Origin and Fate of a One-Male Savanna Baboon Group Formed by Fissioning

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An adult male chacma baboon, Papio hamadryas ursinus, *emigrated from his habituated natal group at age 100 months and joined a neighboring multimale–multifemale group. Subsequently this male, together with eight adult females, all with infants <1 year old, formed a one-male group (OMU). The male was the only adult male in this group for over 200 days. Circumstantial evidence shows that shared parentage of the infants with this male determined which females joined the new group. In addition, 10 juveniles younger than 4.5 years joined the new group. Based upon persistent close physical association, especially at sleeping sites, these juveniles were presumed to be the older independent progeny of the eight adult females. Thus, the founding elements of the new group were the adult male and partial matrilines—mothers, their infants, and their independent juvenile offspring. The OMU status of the group ended with the sequential intrusion of three males known to be low ranking in other groups. The first of these intruders was successful in joining the OMU in spite of the OMU male's earlier successes in rebuffing this and other potentially high-ranking males. Six additional males later entered the fission group during a 6-month interval. Two of them outranked the original male. All additional males present in the last 100 days of observations came from the same group, which was not the group of origin of the females.*

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INTRODUCTION

All long term studies of free-ranging savanna baboons (*Papio hama-dryas* ssp.) report fissioning or fusion events. The only direct observation of formation of a one-male group of savanna baboons is Nash's (1976) account for the Gombe Stream Reserve population of *P. h. anubis*. Observations of *P. h. cynocephalus* groups by Altmann (1980) include the fusion of groups to form Alto's Troop. Here we evaluate the origin and fate of members of a one-male group (OMU) (Stammbach, 1987) of chacma baboons (*Papio hamadryas ursinus*) formed by fissioning and identify males that immigrated into it, changing it from OMU to multimale–multifemale (MM) status.

Primate social group fission and fusion may be a response to changing environmental conditions creating or eliminating environments for additional groups (Hauser *et al.*, 1986; Isbell *et al.*, 1990). There are relatively few accounts of group fissioning, fusion, and extinction in populations of nonhuman primates unperturbed by human activities such as direct or indirect provisioning and agriculture. The complex and confounding relationships of provisioned resources to demography and fissioning are reviewed by Yamagiwa (1985). The site for this study was chosen to avoid equivocal interpretations of demography imposed upon populations by conditions substantially modified by human activities. We feel we are observing a population of chacma baboons undergoing the natural regulation of their numbers including that of numbers of individuals within social groups. We have observed one other fissioning event in the Moremi Wildlife Reserve (Hamilton *et al.*, 1975, 1976) and no group fusions or extinctions.

In addition to environmental factors, social and genealogical relationships within groups may determine patterns and probabilities of fissioning (Chepko-Sade and Sade, 1979). The frequency of fission and fusion modify intragroup and intergroup social relationships. The genetic characteristics of the respective groups and potentially those of populations (Chepko-Sade and Sade, 1979; Melnick and Kidd, 1983; Melnick, 1987) may be substantially modified by these major events.

In cercopithecine monkeys fissioning has been most commonly observed among rhesus and Japanese macaques (Koyama *et al.*, 1975). Among macaques, adult females and their matrilineal kin are one nucleus of new groups (Furuya, 1969; Koyama, 1970; Chepko-Sade and Sade, 1979; Melnick, 1982). Matrilines also are elements of savanna baboon fission fragments (Nash, 1976). Limited evidence suggests that juveniles tend to follow their mothers during fissioning events (Chepko-Sade and Sade, 1979). In addition to matrilines, fissioning segments may also be composed of lineages (Neel and Salzano, 1976), consisting of clusters of relatively more closely

related matrilines. This will be the case if lower ranking matrilines are relatively closely related to one another and if low-ranking females form the core of one of the subgroups following fissioning, as reported for macaques (Chepko-Sade and Sade, 1979). This assumes that maternal rank is inherited by maternal offspring, as has been shown to be the usual case for macaques (Kawai, 1958; Sade, 1967; de Waal, 1991) and savanna baboons [Hausfater *et al.*, 1982; Johnson, 1987; this study (C Troop)].

Thus, there are several possible social and genetic relationships of fissioning adult females to one another.

1. Participating adult females may be a random selection from the parent group.

2   They may share their relative dominance status and thus, by inference, on the average come from relatively closely related matrilines (Melnick, 1987).

3. They may share recent mates that are the behavioral fathers of their infants (Melnick and Kidd, 1983). I.e., they may be the mothers of paternal sibships (Altmann, 1979).

Participation of males, not necessarily as parents, and their possible role as nuclei in group fissioning also have been identified for Japanese macaques (Yamagiwa, 1985). The reasons adult males join fissioning subgroups are neither as well documented nor as extensively considered. Mature males may choose which subgroup fragment to follow or to join based upon their exclusion from or status within other groups, their potential to gain status, their paternal relationships to infants, resource availability, or opportunities to gain access to mates (Packer, 1979), whether fertile or not. Since adult male baboons, unlike females and juveniles, usually move singly and independently, their choices of groups for residence are based upon a wider range of proximate cues than are those of females and juveniles (Pusey and Packer, 1987).

METHODS

We use the nomenclature of Williams-Blangero *et al.* (1990), referring to savanna baboons as the subspecies of *Papio hamadryas* other than the sacred baboon, *P. hamadryas hamadryas.*

Study Area and Subjects

Observations were made in the Moremi Wildlife Reserve in northern Botswana. There are no nearby (<50 km) habitat modifications resulting

from agricultural practices. The study area lies entirely within the Moremi
Wildlife Reserve, where all animal species are protected from poaching
and human induced disruptions other than tourism.

Baboons that we observe live along the floodplain of the Boro River,
one of several river courses forming the Okavango Delta. Several hundred
baboon groups live along these waterways. Northern Botswana is a
semiarid region (325-mm rainfall at Maun, 70 km south and east of the
study area) but the study area within the Okavango Delta is flooded an-
nually, providing suitable vegetation and water to support a high-density
baboon population and an array of ungulate and predator species. Moremi
baboon densities are greater and home ranges smaller than those of most
other savanna baboons which have been observed (cf. Cheney, 1987). Den-
sities are 1 group/2.1 to 6.5 km² (Hamilton et al.,1975, 1976) and 15.4
baboons/km² (1987 calculation: seven groups exclusive of Q Troop). This
compares with densities averaging 3 baboons/km² throughout areas of
southern Africa inhabited by chacma baboons (Anderson, personal com-
munication). Numbers of individuals in these groups were increasing when
(1987, 1989–1990) observations reported here were made (Bulger and
Hamilton, 1987).

We compare behavioral (Hamilton and Bulger, 1992) and demo-
graphic features (this paper) of the fission group, Q Troop, with other
MM groups we have observed in this population. These other MM
groups include A, B, G, and H Troops observed in 1973 on Chief's
Island, 18 km south of the current study area (Hamilton et al., 1975,
1976). Our observations include C Troop, observed since 1977, and W
Troop, observed from 1977 through 1980. Z Troop has been partially
habituated since 1985. D Troop came under close scrutiny only in 1987.
Throughout the interval of observations reported here and until late
1987, C Troop has been under daily observation. Collectively our demo-
graphic observations include over 18 group-years for habituated groups,
including the over 200 days of existence of Q Troop as a one-male
social entity.

Age estimates for Q Troop juveniles and infants are based upon com-
parison with infants of known age resident in C Troop at the time of these
observations. Estimates for infants under 1 year old are judged to be ac-
curate within 2 months (Whitehead et al., 1990). For older juveniles (>18
months) we estimate our accuracy at ± 4 months.

Individual members of the groups of baboons we studied are re-
ported by three-letter acronyms, the first giving the group of birth, when
known and U when unknown. The second two letters abbreviate individual
names.

RESULTS

The New Group

The new group, Q Troop, was first observed during March 1987, foraging near the Boro River along the drying floodplain in a portion of the D Troop home range. Our initial conclusion was that we were observing a part of D Troop, which often foraged and roosted in the area. However, additional observations revealed that Q and D Troops were operating as separate entities and that Q Troop, accompanied by a single adult male, occupied the western sector of the former D Troop home range.

Q Troop members actively avoided contact with all members of the neighboring C and D Troops during 31 intergroup encounters (Hamilton and Bulger, submitted for publication). However, on one occasion, at midday on October 23, 1987, Q and D Troops fused. This amalgamation was followed less than 3 hr later by separation of the members of both groups to their exact respective membership before this fusion event occurred. We have observed complete intermingling of groups in this population in only one other instance, the regular fusion and fissioning of the 148 members of G Troop in 1973. On all other occasions Q Troop and its neighbors, C and D Troops, behaved as distinct and distinguishable groups except for the relationship of males from C and Q Troops to one another, described below.

In combination with the above evidence on ranging patterns and intergroup behavior, our long-term group composition data show that Q Troop was formed by the fissioning of D Troop. In April 1985, D Troop contained 54 individuals, 6 of them carried infants. Q Troop was first censused in June 1987 and was composed of 27 individuals, including 8 carried infants. At that time D Troop membership was 32 individuals, including 11 adult females, only 1 of which carried an infant. Thus, the combined mid-1987 membership of Q Troop and D Troop was 50 exclusive of infants, compared with the 1985 D Troop equivalent of 48, also exclusive of infants. D Troop had divided into two demographically dissimilar fragments (Table I). There were more females with infants in the Q Troop segment (χ^2 = 15.35, df = 1, P < 0.001) and it contained only a single adult male. The adult female:male sex ratio of Q Troop far exceeded that of neighboring MM groups (8.0:1.0 vs 1.6–2.7:1.0). However, the number of postweaning juveniles per female was similar for all groups under observation.

Table I. Composition of Focal Groups in 1987 and 1988

|	Q (5/87)	Q (5/88)	D (5/87)	C (5/87)	Z (5/87)
Adult male	1	8	7	7	9
Subadult male	0	0	1	1	1
Adult female	8	9	11	19	18
Juvenile > 1 year	10	17	12	28	26
Infants < 1 year	8	0	1	5	7
Total	27	34	32	60	61
Adult sex ratio					
(females:male)	8.0	1.1	1.6	2.7	2.0
Juveniles:adult female	1.3	1.9	1.1	1.5	1.4

The Male

CNI (Nigel) was the only adult male with Q Troop until mid-October, 1987. He was born during November 1977 in C Troop and remained in his natal group throughout his youth, as do all males in the groups we observed. At age 100 months, between 5 and 7 March 1986, CNI emigrated from C Troop. He was next seen in May 1986, in D Troop (Fig. 1A). We did not have D Troop under persistent observation then, and CNI's activities in D Troop can only be inferred, more or less precisely, from later observations after contact with him was reestablished in 1987 and from our knowledge of male–female–infant relationships we have observed in this population. The Q–D Troop separation occurred by mid-March, 1987 (Fig. 1B).

Females and Juveniles

In late May 1987, when the female membership of Q Troop was first accurately determined, all eight adult females were carrying dependent infants estimated to be between 3 and 10 months old. It is highly improbable (conditional probability $P = 0.00012$) that these eight mothers were a random assemblage of females from D Troop since they originated from a pool of 19 adult females in the parent D Troop (Table I, Q and D Troops combined), 9 of which had infants.

Subsequent counts of Q Troop identified nine juvenile males and females, between about 2.5 and 4.5 years old, and a subadult female, about 5 years old, that matured to adulthood in 1988. These juveniles persistently associated with particular adult females, a relationship especially evident at sleeping sites. All adult females had at least one juvenile associate estimated to be between 2.5 and 3.5 years old. In addition, two of these females were
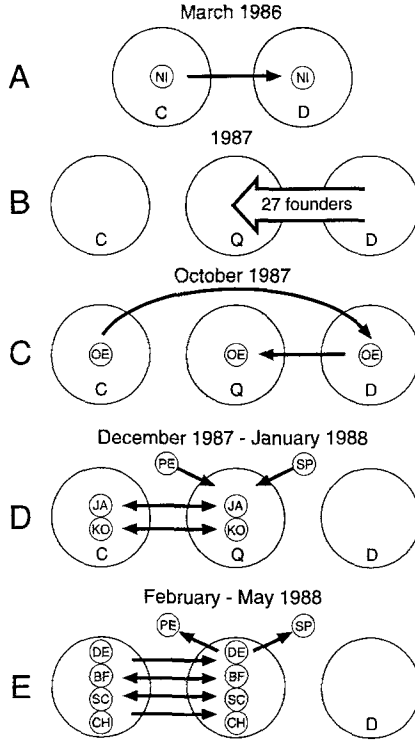
Fig. 1. Chronology of the origins and fate of the membership of a group of chacma baboons formed by fissioning. Large circles represent groups referred to in the text: C, Q, and D Troops. Small circles represent migrating males. (U)PE and (U)SP are males that did not originate in or emigrate to C or D Troops.

associated with a second juvenile, one a 4-year-old female, the other a 4.5-year-old male. We observed no deviations from these initial adult female–juvenile associations from the time individual juveniles were confidently identified in mid-July until the beginning of December 1987.

Survivorship

These founding members of Q Troop all survived and continued to live in Q Troop until persistent observations ended in May 1988 (Table I). All of the infants that we first observed in Q Troop survived to weaning.

In the MM C Troop, for which we have recorded all births since 1977, the observed probability of eight consecutively born infants surviving to 12 months is 0.03 (N = 95 sets of 8 sequential births).

Penetration of Additional Males into Q Troop

Adult male UOE initiated the demise of the one-male status of Q Troop (Fig. 1C). On October 14, he approached Q Troop and a shrieking confrontation with CNI occurred. CNI pursued UOE through the middle story of fig and acacia trees. During his flight UOE raced up a palm tree, and as he reached for its lowest frond, CNI overtook him and seized him by the tail. Both males fell 12 m to the ground. As they dropped through a dead acacia tree a branch punctured CNI's abdomen, breaking off and lodging there. The stick remained protruding from his abdomen for 2 days before coming free. CNI eventually recovered but he did not direct further attacks toward UOE until early December. UOE remained submissive and evasive throughout this interval but CNI was unable or unwilling to displace him from Q Troop.

UOE had immigrated into C Troop in March 1987. When immobilized, he was found to have only one eye and possessed broken upper canines and highly worn molars. Based upon comparison with other males that we have immobilized and that are >13 years old, we estimated UOE's age at >16 years. When he entered C Troop in March 1987, UOE ranked ninth of nine adult males. He transferred to D Troop in July 1987 and there ranked seventh of seven males.

From December 1987 through January 1988, four additional males entered Q Troop (Fig. 1D). UJA and UKO, the next two males to enter Q Troop after UOE, last resided in C Troop, where they ranked seventh and ninth, respectively, immediately before entering Q Troop. UJA entered C Troop early in 1987 and failed to rise far above the bottom of its adult male hierarchy. He settled to eighth of nine males, ranking just above UOE. Examination of his teeth following immobilization revealed that he was also an older male (>16 years). The next male to enter Q Troop, UKO, had declined steadily in rank following the end of his alpha tenure in C Troop in December, 1983.

The origin of immigrants USP and UPE is unknown. These prime males had the sharp canines of young males and probably were making first emigration movement from natal groups (Hamilton and Bulger, 1990). CNI carried infants against USP, which displaced him as alpha male in Q Troop, but not toward any of the other immigrant males. From February through May 1988, males CDE, UBF, USC, and CCH, all C Troop residents, also entered Q Troop (Fig. 1E). CDE was a natal alpha male in C

Troop at the time of this transfer. CDE displaced USP as alpha male. Between February and May 1988, UKO, UJA, USC, and UBF, all postprime males, moved back and forth between C and Q Troops.

DISCUSSION

Group Formation

During 10 years of observations we have never observed a female immigrate into or leave a focal group (15 group-years, >100 resident adult females). Thus, group fission, as far as we know from our observations of this population, is the only way that females of all ages disperse. Nor have we observed juvenile males (<7 years) transfer between groups.

Fissioning macaques and baboons are commonly identified as matrilines (Chepko-Sade and Sade, 1979; Oi, 1988) which also hold adjacent ranks, since females adopt their mother's rank (Pereira, 1988), often for prolonged intervals (Sade, 1967; Hausfater et al., 1982). This is not likely to have been the case for the fissioning event reported here because all eight females were accompanied by dependent infants. We do not know the relatedness of the founder Q Troop adult females to one another or the specific or relative rankings they previously held in D Troop. However, the determinants of fission group membership are strongly suggested by the striking differences in demographic composition between Q and D Troops after fissioning. Q Troop contained only a single adult male, and the eight mother–infant pairs represented virtually all of the most recent cohort of infants from the original D Troop. We have not observed any tendency toward synchrony of births in known lineages of other focal troops where such synchrony could have been recognized, nor are we aware of reports of synchrony for other savanna baboon populations.

That the eight Q Troop females immigrated together and had infants born within 7 months of one another is a finding not readily explained except by common paternity (Altmann, 1979). Since we did not observe sexual consortship or other behavior relating CNI to the adult females with infants that accompanied him, we provide only strong circumstantial evidence that CNI was the father of these infants. Adult females in our study population associate with high-ranking males that consort with them at the time of probable ovulation (Smith, 1986) and that associate closely with them during pregnancy and following parturition (Busse, 1984, 1985; Hamilton, 1984). At the peak of estrus, alpha males are exclusive consort partners on 83% of the conceptive cycles ($N = 66$) that we have observed (Bulger and Hamilton, 1988). We know CNI emigrated from his natal

group and entered D Troop. He was at the age when first transfer and rapid rise to alpha status are likely (Hamilton and Bulger, 1990). The mean alpha tenure in this population is 6 months and may be as long as 16 months (Hamilton and Bulger, 1990). It seems likely that the cluster of females fissioning with CNI to form Q Troop were mothers of his infants that formed a paternal subgroup within D Troop.

If we are correct in our interpretation of the origin of Q Troop, then membership in the fissioned group is accounted for by both matrilineal and paternal relationships. The contingent of juveniles participating as founders of Q Troop almost certainly were the older progeny of Q Troop females and could not have been closely related to CNI. The probability that relatively closely related lineages remained together at the time of fissioning when the new group formed is extremely low.

Nash (1976) observed fission of a group of olive baboons in Tanzania. While she does not report the exact rank of the females that joined the fissioning group, she categorized those individuals as relatively high, middle, and low ranking respectively, suggesting that matrilineal relationships did not account for the membership of the subgroup. While Nash (1976) is often cited as providing evidence for a lineal effect in savanna baboon fissioning, she actually demonstrated participation of matrilines and provided no evidence of a lineage effect. The subgroup was initially accompanied by an older male. His consortship relationship to the females that he accompanied was not reported.

As with other features of savanna baboon sociality, we expect substantial variation in the bases of subgroup formation. Preservation of entire or partial matrilines—mothers and their dependent and recently (1–4 years) independent offspring—is a feature of most Old World monkey fissioning events, including those observed in this study.

Cohorts of paternal sibships may be an additional important basis for adult female membership in fissioning savanna baboon groups. Since both maternity and paternity are bases for social cohesion within baboon groups, no exclusive appeal to maternal kinship as the proximate or ultimate basis for choice of fragment to follow at the time of fissioning is necessary. If there is any unitary explanation for the basis of choices made by social units during group fragmentation in Old World monkeys, it is that current social affinities within families and other positive social relationships tend to be maintained.

Additional Males Joining Q Troop

The number of males in Q Troop swelled from 1 to 8 between October 1987 and May 1988 (Table I), including 10 different males. The OMU

Q Troop was penetrated initially by three of the lowest-ranking males in C Troop. However, these where older and thus more experienced individuals, perhaps better able to deal with attempts at exclusion by CNI as a result of being experienced in effective subordination. Indeed, their entry into Q Troop was in inverse rank order and probably in order of greatest age. Subsequent intrusions included both the highest-ranking and the lowest-ranking adult males of C Troop. When observations were concluded in May 1988, males were passing freely from C to Q Troop and back again (Figs. 1D and E). These transferring males maintained their relative rank relationship in both groups. The eventual ratio of males to females in Q Troop reached and exceeded that of other groups spatially bracketing Q Troop (Table I).

One-Male Group Endurance

Among MM savanna baboon groups, male consortship of estrous females is the usual mating pattern. In the population that we observe reproduction is aseasonal and there is thus relatively even and essentially random timing of fertile female cycles. When CNI held exclusive adult male tenure in Q Troop, only one female, a maturing subadult, was cycling. The other eight females were all nursing and in postpartum amenorrhea. It is possible that the relatively synchronous parturition and subsequent amenorrhea of Q Troop females reduced intruder pressure (Myers *et al.,* 1979), thereby enhancing the endurance of the group as a OMU. This argument assumes that intruder pressure is correlated with numbers of estrous females, as established by Packer (1979) and Manzolillo (1986) for *P. h. anubis.* However, before UOE's penetration of Q Troop, CNI had successfully rebuffed approaches by at least two first-transfer males (Hamilton and Bulger, submitted for publication) and had evicted UOE on several occasions. Q Troop ceased to be a OMU because of CNI's eventual inability to control intruders and his subsequent behavioral shift from defense of group to consortship (Hamilton and Bulger, 1992).

Adult male baboons may exclude competitors from access to receptive females by consortship or by defending entire groups. If males cannot exclude other males from groups, MM groups will form. This may provide a sufficient explanation for the MM and OMU condition of most contemporary savanna baboon societies. Single intruders may be evicted as they arrive by single males maintaining OMUs. After entry of any additional male, consortship may take precedence, thereby precluding any further opportunity to maintain OMU status.

ACKNOWLEDGMENTS

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