



Group size, infant development and social networks in free-ranging rhesus monkeys

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Abstract. The hypothesis that demographic processes are important in determining social structure among non-human primates through their effects on the development of individual social relationships was tested. Changes in maternal behaviour, infants' social milieux and infants' social networks were examined as a function of changes in group size and composition among free-ranging rhesus monkeys, *Macaca mulatta*, on Cayo Santiago, Puerto Rico. Data were analysed for 10 group-years collected between 1974 and 1990 representing a single social group during periods of rapid expansion and fissioning, two daughter groups following fissioning and an unrelated group that did not undergo fissioning. As group size expanded, infants found themselves near (<5 m) larger numbers of group members and smaller proportions of close kin. Mothers spent more time near their infants and sought more proximity with them. Infants developed social networks that were more highly kin biased. When the groups fissioned, these trends reversed. Significant correlations were found between group size, mother–infant interaction and infant social networks across all group-years. Individual variation in the degree to which infant social networks were kin biased was related both directly to the infant's social milieu and indirectly to its relationship with its mother. Given the long-term nature of the mother's influence on social networks, these results suggest that demographic influences on developmental processes can lead to progressive changes in social structure in the absence of resource scarcity.

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Students of primate parent–offspring relations have long recognized the importance of group size, composition and structure for understanding mother–infant relationships and infant social development (e.g. Hinde 1974; Nicolson 1987). Because maternal behaviour and early social relationships are embedded within the social nexus of the group, mothers and infants both influence and are influenced by the constraints and opportunities other group members present.

More recently, this concept has become central to behavioural ecological theories concerned with relationships between demographic processes and social structure in natural groups of primates (Altmann & Altmann 1979; Dunbar 1987).

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Researchers have hypothesized that developmental processes may serve as important mechanisms by which demographic processes influence primate social structure. This hypothesis is based on two major premises: (1) early social relationships have long-term effects on individuals' patterns of social relationships within their groups, and (2) demographic processes influence the size and composition of groups (e.g. Cohen 1969, 1972).

Numerous studies in captivity and in the field have suggested that the presence or absence of particular classes of individuals may influence the degree to which macaque mothers encourage independence in their infants and tolerate their interaction with others (Hooley & Simpson 1981, 1983; Fairbanks & McGuire 1987; Silk 1991; Berman 1992). In general, mothers tend to tolerate interaction with their own close kin and associates. The presence of close kin is associated with relaxed maternal styles and broad infant social networks (Berman 1980; Gouzoules &

Gouzoules 1987; Fairbanks 1990). The latter appears to occur both when infants are young and under their mothers' direct control and when they are older and considerably more independent (Berman 1982a; de Waal 1996). This finding suggests that mothers' responses to the social milieu at the time they rear their infants have long-term influences on infants' social networks. Few empirical studies have examined these hypothesized links between maternal behaviour and infant social networks, however, within the context of demographic processes that affect the availability of social partners in free-ranging and naturally organized social groups.

One reason for this omission may be the difficulty of separating demographic effects from ecological effects. As Altmann & Altmann (1979) pointed out, other environmental factors also affect maternal behaviour both directly (e.g. Lee 1983a; Johnson & Southwick 1987) and indirectly through delayed effects on the size and composition of the group. This difficulty can be overcome, however, through studies in free-ranging, food-enhanced populations, where animals are relatively unmanipulated, but where major environmental influences such as predation and resource availability and distribution are controlled. In one such study of free-ranging rhesus monkeys, *Macaca mulatta*, on Cayo Santiago, Berman (1988) examined changes in maternal behaviour and infant social networks between 1974 and 1984 in an expanding social group (group I). Although no changes were observed in mother-infant contact or nursing, mothers spent less time at a distance from their infants and took larger roles in maintaining proximity with them when the group was large than when it was small. When the group was large, infants spent more time with each of their close kin and less time with more distantly related group members. Berman hypothesized that mothers' responses to the presence of large numbers of distantly related and unrelated group members in large groups led to a focusing of infants' social networks onto kin. Given the correlational nature of the study, however, it was difficult to attribute the observed changes in social behaviour definitively to changes in group size and not to other changes that may have occurred within the group or population during the study.

Here we present an extension of Berman's (1988) study in the form of a natural experiment.

During 1985–1987, group I fissioned into five smaller groups, allowing us to test the prediction that the trends in maternal behaviour and infant social networks observed in group I when it was expanding would be reversed in the smaller daughter groups. We examine the extent to which variations in group size occurring between 1974 and 1990 (i.e. before, during and after the period of fissioning) were related to variations in (1) aspects of the infant's social milieu, (2) measures of mother-infant interaction and (3) aspects of infant social networks. For comparison, we also include data on a large unrelated group (group F) during 1990. Finally, we describe the nature of changes in infant networks in more detail than previously, and assess the hypothesis that changes in infant social networks were mediated by changes in maternal behaviour and were not simply responses of infants and/or other group members to the changing social milieu.

METHODS

Cayo Santiago is a 15.2-ha island, about 1 km off the east coast of Puerto Rico, that supports a closed, free-ranging, provisioned population of rhesus monkeys. The colony was established in 1939 with the introduction of 409 rhesus monkeys from India. Since then, no monkeys have been added to the population except by birth, although a number have been removed over the years. The population has been censused daily since 1956, and hence is well-habituated and made up of known individuals with known histories and maternal kinship relationships (Carpenter 1942a, b; Sade et al. 1977, 1985; Rawlins & Kessler 1986).

Since 1972, management practices have been designed to minimize human interference and have been almost constant. The monkeys are provisioned with high-protein commercial monkey chow at the liberal rate of approximately 0.23 kg per monkey per day from hog feeders located in three 0.25-acre corrals. Water is provided ad libitum. Manipulation is limited to non-invasive measurement during an annual trapping period in January and February. Under this management scheme, the population expanded rapidly at a steady geometric rate of about 13% per year (Rawlins & Kessler 1986), from about 300 monkeys in the beginning of 1974 to nearly 1200 in 1983. A cull of

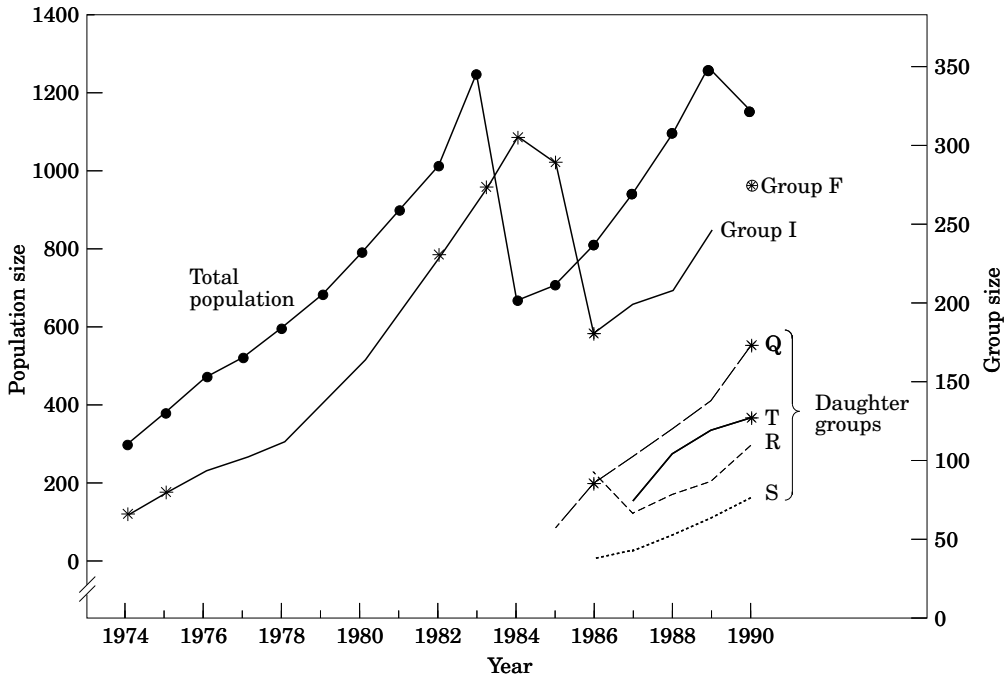


Figure 1. Total population size on Cayo Santiago and group sizes between 1974 and 1990 are shown for group I and its fission products. The size of the unrelated study group (F) in 1990 is also shown. These data were derived from official census sheets for September 1 for each year on Cayo Santiago and/or from published sources (Sade et al 1985; Kessler & Berard 1989; Manson & Perry 1993). Asterisks show the 10 group-years analysed in this study.

three whole social groups in early 1984 reduced the population to about 700. The original study group (I), which was not involved in the cull of 1984, grew at a geometric rate of approximately 16% per year during its period of expansion (1974–1984) (Rawlins & Kessler 1986).

Group I was formed naturally by fissioning in 1961 and was organized in the manner typical of multi-male macaque groups (e.g. Lee 1983b): a number of females and their immature offspring made up the permanent core of the group along with a more transient set of adult males. Male offspring generally left their natal groups at puberty and joined other groups. Adult daughters, on the other hand, remained in their natal groups for life and continued to associate with their mothers and maternal kin. In this way, large maternal lineages that were also subunits of social organization developed over time. Until fissioning, there were three extended lineages in group I with members spanning as many as four generations. The total group membership varied from 53 monkeys at the beginning of 1974 to 321 at the

end of 1984 (Fig. 1). The group did not fission during this period.

In 1985, about 66 monkeys left group I to form group Q. In early 1986, 36 more monkeys fissioned to form group S. A third group (R) of 64 monkeys separated in 1986 and gradually split into two during 1987 (groups R and T). After 1986, only one lineage remained in group I until its removal from the island in early 1990.

When groups fission, they typically split along lineage lines; i.e. the lineages usually remain intact and one or more lineages separate from the rest of the group and form a daughter group. Chepko-Sade & Sade (1979) found only a few exceptions to this rule on Cayo Santiago. In most of these, the lineage split along sub-lineage lines, with the eldest daughter of the matriarch and her descendants splitting off from the rest of the lineage. The probability of fissioning was related to the size of the group or lineage, but a better predictor was the mean degree of relatedness between members (Chepko-Sade & Olivier 1979). When degree of relatedness became small, the group or lineage

became likely to split. Although the fissionings from group I did not follow all of Chepko-Sade & Sade's rules, with few exceptions, infants remained with their mothers and with their close and moderately close maternal relatives (i.e. equivalent of first cousins or closer).

We analysed data for 10 group-years (Fig. 1) and 116 mother-infant pairs. Sixty of the infants were born into group I during its period of expansion from 1974 to 1984 (nine in 1974, 11 in 1975, 19 in 1983 and 21 in 1984). The remaining 56 infants were observed during or after the period of fissioning: 1985: 21 in group I, 1986: 12 in group I and four in group Q, 1990: eight in group Q and seven each in groups T and F. In all groups, infant subjects were drawn from all matriline. The sex ratio of the infants was approximately equal (males: 50.9%, $N=59$; females: 49.1%, $N=57$). All but 11 (9.5%) infants had multiparous mothers.

Focal-animal sampling methods (Altmann 1974) were used to record the social interaction of all infants with their mothers and with other members of the group. All interactions involving the infant were recorded chronologically on checksheets (1974–1986) or on a hand-held computer (1990; Micropalm 4000) along with the identities of the initiator and the recipient of the interaction and the time it occurred. During these sessions, we also recorded point (instantaneous) time samples at 2-min (1974–1986) or 3-min (1990) intervals identifying the individuals in contact with the infant, within 60 cm and between 60 cm and 5 m. Data were analysed for infants 25–30 weeks of age. Between 1974 and 1986, each infant was observed for 9.0 h (1.5 h per week) between 0700 and 1200 hours in sessions that generally lasted 30 min. During 1990, each infant was observed an average of 8.1 h (range=4.5–12.1 h) between 0700 and 1800 hours in sessions that generally lasted 15 min. Although data collection methods in 1990 differed in these aspects from those for earlier years, field comparisons of the two collection protocols in 1990 revealed no systematic differences in measures of behaviour analysed here (K. M. Grosser and C. M. Berman, unpublished data). In all years, measures of distance were checked periodically with tape measures. The senior author (C.M.B.) collected all the data in 1974 and 1975 but was joined by several assistants (trained in the field by C.M.B.)

in later years. There was a high level of inter-observer reliability between C.M.B. and each assistant each year (Kappa coefficients ≥ 0.90 ; Cohen 1960).

We analysed the following measures of mother-infant interaction: (1) time on : the percentage of point time samples during which mothers and infants were neither in ventro-ventral contact nor in nipple contact; (2) maternally initiated nipple contact: the proportion of all nipple contacts initiated by the mother; (3) time on the nipple: the percentage of point time samples infants spent on the mother's nipple; (4) time >5 m: the percentage of time on the mother that was spent more than 5 m from her; (5) relative rejections: the proportion of all attempted nipple contacts, including those initiated by the mother, that were prevented by the mother; (6) proximity index: a measure of the infant's relative role in maintaining proximity to the mother; i.e. the percentage of approaches made by the infant to the mother over a 60-cm limit minus the percentage of departures made by the infant from the mother over a 60-cm limit (Hinde & Atkinson 1970). Descriptions of the infant's social milieu were derived from point time samples and were based on the mean number and composition of individuals observed within 5 m and within 60 cm of the infant at any one time. Descriptions of infant social networks were based on the percentages of observation time that infants spent within 60 cm (touching distance) and within 5 m of particular group members (derived from point time samples).

Kin were classified by their degree of relatedness to the infant through maternal lines, assuming no inbreeding or sharing of paternal genes: degree of relatedness (r)=0.250, 0.125, 0.063 and no more than 0.032. Members of different lineages were considered unrelated ($r=0$). Individual group members were classified as same-sexed peers (same-sexed members of the infant's birth cohort), yearlings (1 year), juveniles (2 and 3 years) and adults (all parous females and females 4 years and older). Adult males were not included in the analyses, except where specifically noted. We described specific methods of data analysis in the results. All statistical tests were two-tailed. We reported results as significant when $P \leq 0.05$, as non-significant tendencies when $0.05 < P \leq 0.10$, and as non-significant () when $P > 0.10$.

RESULTS

Group Size, Population Size and Group Composition

Yearly changes in group size and total population size are shown in Fig. 1 for the study groups between 1974 and 1990. With each fissioning event, group I was reduced in size, and smaller daughter groups formed that subsequently increased in size. The proportions of the groups represented by each age–sex class varied from year to year, but in most cases, changes were not related to group size (adult females: $r=0.15$, ; juvenile females: $r=0.24$, ; yearling females: $r=-0.13$, ; same-sex peers: $r=0.31$, ; yearling males: $r=-0.06$, ; juvenile males: $r=0.72$, $P<0.019$; $N=10$ group-years). Group size was not strongly related to total population size ($r=0.47$, $N=10$ group-years,), particularly after the cull in 1984 ($r=-0.03$, $N=6$ group-years,).

Given the matrilineal organization of macaque groups and the tendency for groups to fission along kinship lines (Chepko-Sade & Sade 1979), it is not surprising that changes in group size were consistently associated with changes in the maternal kinship structure. As group I expanded (1974–1984), mean degrees of relatedness between infants and other group members decreased, and after fissioning, they increased both in group I and the fission product, group Q (Table I). Highly significant negative correlations between group size and mean degree of relatedness were found across all group-years for all group members combined ($r=-0.93$, $N=10$ group-years, $P<0.0004$; Fig. 2a) and for each age–sex class separately (Table II). These results reflect tendencies for infants in large groups to have similar absolute numbers of close kin (siblings, grandmothers and infant offspring of sisters), but for those close kin to represent smaller proportions of the group membership (Table II).

Infants' Social Milieux

As in Berman (1988), changes in group size and composition were reflected in changes in the infant's social milieu. As group I expanded, infants found themselves moderately close (<5 m) to increasing numbers of group members at any given time (Table I). As predicted, this trend reversed in group Q following fissioning, but not significantly so in group I (Table I). Over all

Table I. Changes in mean degrees of relatedness, numbers of individuals less than 5 m from infants, and measures of mother–infant interaction during group expansion (1974–1984) and following fissionings

Measure	Means (Before, After)	$F_{df,df}$ ⁴	$P<$
Mean degree of relatedness			
Expansion ¹	0.032, 0.017	97.5 _{1,56}	0.0005
Group I fission ²	0.016, 0.031	86.2 _{1,31}	0.0005
Group Q fission ³	0.016, 0.038	143.8 _{1,21}	0.0005
Number less than 5 m			
Expansion	2.5, 7.1	148.0 _{1,56}	0.0005
Group I fission	7.5, 6.8	0.5 _{1,31}	
Group Q fission	7.5, 3.8	14.7 _{1,21}	0.001
Time more than 5 m from mother			
Expansion	52.9, 26.9	94.2 _{1,54}	0.0005
Group I fission	24.2, 41.5	17.9 _{1,31}	0.0005
Group Q fission	24.2, 37.4	5.1 _{1,21}	0.035
Proximity index			
Expansion	42.2, 31.8	16.9 _{1,55}	0.0005
Group I fission	35.4, 27.6	1.5 _{1,32}	
Group Q fission	35.4, 29.7	0.0 _{1,22}	

¹Group I data from 1974 and 1975 ($N=20$ infants, group size=63 and 78, respectively) are contrasted with data from 1983 and 1984 ($N=40$ infants, group size=265 and 282, respectively).

²Group I data from 1984 ($N=21$ infants, group size=282) are contrasted with group I data from 1986 ($N=13$ infants, group size=180).

³Group I data from 1984 ($N=21$ infants, group size=282) are contrasted with group Q data from 1986 ($N=4$ infants, group size=85).

⁴ANOVA; lineage status was controlled for all measures except the proximity index (for which infant sex was controlled; see text).

group-years, numbers of group members less than 5 m from the infant were highly correlated with group size ($r=0.90$, $N=10$ group-years, $P<0.0004$; Fig. 2b). This relationship was due primarily to increases in numbers of distantly related group members within 5 m of infants in larger groups; although positive correlations with group size were seen within each kinship category (Table III), they reached significance only for the most distantly related kin (degree of relatedness ≤ 0.032). Numbers of group members within 5 m of infants were not strongly related to total population size ($r=0.043$, $N=10$ group-years,).

In contrast, infants in all group-years were within touching distance (<60 cm) of similar numbers of group members at any given time ($\bar{X}=0.5$,

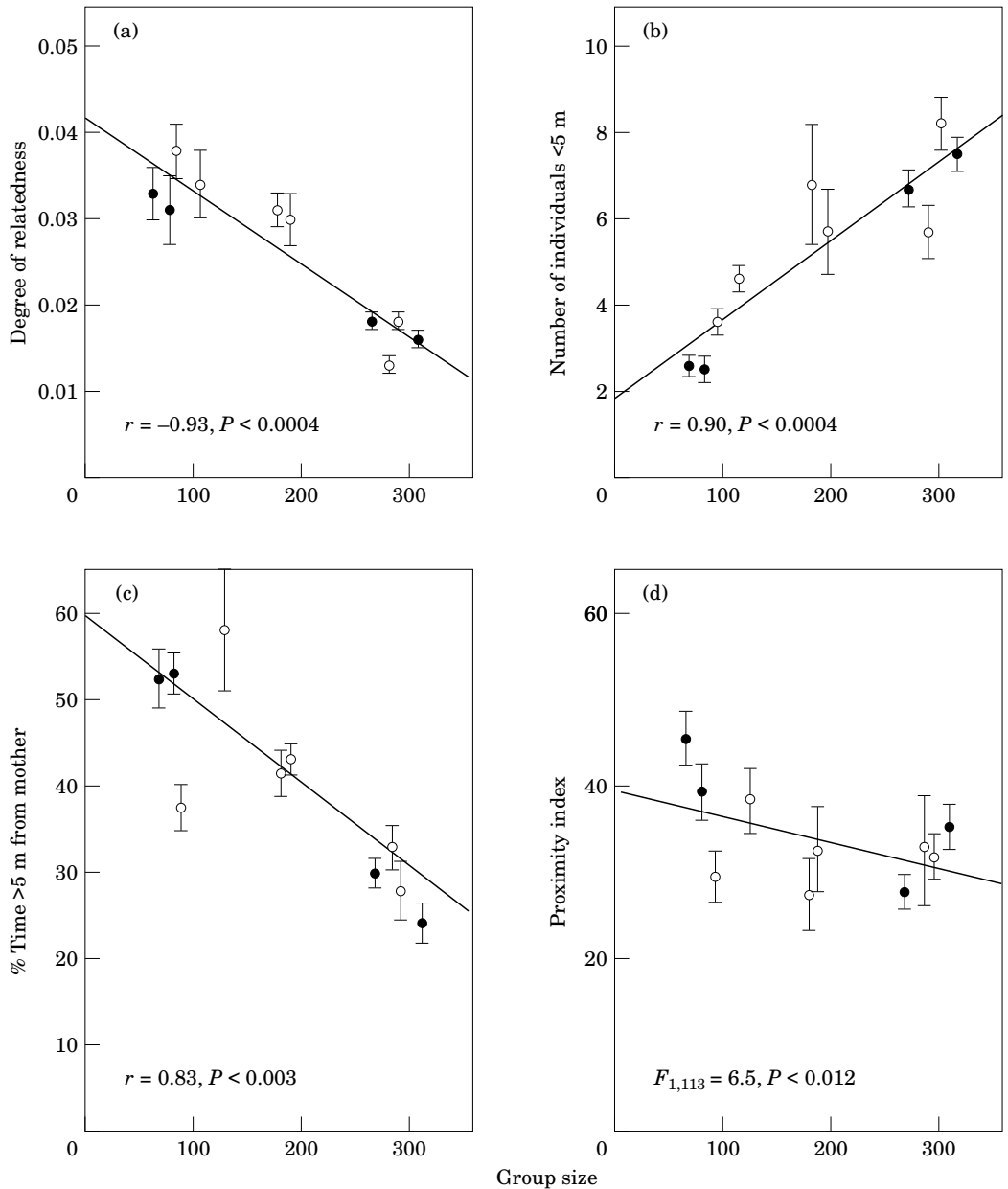


Figure 2. (a) Mean degrees of relatedness of infants to group members, (b) mean numbers of group members less than 5 m from infants at any one time, (c) percentage of time infants spent more than 5 m from the mother and (d) the proximity index as functions of group size across all group-years of the study. Means \pm SE are shown for group I during expansion (●) and for group-years during or after (○) the period of fissioning.

$r=0.36$, $N=10$ group-years,). Since infants were attractive to other group members, and since it was physically possible to have as many as 6–8 other individuals within 60 cm of an infant, these

results suggest that other factors, perhaps factors actively involving generally intolerant mothers or infants, acted to regulate close contact with the infant.

Table II. Mean \pm degree of relatedness between infants and members of other age–sex classes, numbers of close kin (siblings, grandmothers, infant offspring of sisters) and proportions of the each age–sex class they represent

Age–sex class	Degree of relatedness	r^1 with group size	Number of close kin	r^1 with group size	Proportion	r^1 with group size
Adult females	0.047 \pm 0.018	– 0.91****	1.6 \pm 0.6	0.05	0.05 \pm 0.03	– 0.72*
Juvenile females	0.028 \pm 0.008	– 0.79**	0.6 \pm 0.2	0.69*	0.03 \pm 0.01	– 0.58(*)
Yearling females	0.028 \pm 0.010	– 0.82**	0.4 \pm 0.2	0.22	0.03 \pm 0.02	– 0.53
Peers	0.020 \pm 0.008	– 0.50	0.5 \pm 0.4	– 0.33	0.05 \pm 0.05	– 0.70*
Juvenile males	0.030 \pm 0.011	– 0.87****	0.5 \pm 0.3	0.04	0.04 \pm 0.04	– 0.70*
Yearling males	0.029 \pm 0.010	– 0.81**	0.3 \pm 0.1	0.10	0.03 \pm 0.03	– 0.68*
Total	0.026 \pm 0.009	– 0.93****	3.8 \pm 1.2	0.12	0.03 \pm 0.02	– 0.81**

(*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0005$.

¹Pearson correlation coefficients with group size.

$N = 10$ group-years.

Table III. Mean \pm numbers of group members less than 5 m from infants at any time by kinship class, and Pearson correlation coefficients with group size

Kinship (degree of relatedness)	Number of group members within 5 m	Correlation with group size
0.250	0.82 \pm 0.31	0.59(*)
0.125	0.46 \pm 0.17	0.52
0.063	0.40 \pm 0.21	0.61(*)
0.032	1.03 \pm 0.65	0.73*
0 ¹	1.54 \pm 0.78	0.46
All kinship classes ¹	4.25 \pm 1.45	0.85**

¹Includes unrelated adult males.

(*) $P < 0.1$, * $P < 0.02$, ** $P < 0.002$.

$N = 10$ group-years.

Mother–Infant Relationships

The tendency for mothers to spend less time at a distance (> 5 m) from their infants as the group expanded (1974–1984; Berman 1988) also reversed after fissioning (Table I). Over all groups, mothers in large groups spent significantly less time at a distance from their infants ($r = -0.83$, $N = 10$ group-years, $P < 0.003$; Fig. 2c) than mothers in smaller groups. Tendencies for mothers to take smaller roles in maintaining proximity to infants in smaller groups were less consistent. No significant changes were seen in proximity indices after fissioning in group I or in group Q. When we controlled infant sex differences through analysis of covariance, however, we found a significant tendency across groups for mothers to take relatively larger roles in maintaining proximity to

their infants in larger than in smaller groups ($F_{1,111} = 6.49$, $P < 0.012$; Fig. 2d). Using Hinde's (1975) methods for distinguishing the relative responsibilities of partners for differences between relationships, these results tentatively suggest that mothers rather than infants were primarily responsible for variations in proximity related to group size. Mothers in larger groups tended to seek proximity with their infants more than mothers in smaller groups, perhaps because of the proximity of many other monkeys. Given the close relationship between group size and numbers of individuals within 5 m of infants, it is not surprising that mothers spent significantly less time at a distance ($r = -0.78$, $N = 10$ group-years, $P < 0.008$) and took larger roles in maintaining proximity ($r = -0.65$, $N = 10$ group-years, $P < 0.042$) to infants that were observed near large numbers of group members than to those surrounded by few other individuals. No significant correlations were found between total population size and either time spent at a distance from the mother ($r = -0.22$, $N = 10$ group years,) or the proximity index ($r = -0.58$, $N = 10$ group-years,). As in Berman (1988), few marked relationships were found between measures of mother–infant contact and either group size or population size (Table IV).

Infant Social Networks

To test the hypothesis that infant social networks were more highly focused on kin relationships in large groups than in small groups, it was first necessary to confirm that infant social

Table IV. Pearson correlation coefficients: measures of mother-infant contact with group size and population size

Measure	Group size	Population size
Time o	-0.06	-0.36
Time on nipple	0.07	0.24
Relative rejections	-0.50	-0.36
Maternally initiated nipple contact	-0.45	-0.71*

* $P < 0.05$. $N = 10$ group-years.

networks were indeed kin biased. To do this, we used the Z_r partial correlation test (de Vries 1993) to examine the extent to which percentages of time infants spent within 5 m of individual group members were correlated with maternal degrees of relatedness, while controlling for differences between the dominance ranks of the group members (or their mothers, in the case of immatures) and the infant's mother. The partial Z_r test is a row-wise, distribution-free matrix permutation correlation technique based on the Pearson correlation test that uses data in all cells of a social interaction matrix (i.e. from all pairs of animals in a matrix), while avoiding problems of their interdependence. A program for performing the partial Z_r test is a part of the latest version of MatMan, a package of programs for the analysis of sociometric matrices (see also de Vries et al. 1993).

Separate analyses were conducted for each age-sex class within each group-year. Where necessary, the effects of outliers were controlled by Winsorizing (Sokal & Rohlf 1981). Two thousand permutations were carried out in each test. The percentage of time that infants spent near others was positively correlated with maternal degree of relatedness in all age-sex classes and all group-years. The coefficients reached significance in all but six of 60 cases, confirming that infant social networks were indeed biased towards kin. Note that these correlations were not due to a joint correlation with rank distance, because this factor was partialled out.

To compare the relative intensity of kin bias (i.e. the degree to which networks were focused on kin) in groups of different sizes, we calculated the mean percentage of time each infant spent less than 5 m from members of each age-sex-kinship

class (e.g. adult sisters, unrelated juvenile males) on a per capita basis. Hence if an infant had three adult sisters with whom it spent 20, 30 and 40% of its time, respectively, its per capita score for adult sisters was 30%. Next, we examined per capita scores as a function of degree of relatedness separately for each infant with each age-sex class of partner. From these functions, we calculated regression coefficients separately for each infant that had kin in at least three out of the five kinship categories, and plotted them as a function of group size.

Infants' networks were indeed more highly focused on close kin and peers in large groups than in small groups (Fig. 3). Regression coefficients were positively correlated with group size for all age-sex classes, and they reached significance for all classes except juvenile male partners. When the same analyses were repeated substituting total population size for group size, significant results were not found.

To demonstrate the effects of group size on amounts of social interaction separately for different categories of kin, mean per capita scores were also calculated over all infants within a given group-year and were correlated with group size separately for each age-sex-kinship class. The increased focus on kin seen in large groups was apparently due primarily to strong tendencies for infants in large groups to spend more time with each of their closely related kin (Table V; Fig. 4). Infants in large groups tended to spend more time with each of their siblings and/or grandmothers, and with their most closely related peers ($r = 0.125$; i.e. the offspring of their adult sisters) than infants in smaller groups. Correlation coefficients were highly significant for female siblings and for peers, but not for male siblings. Although only a few significant correlations were found for less closely

Figure 3. Degrees of kin bias as a function of group size. Mean \pm regression coefficients for per capita amounts of time infants spent less than 5 m from group members versus degree of relatedness are plotted for each group-year of the study as a function of group size. Separate plots are shown for each age-sex class of group member: (a) adult females, (b) juvenile females, (c) yearling females, (d) same-sex peers, (e) yearling males and (f) juvenile males. ●: Group-years during the expansion of group I; ○: group-years during and after the period of fissioning. Standard error bars are missing for cases in which $N < 4$.

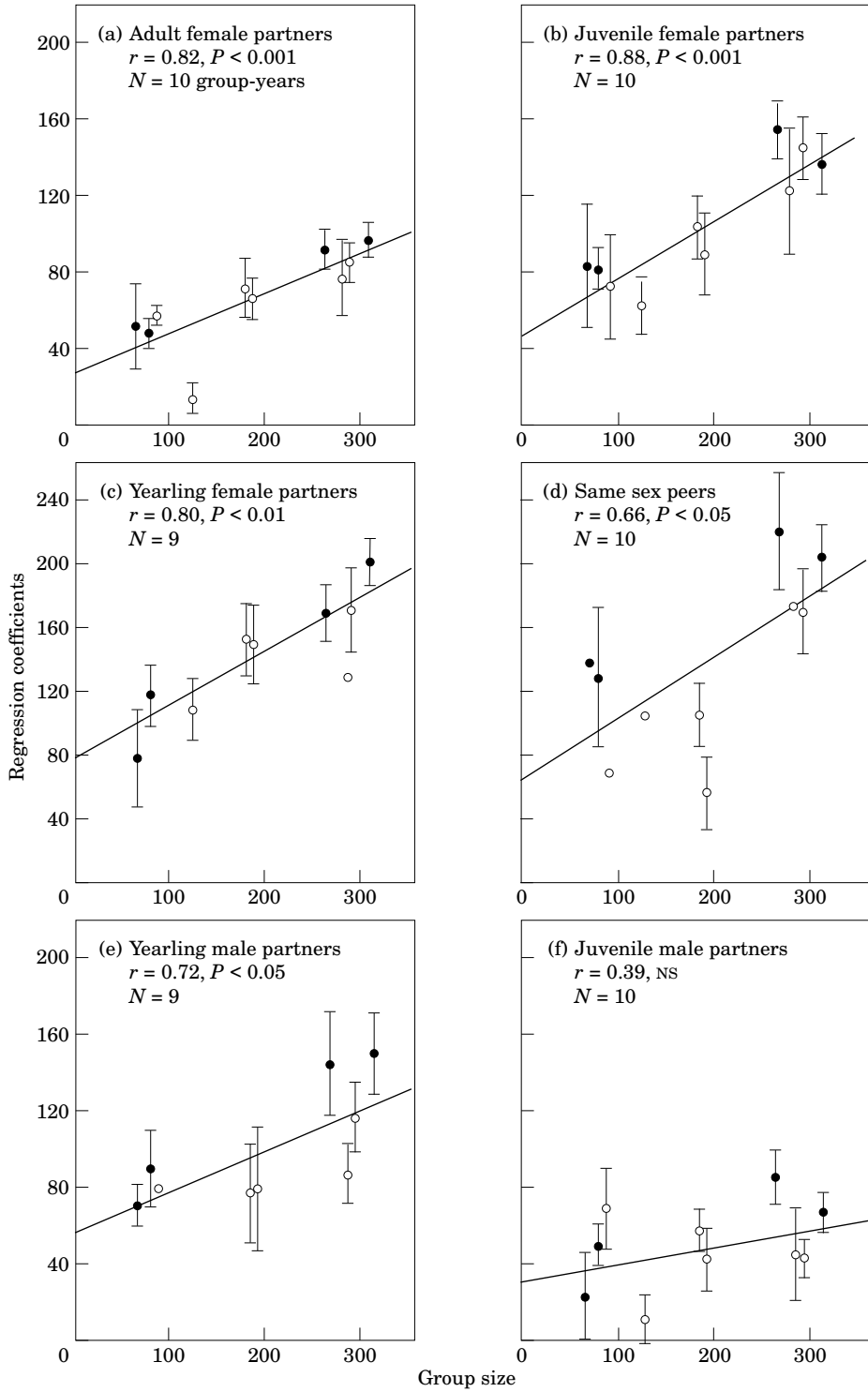


Table V. Pearson correlation coefficients for group size with per capita values for percentage of time infants spent with members of each age–sex–kinship class

Degree of relatedness	Adult females	Juvenile females	Yearling females	Juvenile males	Yearling males	Same-sex peers
0.250	0.83**	0.97****	0.91***	0.60(*)	0.68(*)	
0.125	0.79**	0.38	0.65(*)	0.02	0.17	0.70*
0.063	0.35	0.16	0.11	0.56(*)	0.70*	0.12
0.032	–0.48	–0.63*	–0.41	–0.49	–0.53	–0.47
0	–0.45	–0.38	–0.49	–0.35	–0.40	–0.74*

(*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

$N = 10$ group-years.

related age–sex classes, correlations were uniformly positive for moderately closely related kin ($r = 0.125, 0.063$), and uniformly negative for distantly related ($r \leq 0.032$) and unrelated group members ($r = 0$). The strongest of these correlations indicated that infants in large groups spent significantly less time with unrelated peers than infants in smaller groups.

Group Size Versus Mean Degree of Relatedness

Given the close inverse relationship between group size and mean degrees of relatedness, and the importance of mean degree of relatedness as a predictor of group cohesion (Chepko-Sade & Sade 1979), we next asked whether mean degree of relatedness may have been a better predictor than group size of numbers of individuals near the infant, measures of mother–infant interaction and measures of infant social networks, particularly with close female kin and peers. We used analysis of covariance (ANCOVA) to examine the extent to which correlations with group size were independent of associations with mean degree of relatedness for the following measures: (1) mean numbers of group members less than 5 m from the infant at any one time; (2) time mothers spent more than 5 m from infants; (3) the proximity index; (4) per capita amounts of time less than 5 m from close female kin and peers; and (5) regression coefficients for per capita amounts of time infants spent less than 5 m from group members versus degree of relatedness. The mother's lineage status (top-, middle- or bottom-ranking) was entered as a control factor before the covariates, because several variables differed significantly for infants in different lineages (Table VI). Since only the proximity index differed by infant sex

($F_{1,112} = 10.94, P < 0.001$), we included it as a control factor for only this dependent variable. Sums of squares were partitioned sequentially. Hence, the first covariate was assessed after all the variance associated with the factors was removed, and the second covariate was assessed after all the variance associated with the factors and the other covariate was removed.

Mean degree of relatedness was not a better predictor of the dependent variables than group size (Table VII). When group size was assessed after variance related to mean degree of relatedness was removed (Table VII, first two columns), significant relationships or non-significant tendencies were sustained for nearly all dependent variables. In contrast, except for numbers of group members less than 5 m from infants, no marked associations with mean degree of relatedness were found after the variance associated with group size was removed (Table VII, second two columns).

Infant Relationships and Mother–Infant Interaction

Similar ANCOVA methods were used to examine the hypothesis that mother's responses to changes in the infant's social milieu played a role in mediating changes in the degree to which infant social networks were focused on kin. We examined the extent to which variations in regression coefficients for time spent with group members versus degree of relatedness were related independently to variations in measures of mother–interaction (time spent more than 5 m from the mother and the proximity index) and to numbers of group members less than 5 m from the infant at any one time. If measures of mother–infant interaction were related to the regression

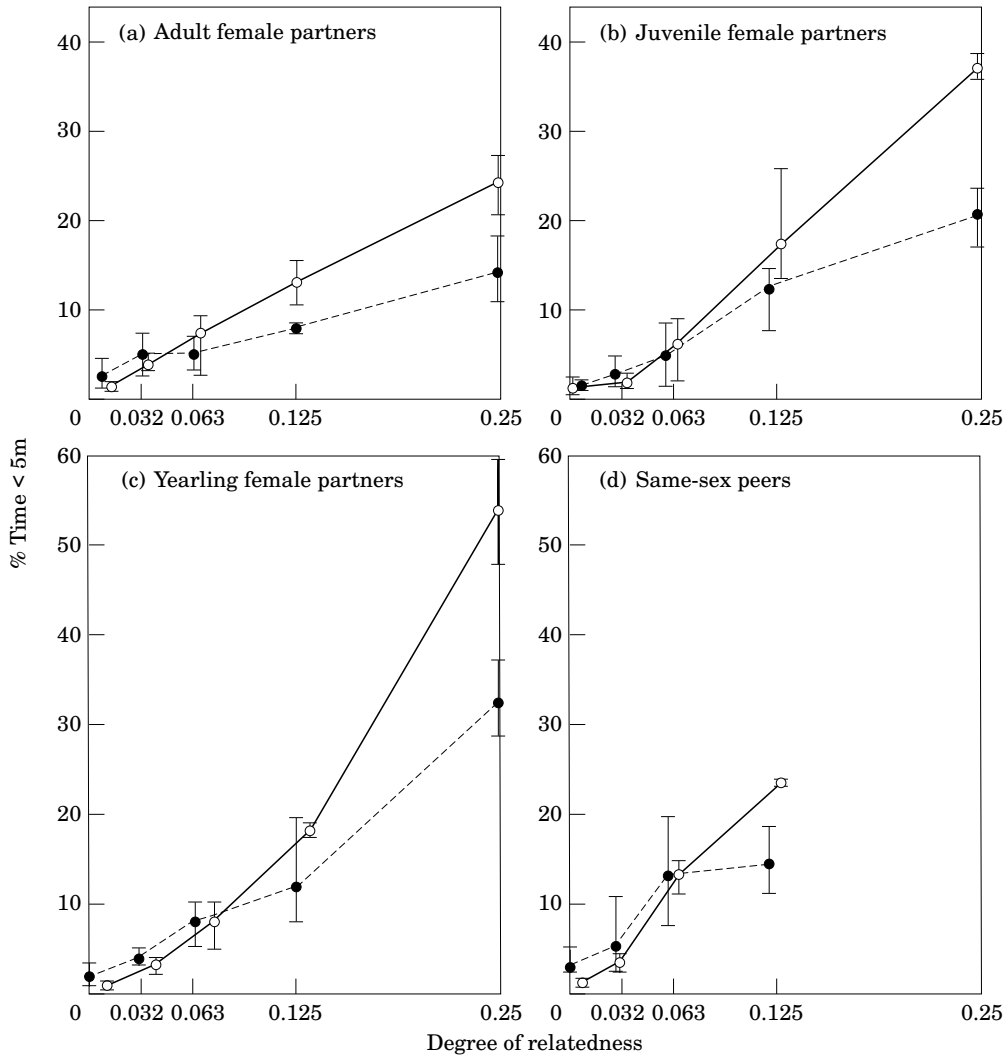


Figure 4. Means and ranges for per capita amounts of time infants in the four largest (\circ) and four smallest (\bullet) group-years spent less than 5 m from group partners are plotted as functions of degrees of relatedness. Separate plots are shown for (a) adult female partners, (b) juvenile female partners, (c) yearling female partners and (d) same sex peers. The four largest group years were group I in 1983, 1984, 1985, and group F in 1990 (group sizes=265, 282, 291 and 284, respectively). The four smallest groups were group I in 1974 and 1975, group Q in 1986 and group T in 1990 (group sizes=63, 78, 85 and 128, respectively).

coefficients independently of numbers of group members near infants, the importance of maternal mediation would be supported. Both lineage status (top-, middle- or bottom-ranking) and infant sex were entered as control factors before the covariates. As before, sums of squares were partitioned sequentially, allowing us to assess the relationship of mother-infant interaction after

all the variation associated with the control factors and with numbers of group members near infants were removed.

Maternal behaviour appeared to mediate variation in the degree to which infants' social networks with other females and peers were focused on kin (Table VIII). In all cases, regression coefficients were significantly related to measures

Table VI. ANOVA: measures of infants' social milieu, mother–infant interaction and infant social networks by lineage status

Measure	Lineage means			ANOVA ²	
	Top	Middle	Bottom	$F_{df,df}$	$P <$
Social Milieu					
Number less than 5 m	6.9	6.9	4.1	12.4 _{2,112}	0.0005
Mother–infant interaction					
Time more than 5 m	37.1	27.4	40.1	4.2 _{2,122}	0.018
Proximity index	32.5	34.5	34.8	0.3 _{2,110}	
Per capita amounts of time less than 5 m from kin					
Adult females	22.7	27.4	17.9	3.4 _{2,89}	0.037
Juvenile females	32.9	39.5	29.6	1.4 _{2,58}	
Yearling females	47.2	53.0	49.7	0.3 _{2,38}	
Peers	17.6	26.4	16.5	1.8 _{2,39}	
Yearling males	40.4	36.7	29.9	2.0 _{2,30}	
Juvenile males	15.7	12.4	17.4	0.7 _{2,46}	
Degree of kin bias in infant social networks¹					
Adult females	80.2	81.3	61.5	1.9 _{2,111}	
Juvenile females	126.6	123.8	100.2	1.5 _{2,107}	
Yearling females	156.2	158.7	154.6	0.0 _{2,90}	
Peers	169.5	192.9	129.5	1.5 _{2,71}	
Yearling males	125.8	121.9	86.2	2.4 _{2,60}	
Juvenile males	63.2	34.3	54.1	2.1 _{2,92}	

¹Regression coefficients (slopes) for per capita amounts of time infants spent less than 5 m from group members versus degree of relatedness.

²Infant sex was controlled.

$N=116$ infants.

of mother–infant interaction independently of numbers of individuals near the infant (first two columns). In most cases, the degree of kin bias in infant social networks was also related to numbers of individuals near infants independently of mother–infant interaction (second two columns), suggesting that infants or others may also have responded more directly to the social milieu.

DISCUSSION

The results of this 'natural experiment' confirm and extend those of Berman (1988). As in the earlier study, we found that, as group I expanded, infants were surrounded by more group members and by proportionally fewer close kin. At the same time, mothers spent progressively less time at a distance from their infants and played larger roles in maintaining proximity with them (Table I). Finally, as the group expanded, infants' social networks became more highly focused on their

close kin (Figs 3, 4). We also established that most of these trends reversed after fissioning both in the main group and in the daughter group, such that strong correlations could be found between group size, mother–infant interaction and infant social networks across all group-years of the study (Figs 2, 4). Taken together, these findings offer strong support for the suggestion that infants' relationships with their mothers and with other group members were influenced by the size and/or composition of their groups, rather than by any unrelated changes that may have accompanied the original expansion of group I. Mothers do appear to seek more proximity with their infants when they are in large than in small groups, and their infants tend to form social networks that are more highly focused on kin.

As in Berman (1988), these results cannot be attributed to changes in resource availability. Amounts of food per monkey per day, as well as other resources, remained virtually constant over the course of the study. Nor can the results be attributed to variations in groups' access to

Table VII. Analysis of covariance: measures of infants' social milieu, mother–infant interaction and infant social networks by group size and infants' mean degree of relatedness to group members

Measure	Group Size ¹		Mean degree of relatedness ²	
	<i>F</i> _{df,df}	<i>P</i> <	<i>F</i> _{df,df}	<i>P</i> <
Social Milieu				
Number less than 5 m	56.7 _{1,111}	0.0005	7.2 _{1,111}	0.008
Mother–infant interaction				
Time more than 5 m	32.9 _{1,111}	0.0005	1.2 _{1,111}	
Proximity index	4.7 _{1,111}	0.033	0.3 _{1,111}	
Per capita amounts of time less than 5 m from kin				
Adult females	2.4 _{1,88}	0.12	0.2 _{1,88}	
Juvenile females	3.4 _{1,57}	0.07	0.0 _{1,57}	
Yearling females	13.9 _{1,35}	0.001	0.1 _{1,35}	
Peers	3.1 _{1,38}	0.09	0.2 _{1,38}	
Degree of kin bias in infant social networks³				
Adult females	5.4 _{1,110}	0.022	0.5 _{1,110}	
Juvenile females	5.8 _{1,106}	0.018	0.2 _{1,106}	
Yearling females	7.6 _{1,89}	0.007	0.0 _{1,89}	
Peers	0.6 _{1,70}		1.1 _{1,70}	

¹Lineage status and mean degree of relatedness were controlled.

²Lineage status and group size were controlled.

³Regression coefficients (slopes) for per capita amounts of time infants spent less than 5 m from group members versus degree of relatedness.

N=116 infants.

resources. Although social groups competed for access to the feeders, it is unlikely that this limited the total amounts of food available to individual animals in either group I or F. Groups F and I consistently ranked first and second, respectively, among the five to six social groups on Cayo Santiago over the course of the study, and as a result, maintained priority of access to at least one of three feeding corrals. Similarly, the results cannot be attributed to variations in overall population size or density on Cayo Santiago, because few relationships were found between population size and measures of group size, mother–infant interaction, infant social milieu or infant social networks. Finally, because the data from group F in 1990 departed little from that of group I and its fission products, the results were probably not due to peculiarities of the main study group or its fission products.

The results of this study also strengthen the hypothesis that maternal responses to demographic changes within the group have predictable consequences for infants' social networks, even

Table VIII. Analysis of covariance: degree of kin bias in infant social networks¹ by measures of mother–infant interaction² and number of individuals less than 5 m from infants

Degree of kin bias in social networks	Mother–infant interaction ³		Numbers of individuals less than 5 m ⁴	
	<i>F</i> _{df,df}	<i>P</i> <	<i>F</i> _{df,df}	<i>P</i> <
Adult females	3.6 _{2,106}	0.031	17.8 _{1,106}	0.0005
Juvenile females	3.7 _{2,102}	0.029	7.0 _{1,102}	0.01
Yearling females	4.5 _{2,85}	0.014	1.9 _{1,85}	
Peers	3.4 _{2,66}	0.038	4.2 _{1,66}	0.046

¹Regression coefficients (slopes) for per capita amounts of time infants spent less than 5 m from group members versus degree of relatedness.

²Measures of time infants spent more than 5 m from mother and the proximity index were analysed together.

³Infant sex, lineage status and numbers of individuals less than 5 m of the infant at any one time were controlled.

⁴Infant sex, lineage status and measures of mother–infant interaction were controlled.

N=116 infants.

for infants as old as 25–30 weeks. For example, infants that spent relatively more time near their mothers and whose mothers took relatively larger roles in maintaining proximity also had social networks that were relatively more highly focused on kin (Table VIII, first two columns). These associations were independent of the number of individuals near the infant at any one time, suggesting that mothers mediated relationships between their infants and other group members to some extent. Although mothers appeared to actively seek more proximity with their infants in large groups than in small groups, it is not clear whether mothers actively promoted more contact between their infants and close kin in large groups. Changes in proximity patterns with others could also have been due to changes in propensities of others to seek proximity with the mother.

In addition to maternally mediated influences, changes in infant social relationships that were related to group size may have also been due in part to more direct influences of the social milieu on infants and other group members; that is, infants and others may also have responded directly to the number of individuals near them by adjusting their propensities to seek proximity specifically with one another (Table VIII, second two columns). It is likely that the balance between maternally mediated and more direct influences may have changed with the infants' ages (Berman 1982b). Such a gradual shift from maternal control to more autonomous control of social networks has been documented in longitudinal studies of captive rhesus monkeys (de Waal 1996).

Taken together, the results of this study lend strong support to the hypothesis that developmental processes are important in mediating relationships between demography and social structure in naturally-organized social groups (Altmann & Altmann 1979). Figure 5 is a revised version of the model presented in Berman (1988). The figure shows hypothesized links between demographic processes, maternal care, development and group structure for this example. Briefly, group growth (which in this case is a result of high natality, low mortality and net immigration into the group; Rawlins & Kessler 1986) appears to lead to specific kinds of changes in group composition: a larger group and one in which each individual has a smaller percentage of close maternal kin. These changes are followed by changes in the infant's social milieu: infants are surrounded by more

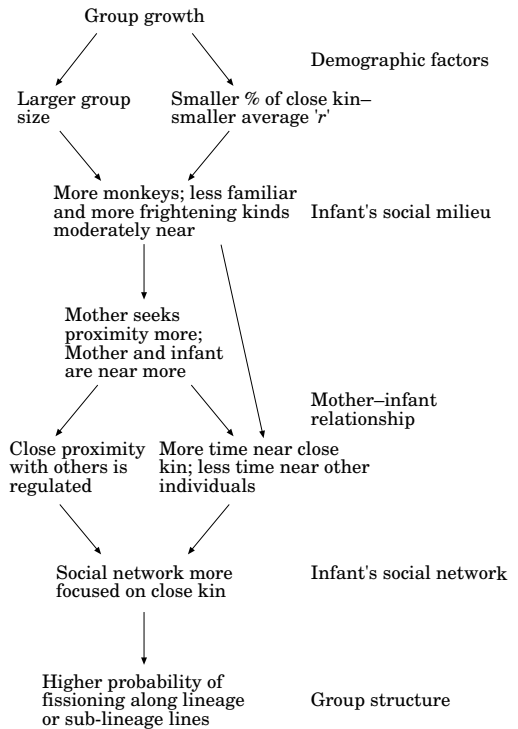


Figure 5. Hypothetical links between group growth, infants' social milieu, maternal behaviour, infants' social networks and group structure.

monkeys, and a larger proportion of them are unrelated and unfamiliar (hence potentially more frightening to them, their mothers and other close maternal kin). As a result, mothers tend to seek proximity with their infants more, and spend more time near their infants. The infants' close proximity is regulated so that they have no more opportunity to associate intimately with other monkeys than did previous cohorts of infants born into the group when it was smaller. Partly as a result of this maternal regulation and partly as a result of responses by the infant or others to the social milieu, infants spend more time with each of their close maternal kin and tend to spend less time with distantly related and unrelated individuals, particularly peers. Given that this focusing of infants' networks onto kin persists as infants develop more independence from the mother (e.g. Berman 1982a; de Waal 1996), and becomes gradually more exaggerated in subsequent cohorts of infants within the group, one would expect a gradual weakening of bonds between families and

eventually a high probability of fissioning along family lines. Such a fissioning would restore many of the conditions present in earlier years (e.g. smaller group size, higher mean degree of relatedness, fewer individuals near the infant, less proximity seeking by the mother and less highly kin biased social networks).

Group fissioning among gelada baboons, *Theropithecus gelada*, also appears to be associated with a narrowing of social networks towards close kin (Dunbar 1984). As the one-male units in which they live increase in size, females tend to groom close female kin progressively more to the near exclusion of others. Dunbar suggested that the lack of cohesiveness that results among females makes the unit particularly vulnerable to fissioning along lineage lines when a follower male joins. As Dunbar pointed out, these phenomena do not constitute an example of the traditional Christian–Calhoun syndrome of behavioural effects when population density increases and migration is prevented (Calhoun 1962; Christian 1970); measures of maternal behaviour and infant relationships were not related to population size (density) on Cayo Santiago.

As in the earlier model (Berman 1988), the hypothesized links in this model are not all necessarily meant to be causal in nature. For example, bonds between families may weaken primarily because older offspring and adults respond immediately and directly to their social environments, and not because they retain their earliest networks into adulthood. Hence, Fig. 5 might best be thought of as a chronology of events until the causal nature of each link can be tested experimentally. Nor are the processes described here meant to be exhaustive of what occurs during group fissioning. Rather they are meant to suggest some of the developmental components of the process in an expanding group. Ecological variables such as predation risk and resource availability and distribution no doubt play a major role through their effects on spatial relationships, demography and patterns of competition (Wrangham 1980; Dittus 1980; van Hoo & van Schaik 1992). Such effects are likely to cause most groups to grow more slowly or decline in the wild than on Cayo Santiago and/or to fission at smaller sizes. Nevertheless, the results of this study suggest that demographic influences on developmental processes can lead to progressive changes in social structure over time (and perhaps to fissioning) in the absence of predation and resource scarcity.

The importance of this finding in a food-rich and expanding population may be easily underestimated, given the current emphasis on research in stable and declining populations commonly found in the wild. Studies of ‘weed’ species (Harper 1977; Richard et al 1989), such as rhesus monkeys, in food-rich and expanding populations, not only allow one to hold certain ecological influences constant, they also permit one to examine behavioural and social processes in conditions under which ‘weediness’ may have evolved (C. Duggleby, personal communication). Indeed, one cannot consider conditions on Cayo Santiago to be highly unrepresentative of extant wild populations of rhesus, some of which grow at higher rates than those on Cayo Santiago (Malik et al. 1984).

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