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# Group fission among wild toque macaques as a consequence of female resource competition and environmental stress

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**Abstract.** At Polonnaruwa, Sri Lanka, four out of 29 groups of toque macaques, *Macaca sinica*, divided in a period of 16 years. Temporary peripheral subgroups of varying sizes and compositions preceded fission by 9–40 months. Fission crystallized within a month through an increase and stabilization of subgroup membership and permanent division. All members in the newly seceded groups had been frequent participants in pre-fission subgroups, and belonged to subordinate matrilineages. Subgroups, and hence group divisions, were initiated by cores of mutually loyal females and occurred mostly along kinship lines. In the year of fissions, the rate of change in female dominance relations was significantly greater among groups that divided than among those that did not. It is hypothesized that low-ranking females secede to form new groups when the costs, especially of intragroup competition for food resources, outweigh the benefits of group membership. Such seceding females were easily available and familiar mates for group males that had recently lost rank. Final division, therefore, resulted from a coalition of subordinate females and males acting according to their respective interests. It was triggered in this population by rapid growth of some groups to large size and by environmental stress (the reduction and fragmentation of food resources caused by drought and a cyclone), which accentuated the costs of resource competition. Male aggression, such as infanticide, which negatively affects female fitness, might also have contributed to one group fission.

Group fission refers to the creation of permanent new social groups through the division of a larger group. The phenomenon is of particular interest among species that normally form cohesive and fairly closed social groups, and so called female-bonded groups (Wrangham 1980), as are typical of most primates and many other mammals (Eisenberg 1966). In such groups, females remain in the group of their birth throughout life and form close social ties with their matrilineal relatives. Males, on the other hand, leave their natal groups at puberty and breed elsewhere. Group fission, as used here then, is distinct from the fission–fusion societies of hamadryas baboons, *Papio hamadryas* (Kummer 1968) and chimpanzees, *Pan troglodytes* (Goodall 1968).

Group fission is rare and of theoretical relevance on at least two counts. First, as female emigration is infrequent (for notable exceptions see Moore 1984), group fission is one way that females may act as carriers in the geographical spread of genes. Small dispersing groups of females may potentially act as founder populations, or, at least, they may accelerate genetic differentiation within a population (Melnick & Kidd 1983).

It also bears directly on the question of the evolution of primate sociality itself. Among typically female-bonded groups, group life and female cohesiveness have been attributed to the advantages that group members gain through cooperating with each other in competing with other groups for resources (Wrangham 1980). Accordingly, intergroup resource competition might favour the formation of large (potentially dominant) groups. Effective anti-predator strategy, too, may favour the formation of large groups. In the opinions of Terborgh (1983) and van Schaik (1983), predator pressure, rather than intergroup competition, is the main selective force for group living, although recent evidence points to the importance of competition (e.g. Dittus 1986). The proponents of both models speculate, however, that as groups increase in size, competition within groups intensifies. Given limited resources, this would be detrimental to individual fitness and group growth as has been shown, for example, in toque macaques, *Macaca sinica* (Dittus 1977a, 1986) as well as some other primates (Dittus 1980).

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My aims in this paper are: (1) to describe the social, ecological and demographic characteristics of four group fissions that occurred in a wild population of toque macaques that inhabit natural forest at Polonnaruwa, Sri Lanka; and (2) to use this empirical evidence to test several hypotheses concerning the causes of group fission.

Most fissions reported to date have occurred in rapidly growing populations of Japanese macaques, *Macaca fuscata*, and rhesus macaques, *M. mulatta*, that have been provisioned with food in managed colonies (Sugiyama 1960; Koford 1963, 1966; Furuya 1968; Nishimura 1973; Chepko-Sade & Sade 1979), or that were fed incidentally at temple or tourist sites (e.g. Southwick et al. 1965; Malik et al. 1984, 1985). Few fissions have been reported among primates living relatively free of such human influence. These include baboons, *Papio ursinus* (Stoltz 1972), *P. anubis* (Nash 1976), colobus monkeys, *Colobus guereza* (Dunbar & Dunbar 1974), rhesus macaques (Melnick & Kidd 1983), blue monkeys, *Cercopithecus mitis* (Cords & Rowell 1986) and redtail monkeys, *C. ascanius* (Struhsaker & Leland, in press).

An examination of group fission in toque macaques offers an important contrast to the above studies for two reasons. First, unlike the provisioned and rapidly growing colonies of macaques, this natural population of toque macaques has shown slow rates of both positive and negative growth, over an 18-year period. And, compared with these toque macaques, most other natural populations have been investigated for substantially shorter terms so that information concerning group fissions is more limited.

## HYPOTHESES: CAUSES OF GROUP FISSION

The following hypotheses concerning the causes of group fission have been put forward.

(1) Surplus males. Group fissions were first noted among Japanese macaques. Referring to these, Sugiyama (1960) suggested that group fission requires that (1) some animals weaken their attachment to the centre of the group, (2) some animals, usually males, act as a social nucleus for the branch group and (3) females join that nucleus. The weakening of social bonds, and hence group fission, has been attributed to instability in the male dominance hierarchy that results from an increase in the number of young males maturing to adulthood or immigrating into a group and challenging the established male leadership (Sugiyama 1960; Furuya 1969; Koyama 1970; Nishimura 1973; Yamagiwa 1985). Nash (1976) came to similar conclusions in her studies of baboons in Tanzania. This view is supported by the fact that new branch groups often: (1) contain either maturing young males which were unsuccessful in their bids to achieve higher rank, or older males which lost to such challengers; and (2) exhibit a higher proportion of such males than the main groups or the parent groups from which they fissioned.

Hence, Furuya (1969) suggested that the existence of a high proportion of subadult and adult males is a cause for fission, and that fission functions to re-establish social stability among the males through a lowering of their numbers in the main group. Carpenter (1942) expressed a similar opinion.

(2) Ecological stress. Furuya (1969) proposed that group fission is a regulatory mechanism by which a growing group will extend its home range through the dispersal of a branch group at times when the size of a group becomes incommensurate with the food supply.

(3) Dilution of kinship. Chagnon (1975), investigating group fissions among growing groups of Yanomamö Indians in Venezuela, believed that ecological factors were of little importance in causing groups to fission. Instead, he suggested that groups fission when the average degree of genetic relatedness among members drops below some critical level, so that solidarity among distantly related kin is lost. An examination of group fissions among the growing rhesus monkey population of Cayo Santiago seemed to confirm this finding (Chepko-Sade & Olivier 1979).

(4) Loss of coordination. Malik et al. (1985) found no unusual aggression accompanying or preceding four fissions of a large group of free-ranging rhesus macaques in India. Genealogical relationships among these macaques were unknown, and they attributed the group fissions to a loss of cohesion and coordination of activities among group members when group sizes increased to more than about 120 macaques.

(5) Female fitness costs. Group life may benefit females in forming defensive coalitions either against other groups which compete for resources, or against predators (Wrangham 1980; van Schaik 1983; Terborgh 1983). However, sociality also has

its costs, especially for low-ranking individuals (e.g. Dittus 1977a, 1979, 1982, 1986).

The working hypothesis proposed here is that group fission occurs when the loss of female fitness, through intragroup competition, outweighs the benefits of membership in a group. Furthermore, it is predicted that most of the costs and benefits of group life will be mediated by way of food competition (ibidem), although direct reproductive competition may also play a role. Fitness loss resulting from the harassment of oestrous, pregnant and/or lactating females by other females, for example, has been suggested in gelada baboons, *Theropithecus gelada* (Dunbar & Dunbar 1977), rhesus macaques (Sackett et al. 1975) and toque macaques (Dittus 1986) as well as marmosets, Callitrichidae, and other mammals which practise obligate monogamy (Kleiman 1977). Aggressive and infanticidal males, too, would contribute to such costs (Hrdy 1979). The female fitness cost hypothesis differs from the others in that it focuses on ultimate causes that can subsume a variety of proximal ones.

## METHODS

### Study Area, Period and Subjects

The data are from a long-term study of a population of toque macaques living in the Nature Sanctuary and Archaeological Reserve at Polonnaruwa, Sri Lanka. Observations were continuous between September 1968 and May 1972 and again from March 1975 to December 1984. Intermittent observations were made between May 1972 and March 1975.

The natural dry evergreen forest, which the macaques inhabit, as well as several aspects of macaque behaviour and sociodemographic relationships have been described earlier (Dittus 1977a, b, 1985). All macaques in the study groups were individually identified. The macaques were well habituated and could be approached to within 1-3 m.

### Individuals, Age Classes and Kin

Toque macaques are highly variable in their individual morphologies. Variations occur in pelage colour, the distribution of red, brown and black pigments in the facial skins, and, especially, in the distinctive structure of the head hair or 'hairdos'. Standard drawings and descriptions (identification cards) were regularly updated for all individuals in the population.

Following Dittus & Thorington (1981), individuals were classified into broad age-sex classes. A female was adult if she had had an infant, or juvenile if she had not. Most females give birth to their first infant in their sixth year of life. A male was adult if he had the physical size and morphological characteristics typical of adults; subadult if he was as large as or larger than an adult female but physically not as fully developed as a typical adult male; and juvenile if he was smaller than a subadult. Among males, the transitions from juvenile to subadult to adult usually occur during the sixth and ninth years of life, respectively. Infants of either sex were typically nursing, carried by the mother and less than a year old.

Chronological ages of individuals born after the onset of the study were known; those of individuals born earlier were estimated retrospectively according to known correlations between age and morphological development based on 15 years of developmental data.

Matrilineal kinships were known through tracing individual identities from birth. From such records of known kinships it has become evident that members of a matriline often shared unique morphological and behavioural traits. I have therefore used this knowledge to assume kinship among older adult females whose kinships were not traced from birth. In making these assumptions, I have probably erred on the conservative side by not assuming kinship among females that might also be close relatives but that were not 'strikingly' similar morphologically. In presenting the results I have distinguished between known and assumed matrilineal kinships.

### Demography

All groups in the population were censused once every month. During the birth season females were checked every 1-5 days in order to determine neonatal birthdates with accuracy. The demographic fates of all individuals were recorded according to their identity.

The mean observed exponential rate of population growth ($\bar{r}$) indicates the rate at which a population increases over time. It was calculated as a regression coefficient from two or more estimates of population size (Caughley 1977). Mean monthly rates of population growth for different years were based on 12 monthly measures of population size per year. Mean annual rates of growth were based on estimates of the mean annual population sizes for different years (Table II).

The mean generation length is defined as the mean interval between the birth of a mother and the birth of a daughter that survives to reproduce herself. This duration is considerably longer (11·8 years in toque macaques at Polonnaruwa) than simply the mean time required for a daughter to reach adulthood (about 6 years; Dittus 1979). It was calculated based on life-table fecundity and survivorship schedules (Caughley 1977), which, for the macaque population at Polonnaruwa, were estimated approximately on the assumption of a more or less stable age distribution (Dittus 1979).

### Mean Degree of Matrilineal Relatedness

The coefficient of relatedness measures the probability that two individuals will share an allele in common that is identical by descent from a common ancestor (Li 1976). The formula for calculating $r$ is

$$r = [(1/2)^{n_1+n_2}]$$

where $n_1$ equals the number of links between one parent of an individual and any ancestor both parents have in common, and $n_2$ equals the number of links between the other parent and the same ancestor. Since only matrilineal relationships were known, the exponent $(n_1+n_2)$ in the above formula simplifies to $n_1$, the number of matrilineal links. To find the degree of relatedness ($r$) between each pair of individuals in a genealogy I counted the number of links between each pair. The $r$ values were then summed and divided by the number of possible pairs in the genealogy, $N(N-1)/2$ (where $N$ = the number of members in the genealogy), to obtain the average degree of relatedness ($\bar{r}$) for the entire genealogy or matriline.

Since $r$ was calculated through the maternal line only, it underestimated the actual genetic relatedness between individuals, since at least some members of a group share fathers. Chepko-Sade & Olivier (1979) give a more detailed account of the calculation of $r$ and $\bar{r}$.

### Social Dominance Ranks

An individual was considered dominant over another if it consistently supplanted it in contests over food, water, resting places, mates, grooming partners or similar resources (Richards 1974). The direction of agonistic signals (threats and appeasement gestures) in all social contexts were in agreement with these measures of dominance (e.g. Sade 1967). Dominance relations among the individuals within all groups were measured at least once per annum in all years of continuous study.

Juvenile females, aged 3 or more years, were often dominant to parous females (6 or more years old). All females that ranked above the lowest-ranking parous female in the group were included in calculations of rates of rank reversal. (However, rank reversals involving juveniles are not illustrated in Fig. 1.)

### Definitions

Daughter groups are the two newly formed independent social groups that are created by the division of the pre-existing parental group. The main group is the daughter group retaining the dominant matrilines of the parental group, and is usually the larger of the two fission products. The branch group is the daughter group consisting of mainly low-ranking matrilines of the parental group, and is usually the smaller of the two daughter groups. Pre-fission subgroups are spatially cohesive parties of individuals that contain less than the full complement of members that normally constitute the group, and that are spatially separated from or peripheral to the remainder of the group. In this study, there was a large asymmetry between the two or more subgroups making up the entire group. Hence, subgroup refers to the smaller fraction and main group to the larger fraction of the entire group.

### Statistical Analyses

The observed exponential rates of growth were expressed as regression coefficients (Caughley 1977). In testing whether such growth rates differed from zero the standard errors were taken into account. The *G*-test is similar to the chi-squared test and William's correction was applied routinely. All statistical tests followed Sokal & Rohlf (1981) and Siegel (1956). All probability values were at the two-tailed level of significance.

## RESULTS

### Probability of Group Fission

At Polonnaruwa, 29 different groups had been observed from 1969 to 1984 for periods varying from 5 to 16 years. Defining 1 group–year as 1 year of observation of one group, there was a total of 295 group–years of observation. Only four group fissions were observed, so that the probability of any one group dividing in any one year was low, $P = 0{\cdot}014$. Hence, one might expect any one group to fission once every 74 years, or once in about six generations, the mean generation length (see Methods) being 11·84 years (Dittus 1979). If three potential (i.e. incomplete) group fissions in 1986 and 1987 are included in the estimate, then group fission occurred with $P = 0{\cdot}019$, or once in 52 years or 4·4 generations.

### Group Fission, Demography and Environment

The entire population, based on 18 groups in 1971, was censused in 1971, and on a monthly basis between 1975 and 1984. In the 14-year period (1971–1984) population size fluctuated between monthly totals of 348 and 502 individuals and the overall mean observed rate of population growth was 2·259% per annum, or $\bar{r} = 0{\cdot}0223$. This rate differed significantly from zero growth ($t$-test $= 5{\cdot}969$, $df = 9$, $P < 0{\cdot}001$).

Over the 14 years, population growth was not constant. For example, between 1971 and 1975, population size decreased by about 15% owing mainly to a severe drought in 1974 (Dittus 1977a). In the 10 years between 1975 and 1984 population growth was variable (unpublished data). Two major environmental events and their negative effects on population growth are noteworthy here. The first concerns a drought in 1976, which was less severe than the one in 1974, but which nevertheless appeared to have underlain the significant negative population growth in 1976 ($r = -0{\cdot}0078$, $t$-test $= 4{\cdot}673$, $df = 12$, $P < 0{\cdot}001$). Second, a cyclone in November 1978 destroyed more than 50% of the woody forest vegetation at Polonnaruwa (Dittus 1985) and reduced the subsequent macaque survivorship (Dittus 1982). The significant negative population growth in 1979 ($r = -0{\cdot}0054$, $t$-test $= 3{\cdot}945$, $df = 12$, $P < 0{\cdot}01$) and zero growth in 1980 ($r = -0{\cdot}0015$, $t$-test $= 0{\cdot}673$, $df = 12$, NS) reflected this situation. The only years of the study after 1975 showing a significant population decline were 1976 and 1979.

There were additional environmental changes specific only to group H. The home range of this group was peripheral to the study site and incorporated an extensive area of scrub forest and abandoned cultivation that was continuous with the mature forest of the study area or sanctuary. In late 1975 and 1976 sections of this scrub forest were partially cleared, thereby reducing and fragmenting the forested feeding sites within group H's home range.

For the 10-year period, 1975–1984, the demographic and environmental data suggested that 1976 and the 2 years following the cyclone, 1979–1980, were ecologically more stressful to the macaques than other times were. The four group fissions occurred during these periods of stress. Three of the groups divided within 19 months of the cyclone: group IH in November 1979; group 22 in December 1979; and group D in June 1980. The fourth, group H, split between August 1975 and January 1977. Fission years were significantly more likely to coincide with a period of environmental stress and significant population decline than with normal years (Fisher exact test, $P = 0{\cdot}016$, two-tailed test).

### Group Growth and Fission

In the year prior to the fissioning of groups, the fission groups were, on average, significantly larger than the 16 groups that did not split. Three of these (22, D and IH) were about twice the mean size of non-fission groups, and they had grown to their maxima in the year of their division (Table I). These three groups ranked among the six largest groups in the population in the year of fission. The fourth fission group (H) was exceptional because it was close to the mean group size of non-fission groups.

The annual means of monthly group sizes were used to calculate the growth rates of groups, or of sets of groups. Together, groups 22, D and IH grew significantly in the 5-year period preceding their division, whereas the set of all non-fission groups had had virtually no growth in the same period (Table II). Most of the growth among the fission groups was attributable to a significant increase in the size of groups D and IH. The demographic history of group H differed from that of the other three fission groups in showing no positive growth in the 5 years (1971–1975) preceding its division (Table II).

Among the groups that did not fission, seven

**Table I.** Annual sizes of fission groups and of sets of groups that did and did not divide, in the year prior to fission and in the 5-year period preceding the splitting of groups

| | Group size | | | |
|---|---|---|---|---|
| | Year of fission (mean) | 5-year period preceding fission | | |
| | | Mean† | Median | Range |
| Fission groups | | | | |
| Group 22 | 47 | 43 | 42 | 41–47 |
| Group D | 41 | 35 | 36 | 28–41 |
| Group IH | 34 | 27 | 26 | 20–34 |
| Group H | 17 | 18 | 18 | 17–19 |
| Subtotal ($N=4$) | 35 | 34 | 34 | 17–47 |
| Non-fission groups | * | | | |
| Subtotal ($N=16$) | 19 | 20 | 15 | 5–47 |
| All groups | | | | |
| Total ($N=20$) | 22 | 22 | 20 | 5–47 |

* $t$-test = 2·226, $df=18$, $P<0{\cdot}04$.
† The mean of the mean annual group sizes.

**Table II.** Mean annual rates of population growth among groups that fissioned and those that did not during the 5- or 6-year periods preceding group fission

| | Fission groups | | | | | Non-fission groups |
|---|---|---|---|---|---|---|
| | 22 | D | IH | H | (22+D+IH) | ($N=14$) |
| Observations period | 1975–1979 | 1975–1980 | 1975–1979 | 1971–1975 | 1975–1979 | 1975–1979 |
| Population growth rate | | | | | | |
| Exponential, *r* | 0·023 | 0·084 | 0·125 | −0·028 | 0·073 | 0·005 |
| Percentage | 2·292 | 8·753 | 13·335 | −2·742 | 7·577 | 0·521 |
| *t*-test | 2·214 | 10·996 | 5·556 | | 8·742 | 0·563 |
| *df* | 3 | 4 | 3 | 0 | 3 | 3 |
| *P* | NS | <0·001 | <0·02 | | <0·01 | NS |

were larger than the median group size ($N=20$) for the population, and three showed significantly positive growth between 1975 and 1979. One of these continued to grow to over 70 members and began dividing in 1986 (unpublished data).

## Process of Group Fission

Group fission occurred in the following two phases.

### *Phase I: subgroup formation*

The first obvious sign of fission was the temporary splitting away from the main part of the group of subgroups (see Definitions) containing non-oestrous females. These subgroups ranged somewhat independently of their main groups, for periods varying from several hours to many days. This phase, during which subgroups were observed, preceded group fission by 9, 17 and 48 months for groups IH, D and 22, respectively. The subgroups eventually developed into new branch groups, but differed from them in four important ways.

(1) In each group, subgroups contained significantly fewer adult females than branch groups did (Table III).

(2) Subgroups were unstable in size and member-

**Table III.** The numbers of adult females observed in subgroups prior to group fission compared with their numbers in the newly formed branch groups

| Fission group | Number of subgroups | Number of adult females in subgroups: Range | Mean | Number of adult females per branch group |
|---|---|---|---|---|
| 22 | 35 | 1–7 | 2·9 | 8 |
| IH | 31 | 1–5 | 2·2 | 5 |
| D | 8 | 1–3 | 2·1 | 3 |
| $U$-test (two-tailed) | | | | $U=28$, $z=2{\cdot}185$, $P<0{\cdot}03$ |

**Table IV.** The observed frequencies with which adult females of branch groups and main groups participated in pre-fission subgroups, compared with those expected if all females had been equally likely to participate in subgroups

| Group | | Frequency of membership in pre-fission subgroups: Branch group adult females | Main group adult females | Total number of female sightings | $G$-test (two-tailed) $df=1$ | $P$ |
|---|---|---|---|---|---|---|
| 22 | Observed | 93 | 9 | 102 | | |
| | Expected | 68 | 34 | 102 | 34·143 | <0·001 |
| IH | Observed | 56 | 12 | 68 | | |
| | Expected | 28 | 40 | 68 | 48·381 | <0·001 |
| D | Observed | 17 | 0 | 17 | | |
| | Expected | 5 | 12 | 17 | 40·420 | <0·001 |

Expected frequencies were computed according to the numbers of adult females in the respective main and branch groups.

ship because individuals frequently shifted their affiliations between the peripheral subgroups and the main groups. Typical subgroup members (see below) were often part of the main group for periods lasting several hours to many months. At such times, however, they often formed spatially distinct parties while coordinating their activities with other members of a main group.

(3) Subgroups ranged within the home range of the main groups, whereas the home ranges of the two daughter groups differed (unpublished data).

(4) Typical intergroup hostility was prevalent between the daughter groups, but not between subgroups (e.g. Cheney 1987).

### *Phase II: branch group formation*

The final composition of the new daughter groups crystallized within a brief period of about 1 month or less. It involved an increase in subgroup size through the coalescence of several typical subgroup females (and their juvenile offspring) and their permanent association with each other and disassociation from members of the main group. During this phase adult males also attached themselves to the branch groups.

## Participants in Pre-fission Subgroups

Of 21 different adult females that were seen in subgroups at least once, 16 eventually became permanent members of the new branch groups; the other five stayed in the main groups. Prior to group fission, one or more of these 16 branch group females were found in subgroups significantly more often than any of the 19 main group females (Table IV). Females in subgroups were significantly more often low ranking than mid ranking, or, especially, high ranking (Table V).

There were no adult or subadult males associated with the females in 75% (six of eight) of

**Table V.** The frequencies with which adult females of different dominance ranks were observed as members of pre-fission subgroups, compared with those expected if rank had no effect on subgroup membership

| Group | | Adult female dominance ranks | | | Total number of female sightings | *G*-test (two-tailed) *df*=2 | *P* |
|---|---|---|---|---|---|---|---|
| | | High | Mid | Low | | | |
| 22 | Observed | 9 | 36 | 57 | 102 | | |
| | Expected | 34·0 | 34·0 | 34·0 | 102·0 | 38·840 | <0·001 |
| IH | Observed | 2 | 14 | 52 | 68 | | |
| | Expected | 22·7 | 22·7 | 22·7 | 68·0 | 62·541 | <0·001 |
| D | Observed | 0 | 3 | 14 | 17 | | |
| | Expected | 5·7 | 5·7 | 5·7 | 17·0 | 20·687 | <0·001 |

**Table VI.** The frequency of sightings of males in pre-fission subgroups containing females, by their dominance ranks and ages, compared with their expected frequencies based on their proportions in the group as a whole

| | Adult males by rank | | All males by age | | | |
|---|---|---|---|---|---|---|
| | (High+mid) | Low | Adult | Subadult | Juvenile | Total |
| Observed frequency | 9 | 16 | 25 | 46 | 54 | 125 |
| Expected frequency | 16·6 | 8·3 | 29·1 | 30·5 | 65·3 | 125 |
| *G*-test | 31·339 | | | 9·642 | | |
| *P* | <0·001 | | | <0·001 | | |

subgroups of group D, and 17% (6 of 35) of group 22. Data were incomplete for male participation in the subgroups of group IH. Males found in subgroups of group 22 were significantly more often subadult than adult or juvenile; and the adult males in these subgroups were significantly more often low ranking than mid or high ranking (Table VI). Among the 35 sightings of subgroups over 4 years in group 22, 19 different adult and subadult males associated with the females, but only four (21%) of them eventually joined the new branch group. This proportion differed significantly from the eight (61%) of 13 different subgrouping adult females that became permanent members of the new branch group ($G=5{\cdot}183$, $P<0{\cdot}05$). Apparently, males were less tied to the females of the subgroups than the females were to each other.

While some females of group 22 were found in subgroups, some males also formed temporary all-male subgroups of variable composition. The latter were often independent of the female subgroups, though individual males wandered between the main group and the female and male subgroups. The final products resulting from the fissioning of group 22 were two permanent daughter groups plus two temporary all-male groups.

## Group Histories and the Timing of Fission

The four fission groups differed in their individual histories prior to group fission. Subgroup development in group IH involved two adult females that had immigrated from a neighbouring group in 1977. Both females were habitually peripheral to group IH. Other females of group IH began to associate with these immigrants to form subgroups in February 1979, shortly after the cyclone. The first signs of subgrouping in group D also occurred shortly after the cyclone, in January 1979. Only group 22 had a 4-year history of subgrouping prior to fission, beginning in January 1976: again, during a year of environmental stress. The pre-fission history of group H is unknown.

There was no significant relationship between the occurrence of subgroups and reproductive seasons (Table VII). The final formation of branch

**Table VII.** The numbers of months during which pre-fission subgroups were observed, in relation to months of conceptions (mating season), births and non-reproduction

| | Mating season no. months | | Birth season no. months | | Non-reproductive no. months | |
|---|---|---|---|---|---|---|
| Group | Total | Subgroups observed | Total | Subgroups observed | Total | Subgroups observed |
| D | 4 | 0 | 8 | 4 | 5 | 2 |
| IH | 2 | 2 | 4 | 4 | 3 | 2 |
| 22 | 19 | 6 | 16 | 10 | 13 | 6 |
| Expected frequencies group 22 | | 8·7 | | 7·3 | | 6·0 |
| *G*-test (two-tailed) | | | | $G=1{\cdot}781$, $df=2$, NS | | |

Expected frequencies were based on the frequency distribution of months per reproductive season per group.

groups, or group fission, occurred at the peak of the mating seasons for groups D and IH, and in the month following the mating season for group 22. The dominant female, Nick, in the new branch group IHN, was oestrous and conceived in the month of group fission. In group 22, fission occurred at least 1 month after the last conceptions. The new branch group D2 was taken over by a group D male, Bfa, and three of the females came into oestrus and conceived within 2 months of fission. Presumably, Bfa sired the three new infants.

### Infanticide and Group Fission

In group D, 3 months before fission, the infant of Nazly had been bitten to death by one of the males in group D, judging from the infant's injuries and the behaviours surrounding the event. Nazly was the matriarch of all individuals that fissioned to form the new branch group D2.

### Group Fission and Female Dominance

The sociodemographic changes among the females of the three fission groups (D, IH and 22) showed the following trends (Fig. 1).

(1) The numbers of adult females had increased by 20%, 38% and 100% for groups 22, D and IH, respectively, owing to the maturation of daughters, and the immigration of two females into group IH.

(2) Several older females lost rank owing either to the maturation of daughters of higher-ranking females (especially in groups IH and D), and/or a series of rank reversals with old and young females (in groups D and 22).

(3) Young adult females of low rank challenged females ranking above them, and dramatically increased their status by three to five ranks, shortly before fission (Gise and Love of group 22, and Amina of group D). For Amina of group D, these gains were short-lived, as she again dropped by four ranks. The ranks that these young females were vying for were those that they would have occupied (through the normal process of the social inheritance of ranks from mothers to daughters, e.g. Baker-Dittus 1985) had their mothers not dropped in rank.

In group 22, at the beginning of 1976, the onset of subgrouping behaviour coincided with the simultaneous maturation of three young females. One of them, Love, challenged higher-ranking females, gained one rank in 1976 and another five ranks about 6 months prior to fission. The highest-ranking females of group 22 in 1975 and 1976 had been Dub and her presumed daughter, Angel. They were first observed in pre-fission subgroups shortly after they began losing ranks in February 1977. Young female Gise (presumed daughter of Dub) avoided loss of rank by ascending in rank over other members of her matriline. In group D, Nazly and her presumed daughter Amina had occupied the upper half of the dominance hierarchy in 1975, but eventually dropped to the lowest ranks.

It was of interest to compare dominance relationships in fission groups with those in non-fission groups (see Methods). Thus, I considered female rank relations in 10 groups that were above the median group size in the 5-year period preceding the splitting of groups D, IH and 22, and excluded

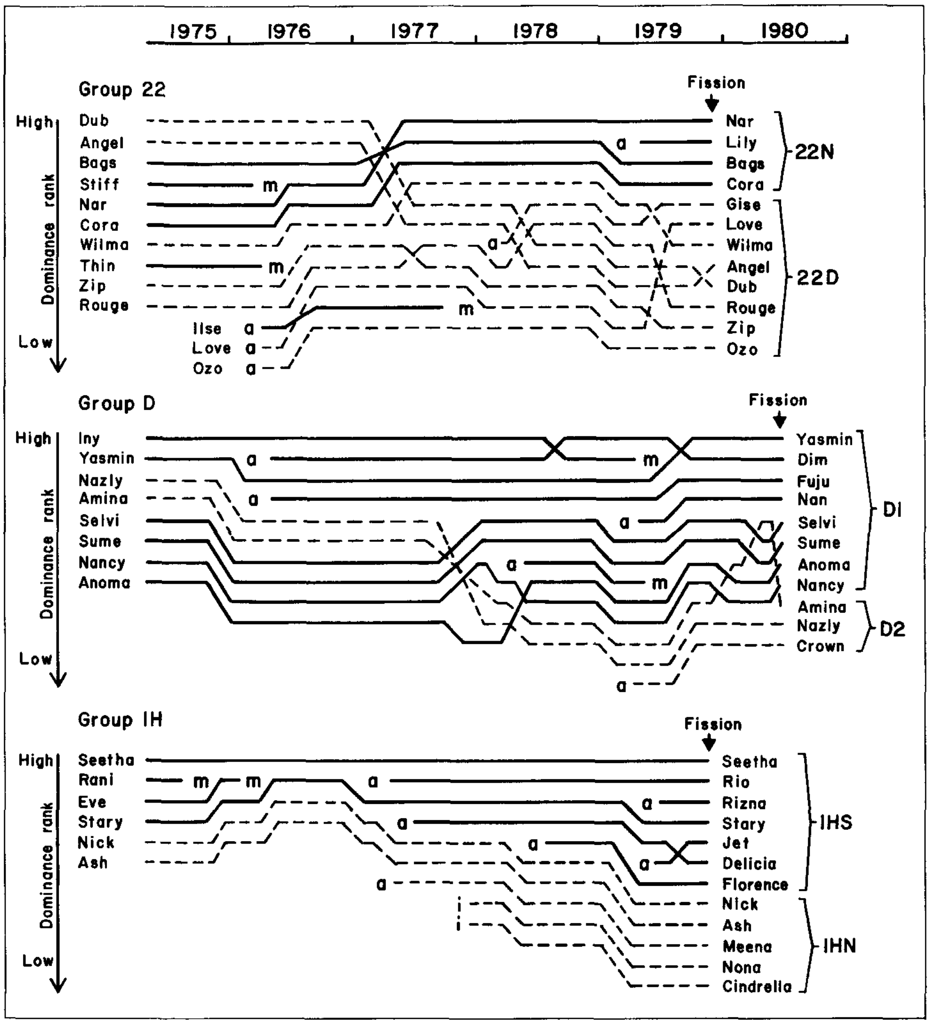

**Figure 1.** Changes in dominance ranks and demographic fates among the adult females of three different groups in the 4–5-year periods preceding group fission. Females that eventually seceded to form branch groups (22D, D2 and IHN) are indicated with broken lines, those remaining with the main groups (22N, D1, and IHS), or dying prior to fission, are indicated with solid lines. The names of individual females identify their sociodemographic fate lines. Demographic fates are a: maturation to adulthood as marked by a female's first infant; i: immigration; and m: death.

these fission groups in the year of their division. In these groups, 220 females were involved in 262 rank reversals in 460 female–years of observation. That is, on average, about 48% of females reversed their dominance rank relationship with one or more other females each year. The majority of these changes involved the daughters of high-ranking females that ascended the dominance hierarchy as they matured. Considering only the year prior to group fissions, out of 74 females distributed among seven non-fission groups, 30 (40·5%) were involved in a reversal of rank. This compared with 28 (75·7%) females reversing their ranks among 37 females in fission groups (D, IH and 22). Thus, there was a significantly greater frequency of rank reversals among fission groups than among those non-fission groups that were above the median group size in the year prior to group fissions ($G = 12{\cdot}481$, $df = 1$, $P < 0{\cdot}001$). Similarly, comparing only fission groups in different periods, in 4 normal years 54·1% (66 of 122) of females transposed their ranks and this rate increased to 75·7%

in the year of fissions; this increase would be significant ($G = 5{\cdot}654$, $df = 1$, $P < 0{\cdot}025$) accepting that frequencies of female rank changes were independent between years. On the other hand, across years among several non-fission groups, rates of rank reversal among females sometimes exceeded those in fission groups. Together, the data suggest that, whereas all group fissions were preceded by a greater than normal rate of rank reversals in the female dominance hierarchy, not all such changes caused group fission.

### Group Fission and Male Dominance

Male dominance ranks were examined for adult and subadult males for 3 years prior to group fission (Fig. 2). The following features were common to three of the groups that fissioned.

(1) Males that seceded to the branch groups upon fissioning had recently lost rank. Thus, in groups D and IH, the males Bfa and Kamal were young, had recently risen in rank, were wounded from lost fights with other challengers, and had dropped to a very low rank and peripheral position just prior to fission. In group 22, Cid and Pep had been the alpha and second-ranking males for more than 1 year, respectively. They lost rank to a young challenger, Acma, several months prior to fission and joined the new branch group 22D. However, whereas Pep remained with the new branch group, Cid, as well as the lower-ranking males, Mer and Oto, shifted back and forth between the daughter groups after fission, Cid finally settling with the main group 22N.

(2) In all three groups, the timing of the final phase of fission was closely tied to the loss of ranks by males that joined branch groups.

(3) A loose relationship also existed between final group fission and an end to the relatively long-term stability of the alpha-male positions. For example, alpha males were deposed 6 months and less than 1 month prior to fission in groups IH and 22, and 7 months after fission in group D. The loss of rank by the second-ranking male, Bfa, at the time of fission in group D was part of the process whereby a coalition of three males (Wri, Henry and Jack) took over group D.

The formation of pre-fission subgroups, however, appeared not to be closely tied to changes in male dominance relations. Also, there were other substantial rank changes among the males which were not tied to group fission.

### Group Fission by Kinship and Dominance

The lines of division in the final formation of new daughter groups were clearly by kinship (Fig. 3). After fission all adult females and juveniles of known and assumed kinships remained in the same groups as other members of their genealogies. The one exception to this concerned a probable intra-genealogical fission between adult female Nick of group IH and her assumed eldest daughter, Jet. Jet was a young adult at the time of fission and she had risen in rank above her assumed mother about 1 year earlier. Jet associated with the higher-ranking genealogies, whereas Nick's known juvenile daughter, Nilani, remained with her.

Adult females and their matrilines were arranged in a hierarchical order according to the behavioural dominance relationships that existed among them just prior to fission (Fig. 3). The three groups split along lines of dominance relationships as might be predicted from pre-fission subgrouping behaviours. Thus, in each case, one daughter group consisted of all members of the higher-ranking genealogies of the pre-existing parental group, whereas the other consisted of all of its low-ranking genealogies. For groups D and IH, the lower-ranking daughter groups were also the smaller of the fission products, but for group 22 the smaller daughter group was composed of the high-ranking genealogies.

Kinships were only partly known for group H in 1975. But dependent young remained with their mothers after group fission, and the division resulted in two daughter groups containing the adult females ranking first and fourth, and second and third, respectively.

### Group Fission and Relatedness

I wished to test the hypothesis that group fission occurs when the mean degree of relatedness among group members falls below some critical level. To this end, I compared the mean degrees of relatedness among natal group members ($r$) between groups that fissioned and those that did not. Degrees of relatedness were calculated based on the demographic compositions of groups as they stood either in the months of fissions for fission groups, or in December 1979 for all other groups (group H was omitted). Two estimates of $r$ were made. The first used only kinship links that were known through birth, the second also incorporated some estimated links (see Methods). The latter was

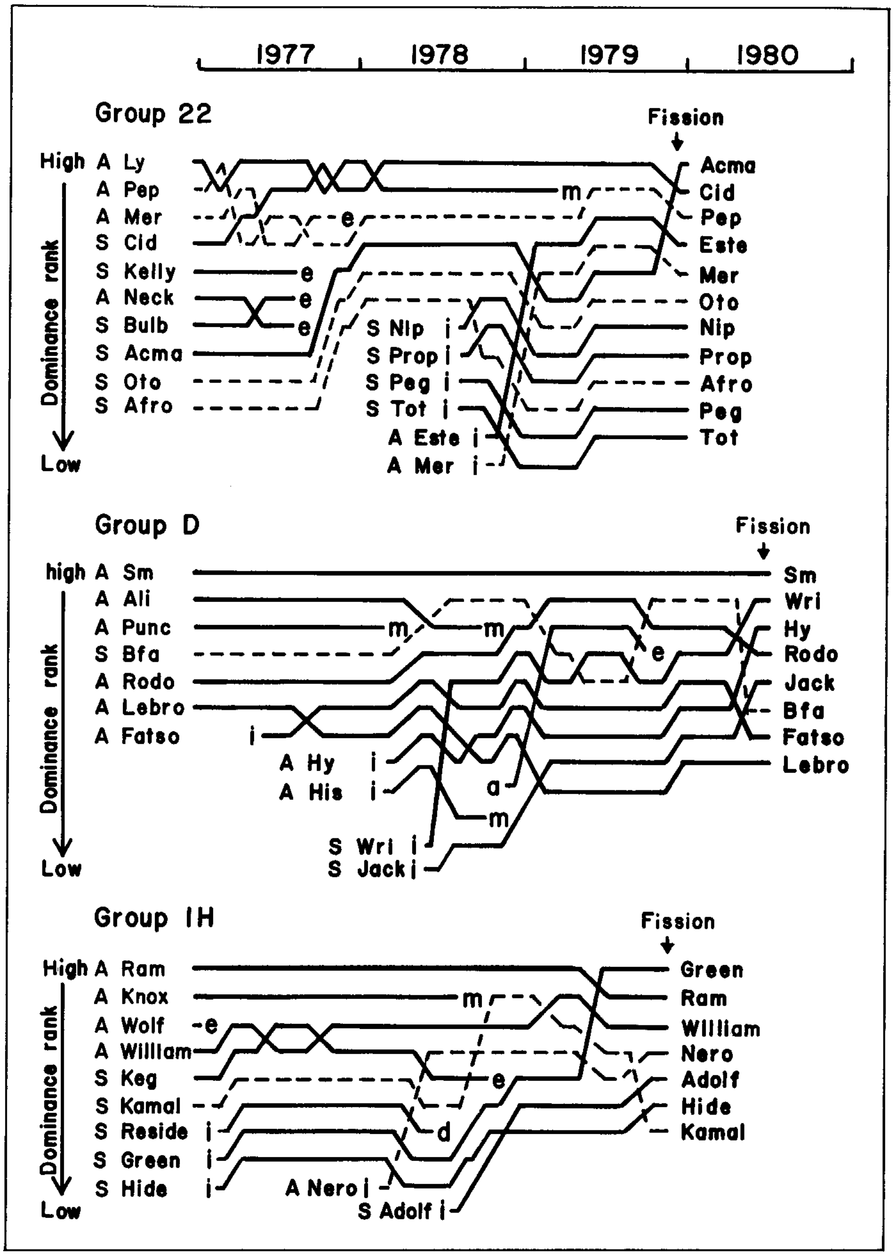

**Figure 2.** Changes in dominance ranks and demographic fates among adult and subadult males of three different groups in the 3 years preceding group fission. Males that eventually joined branch groups are indicated with broken lines, those remaining in the main groups are indicated with solid lines. The names of individuals and their age classes are shown on the left-hand side. Age classes are *A*: adult; *S*: subadult. Demographic fates are a: maturation to subadulthood; d: disappearance; e: emigration; i: immigration; and m: death.

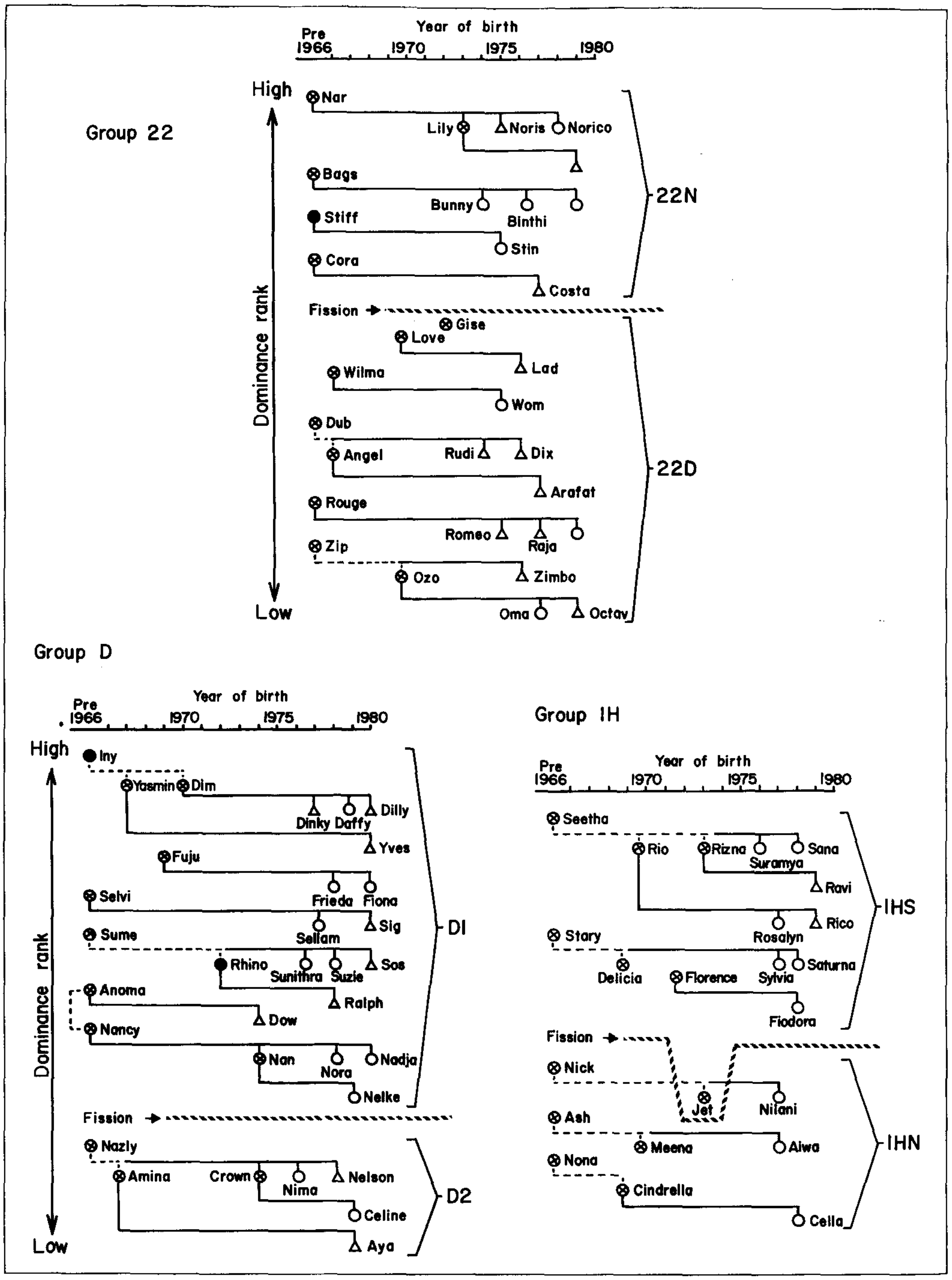

**Figure 3.** Matrilineal kinships among the natal members of the three different groups that fissioned, and the dominance rank relationships among matrilines within these groups. Solid lines indicate kinships known through birth, broken lines indicate estimated ones. The names of all individuals more than 6 months old at the time of fission are indicated. Circles: female; triangles: male; black: dead individual at the time of group fission; crossed circles: adult; open: juvenile or infant. Brackets indicate the daughter groups created by fission. In group 22, the female Gise is an assumed daughter of Dub.

**Table VIII.** Mean degrees of relatedness ($\bar{r}$) among fission groups prior to group division, non-fission groups and of daughter groups after fission

| Group | Number of natal members | Known kinship links only | | Known plus estimated kinship links | |
|---|---|---|---|---|---|
| | | Number of matrilines | $\bar{r}$ | Number of matrilines | $\bar{r}$ |
| Non-fission groups ($N=16$) | | | | | |
| Means | 13·4 | 5·7 | 0·064 | 4·8 | 0·079 |
| Fission groups | | | | | |
| D | 31 | 10 | 0·032 | 7 | 0·043 |
| IH | 23 | 12 | 0·025 | 6 | 0·054 |
| 22 | 30 | 12 | 0·027 | 9 | 0·037 |
| Means | 28·0 | 11·3 | 0·028 | 7·3 | 0·045 |
| Daughter groups | | | | | |
| D1 | 24 | 8 | 0·041 | 6 | 0·052 |
| D2 | 7 | 2 | 0·179 | 1 | 0·277 |
| IHS | 15 | 7 | 0·045 | 4 | 0·095 |
| IHN | 8 | 5 | 0·054 | 3 | 0·107 |
| 22N | 12 | 4 | 0·091 | 4 | 0·091 |
| 22D | 18 | 8 | 0·038 | 5 | 0·066 |
| Means | 14·0 | 5·7 | 0·075 | 3·8 | 0·115 |
| *U*-test of $\bar{r}$ | | | | | |
| Non-fission versus fission group | | $U=9$, NS | | $U=10$, NS | |
| Fission versus daughter group | | $U=0$, $P<0·05$ | | $U=1$, $P<0·05$ | |

considered to be a closer estimate of true kinship. Although the means of $r$ for all fission groups were less than those for non-fission groups, there was no significant difference in the distributions of $\bar{r}$ for groups that fissioned and those that did not, using both kinds of estimates of kinship (Table VIII). High variance in $\bar{r}$ among non-fission groups combined with the small sample size of fission groups might have contributed to this lack of significance. Also, there were significant inverse correlations between values of $\bar{r}$ and the number of natal animals in a group (Pearson's $r=-0·556$, $t$-test$=2·76$, $df=17$, $P<0·02$ for degrees of relatedness using known links only, and Pearson's $r=-0·831$, $t$-test$=6·15$, $df=17$, $P<0·001$, for degrees of relatedness using some estimated kinships). Therefore, the potential effect on fission of dilute relatedness among group members was partly clouded by the effects of group size on fission, since large groups were more prone to fission than small ones (Table I).

### Relatedness After Group Fission

Fission products were unequal in size, and markedly so in the case of groups D1 and D2, where group D2 consisted essentially of only one matriline (Fig. 3, Table VIII). The splitting of members of the same matriline did not occur, with one probable exception in group IH. Hence, with the exception of group IHN, the mean coefficient of relatedness within matrilines did not change before and after fission. But, considering the mean coefficient of relatedness among all natal members of the group, fission resulted in significant increases in the degrees of relatedness among members of all daughter groups compared with their respective pre-existing parental groups (Table VIII).

### Group Fission and Sex Ratios

Was there a build-up towards a disproportionate number of males in groups of toque macaques before fission as might be expected from the Surplus Males hypothesis? Sex ratios were compared between groups that fissioned and those that did not for 6 years prior to their divisions. The male component of the ratio included adult males 9·0 or more years old, plus subadult males aged 6·0–8·9 years, and was compared with adult females aged

**Table IX.** Annual sex ratios* of groups that fissioned and those that did not, during the 6-year period preceding group fission

| | (AM+SM) : 100 AF† | |
|---|---|---|
| Year | Fission groups ($N=3$) | Non-fission groups ($N=16$) |
| 1974 | 74·9 | 78·6 |
| 1975 | 95·6 | 89·3 |
| 1976 | 85·8 | 88·8 |
| 1977 | 80·5 | 73·7 |
| 1978 | 76·3 | 82·7 |
| 1979 | 89·4 | 72·1 |
| Wilcoxon test | $T=6$ | |
| $P$ | NS | |

* Sex ratios are unweighted annual means.
† AM: adult male; AF: adult female; SM: subadult male.

**Table X.** Sex ratios of parent groups, in the 2 months preceding group fission, and those in daughter groups (main and branch groups) in the 2 months following fission

| | (AM+SM) : 100 AF† | | |
|---|---|---|---|
| Group | Parent group | Main group | Branch group |
| D | 90·9 | 112·5 | 33·3 |
| IH | 62·5 | 57·1 | 60·0 |
| 22 | 95·8 | 175·0 | 43·8 |
| 22+Oto* | 100·0 | 175·0 | 62·5 |
| Mean (D+IH+22) | 82·9 | 105·3 | 56·3 |

Fisher exact test, $P>0{\cdot}05$ for all ratios compared

* Group census includes temporary all-male group (Oto) in the group with which it was most closely associated.
† AM: adult male; AF: adult female; SM: subadult male.

6·0 or more years. The ratio therefore compared all males and females 6·0 or more years old. Computations of sex ratios were based on the mean numbers of monkeys residing in groups per annum (see Methods). There were no significant differences in the distributions of these sex ratios, between groups that fissioned and those that did not, for 6 years prior to group division (Table IX). Nor was there a trend for sex ratios to change over time in either subpopulation. A slightly higher unweighted mean proportion of adult plus subadult males was evident among fission groups in 1979 just prior to group fission (Table IX). But the weighted mean sex ratio of adult plus subadult males of fission groups (88·3) did not differ significantly from that (75·1) of non-fission groups ($G=0{\cdot}224$, $df=1$, $P>0{\cdot}50$). These trends were true also for ratios comparing only adult males with adult females.

To assess changes in sex ratios caused by fission, I compared the mean sex ratios among parent groups, for 2 months prior to fission, with those among the newly created daughter groups, for 2 months after fission (Table X). Among the newly created daughter groups, the sex ratios in two of the three main groups were greater than those in their pre-existing parental groups, respectively. There were no disproportionate numbers of adult plus subadult males in the branch groups following fission; the sex ratios in two of the branch groups were lower than those in their pre-existing parental groups (Table X). There were no statistically significant changes in the sex ratios either of any parent group compared with any of its daughter groups, or of the subpopulation of all parent groups combined compared with that of all daughter groups (Table X). These trends were true also when only adult males were considered in the sex ratio comparisons.

## DISCUSSION

Over a 14-year period, the population of macaques at Polonnaruwa grew significantly at a mean rate of slightly more than 2% per annum. But this overall rate varied annually and included significant negative population growth during years of ecological stress (drought and cyclone). Group fission, though rare in this population, coincided with these stress years, and occurred mainly in those groups whose long-term rates of growth were significantly greater than those of groups that did not fission (Table II). Also, considered together, fission groups were significantly larger than intact groups (Table I). The exception to this, group H, was approximately of median size and had not grown in the 5 years prior to its division.

The cause of group fission could not be attributed to any single proximal factor. Instead, there appeared to be an interplay between several events and conditions that contributed towards the breakdown of cohesion in some groups. What, then, was the nature of each factor and its role in fission? And is there a single ultimate factor that might explain why groups divide?

Before evaluating these factors, it is useful first to review the ecological significance of subordinate behaviour in toque macaques.

### Costs of Subordinate Behaviour

When not vying for mates, more than 80% of the toque macaques' agonistic interactions concern the displacement of individuals at contested feeding sites; dominant individuals usurp the foods that subordinates have found. Such competition influences foraging success so that, compared with dominant animals, subordinate ones expend more time and energy in seeking food, feed at slower rates and consume greater proportions of foods of inferior caloric and nutritional quality (Dittus 1977a). These socially mediated differences in feeding success underlie variance in rates of maturation, survivorship and reproductive success, so that dominant individuals experience greater fitness than subordinate ones. Furthermore, the sizes of groups, and of the total population, are regulated at Polonnaruwa in relation to the availability of food resources (Dittus 1979, 1982, 1986).

### Ecological Stress and Sociodemographic Change

The cyclone had three measured effects on the forest vegetation: first, about 40% of trees either were uprooted or died from damage shortly after the cyclone; second, the production of flowers and fruits by trees and shrubs was significantly diminished for more than a year after the cyclone; and, lastly, trees lost an average of 34% of their large branches so that the crowns of fruit-bearing trees were greatly reduced in size (Dittus 1985).

These vegetational changes influenced the macaque's feeding ecology in two ways. First, more than 65% of the toque macaques' diet by dry weight consists of the fruit of trees (Dittus 1974). Hence, there was a great decrease in the macaques' food supply, that normally would have been available from trees. Second, the reduction in the sizes of tree crowns (food patches) meant that, compared with normal times, fewer group members could be accommodated at such diminished sites.

These cyclone-related environmental changes affected all macaque groups at Polonnaruwa about equally. In the year following the cyclone, mortality increased significantly among infants, old and subordinate individuals in many groups (Dittus 1982). That is, the post-cyclone environmental changes raised the costs of food competition in general.

Environmentally based hardship may have been especially marked in large groups, particularly those, like the fission groups, that had grown rapidly (8% per annum) in the years just preceding the cyclone (Tables I and II). The onset of subgrouping behaviour by subordinate females (Table V) in two of these groups (D and IH) immediately after the cyclone suggests that these individuals were competitively excluded from food resources. In group 22, too, subgrouping began in a year (1976) of ecological stress and the participants were subordinate females (Table V).

Much of the growth of the fission groups occurred among the females; their numbers increased by 20–100% in the 5-year period prior to fission. Except for two female immigrations in group IH, the increase in adult females was due to the maturation of daughters. The frequency of dominance rank reversals was significantly greater in fission groups than in intact groups immediately after the cyclone. Strife among these females concerned the acquisition or defence of social positions, or 'priority of feeding rights', that would directly determine their abilities to survive and reproduce. The losers in these contests presumably experienced greater foraging success in small independent parties moving peripheral to the main group, where they had less interference from dominant competitors.

In the home range of group H, also, food resources were greatly reduced in their availability and size by humans in a drought year. The division of group H is of special interest because it implies that even small groups, with very few intragroup competitors, may be subject to fission if the ecological stresses are very severe.

In the absence of environmental changes, groups D, IH and 22 might have fissioned eventually owing to their sizes and other characteristics. The effect of the sudden environmental stresses brought on by the cyclone was apparently to synchronize fission in these susceptible groups within the same year.

### Influence of Males on Group Fission

Subadult and adult males are generally dominant to the smaller adult females and compete with them for resources (Dittus 1977a). Subordinate females, therefore, were subject to supplantation by such males as well as by dominant females. Many pre-fission female subgroups had no or only a few males associated with them, suggesting that the subordinate females had been avoiding male as well as dominant female competitors.

Subadult and subordinate adult males associated with prefission subgroups significantly more often than did males of other ages or rank (Table VI), suggesting that they too avoided dominant foraging competitors. Some males shifted back and forth between the new daughter groups immediately after fission. They were probably adjusting their group affiliation according to the new distribution of females and other group members, rather than being important agents of fission.

The formation of female subgroups prior to fission was not obviously related to male rank changes, nor to the reproductive condition of females (Table VII). But the final formation of branch groups did coincide with major reorderings of male dominance relationships (Fig. 2), which were generally a consequence of male-male contests for mates (Dittus 1977a). The precise timing of final fission also overlapped with the presence of oestrous females in groups D and IH (but not in group 22), and was loosely associated with an infanticide (before fission) and the onset of oestrus shortly after fission among females of branch group D2. These data suggest, albeit somewhat equivocally, that male aggression and reproductive competition may have influenced the precise within-year timing of final fission. Males, however, were not the sole agents causing fission, because male competition for mates and rank changes were fairly common in the population and most did not result in group division.

Generally, males that lose rank often emigrate and attach themselves to a new group (Dittus 1975). The peripheral female subgroups seemed to be attractive 'new groups' for these subordinate males to take over, because they were already familiar with the females and there were no other males to contend with. Once these males began defending the new branch group females against the main group and other groups, they may well have drawn other typical subgroup females to join them and so to form the new branch groups. Thus, the final crystallization of new branch groups appears to have resulted from a coalition of males and females, each behaving according to their own best interests. One might speculate that females in peripheral subgroups would continue to associate with their main groups until males are available and willing (or able) to join them in the formation of an independent new group.

In contrast to reports of group fissions in some other species (Sugiyama 1960; Furuya 1968; Nash 1976; Yamigawa 1985) there was no significant build-up of disproportionate numbers of subadult and subordinate adult males in groups of toque macaques that fissioned (Table IX). Nor did fission result in a shift of an unusual number of males out of the main group and into the branch groups. In fact, for two of the groups, a greater proportion of males stayed with the main group than shifted to the new branch groups (Table X), although none of these changes in sex ratios was statistically significant.

Greater than normal degrees of male aggression and dominance rank changes (resulting from disproportionate numbers of males) have often been cited as a cause for group fission in other species (e.g. Japanese macaques: Sugiyama 1960; Furuya 1968, 1969; Yamigawa 1985; baboons: Nash 1976; rhesus macaques: Southwick et al. 1965; and redtail monkeys: Struhsaker & Leland, in press). On the other hand, no unusual degree of male aggression accompanied the division of groups of blue monkeys (Cords & Rowell 1986) or of rhesus macaques in India (Malik et al. 1985) or on Cayo Santiago (Chepko-Sade 1982). Group division in blue monkeys is initiated solely by females (Cords & Rowell 1986), and in redtail monkeys females initiate fission in response to male aggression (Struhsaker & Leland, in press). Together with the data from toque macaques, these data imply that the role of males may vary considerably between groups or social contexts. Part of this variance might also relate to species differences in life-history strategies.

## Fission and Solidarity Among Kin

The importance of close kinship ties to social life has often been stressed (e.g. Hamilton 1964; Eisenberg 1966; Alexander 1974; West-Eberhard 1975). This was indicated by the occurrence of group division mostly between, rather than within, matrilineages in toque macaques (Fig. 3) as well as in other primates: Japanese macaques (Koyama

1970), rhesus macaques (Missakian 1973) and baboons (Nash 1976). Possibly owing to small sample sizes, there was no significant link between fission and dilute relatedness in toque macaques, as had been noted in rapidly growing human and rhesus populations (Chagnon 1975; Chepko-Sade & Olivier 1979).

In the rhesus population at Cayo Santiago, eldest daughters typically occupy the lowest ranks in their matrilines, and when groups divide they leave with the splinter group (Chepko-Sade & Olivier 1979). The intragenealogical fission in group IH, at Polonnaruwa, departed from the above pattern because the eldest daughter, Jet, outranked her own (assumed) mother and stayed with the dominant genealogies, whereas the mother, Nick, left with the subordinate branch group.

## Consequences of Group Fission

Daughter groups established independent home ranges. Notwithstanding, these ranges overlapped with each other and with those of their respective pre-existing parental groups. The main groups, consisting of the dominant matrilines, however, inherited the largest portions of the parental home ranges. The ranges of all daughter groups also expanded into previously unused or little used habitats (unpublished data). Similar changes have been noted in Japanese macaques (Furuya 1969), rhesus macaques (Southwick et al. 1965; Melnick & Kidd 1983) and baboons (Nash 1976).

If, by splitting from their parental group, the members of new branch groups improved their socioecological conditions, one might expect this to translate into enhanced fitness. For instance, after fission, an increase in birth rate among branch groups has been reported in rhesus macaques (Malik et al. 1985), redtail and blue monkeys as well as some Japanese macaques and baboons (Maruhashi 1982; Struhsaker & Leland, in press). In toque macaques, too, natality improved significantly following group fission (unpublished data). However, it remains to be seen whether members in branch groups also gained in their survivorships and hence in their overall long-term fitnesses.

Daughter groups were smaller than their pre-existing parental groups and had higher mean degrees of relatedness (Table VIII). One daughter group (D2) consisted of only one matriline (Fig. 3). If such groups disperse and survive to found new populations, they may add to genetic drift.

## Conclusions

Group fission was initiated primarily by low-ranking females whose individual fitnesses were probably in jeopardy owing to more than usual intragroup resource competition. The following proximal factors combined to increase the negative effects of intragroup competition: (1) a significant increase in group size to well above the mean for the population, which involved especially (2) the maturation of several daughters to adulthood, and (3) their challenges to the established order of female dominance relations, which resulted in (4) a significant increase in the rate of rank reversals among females of fission groups. (5) These socioecological stresses were exacerbated by an abrupt decrease in the size of important feeding sites and in the overall availability of foods in the environment. This sudden hardship appeared to synchronize the division of three susceptible groups. Even small groups may divide under acute environmental stress (e.g. food shortage) which may accentuate social disparities among a few group members.

I hypothesize that males promote group fission in two ways. First, dominant males, like dominant females, add to the burden of subordinate females in food competition. Also, high levels of male aggression, involving competition for mates, may similarly adversely affect female fitness especially if it results in infanticide. Second, however, females in peripheral subgroups require willing and able male defenders to form an independent new group. Fission is of advantage to low-ranking males because they too may improve their foraging success, and they gain greater access to mates than they would have in large groups with many dominant male competitors. Fission, then, appears to occur as a result of a coalition between subordinate males and females, both of which may potentially benefit from forming an independent new group. It seem unlikely that males, acting in their own interests but against those of females, would be successful in causing fission, at least not in large groups with many defenders against potential 'raiders'.

A breakdown of cohesion prior to fission was, in itself, probably not a cause of fission, as suggested by Malik et al. (1985). Rather, it was simply a manifestation of the peripheral and independent tendencies of subordinate females and males for reasons outlined above.

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## REFERENCES

Alexander, R. D. 1974. The evolution of social behavior. *A. Rev. Ecol. Syst.*, **5**, 325–383.

Baker-Dittus, A. 1985. Infant- and juvenile-directed care behaviors by adult toque macaques, *Macaca sinica*. Ph.D. thesis, University of Maryland.

Carpenter, C. R. 1942. Societies of monkeys and apes. *Biol. Symp.*, **8**, 177–204.

Caughley, G. 1977. *Analysis of Vertebrate Populations*. New York: John Wiley.

Chagnon, N. A. 1975. Genealogy, solidarity, and relatedness: limits to local group size in an expanding population. *Ybk Phys. Anthropol.*, **19**, 95–110.

Cheney, D. L. 1987. Interactions and relationships between groups. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 267–281. Chicago: University of Chicago Press.

Chepko-Sade, B. D. 1982. Role of males in group fission in *Macaca mulatta*. Ph.D. thesis, Northwestern University.

Chepko-Sade, B. D. & Olivier, T. J. 1979. Coefficient of genetic relationship and the probability of intragenealogical fission in *Macaca mulatta*. *Behav. Ecol. Sociobiol.*, **5**, 263–278.

Chepko-Sade, B. D. & Sade, D. S. 1979. Patterns of group splitting within matrilineal kinship groups. *Behav. Ecol. Sociobiol.*, **5**, 67–87.

Cords, M. & Rowell, T. E. 1986. Group fission in blue monkeys of the Kakamega Forest, Kenya. *Folia primatol.*, **46**, 70–82.

Dittus, W. P. J. 1974. The ecology and behavior of the toque monkey, *Macaca sinica*. Ph.D. thesis, University of Maryland.

Dittus, W. P. J. 1975. The dynamics of migration in *Macaca sinica*, and its relation to male dominance, reproduction and mortality. *Am. J. Phys. Anthropol.*, **42**, 298.

Dittus, W. P. J. 1977a. The social regulation of population density and age–sex distribution in the toque monkey. *Behaviour*, **63**, 281–322.

Dittus, W. P. J. 1977b. The ecology of a semi-evergreen forest community in Sri Lanka. *Biotropica*, **9**, 268–286.

Dittus, W. P. J. 1979. The evolution of behaviours regulating density and age-specific sex ratios in a primate population. *Behaviour*, **69**, 265–302.

Dittus, W. P. J. 1980. The social regulation of primate populations: a synthesis. In: *The Macaques: Studies in Ecology, Behavior and Evolution* (Ed. by D. G. Lindburg), pp. 263–286. New York: Van Nostrand Reinhold.

Dittus, W. P. J. 1982. Population regulation: the effects of severe environmental changes on the demography and behavior of wild toque macaques. *Int. J. Primatol.*, **3**, 276.

Dittus, W. P. J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica*, **17**, 1–14.

Dittus, W. P. J. 1986. Sex differences in fitness following a group take-over among toque macaques: testing models of social evolution. *Behav. Ecol. Sociobiol.*, **19**, 257–266.

Dittus, W. P. J. & Thorington, R. W., Jr. 1981. Techniques for aging and sexing primates. In: *Techniques for the Study of Primate Population Ecology* (Ed. by the Subcommittee on Conservation of Natural Primate Populations), pp. 81–131, Washington, D.C.: National Academy Press.

Dunbar, R. I. M. & Dunbar, E. P. 1974. Ecology and population dynamics of *Colobus guereza*. *Folia. primatol.*, **21**, 188–208.

Dunbar, R. I. M. & Dunbar, E. P. 1977. Dominance and reproductive success among female gelada baboons. *Nature, Lond.*, **266**, 351–352.

Eisenberg, J. F. 1966. The social organization of mammals. *Handbk Zool.*, **10**, 1–92.

Furuya, Y. 1968. On the fission of troops of Japanese monkeys I. *Primates*, **9**, 323–350.

Furuya, Y. 1969. On the fission of troops of Japanese monkeys II. *Primates*, **10**, 47–69.

Goodall, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.*, **1**, 161–311.

Hamilton, W. D. 1964. The genetical evolution of social behavior. *J. theor. Biol.*, **7,** 1–52.

Hrdy, S. B. 1979. Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.*, **1,** 13–40.

Kleiman, D. 1977. Monogamy in mammals. *Q. Rev. Biol.*, **52,** 39–69.

Koford, C. B. 1963. Group relations in an island colony of rhesus monkeys. In: *Primate Social Behavior* (Ed. by C. H. Southwick), pp. 136–152, New York: D. Van Nostrand.

Koford, C. B. 1966. Population changes in rhesus monkeys, Cayo Santiago, 1960–1964. *Tulane Stud. Zool.*, **13,** 1–7.

Koyama, N. 1970. Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. *Primates*, **11,** 335–390.

Kummer, H. 1968. Social organization of hamadryas baboons. *Biblthca primatol.*, **6,** 1–189.

Li, C. C. 1976. *Population Genetics*. Pacific Grove, California: Boxwood.

Malik, I., Seth, P. K. & Southwick, C. H. 1984. Population growth of free-ranging rhesus monkeys at Tughlaqabad. *Am. J. Primatol.*, **7,** 311–321.

Malik, I., Seth, P. K. & Southwick, C. H. 1985. Group fission in free-ranging rhesus monkeys of Tughlaqabad, Northern India. *Int. J. Primatol.*, **6,** 411–422.

Maruhashi, T. 1982. An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, **23,** 317–337.

Melnick, D. J. & Kidd, K. K. 1983. The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). *Behav. Ecol. Sociobiol.*, **12,** 229–236.

Missakian, E. A. 1973. The timing of fission among free-ranging rhesus monkeys. *Am. J. Phys. Anthropol.*, **38,** 621–624.

Moore, J. 1984. Female transfer in primates. *Int. J. Primatol.*, **5,** 537–589.

Nash, L. T. 1976. Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. *Am. J. Phys. Anthropol.*, **44,** 63–78.

Nishimura, A. 1973. The third fission of a Japanese monkey group at Takasakiyama. In: *Behavioral Regulators of Behavior in Primates* (Ed. by C. R. Carpenter), pp. 115–123. Lewisburg: Bucknell University Press.

Richards, S. M. 1974. The concept of dominance and methods of assessment. *Anim. Behav.*, **22,** 914–930.

Sackett, G., Holm, R. & Landesman-Droyer, S. 1975. Vulnerability for abnormal development: pregnancy outcomes and sex differences in macaque monkeys. In: *Aberrant Development in Infancy. Human and Animal Studies* (Ed. by N. R. Ellis), pp. 59–76. New York: John Wiley.

Sade, D. 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: *Social Communication in Primates* (Ed. by S. Altmann), pp. 99–114. Chicago: University of Chicago Press.

van Schaik, C. P. 1983. Why are diurnal primates living in groups? *Behaviour*, **87,** 120–144.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. San Francisco: W. H. Freeman.

Southwick, C. H., Beg, M. A. & Siddiqi, M. R. 1965. Rhesus monkeys in north India. In: *Primate Behavior* (Ed. by I. De Vore), pp. 111–159. New York: Holt, Rinehart & Winston.

Stoltz, L. P. 1972. The size, composition and fissioning in baboon troops (*Papio ursinus* Kerr, 1792). *Zool. Afr.*, **7,** 367–378.

Struhsaker, T. T. & Leland, L. In press. Group fission in redtail monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. In: *A Primate Radiation: Evolutionary Biology of the African Guenons* (Ed. by A. Gautier-Hion, F. Bourliere, J.-P. Gautier & J. Kingdon), Cambridge: Cambridge University Press.

Sugiyama, Y. 1960. On the division of a natural troop of Japanese monkeys at Takasakiyama. *Primates*, **2,** 109–148.

Terborgh, J. 1983. *Five New World Primates. A Study in Comparative Ecology*. Princeton: Princeton University Press.

West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Q. Rev. Biol.*, **50,** 1–33.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75,** 262–300.

Yamagiwa, J. 1985. Socio-sexual factors of troop fission in wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, **26,** 105–120.

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