differences between species in group structure are to be understood.

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