

Social Behavior in Aged Rhesus Macaques

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ABSTRACT

*This study investigated the relationship between chronological age and social behavior in 42 adult male and female rhesus macaques (*Macaca mulatta*) in three specific areas: social interactions, social roles, and social networks. While both old males and old females share behavioral differences associated with senescence, this study reports that old females and old males are distinct in their social behaviors, both from each other and from other adults. Many of these differences appear progressive across age classes, e.g., declining across age classes in females and increasing across age classes in males. Old females are less social and have smaller social networks than other females, while the opposite was found to be true of old males. An explanation for the sex-based differences in aged social behavior and social networks reported in this study may originate in rhesus matrifocal social structure.*

Keywords: non-human primates, aging, behavior, social networks

Introduction

Human demographics are shifting toward an increasing proportion of aged individuals, particularly in industrialized nations. Across disciplines, greater efforts are being made to secure and improve quality of life for growing numbers of elderly. All primates pass through an orderly sequence of life stages: infant, juvenile, adult, and aged. Patterns of normal, programmed development and behavior are well known for each life stage, except *aged*. There is, then, a growing need for information about the basic pro-

cesses of senescence and aging. Further, the emerging field of primate gerontology, using the traditional tools of biological anthropology (the life history perspective, comparative data, and a focus on variation), is well suited to investigate senescence and aging¹⁻³.

This project addresses the effects of aging (becoming old) on nonhuman primate social behavior. While human and nonhuman primate social systems are not wholly and directly comparable in terms of sociality, there are areas of com-

mon interest which can be investigated to provide a broader, cross-species perspective on the process of aging⁴⁻⁶.

Materials and Methods

Study population and site

The Caribbean Primate Research Center, administered by the University of Puerto Rico, maintains and manages a rhesus macaque (*Macaca mulatta*) colony on the island of Cayo Santiago and supports noninvasive research on the biology and behavior of these monkeys⁷. In 1938, 409 rhesus monkeys were brought to the island from India by C. Ray Carpenter, and now number approximately 1,000 animals. They are provisioned, although also forage heavily, and are organized into seven voluntary social groups. The Cayo colony was selected for this study because it has been under constant census since the 1950’s. Family histories, birth dates, and reproductive histories are known for all animals⁸.

Doing an aging study in a wild monkey population is difficult for several reasons. First, unless the animals have been under observation for some time, ages are not known and must be estimated (from, for instance, dental casting). Second, old animals are rare in wild populations due to predation and increased mortality in the aged¹. Even on Cayo, a somewhat protected environment, few old animals were available. The macaque lifespan is estimated at 30 years, which have been divided into trimesters⁹. Therefore, in this study, aged (or old) monkeys were defined as those in their third trimester of life.

Procedures

Six study groups were formed, three female and three male, containing all available individuals at or over the age of 20 years, and randomly selected comparison samples of younger adults (Table 1).

Middle and young female age groups contained at least one individual from each birth cohort, was balanced for matrilineal membership across and within study groups, and spread across dominance ranks when possible. Male comparison subjects were selected randomly by age and group membership. Age in the young male group was adjusted to allow for slower rates of social and reproductive maturity. Additional animals were included in the female middle group, to ensure surviving animals for future, longitudinal study.

TABLE 1
FEMALE AND MALE AGE-BASED STUDY GROUPS

	Female	Male
Old:	20+ (N= 6)	20+ (N= 5)
Middle:	15–19 (N= 11)	15–19 (N= 7)
Young:	7–11 (N= 7)	9–13 (N= 6)

Between July 1997 and August 1998, 627 hours of observational data were collected, using a Psion Workabout handheld computer, programmed with Observer™ software. Behaviors, including social interactions, were recorded by focal subject, partner, occurrence, time of onset and time of completion. In each randomly ordered data set, subjects were sampled for a 15-minute period, once in the morning and once in the afternoon, to control for effects of time and day. Data was taken for a calendar year to control for effects of seasonality. Following a similar research protocol on aged Japanese macaques (*Macaca fuscata*), three specific questions were asked⁶: (1) does sociality vary across age groups? (2) are old monkeys a behaviorally distinct subgroup?, and (3) do the characteristics of an individuals social network vary across age groups?

Statistical analysis

First, males and females were grouped into age categories. Second, tables were constructed to allow data comparisons between individuals and groups. Age groups were tested for significant differences using either a One-Way ANOVA or Kruskal-Wallis analysis of variance where appropriate.

Results

Does time spent in social contact vary with age? Two measures of sociality were considered here: time spent in social contact (measured at body contact, arm's length, and two-meters) and social network size (a count of the animals a subject was with for 15 seconds or more). Within age groups, old females had significantly smaller network sizes, and spent significantly less time in social contact (Tables 2 and 3). There were no significant differences in social network size

or social contact time across male age groups (Tables 4 and 5). Both network size and social contact time showed opposite trends with age in female and male rhesus (Figure 1).

Do behaviors vary across age groups? In this analysis, for all subjects and age groups, 19 behaviors and four behavior groupings were measured. The groupings included social behavior received and directed and agonistic behavior received and directed. These were measured ei-

TABLE 4
SUMMARY STATISTICS FOR MALE SOCIAL NETWORK SIZE BY INDIVIDUALS

	Min.	Max.	X	SD
Total (N=18)	8	38	18.2	8.12
Old (N=5)	10	38	24.4	12.01
Middle (N=7)	12	25	16.9	4.74
Young (N=6)	8	23	16.5	5.86

F = 1.82, $\alpha = 0.20$

TABLE 2
SUMMARY STATISTICS FOR FEMALE SOCIAL NETWORK SIZE BY INDIVIDUALS

	Min.	Max.	X	SD
Total (N=24)	6	36	19.0	8.41
Old (N=6)	7	25	12.8	6.34
Middle (N=11)	6	27	17.0	6.16
Young (N=7)	16	36	27.9	6.12

F = 10.70, $\alpha = 0.0006$

TABLE 5
SUMMARY STATISTICS FOR MALE SOCIAL CONTACT TIME IN MINUTES

	Min.	Max.	X	SD
Total (N=18)	151.4	1256.4	335.5	250.41
Old (N=5)	521.9	1256.4	521.9	417.30
Middle (N=7)	151.4	486.6	295.2	126.21
Young (N=6)	169.6	320.6	227.2	60.66

F = 2.36, $\alpha = 0.40$

TABLE 3
SUMMARY STATISTICS FOR FEMALE SOCIAL CONTACT TIME IN MINUTES

	Min.	Max.	X	SD
Total (N=24)	88.5	418.0	295.2	82.8
Old (N=6)	88.5	362.1	225.4	107.8
Middle (N=11)	270.2	410.2	312.1	47.9
Young (N=7)	212.8	418.0	328.3	78.2

F = 3.57, $\alpha = 0.05$

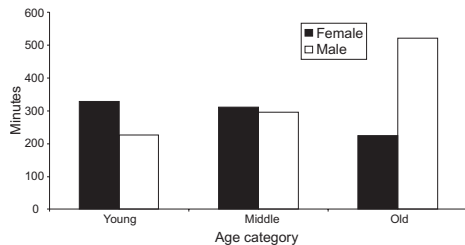


Fig. 1. Social network size by male and female age groups.

TABLE 6
ETHOGRAM OF SELECTED BEHAVIORS

Behavior	Type	Description
Proximity	State	Measured at body contact, arm's length, 2 meters
Sit alert	State	How long an animal remained watchful
Sleep doze	State	How long an animal rested sitting up with eyes closed
Groom alone	State	How long an animal groomed it's own coat
Groomed by	State	How long an animal is groomed by another
Social behavior received	Event	Several behaviors, how often an animal is groomed by another, approached by another, defended by another
Social behavior directed	Event	Same as above, except behaviors are directed at another by focal subject
Chase	Event	How often individual chases another
Chased by	Event	How often a focal individual chases another
Agonistic behavior directed	Event	How often a focal subject chases, bites, threatens, displaces, etc. another

ther by frequency (event behaviors) of occurrence or duration times (state behaviors) and tested for significance. Table 6 describes the ethogram presented in Tables 7 and 8. Old females sat alert less often, sleep-doze more, and groomed themselves less than younger females (Table 7). Table 8 shows that the same occurred in old males. Old females also groomed

others significantly less than younger females, and showed less social behavior, both received and directed. They fear grimaced more and are chased by others more frequently.

In males, proximity did not reach significance. As in old females, males sit-alert, sleep-doze, and groom alone were significantly different across age groups.

TABLE 7
FEMALE BEHAVIORS: RESULTS OF ANOVA ANALYSES

Behavior	ANOVA F (p)
Proximity (D)	3.57 (0.05)
Sit alert (D)	4.21 (0.03)
Sleep-doze (D)	3.02 (0.07)
Groom alone (D)	3.02 (0.07)
Groom (D)	5.1 (0.02)
Groomed by (D)	0.62 (0.55)
Social behavior received (F)	4.45 (0.02)
Social behavior directed (F)	3.57 (0.05)
Approached by (F)	3.29 (0.06)
Fear grimace (F)	3.60 (0.05)
Chased by (F)	8.3 (0.002)

TABLE 8
MALE BEHAVIORS: RESULTS OF ANOVA ANALYSES

Behavior	ANOVA F (p)
Proximity (D)	1.82 (0.20)
Sit alert (D)	5.54 (0.02)
Sleep-doze (D)	6.93 (0.007)
Groom alone (D)	3.63 (0.05)
Groomed by (D)	3.08 (0.08)
Social behavior received (F)	2.79 (0.09)
Social behavior directed (F)	2.20 (0.15)
Chase (F)	4.50 (0.03)
Agonistic behavior directed (F)	4.42 (0.03)

D = Duration; F = Frequency

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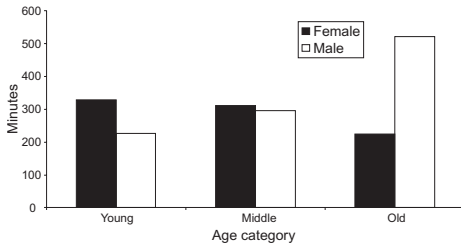


Fig. 2. Social contact time by male and female age groups.

Groomed-by another was also significant in old males, as is social behavior received. Social behavior directed was not significantly different across age groups, while chase and agonistic behavior are. Old males were groomed by others more than younger males, show higher rates of directed social behavior, and have significant reductions in chase and agonistic behaviors (Table 8).

Do social networks vary across age groups? This question was addressed by looking at the relationship between advancing age and the age and kinship affiliations of preferred social partners. Sev-

eral characteristics of the social network were identified (age of network, rank of network, and degree of kinship in the network). Calculated scores were then weighted by the proportion of time spent with each partner and tested for significance differences across age groups. Weighted scores were used because all others are not equally important to each subject. A subject may, for instance, spend the majority of time in social contact with a single other, or with many others.

Table 9 shows female age categories by weighted characteristics of the social network. Of the three network characteristics that are significantly different across age groups: variance in age, degree of kinship, and time spent with others, the group means show that the differences in these categories lay in the young age group. In all three significant variables, the old and middle-aged means are nearly alike. In males, the same data were analyzed, with the exception of degree of kinship due to lack of paternity data, and no significant differences in rank, age, or time spent with others were

TABLE 9
FEMALE AGE CATEGORIES BY WEIGHTED CHARACTERISTICS OF THE SOCIAL NETWORK

Network characteristics	Old X	Middle X	Young X	F or H value (p)
Rank	2.59	2.15	2.01	0.47 (0.63)
Variance in rank	0.15	0.39	0.19	0.97 (0.62)
Relative variation in rank	0.58	2.24	2.15	0.77 (0.48)
Age	7.11	7.51	7.79	0.94 (0.63)
Variance in age	1.16	1.50	0.44	4.76 (0.02)
Relative variation in age	2.10	3.61	1.64	3.62 (0.16)
Degree of kinship	0.43	0.42	0.16	11.55 (0.003)
Variance in degree of kinship	-7.44	-6.84	2.34	0.50 (0.61)
Relative variation in degree of kinship	-0.28	-0.11	-0.25	0.60 (0.94)
Time with others	610.64	621.39	370.51	3.75 (0.04)
Variance in time with others	778344	983778	619810	4.56 (0.102)
Relative variation in time with others	1082.73	1640.72	1393.15	0.68 (0.52)

found (Table 10). Interesting differences were found between male and female social networks, however, in the identity of those whose primary social time was spent with.

Table 11 shows male and female primary social partners. In females, daughters are the preferred primary social partners. In all female groups, preferred

partners are offspring; if sons are added to daughters, 100% of the middle-aged female’s primary partners are accounted for. In old males, 80% of their primary social contact partners are infants. The young and middle-aged male groups, however, spend at least 50% of their primary social contact with adult, reproductive females.

TABLE 10
MALE AGE CATEGORIES BY WEIGHTED CHARACTERISTICS OF THE SOCIAL NETWORK

Network characteristics	Old X	Middle X	Young X	F or (H) value (p)
Rank	1.39	1.85	1.98	0.98
Variance in rank	0.0246	0.112	0.078	(2.72) (0.26)
Relative variation in rank	0.334	0.845	0.551	(1.44) (0.49)
Age	6.81	6.88	6.90	(0.0) (0.99)
Variance in age	0.161	1.54	0.931	(6.03) (0.04)
Relative variation in age	0.51	2.75	1.65	(6.03) (0.05)
Time with others	470.6	5.61	409.7	0.60 (0.56)
Variance in time with others	167,240.0	522,731.0	30,547.0	1.71 (0.22)
Relative variation in time with others	748.6	821.7	594.2	0.43 (0.66)

TABLE 11
FEMALE AND MALE PRIMARY SOCIAL PARTNERS BY PERCENT

Age group	Female			Male		
	Old	Middle	Young	Old	Middle	Young
Daughter	50%	91%	43%			
Son		9%	14%			
Sister	1%		29%			
G. daughter	16%					
Cousin			14%			
Male No relation	33%					
Infants				80%		16%
Yearlings					14%	16%
Juveniles						16%
Young female				20%	14%	2%
Adult female					58%	50%
Adult male					14%	
Total	100%	100%	100%	100%	100%	100%

Discussion

This study examined associations of age with social behavior of male and female rhesus macaques in three specific areas: social interactions, social roles, and social networks. The objective of this research was to explore behavioral differences between male and female rhesus macaque age classes by looking at the general relationship between an individual's age and (1) degree of sociability, (2) individual behaviors, and (3) characteristics of their social networks. These data indicate that over the adult life span, important differences occur in rhesus sociability, behavior, and social networks.

Old monkeys (over 20 years) spend more time resting and sleeping than other adult monkeys, which may be secondary to the underlying processes of senescence. Beyond this characteristic, which is shared by both males and females, the data show clear, sex-based differences in social behaviors. Interestingly, these differences often appear progressive across age classes, e.g., declining across age classes in females and increasing across age classes in males. For instance, female rhesus social networks decrease in size across age classes, while male social networks increase in size across age classes. Also, old females spend less time in proximity with others, less time in social contact, and groom less than other adult females, while males exhibit an almost *mirror-image* increase in these behaviors across age classes. Old male rhesus monkeys spend more time in proximity with others, more time in social contact, and are groomed more than other adult males. Clearly, these results show that old females and old males are distinct in their social behaviors, both from each other and from other adults.

An explanation for the sex-based differences in social behavior reported in this study may originate in rhesus social

structure. Rhesus society is matrifocal with related females remaining in their matriline for life. Males, on the other hand, leave their natal group at adolescence and do not normally spend their adult social and reproductive lives in a related group. From the beginning of adulthood, male and female rhesus macaques live very different lives. It follows then, especially given the sex-based differences reported here, that *successful* aging could require different social strategies for male and female rhesus. Perhaps to be *successful* in old age (i.e. to survive), males must reduce agonistic behaviors that could lead to debilitating physical injuries, and increase social activity to maintain their position within a social group.

Old rhesus males spend the majority of their social contact time with infants and yearlings rather than adult females, which may serve to avoid dangerous challenges from younger adult males. Females, on the other hand, are socially secure within their matriline at any age and, to be *successful* in old age, may only need to maintain already stable familial relationships. While it is reported here that females become less social with increasing age, agonistic behaviors do not decrease and daughters remain their preferred social partners. For males, the 'old' age class has the highest level of social behaviors and the lowest level of agonistic behaviors.

This study demonstrates that old male and old female rhesus behaviors differ significantly from those of younger adults. Aging is a complex and variable process. An individual ages chronologically through the passage of time, biologically, through changes in physiological function, psychologically, through changes in personality and cognitive function, and socially, through changes in patterns of behavior⁶. If we are to enhance our understanding of these complex processes to the benefit of

the world's growing numbers of *aged*, a wider, biocultural view, inclusive of both biology and behavior should guide our investigations. Additionally, since aged

male social behavior has not specifically tested prior to this study, more research in this area is needed.

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DRUŠTVENO PONAŠANJE STARIH REZUS MAKAKA

S A Ž E T A K

Ova studija proučava odnos između kronološke dobi i društvenog ponašanja u 42 odrasla rezus makaka oba spola (*Macaca mulatta*) u tri specifična područja: socijalna interakcija, socijalne uloge i socijalna mreža. Dok su i starim mužjacima i ženkaama zajedničke razlike u ponašanju koje su vezane uz starost, ova studija pokazuje da se stare ženke i stari mužjaci razlikuju u socijalnom ponašanju, kako međusobno tako i u odnosu na druge odrasle jedinice. Mnoge od ovih razlika javljaju se progresivno pre-laskom iz jedne dobne klase u drugu, i to uz smanjenje socijalnih aktivnosti u ženki te porast u mužjaka. Stare ženke manje su društvene i imaju manju društvenu mrežu od drugih ženki, dok je suprotno nađeno kod starih mužjaka. Jedno tumačenje spolno zasnovanih razlika u socijalnom ponašanju i socijalnim mrežama starih makaka o kojem je ovdje izviješteno jest da ta razlika proizlazi iz matricentrične socijalne strukture rezus makaka.