Behav. Ecol. Sociobiol. 2, 31–40 (1977)

Behavioral Ecology and Sociobiology

Agonistic Aids and Kinship in a Group of Pigtail Macaques

Adrianne Massey*

University of Georgia, Athens, Georgia 30602, USA

Received July 15, 1976

Summary. 1. An analysis of aiding behavior in a group of 49 pigtail macaques (*Macaca nemestrina*) demonstrated that these animals were very selective in the performance of these aids.

2. Not only did these monkeys discriminate between relatives and nonrelatives, but they also chose to aid relatives of a closer degree of relatedness more often than relatives more distantly related.

3. Kinship, however, was not the only factor that affected the performance and receipt of aids, for age and sex were also relevant. Although females were more active than males in performing acts of aid, neither sex received significantly more aids. While older animals performed more aids than younger animals, younger animals received significantly more aids than did older animals.

Introduction

In recent years evidence that genealogical relationships are an important factor in the organization of macaque societies has grown considerably. Studies of Japanese macaques (*Macaca fuscata*) (Kawai, 1958a, b; Kawamura, 1958; Koyama, 1967) and rhesus monkeys (*Macaca mulatta*) (Koford, 1963; Sade, 1967; Missakian, 1972) show that the dominance rank an animal assumes is related to the rank of its mother. Sade (1965) has also shown that the rhesus on Cayo Santiago tend to develop the strongest ties with animals of their own genealogy. Given that to be true, it is not surprising then that when troops divide they do so along matrilineal lines (Furuya, 1969; Koyama, 1970; Missakian, 1973) or that rhesus male acceptance into an all male band is greatly facilitated by the presence of a relative in that band (Wilson, 1968).

Similarly strong genealogical ties have been illustrated for pigtail macaques (*Macaca nemestrina*). In an initial study comparing pigtail and bonnet macaques (*Macaca radiata*), the pigtails showed a striking lack of physical contact (Kauf-

---

* Present address: Department of Zoology, North Carolina State University, Raleigh, North Carolina 27607, USA

man et al., 1964). While the bonnets tended to sit in clumps, the pigtails rarely came into contact. Yet, when this artificially formed group of pigtails was observed a number of years later, significantly different results were obtained. Physical contact within consanguineous units was found to be as frequent as in the bonnet group (Rosenblum, 1971).

It is obvious then that kinship ties are a significant force underlying the structure of pigtail societies, but just how strong are these "ties that bind"? If "family" is as important to pigtails as it seems to be, is it conceivable that they not only contact and groom relatives more, but that they also might risk their own welfare for a relative? Pigtail monkeys do come to the aid of animals that are under attack. Anyone who has witnessed aggression in macaques will attest to the fact that there is considerable risk in becoming involved in any aggressive encounter. Because this risk does exist, aiding behavior can be classified as altruistic behavior, for it is potentially detrimental to the altruist while being beneficial to the recipient. The purpose of this study was to determine if pigtail monkeys are discriminant in their aiding behavior, and if so, the parameters that define this discrimination.

Methods

Subjects. At the start of the study (March, 1975) there were 44 pigtail monkeys in the study group. During the study five additional animals were born. All except the five eldest animals were born into this group, which was formed in 1963. Genealogical data have been collected systematically over more than 12 years and through four generations. This group is maintained at the Yerkes Regional Primate Research Center Field Station with minimal disturbance. No animal has been added to or removed from the group except by agency of birth or death since 1963. Data on group formation and social activities of this group appear in Bernstein (1969a, b, 1972). A list of subjects, their birth dates, and genealogical relationships are shown in Figure 1, with deceased animals represented by blank boxes.

Apparatus. The group was housed in a 30.5 square meter outdoor compound with unrestricted access to a 9.2 m × 30 m × 20 m indoor quarters. Details of the living quarters are provided in Bernstein (1972). The subjects were observed from a vantage point 4.9 m atop the outdoor compound.

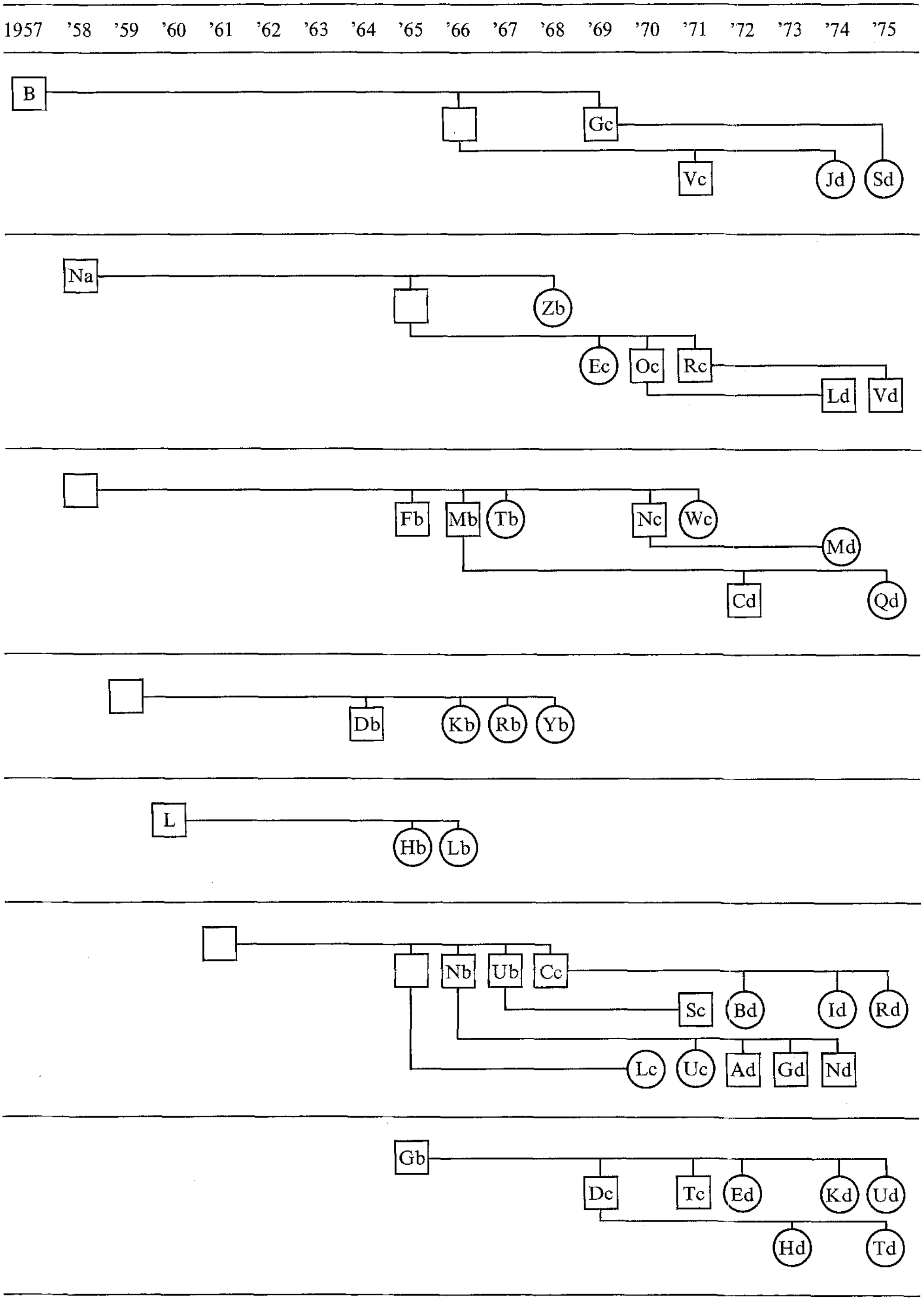
Procedure. The subjects were observed a total of 120 h, 80 of which were devoted to data collection. The other 40 h were spent acquiring individual recognition skills, becoming acquainted with the behavioral repertoire of pigtail monkeys, and habituating the monkeys to my presence. Scores were kept on the following kinds of agonistic encounters:

1. Encounters in which one individual chased or charged another individual who fled or crouched.
2. Encounters that included vocalizations characteristic of aggression and/or submission.
3. Any encounter that included a sequence of 5 displays considered to be aggressive, but not accompanied by vocalization. These include the open mouth gesture, slap, push, pull, and bite. The pucker characteristic of pigtails (also defined as jaw thrust in Kaufman and Rosenblum, 1966) was also scored as a significant display occurring in agonistic contexts at times.

Restriction of scoring to the foregoing situations was based on the belief that failure to receive aid could only be scored as such if most of the group members had the opportunity to detect the individuals engaged in an agonistic encounter. Because of the large size of the compound a single threat or slap could easily go unnoticed by the other animals.

Not only were agonistic encounters of the type described above tallied, but all aids were also recorded. Aiding was defined as participating in an aggressive encounter in support of one animal against another and was manifested in a variety of ways. Some of the more common forms of aiding are described below:

Fig. 1. Subjects, birthdates, and genealogical relationships



Animals Ⓠ, born in 1959; O, born in 1960, have no relatives in the group

□, females; ○, males; blank boxes, deceased animals

1. The aider chases or threatens the aggressor in support of the defender. Actual contact aggression by the aider was seen on very few occasions.
2. The aider places his body between the aggressor and the animal under attack, crouches, and sometimes squeals and/or grimaces at the aggressor.
3. The aider mounts the aggressor. Often this is followed by a mount of the aider by the aggressor. Such mounting behavior usually served to terminate further aggression and was considered to be supportive of the defender.
4. The aider assists the aggressor in chasing, threatening, or actually attacking the defender. This type of aid was scored as an aid to the aggressor, while the other three forms of aiding were scored as aids to the defender.

Scores were tabulated in accordance with who aggressed against whom and whether or not an aid was received by either party. From this was calculated (1) the total number of times a given animal aggressed against a second animal, (2) the total number of times a given animal aided or received aid from each animal, (3) the proportion of the total number of aids an individual did to or received from each other individual, and (4) the number of aids an individual received from a second animal divided by the number of aggressive encounters in which that individual was involved.

Statistical Tests. To determine if there was a significant tendency to direct aggression more often to related or nonrelated individuals, the probabilities of an individual attacking a relative or a nonrelative were calculated based on the number of relatives an animal had in the group and the number of group members. These expected probabilities were then compared to the observed results and checked for significance ($p < 0.01$) using a partial sums table of the binomial probability distribution (National Bureau of Standards, 1949).

In determining if animals aided relatives significantly more often than nonrelatives, the same procedure was used. My null hypothesis was that aiding was random and that kinship had no effect on the probability of giving or receiving aid. The expected probabilities of an individual aiding a family member or a nonfamily member were calculated based on the number of relatives an animal had in the group and the number of group members. These expected probabilities were then compared to the observed results and checked for significance ($p < 0.01$) using the method described above. The number of individuals that aided family members significantly more often than one would expect, had acts of aid been random, was then compared to the total number of animals that performed any acts of aid. If significantly more than half of the group members showed the tendency to aid relatives more often than other group members, I assumed this was a general characteristic of animals in the group and not just a special property of one or two individuals.

Results

During 80 h of observation, 729 agonistic episodes of the type described above were recorded. Only one individual of the 38 animals who attacked others directed his attacks significantly more often to family members, while one other individual attacked nonrelatives significantly more often. The remaining 36 animals who attacked others showed no tendency to fight more or less often with related or nonrelated individuals.

Although kinship ties seem to have no effect on which individual was aggressive to whom, they do appear to influence whether individuals will become involved in aggressive encounters involving other animals by aiding one another. In 338 agonistic episodes at least one antagonist received aid from another animal. Because multiple aids were possible during a single encounter, a total of 397 animals were observed aiding in these 338 encounters. Eighty-eight percent of these aids (350) involved animals aiding members of their own genealogy, yet only 37.8% of the aids involved mothers aiding children. Three hundred and nine of the aids were aids to the defender; only 88 were aids in which the aider joined in an attack on another. Of the 30 individuals that performed these 309 aids, 22 aided family members under attack significantly more often than one would expect had they simply aided group members under attack at random. Therefore, significantly more than half of the members of the group aided family members more often than nonfamily members ($p < 0.008$).

In addition, there were 23 animals that aided other individuals in attacking others. Of these only 13 individuals aided family members significantly more often than they aided nonfamily members. Thus, the tendency to aid family members more than nonfamily members in attacking others could not be demonstrated for significantly more than half of the animals in the group.

Consideration of aids to defenders and aids to attackers conjointly revealed that 24 of the 34 animals that aided did so significantly more often for family members than for nonfamily members. Because this proportion represents significantly more than half of the group members, there existed a general tendency within the group to aid relatives more often than nonrelatives ($p < 0.01$). Of the 15 animals that performed no acts of aid six were less than six months old, five were between six months and two years old, and the remaining four were adult males.

Once again aiding behavior within the matrilines was not restricted to mother-to-child aids, but was observed for relatives of varying degrees of relatedness. Minimal degrees of relatedness, based on data available from matrilineal descent, that were present in the pigtail group were as follows:

1. Parent–offspring;	may be as low as 0.5
2. Grandparent–grandchild; aunt/uncle–niece/nephew; half siblings	may be as low as 0.25
3. Great-grandparent–great-grandchild; Great-aunt/uncle–great-niece/nephew; cousins	may be as low as 0.125
4. Nonrelated individuals	may be as low as 0.00

Since paternity is unknown to the monkeys in macaque societies, all maternal siblings were treated as half-siblings.

A breakdown of the aids performed by relatives of the three coefficients of relatedness is shown in Table 1. Considering the three degrees of relatedness as three populations of animals, Student's *t* tests revealed significant differences in the mean number of aids. In terms of animals receiving aid, first, almost all (88.2%) aids were to family members. Secondly, receiving aid was significantly different according to the degree of relatedness in terms of (1) the average frequency of aids an animal received from a relative of a given degree of relatedness, (2) the proportion of all the aids an individual received that were from a relative of a given degree of relatedness, and (3) the number of aids an individual received from a relative of a given degree of relatedness with respect to the number of agonistic episodes in which that individual was involved.

An examination of the mother–infant dyads using paired *t* tests revealed a significant tendency for mothers to aid offspring more than to be aided

Table 1. Aids received by individuals of the specified degree of relatedness

	Degrees of relatedness		
	0.5 ($n=38$)	0.25 ($n=156$)	0.125 ($n=48$)
Total number of aids	173	164	13
Average number of aids	4.55	1.05	0.271
Average proportion of aids	0.387	0.113	0.029
Average number of aids/number of aggressive encounters	0.149	0.035	0.009

All differences in the means of the 0.5 and 0.25 classes of relatives are significant at $p<0.001$
All differences in the means of the 0.25 and 0.125 classes of relatives are significant at $p<0.01$

Table 2. Aids that occurred within the mother-infant dyad

	To offspring from mothers	To mothers from offspring
Average number of aids	7.89	1.21
Average proportion of aids	0.657	0.103
Average number of aids/number of aggressive encounters	0.258	0.033

All differences in the means are significant at $p<0.01$

by them, although the degree of relatedness is the same. Furthermore, the difference in mother-to-child and child-to-mother aids proved significant for all three types of aiding (see Table 2). Mothers consistently aided their children more than the reverse.

Of the 47 aids that occurred outside the family during this study, only ten, significantly less than half, were reciprocated. No pattern was evident in these ten aids: they did not consistently involve any of the special relationships that exist in primate societies such as consort pairs, adult male coalitions, or peer relationships.

In addition to kinship, a number of other factors were observed to have an effect on the performance and receipt of aids. It was found that an animal was much more likely to receive aid when under attack than when attacking. A 2×2 chi square contingency table showed this difference to be significant at $p<0.005$. Spearman rho analysis revealed that those animals receiving the majority of these defensive aids were those that were attacked the most ($r=0.85$; $p<0.01$).

Finally both age and sex have a profound effect on the performance of aids. A total of 302 of the 397 acts of aid were performed by the 25 animals that were four years or older, while the remaining 95 were attributed to animals younger than four years. A 2×2 chi square contingency table showed this difference to be significant at $p<0.005$. The 19 females over three years of age performed 294 aids while the 12 males of the same age aided animals only 74 times. In total, 303 acts of aid were attributed to the 24 females older than six months; 94 aids were performed by the 19 males. Chi square contingency analysis proved both of these differences significant at $p < 0.005$. Of the 94 acts of aid by males, 57 were to relatives. Twenty-four of the 37 aids to nonrelatives were aids by the alpha male, five were aids by other adult males in support of the alpha male, and the remaining eight were performed by adult and subadult males for various group members. Finally, although females aided more often than males, neither sex received significantly more aids than the other.

Discussion

These findings are pertinent to the current questioning of the selective mechanism responsible for the evolution of altruistic behaviors if one is willing to accept aid in agonistic encounters as an indicator of altruistic behavior. Two alternative models of such selective mechanisms are Hamilton's (1964a, b) model of kin selection and Trivers' (1971) hypothesis of reciprocal altruistic behavior.

The pivotal concept of Hamilton's theory is that an altruistic trait will evolve provided the loss to the altruist is offset by a gain in "inclusive fitness". The gain to a relative must exceed the loss to the altruist by a factor greater than the degree of relatedness between the altruist and the recipient. This degree of relatedness, or coefficient of relationship (Wright, 1922), represents "the fraction of genes in two individuals that are identical by descent, averaged over all loci" (Wilson, 1975). In other words, an individual is more likely to be altruistic to relatives that are closest to him.

Trivers' model does not restrict altruistic behavior to relatives but provides for the evolution of such behavior in situations where pairs of individuals reciprocate altruism provided the cost to the altruist is less than the gain to the recipient. Protection of a vulnerable family member against attack seems to be truly related to kin selection, for the performance of such aids was found to be directly related to Wright's coefficient of relatedness (Wright, 1922). Of course, it was expected that a significant difference would exist between the 0.5 class and other degrees of relatedness due to the preponderant tendency for mothers to protect their offspring. What is striking, however, is the fact that a significant difference was also present between the 0.25 and 0.125 classes of relatives. That is, they discriminated between individuals that were more closely and more distantly related, with dyads that shared an average of 25% of their genes aiding each other more often than individuals that shared on the average only 12.5%. This finding lends support to Hamilton's model of the evolution of altruism through kin selection by offering experimental verification of the hypotheses he generated. The results of several of the analyses could also be used to support Trivers' model of reciprocal altruism, particularly his hypothesis that kin selection and reciprocal altruistic selection may act conjunctively, for family members do reciprocate aids. Trivers could explain the failure to find significant reciprocation in extra-familial aids by invoking Rosenblum's (1971) work, which illustrates that in pigtails, related individuals spend more time in proximity than do nonrelated individuals. Consequently, the nonsignificant reciprocation that occurred in nonrelated individuals could be attributed to their not being in proximity to one another, while the significant reciprocation within family units could be due to relatives being in close proximity. This study may simply have been too short for reciprocation to be seen in unrelated animals not frequently in proximity to one another.

The result that mothers aid children more than the reverse despite the fact that the coefficient of relatedness is 0.5 in both cases is due to the highly unequal cost-benefit ratios involved in mother-to-child and child-to-mother aids. A number of factors are responsible for the cost of performing an aid and for the benefits gained from receiving an aid being greater for the child than for the mother. First, age would seem to have an effect on the performance and receipt of aids, for young animals are not able to fend for themselves. In fact, the data do show that the age of an animal definitely influenced the likelihood of aiding another. The difference between the animals older than four years and younger than four years was significant at $p < 0.005$. So, as an individual matures, you would expect to see an increase in aids to his mother. However, even if the offspring is fully adult, one might argue that there will still be a higher proportion of aids being directed toward the child inasmuch as, since the reproductive potential of an individual decreases with age, the benefits reaped from the receipt of an altruistic act must decline. Though the degree of relationship is the same, a parent has more invested in its offspring than the child has in its parent. As that parent ages, the loss rendered to it by the performance of an altruistic act also declines, for its genetic fitness in terms of numbers of offspring produced is set. The only method now open to the parent interested in increasing its fitness is to be extremely active in assuring the survival of these offspring and their children. Consequently, the older a mother is the more prone to altruism she should be.

In addition to kinship, sex was found to have an effect on the performance of aids, for females aided significantly more often than males ($p < 0.005$). One would expect males to be less involved than females in aiding because, having no knowledge of their offspring, the only relative of 0.5 degree of relatedness they can be aware of is their mother; and, as discussed above, offspring are not as active in aiding their mothers as the reverse. While the female's role in macaque societies is directed toward the group by maintaining relationships and enforcing the relative positions of themselves and their offspring, the male's is oriented outward toward the protection of the group against external threats (Bernstein, 1976).

Finally, it was found that those animals receiving the majority of the defensive aids were those that were attacked the most. Therefore, it is those animals with the greatest need of aids that are most likely to receive aid, for aiding is potentially detrimental to the aider and should not be performed without regard for this potential danger.

Of course, it may well be that the aid an individual receives when attacked comes from those animals that are physically closest to him. In pigtail societies this would be difficult to separate from the fact that kinship does have an effect on aiding behavior. Yet it is the subjective impression of this author that spatial proximity, though perhaps related to aiding, is not the cause of it. A great many times animals interrupted grooming bouts, feeding, and other activities to speed across the enclosure and come to the aid of a relative in need. However, no data were collected on the spatial separation of aider and aided.

In conclusion, pigtails do come to the aid of relatives under attack significantly more often than they aid nonrelatives. Not only do they selectively aid related versus nonrelated individuals, but they also discriminate between relatives of varying degrees of relatedness. If such aiding can be viewed as altruistic, then these findings can be used in support of Hamilton's model of kin selection as the mechanism responsible for the evolution of altruism. Certain findings of this study also lend support to Trivers' model of reciprocal altruistic selection.

In addition to kinship, both age and sex affect the possibility of an individual performing an aid. Older animals are more likely to aid than younger animals, and females aid more often than males.

Acknowledgments. I wish to thank I.S. Bernstein for reading the manuscript, D.C. Justice and A.J. Volpi for supplying expert technical assistance, and P.A. Gowaty and R.R. Sinden for providing critical comments, helpful discussions, and indispensable support. This research was supported by NIMH Grant 13864 and NIH Grant RR 00165 to Yerkes Regional Primate Research Center.

References

Bernstein, I.S.: Spontaneous reorganization of a pigtail monkey group. Proc. 2nd Intern. Congr. Primate Behavior, p. 48–51. Basel: Karger 1969a

Bernstein, I.S.: Introductory techniques in the formation of pigtail monkey troops. Folia Primat. **10**, 1–19 (1969b)

Bernstein, I.S.: Daily activity cycles and weather influences on a pigtail monkey group. Folia Primat. **18**, 390–415 (1972)

Bernstein, I.S.: Primate genetic fitness. J. Theor. Biol. **60**, 459–472 (1976)

Furuya, Y.: On the fission of troops of Japanese monkeys II: General view of the troop fission in Japanese monkeys. Primates **10**, 47–70 (1969)

Hamilton, W.D.: The genetical evolution of social behavior I. J. Theor. Biol. **7**, 1–16 (1964a)

Hamilton, W.D.: The genetical evolution of social behavior II. J. Theor. Biol. **7**, 17–52 (1964b)

Kaufman, I.C., Rosenblum, L.A., Stynes, A.J.: Individual distance in two species of macaque. Anim. Behav. **12**, 338–342 (1964)

Kaufman, I.C., Rosenblum, L.A.: A behavioral taxonomy for *Macaca nemestrina* and *Macaca radiata*. Based on longitudinal observation of family groups in the laboratory. Primates **7**, 205–258 (1966)

Kawai, M.: On the system of social ranks in a natural troop of Japanese monkey I: Basic rank and dependent rank. Primates **1**, 111–130 (1958a)

Kawai, M.: On the system of social ranks in a natural troop of Japanese monkeys II: Ranking order as observed among monkeys on or near the test box. Primates **1**, 131–148 (1958b)

Kawamura, S.: Matriarchal social ranks in the Minoo-B troop: A study of the rank system of Japanese monkeys. Primates **1**, 148–156 (1958)

Koford, C.B.: Ranks of mothers and sons in bands of rhesus monkeys. Science **141**, 356–357 (1963)

Koyama, N.: On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates **8**, 189–216 (1967)

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

Missakian, E.A.: Genealogical and cross genealogical relations in a group of free-ranging rhesus monkeys on Cayo Santiago. Primates **13**, 169–180 (1972)

Missakian, E.A.: The timing of fission among free-ranging rhesus monkeys. Amer. J. Phys. Anthrop. **38**, 621–624 (1973)

Rosenblum, L.A.: Kinship interaction patterns in pigtail and bonnet macaques. Proc. 3rd Intern. Congr. Primat. 3, p. 79–84. Basel: Karger 1971

Sade, D.S.: Some aspects of parent-offspring relations in a group of rhesus monkeys with a discussion of grooming. Amer. J. Phys. Anthrop. **23**, 189–200 (1965)

Sade, D.S.: Determinants of dominance in group of free-ranging rhesus monkeys. In: Social communication among primates (ed. S.A. Altmann). Chicago: Univ. Chicago Press 1967

Trivers, R.L.: The evolution of reciprocal altruism. Quart. Rev. Biol. **46**, 35–59 (1971)

Wilson, A.P.: Doctoral Dissertation, Univ. Calif. Berkeley, August 1968

Wilson, E.O.: Sociobiology. p. 74. Cambridge: Harvard Univ. Press 1975

Wright, S.: Coefficient of relationship. Am. Naturalist **56**, 330–338 (1922)