Behav. Ecol. Sociobiol. 5, 67–86 (1979)

Behavioral Ecology and Sociobiology

Patterns of Group Splitting Within Matrilineal Kinship Groups

A Study of Social Group Structure in *Macaca mulatta* (Cercopithecidae: Primates)

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Received May 19, 1978

Summary. 1. When social groups of free-ranging rhesus monkeys on Cayo Santiago, Puerto Rico, undergo fission, they usually divide between genealogies.

2. If a genealogy divides, it is usually between an eldest daughter with her family and the rest of the genealogy.

3. The separation of the eldest daughter from her genealogy is the extreme case of peripheralization of low-ranking females among rhesus monkeys.

4. The founders of new groups that disperse from the former home range are likely to be subordinate individuals in the parent group, as predicted by Christian (1970).

5. The dispersal of families as units is likely to lead to 'lineal effects' (Neel and Salzano, 1967) in the genetical substructure of the population.

Introduction

The purpose of this paper is to describe one aspect of group fission among rhesus monkeys, based on observations of the fission of a social group of 106 free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, analysis of census records of four other fissions, and review of the literature. This paper identifies the places where the network of social attachments (Sade, 1972a) among females are likely to break during a group fission. The role of males in group fission will be described in a later paper. The changes in interactional patterns both among females and males that precede, accompany, and follow a group fission will also be described in a later paper.

Group fission results in dispersal, an event of importance for the spread, isolation, and speciation of organisms. In cases in which one of the new groups formed is smaller than the other, Nash (1976), Furuya (1960, 1968, 1969), and Southwick et al. (1965) have found that the smaller groups disperse from the home range of their mother groups into less inhabited adjacent areas.

Groups may divide into equal or unequal parts. Furuya (1969) mentions 'peripheral females' as those most likely to form a new group. Missakian (1973a)

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notes that in most cases, animals related to one another stayed together in the new groups. If interactional subgroups can be detected within social groups, it might be possible to detect the probable lines along which a group will split.

Sade (1965, 1966, 1972a) and Missakian (1972, 1973a and b, 1974) have shown that kinship groups form strong interactional subunits within social groups of rhesus monkeys. The same has been shown for all other species of primates in which kinship relations among members of a social group were known (Goodall, 1967; Nash, 1976; Koyama, 1970; Jolly, 1972; Chagnon, 1975). The most likely place for the integration of a social group to break down is between kinship groups. But what if all of the members of a social group belong to the same kinship group? Are there interactional subunits within the kinship groups? Along what lines can a group of closely related animals divide when group fission occurs?

Most studies of group fission have been on animals under observation for too short a time for familial relationships beyond one generation to be known. Nash's (1976) study used 5 consecutive years of genealogical information. Since baboons have a life span of up to 20 years or more, even this study does not allow an examination of kinship relations between adult members of the main group and adult members of the splinter group.

The Cayo Santiago colony of free-ranging rhesus monkeys offers a unique opportunity for the study of topics requiring long-term information. All individuals were marked permanently with a unique tattoo. Records of genealogical relations have been kept on individuals born on the island since 1956 (Altmann, 1962). Monkeys range at will over the 40-acre island, and remain or do not remain in social groups according to their own motivations, rather than because of constraints imposed by humans.

Missakian's (1973a) study of the fission of Group A at Cayo Santiago between 1968 and 1970 utilized 14 years of genealogical data. Group A divided mainly along genealogical lines, but with exceptions that are discussed below. A few years later, Group F divided also mainly along genealogical lines, but with similar exceptions, also discussed below.

Materials and Methods

Cayo Santiago's physical characteristics have been described elsewhere (Heatwole et al., 1963). The island's high relief and dense vegetation provide many more sites for monkeys to forage and groom out of sight of one another than an island of similar size, but more uniform topography. Two social groups of monkeys may be visually isolated from one another while only 100 m distant.

The history and characteristics of the population are described in Sade et al. (1976).

Definitions

A 'genealogy' is the set of all individuals known to be related to one another through the female line. They are all descended from the single female who is the eldest of the genealogy known to the colony's census records. She is the 'matriarch' of the genealogy. A 'family' is a mother and her offspring. Depending on the duration of the census, a genealogy may contain several families of different generations. 'Fission,' 'division,' and 'split' are used interchangeably.

Males who are still members of the group into which they are born are referred to as 'natal males.' Males who have migrated into other groups are called 'non-natal males.'

For any pair of monkeys, the 'dominant' individual consistently elicits signs of subordination from the other individual in aggressive encounters involving only those two individuals (Sade, 1964; Missakian, 1972).

Sade (1972b) showed that female rhesus monkeys have a very stable linear dominance hierarchy, and that maturing females take their places in the adult dominance hierarchy in a very predictable way. Using the unambiguous criterion for dominance of a clear display of subordination in fights involving only two animals, Sade (1972b) showed that usually each young female assumes a position in the dominance hierarchy directly below her mother's position, remaining subordinate to her mother and to all of the females who are dominant to her mother. The daughter is dominant to all of the females that her mother dominates, including the daughter's older sisters. Younger sisters will in turn rise in rank over her when they mature. Thus any set of sisters, once they are all mature, will rank in the inverse order of their ages, the youngest being dominant to all, and the eldest being subordinate to all.

Linearity, predictability, and stability over time of the position of adult females in the dominance hierarchy of the group allows us to rank not only individuals, but whole genealogies with respect to one another in the group.

Criteria for Recognizing Independent Social Groups

The criteria used for designating Group M as an independent social group, and no longer a subgroup of Group F were:

1) consistent spatial separation from Group F;

2) stabilization of adult female membership of the two groups;

3) the occurrence of aggressive intergroup encounters (Hausfater, 1972) between the daughter group and parent group, in which monkeys attacked relatives and former friends.

These criteria were met in November 1973, exactly 2 years after the first signs of splitting were seen.

Missakian (1973a) used an additional criterion for the completion of the fission process: cessation of grooming between adult females of the different groups. By 1976 this criterion had still not been met for Groups F and M. One female in Group M still occasionally groomed her sisters in Group F when the two groups came close to each other (Rhodes, personal communication). Cayo Santiago is too small to permit a very great shift in home range for the new group, as seems to occur following group fission in less limited space (Nash, 1976; Furuya, 1969). Since the two groups are confined on a small island they come into contact frequently. There is nothing to prevent the old bonds between the siblings from reverberating (Count, 1967; Sade, 1968) even though they are now in different groups. Grooming between adult females of different groups has also been seen occasionally when other pairs of groups come into contact (Chepko-Sade, field notes; K. Cushing, field notes; Sade, field notes), though it is comparatively infrequent. Therefore, this criterion for separation of groups was considered less important than the three criteria mentioned above.

Methods

A census of births, deaths, maternity, and group membership is collected by direct observation. Most monkeys are recognized individually by trained observers, and all identifications can be verified by a close look at the animal's tattoo. This paper uses information collected from 1960 through 1976, and maintained in a computerized data base at Northwestern University.

The growth and division of the social groups are shown in Fig. 1. Sudden large decreases in the sizes of groups are due to removals. The formation of new groups by group fission is indicated by sections which branch out of other groups.

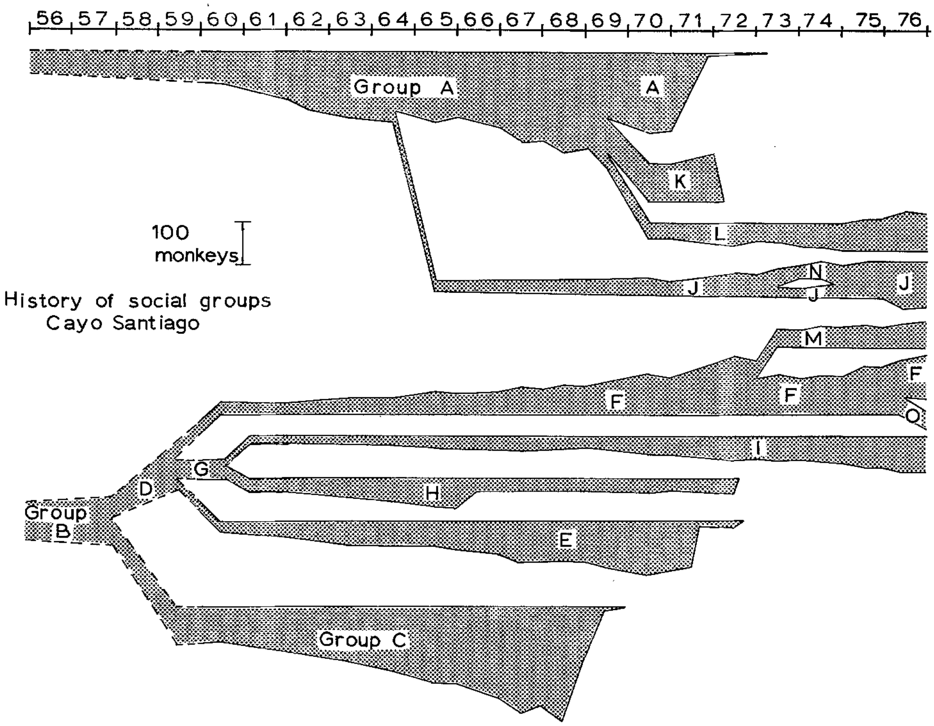


Fig. 1. History of social groups at Cayo Santiago (modified from Sade et al., 1976). Years are given at the top

Results

The First Fission of Group F

There were 106 monkeys in Group F in late September 1971. The 87 animals who were either original members of the group or who had been born into the group were members of six genealogies (Fig. 2). One infant female, presumably born in another group, had been adopted by a female from Group F. The other 18 members (not shown) were males who had migrated into Group F.

In late November 1971 a subgroup of males and females (stippled individuals in Fig. 2) began to separate from the rest of Group F. Some individuals were at first sometimes found with the subgroup and sometimes with the main group, but membership stabilized by the time fission was complete. As in the fission of Group A described by Missakian (1973a), there were periods during which the two groups were more separated from one another, and other periods during which all of the members acted as one group. This process shall be described in a later paper.

When the subgroup became separate enough from Group F to be called an independent social group, it was named Group M. The females of the subgroup initially included most of the members of 022's genealogy and a few

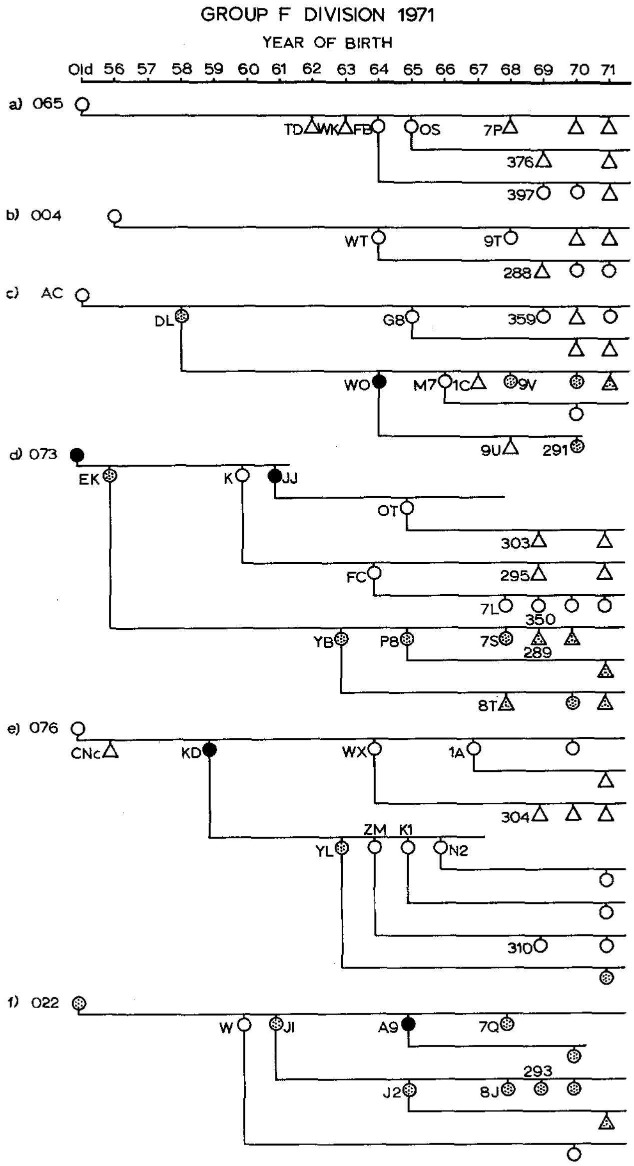


Fig. 2. Genealogical relations of the natal members of Group F in October 1971. *Circles* represent females, *triangles* represent males. The name (*tattoo*) of each monkey over two years of age is given. *Black symbols* represent 'connector females' who died before October 1971. *Stippled symbols* indicate the original members of the subgroup. The genealogies are arranged in order of decreasing dominance rank from top to bottom. In 073's genealogy, 073's eldest daughter, EK, along with all of EK's offspring, joined the subgroup, while the rest of 073's genealogy remained with Group F. 022's genealogy showed the reverse pattern: 022's eldest daughter, W, and W's offspring remained in Group F while the rest of 022's genealogy joined the subgroup. In 076's genealogy, 076's eldest daughter was KD, who was dead. KD's eldest daughter, YL (plus her offspring) joined the subgroup, while the rest of KD's family as well as the rest of 076's family remained in Group F. AC's genealogy represents a case within a case of an eldest daughter leaving her family: Female 291, AC's eldest daughter's granddaughter, by WO, was orphaned when WO died within a few days of her birth. Female 291 was adopted and raised by her grandmother, DL, from the time her mother became ill (Breuggeman, 1973). Female 291 has always acted exactly as if she were DL's daughter, in terms of dominance rank and grooming partners, even though her biological mother was WO. M7 was DL's eldest living daughter at the time of the group division. M7 and her offspring stayed with Group F, while DL and the rest of DL's family, including adopted 291, joined 022's group. Meanwhile, AC and the rest of the genealogy stayed with Group F: M7 (DL's eldest daughter) left DL's family, while DL (AC's eldest daughter) left AC's family

mother-and-offspring families from genealogies AC, 073, and 076 (Fig. 2). These were the low- and middle-ranking genealogies of the group. These four genealogies all showed intragenealogical splitting. In each case splitting was a variant of a female's eldest daughter separating from her mother's family.

A 'connector female' is the matriarch of a genealogy or any other female who has offspring living in a group (Missakian, personal communication). Missakian (personal communication) noted that a connector female was dead in all the genealogies that split internally during the division of Group A in 1968–1970. However, connector females were also dead in some genealogies that did not split internally during both the Group A and the early Group F divisions. Later during the fission of Group F, between May 1972 and August 1973, seven connector females died: DL, K, 065, 004, WT, 076, and 022 (Fig. 3).

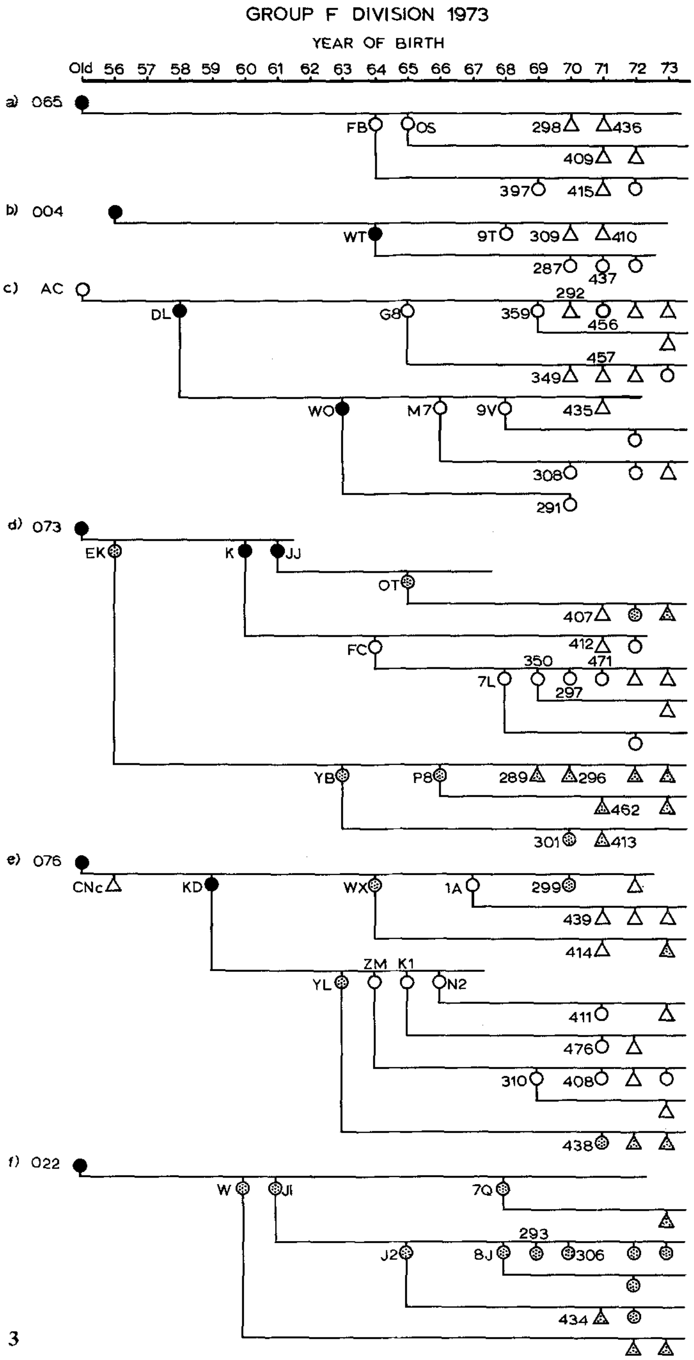
The events following these deaths (Fig. 3) suggest the roles that are played by factors such as size of genealogy, rank of genealogy, and presence or absence of connector females in determining whether a genealogy will or will not divide during a group fission.

Other Group Divisions at Cayo Santiago

In order to determine whether the patterns seen in split genealogies of Group F were general, census information was examined for other divisions that have occurred on Cayo Santiago. Group fissions have occurred six times since 1960 when a continuous census was begun: the division of Group G into Group H and Group I; the division of Group A into Group A and Group J; the division of Group A into Group A, Group K, and Group L (Missakian, 1973a); the division of Group F into Group F and Group M; the division of Group J into Group J and Group N; and the division of Group F into Group F and Group O.

Group G into Group I and Group H. There were no breaks within any of the genealogies of Group G, as far as can be seen from the amount of genealogical

Fig. 3. Genealogical relations of the natal members of Group F in November, 1973, showing final members of Group M (*stippled symbols*) and Group F (*open symbols*). Other conventions are as in Figure 2, except that dominance relations of females in Group M are not implied by this figure. Genealogies 065 and 004, both small and high-ranking, did not divide in spite of the death of their matriarchs. Following DL's death, genealogy AC reunited within Group F. More complex results were seen in the larger and lower ranking genealogies 073 and 076: Genealogy 073, now lacking both its matriarch and two of the matriarch's three daughters, acted as 3 independent families: EK's family moved with the subgroup, as before. K's family stayed in Group F, as before. OT's small family joined the subgroup. Genealogy 076, another large genealogy, also broke into small subgroups after losing its matriarch. Each of 076's offspring acted independently of the others. WX, her family, and her sister 299 joined the subgroup, while the male castrate CN, his sister 1A, and their yearling brother remained with Group F. KD's family did not change: YL remained in the subgroup, while her sisters remained in Group F. In genealogy 022, W returned with her offspring to the subgroup after her mother 022 died, but W did not affiliate closely with members of her own genealogy. Rather, her closest ties appeared to be with males in the group (Conley, field notes)


GROUP F DIVISION 1973
YEAR OF BIRTH
Old 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73
a) 065
FB
OS
298
436
409
397
415
b) 004
WT
9T
309
410
287
437
c) AC
DL
G8
292
359
456
457
349
WO
M7
9V
435
308
291
d) 073
EK
K
JJ
OT
407
FC
412
350
471
7L
297
YB
P8
289
296
462
301
413
e) 076
CNc
KD
WX
1A
299
439
414
ZM
K1
YL
N2
411
476
310
408
438
f) 022
W
JI
7Q
293
J2
8J
306
434

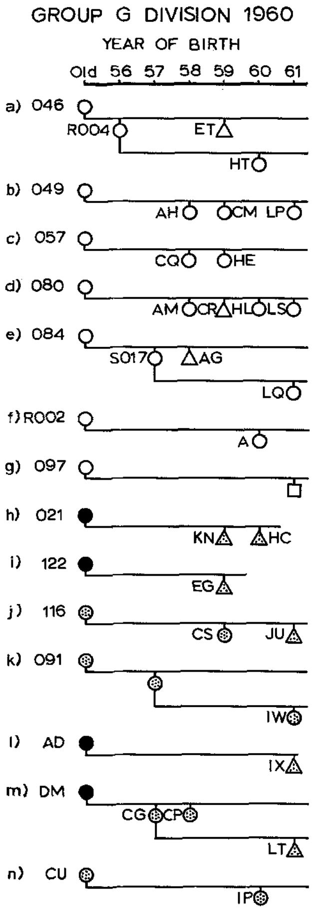


Fig. 4. Genealogical relations of the natal members of Group G in late 1960. *Stippled symbols* represent monkeys who joined Group I. *Open symbols* represent monkeys who joined Group H. Dominance relations are not known among these females. Other conventions are as in Fig. 2. In 1960, prior to group fission, Group G contained 48 members, 39 of which were natal, belonging to 14 different genealogies. By December 1960, Group G had divided into two new groups, Group I and Group H (Koford, 1963). Group I contained 18 members, 15 of which were natal, belonging to 7 genealogies (*stippled individuals*), and Group H contained 31 members, 24 of which were natal, belonging to 7 other genealogies (*unstippled individuals*)

information available (see Fig. 4). However, genealogical information was available for only some of the adults prior to the Group G split. It is likely that if information had been available for earlier years, some of the genealogies of Group G would have been shown to be related to one another. No genealogical relations are known beyond two generations. The largest known genealogy in Group G before the split had only five members.

Group A into Group A and Group J. This division is illustrated in Fig. 5 and described in the caption.

Group A into Group A, Group K, and Group L. This division is illustrated in Fig. 6 and described in the caption.

Group J into Group J and Group N. This division will be described in a later paper. As noted above, the females of Group J were members of two genealogies, 031 and 092, that had previously separated from Group A.

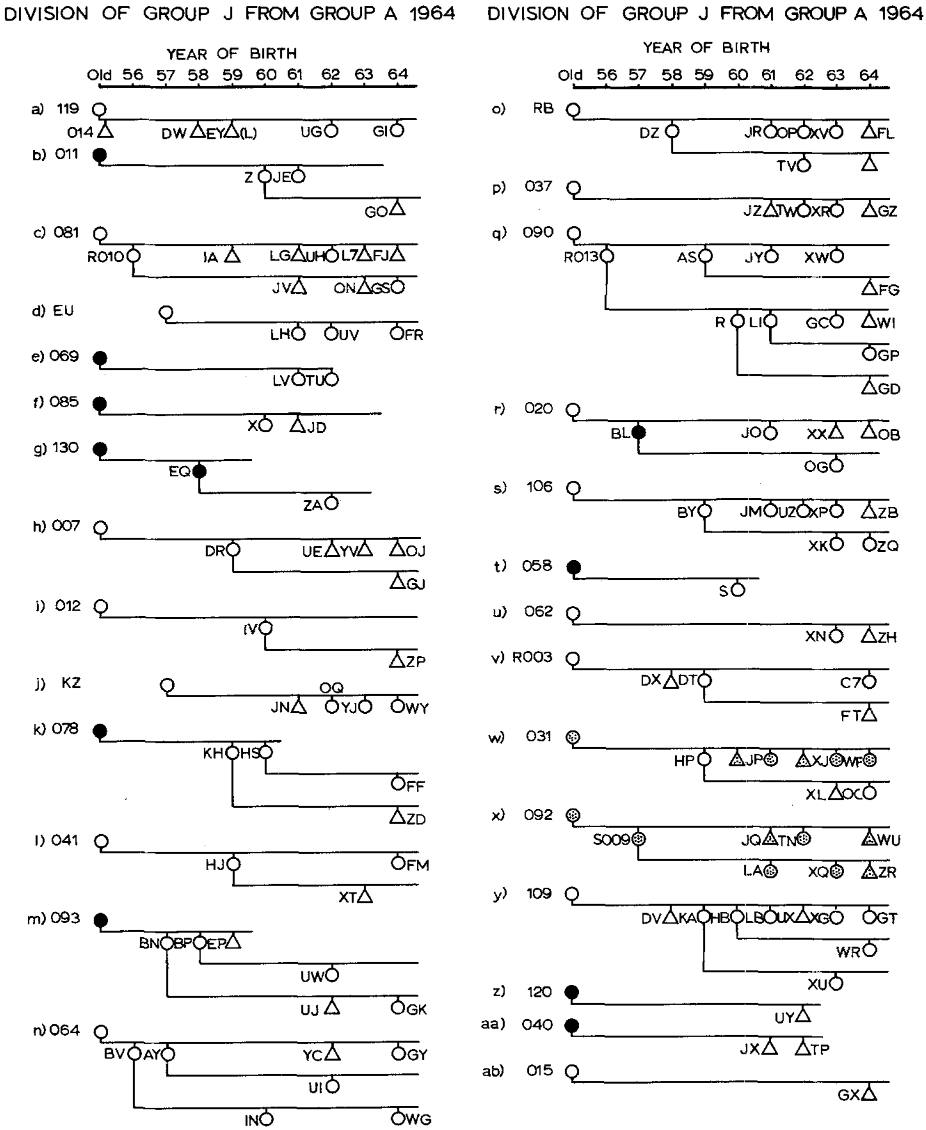
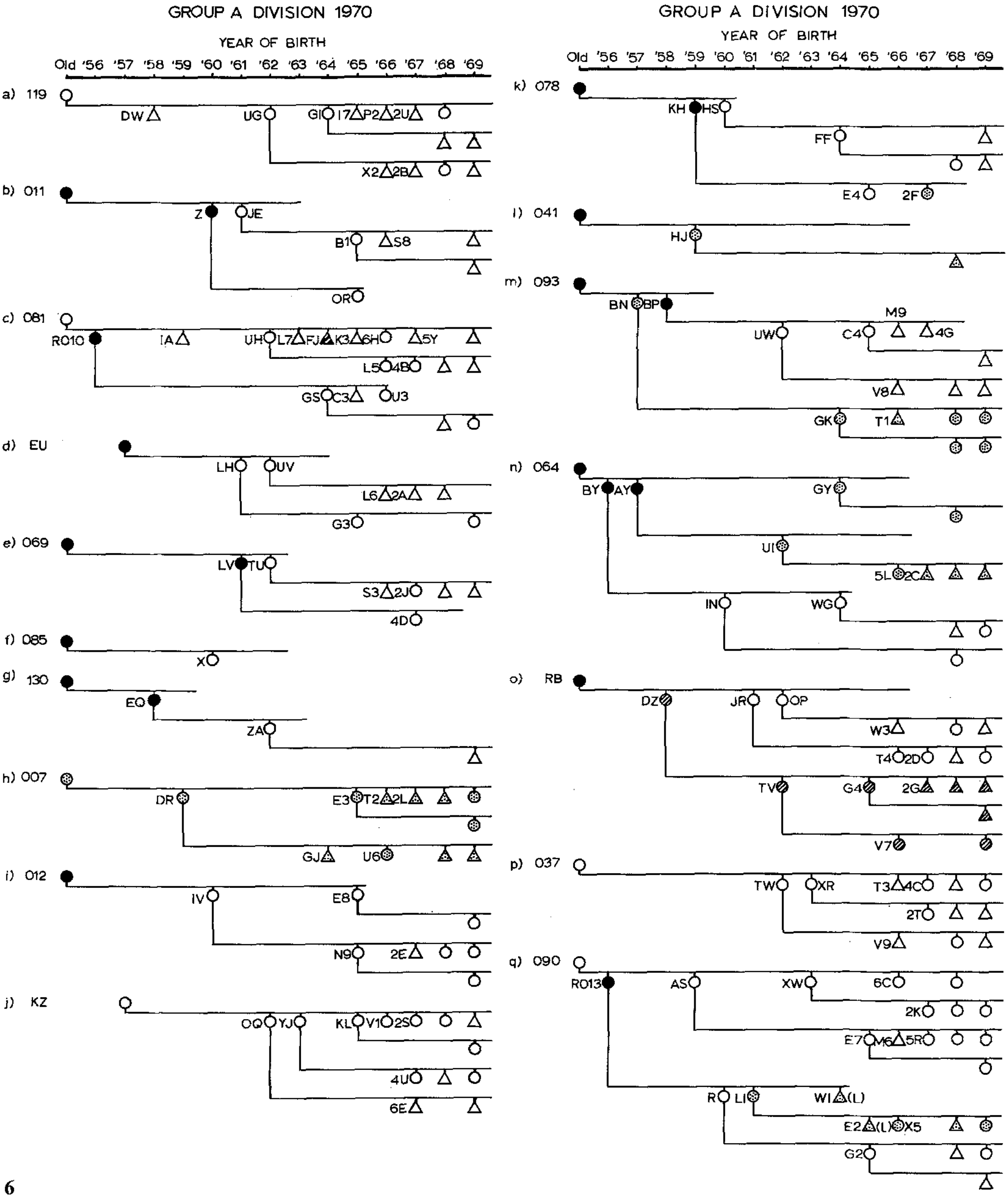


Fig. 5. Genealogical relations of the natal members of Group A in August 1964. *Stippled symbols* represent monkeys who joined Group J. *Open symbols* represent those that remained in Group A. Dominance relations are not known for the females in 1964. The genealogies are listed in order of decreasing dominance rank as determined by Missakian (1972) in 1968–1969. Other conventions are as in Fig. 2. – Group J consisted of 2 genealogies, 031 and 092, which left their mother group, Group A. This division occurred in 1964, at which time 7 years of genealogical information were available. Group A at this time had 143 natal members, belonging to 28 genealogies. Genealogy 031 had 9 members at this time and genealogy 092 had 8 members. They were joined by 3 non-natal males in forming the new group. One of the two genealogies, genealogy 031, showed intragenealogical splitting: the matriarch's oldest daughter, HP, and her two offspring, XL and OC, remained in Group A while the rest of 031's genealogy joined Group J


GROUP A DIVISION 1970
YEAR OF BIRTH
Old '56 '57 '58 '59 '60 '61 '62 '63 '64 '65 '66 '67 '68 '69
a) 119
DW UG GI 17 P2 2U X2 2B
b) 011
Z JE B1 S8 OR
c) 081
R010 IA UH L7 FJ K3 6H 5Y L5 4B GS C3 U3
d) EU
LH UV L6 2A G3
e) 069
LV TU S3 2J 4D
f) 085
X
g) 130
EQ ZA
h) 007
DR E3 T2 2L GJ U6
i) 012
IV E8 N9 2E
j) KZ
OQ YJ KL V1 2S 4U 6E
GROUP A DIVISION 1970
YEAR OF BIRTH
Old '56 '57 '58 '59 '60 '61 '62 '63 '64 '65 '66 '67 '68 '69
k) 078
KH HS FF E4 2F
l) 041
HJ
m) 093
BN BP M9 UW C4 4G V8 GK T1
n) 064
BY AY GY UI 5L 2C IN WG
o) RB
DZ JR OP W3 T4 2D TV G4 2G V7
p) 037
TW XR T3 4C 2T V9
q) 090
R013 AS XW 6C 2K E7 M6 5R R LI WI (L) E2 (L) X5 G2

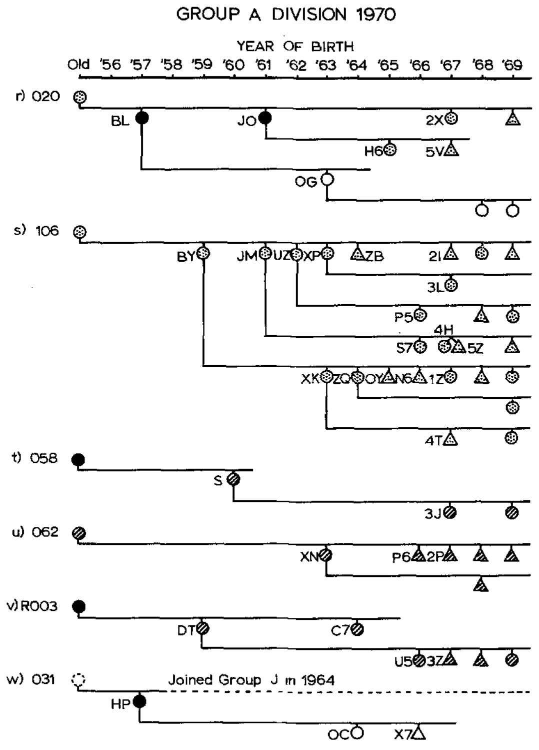
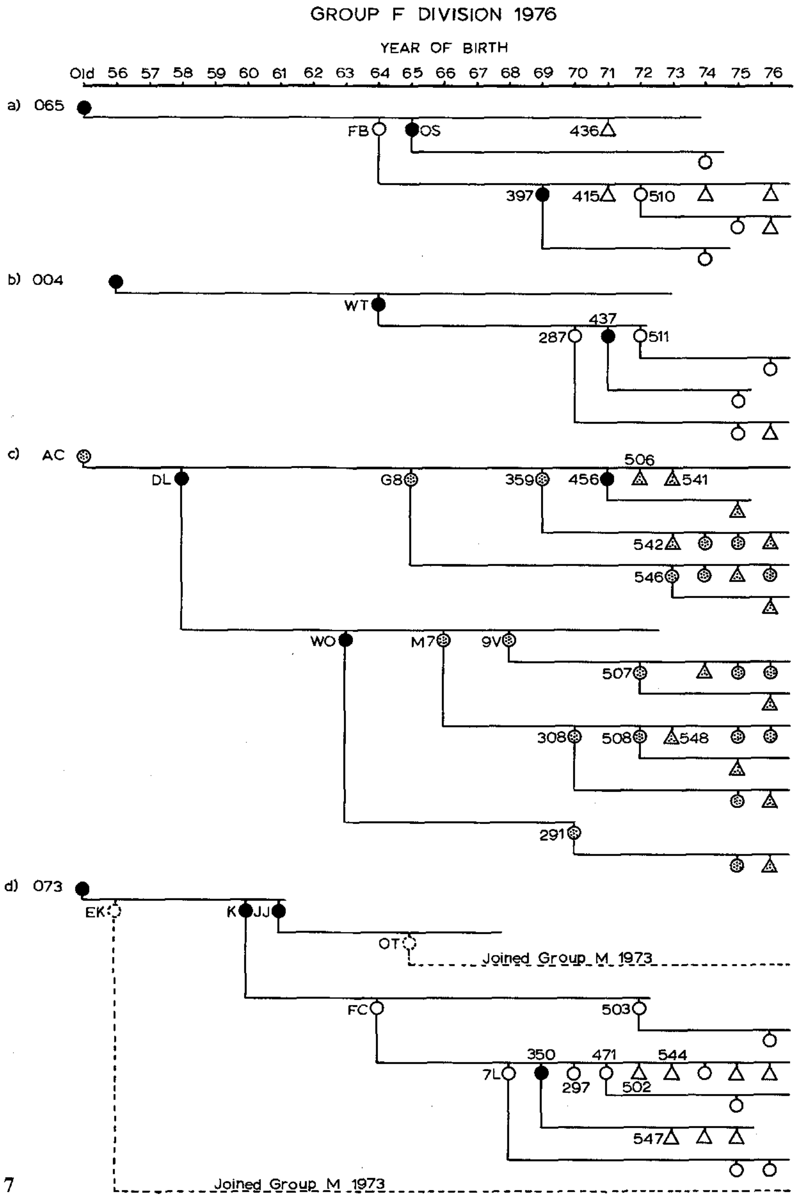


Fig. 6. Genealogical relations of the natal members of Group A in July 1969. *Stippled symbols* represent individuals who joined Group K. *Diagonally marked symbols* represent individuals who joined Group L. *Open symbols* represent individuals who remained in Group A. Other conventions are as in Fig. 2. Group A (Fig. 6) had 275 members in July 1969. Of these, 233 were natal to the group, and belonged to 23 genealogies, one of which (genealogy 085) contained only one living member, and so could not divide internally. Of the 22 remaining genealogies, 6 showed intragenealogical splitting: genealogies 078, 093, 064, RB, 090, and 020. The eldest daughter of the matriarch in the splitting of genealogies 093, 064, RB, and 020 joined a separate group from the rest of her genealogy. The other two genealogies, genealogies 078 and 090, showed double splitting: The eldest daughter of the matriarch (KH and R013, respectively) and their families joined a separate group from their mothers and siblings, but their own eldest daughters (E4 and R), accompanied by their families, remained behind in the same group as the matriarch (their grandmother). In both of these cases, the eldest daughter (KH and R013) was dead by the time group fission was completed, but both had adult daughters. After group fission was completed in January 1970, Group A contained 164 animals, 140 of which were natal, and belonged to 10 complete genealogies plus 6 partial genealogies. Group K contained 83 animals, 67 of which were natal, belonging to 3 complete genealogies, plus 5 partial genealogies, and Group L contained 30 members, 26 of which were natal, and belonged to 3 complete genealogies plus 1 partial genealogy. Other changes in the compositions of the three groups were the result of deaths and migration of males into and out of the 3 new groups (Missakian, 1973a)


GROUP F DIVISION 1976
YEAR OF BIRTH
Old 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76
a) 065
FB
OS
436
397
415
510
b) 004
WT
437
287
511
c) AC
506
DL
G8
359
456
541
542
546
WO
M7
9V
507
308
508
548
291
d) 073
EK
K
JJ
OT
Joined Group M 1973
FC
503
350
471
544
7L
297
502
547
Joined Group M 1973

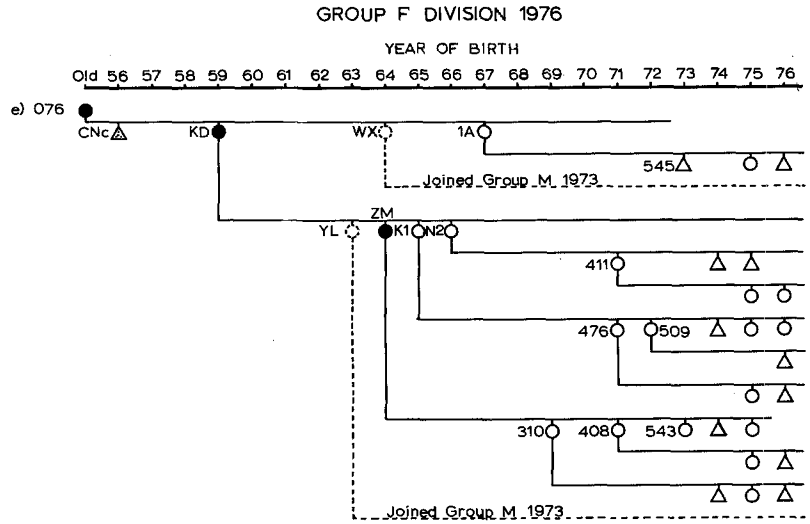


Fig. 7. Genealogical relations of the natal members of Group F in September 1976. *Stippled symbols* represent monkeys who joined Group O. *Open symbols* represent monkeys who remained in Group F. Other conventions are as in Fig. 2. At this time, Group F had 118 members, 96 of whom were natal, belonging to 5 genealogies. After the second fission Group F consisted of 76 members, 62 of whom were natal to Group F. All of the natal Group F members (*unstippled individuals*) belonged to 4 genealogies (genealogies 065, 004, 073, and 076). Group O consisted of one large intact genealogy, genealogy AC, which had 33 members in the group at this time (*stippled individuals*), plus 9 non-natal males; a total of 42 members. The old male castrate, CN, joined Group O rather than Group F where his relatives remained (genealogy 076). Other natal males either remained with their genealogies or left Groups F and O completely, joining other social groups on the island or becoming solitary

In late 1973 and early 1974 the members of the two genealogies separated, 092's genealogy remaining with most of the non-natal males while 031's genealogy acquired new males and became Group N. Later in 1974, however, the two groups rejoined and became reintegrated into a single group again.

Group F into Group F and Group O. In 1976 Group F divided again. The division is illustrated in Fig. 7 and described in the caption.

Summary of Results

Seventy genealogies were involved in six group splits. Groups A and F each divided twice, with the second division involving most of the genealogies involved in the first division. These genealogies are counted twice. Of these 70 genealogies, nine showed intragenealogical splitting.

There are two kinds of intragenealogical splitting that have been observed. Of nine genealogies that split, seven split between eldest daughters with their families and the rest of the genealogy. The other two genealogies dissolved into independent family groups, each with a daughter of the original matriarch as its focus.

Discussion

The important tendencies in intragenealogical splitting appear to be:

1) The larger the genealogy, the more likely it is to divide internally.

2) The higher the rank of the genealogy, the less likely it is to divide.

3) The most likely part of the genealogy to separate from the rest is the eldest daughter with her offspring.

4) The loss of connector females increases the likelihood that the genealogy will divide.

5) Following the loss of a connector female who has several adult daughters, each daughter with her offspring may act as an independent unit, irrespective of the daughter's age and rank.

Several patterns of dispersal are known among primates. Among solitary species such as pottos and lorises (Lorisidae) (Jolly, 1972), males and females associate only for mating, and offspring leave their mother shortly after weaning. Siblings of different ages never associate with their mother at the same time, because older offspring disperse before their younger siblings are born. This pattern is similar among all solitary mammals (Wilson, 1975), and may be considered the primitive mammalian pattern of dispersal.

Another pattern found among primates occurs in territorial family groups: siamangs and gibbons (Hylobatidae) live in small groups of 2–6 animals, consisting of a mated pair and their offspring. Male and female young disperse from their natal groups as they approach puberty, but not necessarily before their younger siblings are born. Females give birth at approximately 3-year intervals, and young animals reach puberty when they are 6–7 years old. Thus, a pair of adults may have with them at one time an infant, a 3-year-old, and an adolescent offspring. Since all offspring disperse as adolescents, it is always the oldest offspring of the family group that disperse from the rest of the family (Fox, 1972, 1974; Chivers, 1972). In caged families in which it is impossible for adolescents to disperse, the adolescent is peripheralized by other family members, who direct less and less friendly behavior and more and more threats toward the adolescent. Eventually adolescents received so much physical abuse from family members that they had to be removed from the cage (Fox, 1974).

Primates that live in large social groups containing many adults of both sexes, such as the macaques and baboons (Cercopithecidae), show more complex patterns of dispersal than do the solitary and small-group-living primates, or the primates that live in territorial family groups. Macaque and baboon males, like gibbon and siamang males, usually leave their natal groups around the time they reach puberty (Koford, 1966; Drikamer and Vessey, 1973). The dispersing young males become solitary, join all-male groups for a period of time, or attach themselves to heterosexual social groups other than their natal groups. Female macaques and babbons, on the other hand, usually do not disperse as individuals from their natal groups, but rather leave in groups composed of both males and females, when the entire social group undergoes fission.

The most intriguing finding of this study is the regularity of eldest daughters and their families separating from the rest of the genealogy, when a genealogy divides during a group fission. We suggest that this tendency represents the extreme case of peripheralization of low-ranking females among rhesus monkeys. Peripheralization and migration of male rhesus monkeys is well documented (Lindberg, 1971; Sade, 1972a; Drickamer and Vessy, 1973), but females are considered the stable core of the social group and usually do not migrate.

However, the dominance status of the matriarch's eldest daughter and her family is the least favorable within the genealogy, since any set of sisters, once they are mature, will rank in the inverse order of their ages, the youngest being dominant to all, and the eldest being subordinate to all (see definition of dominance, under Definitions). As a female matures she loses rank within her genealogy and also finds her mother's attention focusing less on her and more on her younger siblings (Sade, 1965). At the same time, she is developing friendly ties with females in other genealogies.

A sociometric analysis of interactional patterns (Sade, 1972b) might reveal that:

1) An infant monkey receives the greatest proportion of attention that its mother gives to any individual monkey. As the infant matures, however, this attention wanes. As younger siblings are born, older siblings receive less and less of their mother's attention.

2) Most aggressive interactions between members of the same family involve attacks by dominant animals on subordinate animals. The majority of these interactions are probably cases of redirected aggression, in which an animal that feels threatened or frightened takes out her aggression on a subordinate family member.

3) Positive social behaviors between adults in the family are directed toward dominant individuals. That is, when an animal chooses another animal to groom, sit next to, or lie in contact with, she is more likely to choose a dominant than to choose a subordinate. Young monkeys, 2 years old or younger, are exceptions to this rule, being frequently chosen over other animals as recipients of positive social behavior, regardless of rank.

If these hypotheses are correct, social behavior within the family should follow the pattern illustrated in Figures 8 and 9. The directionality of aggression and affiliation within the family described here and illustrated in these figures, would result in the eldest daughter of the matriarch of the family receiving the greatest amount of aggression from family members, and the least amount of friendly interactions from family members. She tends to be a social outcast from her family, just as the siamang adolescent is from hers. The greater degree of tolerance among rhesus monkeys, however, allows her to remain a member of the social group in spite of being a peripheralized member of her own family.

There are two ways that the peripheralized female can increase the amount of positive attention that she receives from other members of the social group. One is to have more offspring of her own. The other is to develop positive or friendly relationships with unrelated members of the social group.

The tendency for large genealogies to divide is consistent with the hypothesis that eldest daughters are the most peripheralized females: the more younger siblings a female has, the larger the genealogy becomes, and the worse her position within the intragenealogical dominance hierarchy. The more offspring of her own that she has, the larger the genealogy becomes, and they become

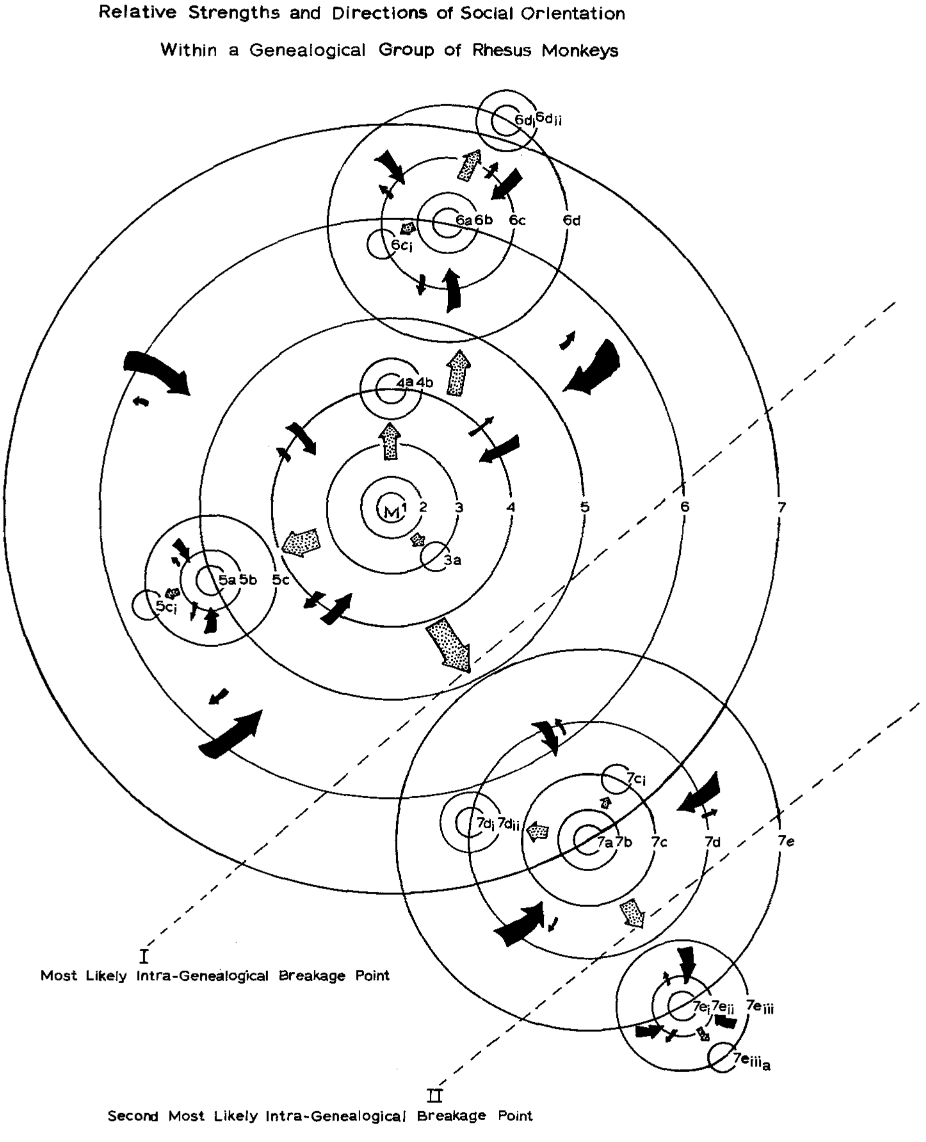


Fig. 8. Relative strengths of social bonds within a genealogical group. M in the center of the figure is the mother of the 7 females represented as concentric circles. The *smallest circle* around M represents M's youngest daughter, 1, who will rank highest in the dominance hierarchy among the 7 sisters, by the time all are adults. 7, M's oldest daughter, will rank 7th among the sisters, while M will continue to rank above all of her daughters. The daughters of each of M's daughters are represented by *concentric circles* centered on the circle that represents their mother. Again, age increases out from the center of the circle. Rank of these females will be just below their mother's rank, represented by the subscripts *a–e*. Younger sisters will outrank their older sisters by the time they reach adulthood. The *dashed lines*, I and II, represent predicted fracture points within the genealogical group. *Black arrows* show direction of affiliative behavior. *Stippled arrows* show direction of aggressive behavior

Disintegration of a Genealogy with the Death of a Matriarch

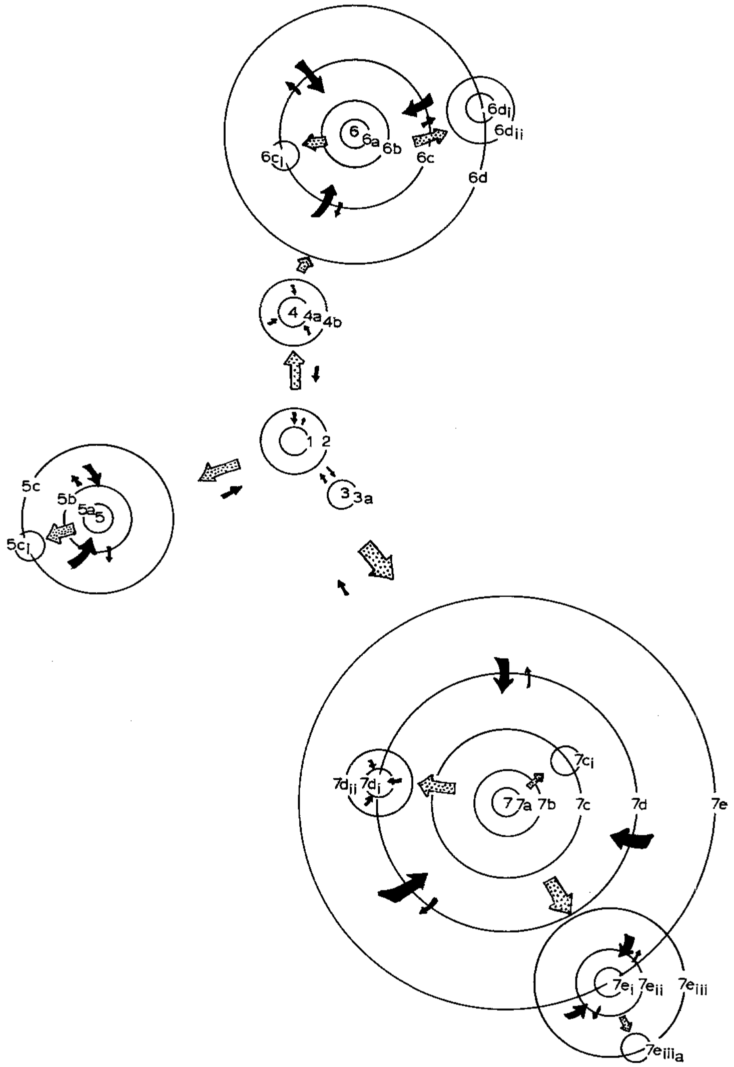


Fig. 9. Disintegration of genealogy following death of matriarch. This genealogy, formerly a single social unit (see Fig. 8), now consists of 3 well-knit social units, the families of females 5, 6, and 7, plus one more diffuse social unit consisting of the younger 4 offspring of the dead female. *Arrows* as in Fig. 8

the focus of her attention, weakening her interactions with the rest of her relatives. At the same time, her own oldest daughter may split from her and her younger offspring.

The tendency for genealogies to divide following the loss of a connector female is also consistent with the hypothesis of the peripheralized eldest daughter: the primary tie of every female to her matrilineal group is through her mother. A split within a genealogy should therefore be more likely if the mother of a group of sisters is dead than if she is still living.

The tendency for the lower-ranking genealogies to divide is also consistent with the hypothesis of the peripheralized eldest daughter: the higher the rank of her genealogy, the more unrelated females there are that rank below an eldest daughter. The opportunity to redirect aggression onto them may relieve her unfavorable status within her own genealogy. Eldest daughters within low-ranking genealogies are at the end of the chain of aggression both within their own genealogy and within the group as a whole.

The tendency of low-ranking females with their young to disperse from the parent group also is consistent with Christian's (1970) hypothesis that socially subordinate animals are the migrants, and therefore the pioneers, in many mammalian species.

A dispersing mother and her offspring may be considered founders of a new breeding group. Genetically the consequences are likely to be equivalent to the 'lineal effect' (Neel and Salzano, 1967) in that a closely related group of individuals will not be likely to have genotypes selected randomly from the population.

The genetical consequences of these group fissions are being studied intensively (Duggleby, 1976, 1978; Cheverud and Buikstra, 1978; Cheverud et al., 1978; Olivier et al., 1978; Chepko-Sade and Olivier, 1979).

Acknowledgements. This paper is based in part on Chepko-Sade (1974) and on a Master's Dissertation by B. Diane Chepko-Sade through the Departamento de Biologia del Universidad de Puerto Rico, Rio Piedras. This work was supported by Grant BNS77-14882 and other grants from the NSF, and grant 1RO1MH23809 from the NIMH, NIH, PHS. The Cayo Santiago colony is part of the Caribbean Primate Research Center supported by a contract from the DRR, NIH, PHS to the University of Puerto Rico. The data were collated and retrieved by programs written by Jonathan Schneider and Mark Singer at Northwestern University. Jean DeRousseau and Ann Wasserman provided essential technical assistance. Douglas Rhodes and Richard Rawlins provided information on the division of Group F into Group F and Group O. Clinton H. Conaway and William Kerber, former directors of the CPRC, provided essential support. The work profited from comments by Earl Count, Peter Cushing, Saroj Datta, Janet Dunaif, Jay Kaplan, Katherine Cushing Kaplan, and Elizabeth Missakian. Angel Figueroa provided continuity in the census program for many years at Cayo Santiago, and this and many other studies have been made possible through his diligence.

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