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Birth-Season Interactions of Adult Female Japanese Macaques *(Macaca fuscata)* Without Newborn Infants

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The affiliative interactions of 11 adult female Japanese macaques that did not deliver an infant during the 1981 birth season of the Arashiyama West troop were examined. Consideration was given to the effects of kinship as a structuring element in these birth-season interactions and to the degree of association with various categories of troop members based on age, sex, and (in the case of adult females) whether or not the females were new mothers. Females without infants interacted predominantly with their yearling offspring, although it was the behavior of the offspring that precipitated the interaction. These females were active in soliciting affiliation with nonkin new mothers, whereas female matrilineal relatives with new infants approached and remained in proximity to them more than did nonrelated new mothers. Females without newborns groomed and approached nonkin infants more than infants within their own matriline, and these infants were predominantly those of females in the highest-ranking matriline of the troop. Adult males were responsible for 40% of all grooming received from nonkin by the females without newborns, and these males approached them significantly more than did other adult females without infants. These patterns demonstrate that the structure of social relationships is influenced by the particular dynamics of troop contexts such as birth seasons, as well as by enduring, broad-based affinities which are less affected by cyclic changes in troop context.

KEY WORDS: Japanese macaques; *Macaca fuscata;* adult females; affiliation; kinship; birth season.

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INTRODUCTION

The birth season of seasonally breeding primates is a period in which affinities among various group members may be modified by the demands of motherhood and infancy. The presence of other troop members directly and indirectly influences new mothers and their infants (Altmann, 1980; Berman, 1978, 1982a, b; Hinde, 1983; Hooley and Simpson, 1983). At the same time the presence of new mothers influences other animals (Dunn and Kendrick, 1980) in modifying both their associations with the mothers and their interactions with one another. The result is a pattern of changed relationships and potential for new interactive opportunities.

Although the reported percentages of reproductive-age females that successfully deliver an infant in a particular birth season are variable (Bernstein, 1983; Dittus, 1975; Drickamer, 1974; Kaufman, 1965; Wilson *et al.*, 1978), it is clear that there is likely to be a fairly substantial cohort of adult females without new infants. For example, Gouzoules and Goy (1983) reported that between 1972 and 1979, sexually mature females of the semi-free-ranging Arashiyama West troop of Japanese macaques *(Macaca fuscata)* in south Texas gave birth an average of every 1.96 reproductive years. Given the significance of the female core in matrilineally organized macaque groups, females without neonates represent an important subset that may differ in significant respects from their female counterparts that do produce an infant in a particular year. Freed from the extra demands associated with caring for a newborn infant, these females may be expected to differ in both activity patterns and interactive behavior. This is not to say, however, that these females without newborn infants are freed from all care activities, since they are likely to have yearling infants that may continue to exert demands and may not yet be fully weaned. For this reason, such females should not be referred to as "nonmothers."

Small (1980, 1982, 1983) focused on both rhesus *(Macaca mulatta)* and bonnet (*M. radiata*) macaque mothers and "nonmothers" (i.e., those without neonates), documenting differences in time budgets and levels of interaction. During the birth season, new rhesus mothers spent less time moving, feeding, grooming, and aiding others than did "nonmothers", and they were approached significantly more. Bonnet macaque mothers were quite similar to rhesus in these characteristics and were also groomed and embraced more than "nonmothers." The presence of a newborn infant restricts a mother's mobility and decreases her initiation of interaction with others, while she simultaneously becomes the focus of attention from others (Altmann, 1980; Hrdy, 1976; Lancaster, 1971).

Presented here is an analysis of the structure of social interactions of a sample of Japanese macaque females of the Arashiyama West troop that did not produce an infant in the annual birth season. The importance of

matrilineal kinship in the social organization of these macaques (Ehardt and Blount, 1984; Gouzoules, 1980; Grewal, 1980; Kawai, 1958; Kawamura, 1958; Koyama, 1967, 1970; Kurland, 1977; Yamada, 1963) implies that females without newborns should preferentially associate with kin, particularly with their previous offspring and possibly with new mothers within their matriline. The interest in females with new infants might also be predicted to be more generalized and less restricted to kin (Breuggeman, 1973; Hrdy, 1976; McKenna, 1979), although Japanese macaque mothers and their new infants reportedly receive only limited attention from other group members (Fedigan, 1982; Itani, 1959; Sugiyama, 1965). If interest is low, or discouraged, the presence of new infants might restrict the range of interactions for females without neonates and promote a greater degree of interaction among these females themselves, particularly among relatives. Finally, given that females that do not produce an infant during one birth season are likely to be the first to enter estrus in the subsequent breeding season (Kaufman, 1965; Small, 1983; Tanaka *et al.*, 1970; Wilson *et al.*, 1978), females without newborns may also show significant levels of interaction with adult males.

METHODS

Subjects

The 287-member Arashiyama West troop, free-ranging on 50 acres near Dilley, Texas, produced 51 new infants in the 1981 birth season. From the 29 remaining females that could have produced an infant but did not, a sample of 11 was selected. These females ranged in age from 9 to 16 years ($\bar{X}$ = 12.1 years); each had at least one surviving offspring from previous years, and eight had a yearling offspring born the previous birth season (five females, three males). Animals were individually recognized, and the genealogical records maintained for the troop since 1954 have documented the matrilineal relatedness of all troop members.

Procedures

Data were collected during the 6-week period following the birth of the last infant and preceding the onset of the mating season. This time period was chosen to minimize variability in interactive patterns that might result as a consequence of a new birth or of the beginning of consort behavior. Eighty-eight hours of focal data (Altmann, 1974) was collected, utilizing 20-min samples and observing each female equally, both in total time and in distribution across morning and afternoon testing sessions.

Analysis focused on six categories of affiliative behavior: grooming performed by the focal females and received by them, passive contact (sitting or lying in incidental contact, not involving holding or embracing), proximity within 1 m, and social approaches performed by the focals and received by them. These measures were scored hierarchically: If an animal was scored as grooming, then proximity or contact were not scored, and if contact was scored, then proximity was not.

To determine whether there was a significant tendency to interact more often with related individuals, or with more precise classes of individuals, probabilities of interaction were calculated based on the number of individuals in the class (for example, the number of relatives an animal had) and the total number of group members. These expected probabilities were then compared with the observed values and tested for significance ($P < 0.01$), using a partial-sums table of the binomial probability distribution. If significantly more than half of the focal females interacted with a class significantly more than expected, this nonrandom pattern was considered to be characteristic of the sample and not a property of only a few individuals (see Massey, 1977).

Comparisons between categories of interactions were made using one-way analysis of variance and Scheffé's (1959) range tests ($P < 0.05$). Two separate analyses were made: one comparing categories of matrilineal relatives and another comparing categories of nonkin. Significant differences in rates of interaction between kin and nonkin categories ($P < 0.05$) were determined by the Mann–Whitney U test (Siegel, 1956). Frequencies of interaction with each class for each female were corrected for unequal representation before comparative analysis. As such, it is the frequency of interaction per the possible number of interactants within each class that is being compared.

Analytical comparisons were based on four categories of kin and four categories of nonkin. Among kin, these interactant categories were (1) the surviving year-old offspring of the focal females, (2) related adult females with new infants born in the current birth season, (3) new infants born to related females in the current birth season, and (4) other related adult females without neonates. Among nonkin, the categories compared were (1) adult males, (2) nonrelated adult females with new infants, (3) new infants of nonkin females, and (4) nonkin adult females without new infants. Interactions with these categories comprised over 88% of all interactions between the focal females and other troop members.

RESULTS

Table I summarizes all kinship effects and Table II presents significant differences in interactions between the females without neonates and other

Table I. Kinship Effects for Each Category of Behavior

Behavioral category	% total interaction with kin	% kin interaction with yearlings	Kin > expected?*
Grooming performed	61	62	Yes/no[a]
Grooming received	67	34	No/no
Passive contact	66	69	Yes/no
Proximity	42	37	Yes/no
Social approaches performed	38	14	No/no
Social approaches received	69	73	Yes/no

[a]Left-side analysis includes yearling offspring; right-side analysis excludes yearlings.
*Binomial test, $P < 0.01$.

kin and nonkin classes. Proportions of interaction with kin and nonkin categories are presented in Tables III (kin) and IV (nonkin). These tables are referred to in the results summarized below.

Overall Interactions with Matrilineal Relatives

Interaction with kin was significantly greater than with nonkin for all behavioral categories, and interaction with relatives was significantly greater than expected for all behavior other than grooming received and social approaches performed by the focals (Table II). When comparisons were made between kin classes, this kinship bias appeared to be due principally to interaction with yearlings born to the focal females in the previous birth season and (less importantly) to interaction with related females with new infants (Table III). The degree to which the females' yearlings influenced the amount of kin interaction was illustrated when their scores were removed from the analysis; interaction with kin was no longer significantly greater than expected for any behavioral category.

Interactions with Yearling Offspring

As indicated in Table III, the eight females without neonates that had a surviving infant from the previous birth season interacted significantly more

Table II. Significant Differences in the Interaction of Females Without Newborns with Kin and Nonkin Categories

Behavioral category	Direction of difference
Grooming performed	Yearling offspring > all other kin*
	Yearling offspring > adult male nonkin**
Grooming received	Adult male nonkin > other nonkin females without newborns*
Passive contact	Yearling offspring > all other kin*
	Yearling offspring > adult male nonkin**
	Related new mothers > adult male nonkin**
Proximity	Yearling offspring > all other kin*
	Yearling offspring > adult male nonkin**
Social approaches performed	Nonkin new mothers > other nonkin females without newborns*
	Related new mothers > adult male nonkin**
Social approaches received	Yearling offspring > all other kin*
	Yearling offspring > adult male nonkin**
	Related new mothers > adult male nonkin**
	Adult male nonkin > other nonkin females without newborns*

*Analysis of variance and Scheffé post hoc analysis ($P < 0.05$).
**Mann-Whitney U test ($P < 0.05$).

Table III. Mean Proportions of Interaction with Kin Categories

	Yearlings	New mothers	Other females without newborns	New infants
Grooming performed				
Mean proportion of total kin interactions[a]	0.62	0.22	0.04	0.02
Mean proportion of entire category[b]	–	0.45	0.54	0.09
Interaction with category > expected?	$P < 0.001$	No	No	No
Grooming received				
Mean proportion of total kin interaction	0.34	0.28	0.16	0.00
Mean proportion of entire category	–	0.56	0.81*	0.00
Interaction with category > expected?	No	No	No	No
Passive contact				
Mean proportion of total kin interaction	0.69	0.17	0.01	0.04
Mean proportion of entire category	–	0.42	0.10	0.33
Interaction with category > expected?	$P < 0.001$	No	No	No
Proximity				
Mean proportion of total kin interaction	0.37	0.25	0.07	0.11
Mean proportion of entire category	–	0.32*	0.32	0.24
Interaction with category > expected?	$P < 0.001$	No	No	No
Social approaches performed				
Mean proportion of total kin interaction	0.14	0.56	0.11	0.04
Mean proportion of entire category	–	0.40	0.38	0.09
Interaction with category > expected?	No	No	No	No
Social approaches received				
Mean proportion of total kin interaction	0.73	0.11	0.06	0.04
Mean proportion of entire category	–	0.45*	0.75*	0.20
Interaction with category > expected?	$P < 0.001$	No	No	No

[a]Mean proportion of all kin interactions that was with the category.
[b]Mean proportion of all interaction with the category (kin and nonkin) that was with kin.
*Interaction with related members of the category was significantly greater than with nonkin (Mann-Whitney U, $P < 0.05$).

than expected with these year-old offspring for all behavioral categories other than grooming received and social approaches performed, the same two that did not show a significant overall kin effect. For grooming performed, passive contact, and social approaches received, interaction with yearlings comprised more than half of all interactions with kin (62, 69, and 73%, respectively). Those focal females with female yearling offspring were also groomed by their daughters significantly more than expected, while those females with year-old sons were not.

Among matrilineal relatives, females without neonates groomed, were in passive contact with, and were in proximity to their year-old offspring at significantly higher rates than with other kin, and these yearlings approached their mothers significantly more than did other relatives (Table II). The focal females, however, actively approached related females with new infants at a mean rate nearly twice that at which they approached their own yearling offspring, with 56% of all kin-directed approaches made to related new mothers and 14% to yearlings (Table III).

Interactions with Adult Females with New Infants

Overall, the females without newborns approached and were in proximity to new mothers significantly more than expected. They did not, however, interact significantly more than expected with related new mothers for any behavior (Table III), but did approach nonkin new mothers more than expected (Table IV), indicating that their preference for approaching females with new infants was due to a greater interest in nonkin mothers than in relatives of this category. The focal females were in proximity to related females with new infants significantly more than to nonkin new mothers, and these matrilineal females with infants approached the focals significantly more than did their nonkin counterparts (Table III), suggesting that proximity was precipitated by the new mothers.

Specifically among nonkin, females without neonates did not show a preference for females with infants over those without for any behavior except approaches performed (Table II). For this active behavior on the focal females' part, 51% of all approaches to nonkin were to new mothers, as opposed to only 11% to other adult females without new infants (Table IV).

Interactions with New Infants

Among the new infants born during the season, females without newborns groomed and approached nonkin infants that were not in contact with their mothers significantly more than they groomed and approached infants

Table IV. Mean Proportions of Interaction with Nonkin Categories

	Adult males	New mothers	Other females without newborns	New infants
Grooming performed				
Mean proportion of total nonkin interaction[a]	0.15	0.42	0.05	0.26
Mean proportion of entire category[b]	–	0.55	0.46	0.91*
Interaction with category > expected?	No	No	No	No
Grooming received				
Mean proportion of total nonkin interaction	0.40	0.43	0.08	0.00
Mean proportion of entire category	–	0.44	0.19	0.00
Interaction with category > expected?	No	No	No	No
Passive contact				
Mean proportion of total nonkin interaction	0.05	0.46	0.23	0.15
Mean proportion of entire category	–	0.58	0.90	0.67
Interaction with category > expected?	No	No	No	No
Proximity				
Mean proportion of total nonkin interaction	0.14	0.40	0.11	0.26
Mean proportion of entire category	–	0.68	0.68	0.76
Interaction with category > expected?	No	No	No	No
Social approaches performed				
Mean proportion of total nonkin interaction	0.10	0.51	0.11	0.25
Mean proportion of entire category	–	0.60	0.62	0.91*
Interaction with category > expected?	No	$P < 0.05$	No	No
Social approaches received				
Mean proportion of total nonkin interaction	0.14	0.30	0.05	0.35
Mean proportion of entire category	–	0.55	0.25	0.80
Interaction with category > expected?	No	No	No	No

[a]Mean proportion of all nonkin interactions that was with the category.
[b]Mean proportion of all interaction with the category (kin and nonkin) that was with nonkin.
*Interaction with nonkin members of the category was significantly greater than with kin (Mann–Whitney U, $P < 0.05$).

of their own matriline (Table IV). This effect, however, is due to inordinate interest in a few specific infants. Approaches to nonrelated infants were predominantly to those of the alpha female, her oldest daughter, and three other females of this highest-ranking matriline.

Interactions with Other Females Without Newborns

Overall, interaction between the focal females and other females without a new infant was minimal, and in no case did frequencies significantly exceed expectation or surpass those of interaction with other classes of group members. A significant kin preference was found only for the categories grooming received and approaches received: 81% of all grooming and 75% of all approaches received from other females without newborns were from relatives of the focals (Table III).

Interactions with Adult Males

The focal females interacted significantly more with their year-old offspring than with adult males for all behavioral categories except grooming received and approaches performed (Table II). Females without neonates also approached related new mothers, were approached by them, and were in passive contact with them significantly more than with adult males (Table II).

Among nonkin, the focal females were approached and were groomed significantly more by adult males than by other females without new infants (Table II), suggesting an initiating, active role on the part of the males. This result is perhaps most meaningful for grooming received from adult males; 40% of all grooming of the focal females by nonkin was by these males, as opposed to 8% by other females without newborns (Table IV).

DISCUSSION

If the interactive pattern of the females without new infants can be described as being dominated by any one subset of troop members, it would be the yearling sons and daughters of these females. This result, however, is due largely to active solicitation on the part of the yearlings. The females frequently attempted to avoid persistent interaction, sometimes threatening their approaching offspring or quietly, but consistently, moving away. Yet despite the obvious cases of avoidance, yearlings received 62% of all grooming directed to matrilineal relatives. This emphasizes the fact that females of this species continue to be interactively involved with their youngest offspring,

although it is the offspring that are now primarily responsible for precipitating interaction, as has been shown for rhesus macaques (Hinde and Atkinson, 1970; Hinde and Spencer-Booth, 1967).

When females without newborns actively sought interaction, they preferentially approached and remained in proximity to mothers with new infants. Although this seems contrary to observations that Japanese macaque mothers receive relatively little attention from other troop members (Itani, 1959; Sugiyama, 1965), approaching new mothers and spending time in proximity with them are not inconsistent with reports of interest involving rather nonintrusive behavior, such as looking at a new infant or trying to touch it, as reported by Sugiyama (1965). It appears that females without new infants of their own are interested in new mothers and their infants, although this interest is expressed through rather subtle affinitive behavior (cf. Altmann, 1980; Fedigan, 1982).

Although Japanese macaques have been reported to be highly matrilineal in their overall associations, kin biases on the part of the subject females were not uniform across categories of affiliative behavior, and all significant kin biases disappeared when interactions with the females' yearling offspring were excluded from analysis. For the categories grooming received and approaches performed, *overall* interaction with kin (even including yearlings) did not significantly exceed expectation based on representation of relatives within the group. This is due to variance in interactive patterns with differing classes of troop members. For instance, interaction with related new mothers was not significantly different from that with nonrelated mothers for the majority of the behavioral categories, despite correction for unequal representation in the two classes. Females without newborns were approached by and were in proximity to related mothers significantly more than with nonrelated mothers; but for more active behavior on the subject females' part, such as grooming performed and approaches performed, the difference was once again not significant. As a matter of fact, females without neonates approached nonkin new mothers, but not matrilineal new mothers, more than expected. Altmann (1980) has pointed out that the time of birth is a period in which individuals that are relaxed with one another are drawn together. Therefore, nervous or prohibitive mothers, which are less likely than other troop members to initiate interaction (Altmann, 1980), should be most comfortable in approaching their kin, as were the new mothers that approached the focal females. The females without new infants, on the other hand, were attracted to the new mothers and infants as a class, and although they may have greater ease of access to related mother-infant dyads, they are less restricted in their movements (having no newborn infant to constantly protect, feed, and support) and are somewhat freer to maximize other interactive possibilities. Several researchers have discussed the potential

benefits of relationships with high-ranking animals (Chapais and Schulman, 1980; Cheney, 1977, 1983; Silk, 1981), and females without newborns may prefer to approach and may more easily approach nonkin high-ranking mothers, which are less likely to be distressed by such approaches than low-ranking new mothers (Altmann, 1980; Cheney, 1978; Seyfarth, 1976).

Females without neonates, in fact, showed a definite preference for approaching and grooming infants of high-ranking mothers. This is in agreement with Gouzoules' (1980) finding that infants in the first 3 months of life show lower scores for proximity to nonrelatives if they are infants of lower-ranking females. Such a preference on the part of females without newborns may be facilitated by the earlier independence of infants of high-ranking females, in conjunction with decreased restrictiveness by high-ranking mothers (see Altmann, 1980; Rowell *et al.*, 1968). Females without new infants would thus have a greater opportunity to interact specifically with these infants during the early weeks after their birth.

Thus, it appears that for adult Japanese macaque females without newborns, the effects of kinship may become less apparent during the birth season, particularly with respect to new mothers. This is congruent with Small's (1980) findings for rhesus and bonnet macaque "nonmothers" and with the absence of strong kin effects which can also be seen in Altmann's (1980) data for the Amboseli baboons (although females without infants were not a specific focus of the latter study). The absence of strong kin effects for these females was also graphically illustrated when all overall kin biases disappeared with the removal of mother–yearling interactions, a result that should be further examined beyond the birth season.

Contrary to what might have been predicted, females without neonates are apparently not excluded from interacting with other classes of group members (particularly, new mothers) to a degree that might produce a high rate of association among themselves. For no behavior did interaction between females without new infants, kin or otherwise, exceed expectation. In fact, the focal females were approached and groomed by adult males significantly more than by other adult females without infants. Interestingly, several of the focal females were very conspicuous in their active solicitation of adult male interaction, and their interest was also reciprocated. These interactions between males and females without new infants may be related to the fact that the first consorts of the subsequent breeding season were between these adult males and females that did not produce an infant in the previous birth season. This also accords with the data of Small (1983; cf. Tanaka *et al.*, 1970), who argues that there may indeed be distinct advantages to early breeding (for example, decreased female competition) that can be realized by females that are not actively caring for a very young infant. However, beyond

reproductive advantage, females may also benefit in other respects through their association with adult males. These potential benefits may include protection from interference with maintenance activities by other, higher-ranking adult females and other adult males (Altmann, 1980), as well as a possible decrease in the risk of injury from other males (Smuts, 1982).

At a more proximate level, the presence of mothers and infants during the birth season facilitates association between adult males and adult females without newborns. Aside from kin, new mothers do not frequently approach adult males, and mothers also appear anxious when their infants approach these males. Adult males have often been observed to show exaggerated avoidance of an infant that approaches or stumbles into the male unexpectedly (Fedigan, 1982; Gouzoules, 1980). Hence, preference by males for adult females without infants is predictable. At the same time, a female that is not encumbered by a new infant demanding constant attention and protection may be less hesitant to participate in interactions involving adult males, taking advantage of the male's preference and the relative decrease in interest by females nursing new infants.

To summarize, the interactive pattern described for these adult females that do not produce a new infant during the circumscribed birth season is essentially twofold. On one hand, the behavior of the females without newborns reflects enduring bonds and relationships that remain relatively stable across seasonally changing troop contexts. This includes affiliation with closely related kin, predominantly young offspring; however, even these relationships are not without some modification. On the other hand, many facets of the behavior of females without newborns reflect the particular context of the birth season and the somewhat unusual position of these females, i.e., their lack of a highly dependent newborn infant. Examples include the subject females' increased interactive frequency outside of their matriline, their attraction to females with infants and to the infants of high-ranking females, and their increased association with adult males, which also show a preference for such interaction.

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