

The Behavior of Peripheral Males During the Mating Season in *Macaca fuscata*

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ABSTRACT. The mating season behavior of peripheral male Japanese macaques (*Macaca fuscata*) at Arashiyama West were studied during the 1994/1995 mating season. Although all peripheral males increased their proximity to the main troop, there was great variation in this behavior, from those who became virtually indistinguishable from the main troop males to those who moved in and out of the main troop in a clandestine fashion, to those who had only visual contact, from a distance of 25 m, with the main troop. The subsequent behavior of males displaying these three patterns was compared, as was the behavior of peripheral to main troop males. Specifically, they were investigated for variation in three behavioral strategies which may function to increase access to mates: aggressive intimidation; affiliation with unrelated main troop females; and courtship display. The results show that peripheral males are a more diverse group than previously described, and that one group of peripheral males was able to successfully join the main troop, becoming indistinguishable from main troop males with regard to these behaviors which enhance access to mates.

Key Words: Peripheral males; Access to mates; Japanese macaques; Proximity; Provisioning.

INTRODUCTION

Emigrating male Japanese and rhesus macaques become solitary for a period of time, transfer directly into another heterosexual troop, or join a peripheral male subgroup (FUKUDA, 1991). Peripheral male subgroups have been reported for both Japanese (SUGIYAMA, 1976; FEDIGAN, 1976; NISHIDA, 1966; PAVELKA, 1993) and rhesus macaques (BERARD, 1990, 1993; COLVIN, 1983, 1986; BOELKINS & WILSON, 1972), although the information available on these subgroups is limited. Peripheral male subgroups are usually only anecdotally noted and in most studies members have not been individually identified (see NORMAN, 1994; FEDIGAN, 1976, for exceptions). The amount of time males spend in peripheral male subgroups and the relationship of these subgroups to heterosexual troops is unclear.

A peripheral male group is best defined as a spatially distinct subgroup comprised of subadult males (4.5–9.5 yrs), adult males (10+ yrs), and occasionally “floating females” (low ranking females found away from the main troop area) (FEDIGAN, 1976). These peripheral male subgroups occupy the peripheral, usually suboptimal, portions of the main troops range (PUSEY & PACKER, 1987). Immigrating males often join peripheral male subgroups of the troops they are attempting to enter, as affiliative interactions with the peripheral males may facilitate troop acceptance (Japanese macaques: SUGIYAMA, 1976; FURUICHI, 1985; MATSUMURA, 1991, 1993; rhesus macaques: COLVIN, 1983). FEDIGAN’S

1976 study of Japanese macaques at Arashiyama West, provides a description of a peripheral male subgroup and their behavior during the non-mating season.

Despite a high level of interest in variables which influence male mating activity, and although the movement of peripheral males into the main troop area at the commencement of the breeding season has been reported by several researchers (NORMAN, 1994; PAVELKA, 1993; HUFFMAN, 1987, 1992), the mating activity of peripheral males has not been a focus of study. Peripheral male Japanese and rhesus macaques have been reported to be successful in mating (Japanese macaques: SUGIYAMA, 1976; NORMAN, 1994; PAVELKA, 1993; HUFFMAN, 1987; rhesus macaques: BERARD et al., 1993), however, their mating strategies have not been fully documented.

This paper reports on a study of variation in the behavior of peripheral males during mating season and a comparison of peripheral to main troop (central) males, with a focus on behaviors which may increase access to mates.

STUDY SITE AND METHODS

The study was conducted at the site of the Arashiyama West colony of Japanese macaques, 125 km southwest of San Antonio, Texas. The troop has fully adapted to and is thriving in the desert-like environment of South Texas. The population has grown from an original 150 animals in 1972 to over 600 animals in 1994 at the time of the study. A large population is not uncommon for provisioned groups. The troop was not enclosed within any physical barriers at the time of the study, and ranged over an area of approximately 100 ha of ranch land, foraging extensively on native vegetation. The native food supply is enhanced with a daily provision of monkey chow and grain.

SUBJECT ANIMALS

A total of 25 focal animals were chosen for this study. Upon commencement of this study in September 1994 there were approximately 67 males over 4.5 yrs of age including main troop ($N=24$), peripheral ($N=37$), and solitary ($N=6$) males. Main troop males are those males which do not normally leave the main troop area (the area where the core of related females and their immature offspring spend their time). Peripheral males are defined as being both spatially and socially separated from the main troop. Subjects were selected to represent a variety of ages, ranks, and family lines, and according to the ease with which they could be located and observed. Fifteen main troop and ten peripheral males were selected as subjects.

DATA COLLECTION METHODS

A total of 125 hr of focal animal data (20–15 min sessions for each male) were collected on a rotational basis from September 19 through December 21, 1994, and January 8 through January 13, 1995. In addition, during this time frame 49 scans of 45 min in length were also collected (36.75 hr) in which a male's location was mapped and reproductive status assessed. A one-month period prior to the commencement of data collection was utilized for reconnaissance observations and refinement of study questions and data collection techniques. As the Arashiyama West macaques are provisioned, at least one hour elapsed after provisioning prior to data collection.

BEHAVIORAL CATEGORIES AND MEASUREMENT

By the end of the first week in October a noticeable difference in the daily locations of peripheral males had occurred. Daily observations along with an examination of ad lib notes, daily scan maps, and focal animal data revealed that most peripheral males had decreased, or were attempting to decrease, the distance between themselves and the main troop. Three major patterns of increasing proximity to the main troop were readily recognizable, and these heuristically identified categories were used as the basis for the quantitative comparison of male behavior.

Proximity Pattern 1 (PP1) was characterized by a gradual increase in spatial proximity to, and eventual entrance into, the main troop. Four of the ten peripheral male focal animals (mean age=9.5) joined the main troop during the mating season. These males remained highly visible within the main troop area and interacted with main troop members on a continuous basis.

Proximity Pattern 2 (PP2) was characterized by a gradual increase in spatial proximity accompanied by frequent movement into and out of the main troop area. These males usually remained out of sight from main troop members and generally interacted with troop females for copulatory purposes only. Four subject males followed this pattern (mean age=7).

Peripheral males following Proximity Pattern 3 (PP3) gradually increased their proximity to the main troop, however, a distance of approximately 25 m was maintained between these males and main troop animals. PP3 males often sat watching the main troop from a non-interactive distance. Two subjects followed this pattern (mean age=10.5).

These three categories of peripheral males were quantitatively compared with each other and with main troop males ($N=15$; mean age=10.8) for their use of behaviors which are known or believed to assist males in gaining access to females during the mating season: aggressive intimidation (SMUTS & SMUTS, 1993), affiliation with potential mates (SMUTS, 1985; STRUM, 1987; MANSON, 1992), and display (PAVELKA, 1993; SPRAGUE, 1991; WOLFE, 1981; MODAHL & EATON, 1977).

Aggressive behaviors for this study were scored as events, as they were brief in duration, and included: gape, growl, lid, stare, head bob, chase, lunge, bluff charge, pinch, slap, grab, push, pull, and bite. Each male received an aggression score which represented the total number of aggressive incidents he directed against any unrelated adult females. Stalking is a distinct aggressive behavior which is essentially a mode of traveling during which a male keeps his body low to the ground with his head protruding out in front of him as he constantly scans his surroundings. Male stalking behavior is unique to the mating season (PAVELKA, 1993). A male engaged in stalking moves quickly and appears to be searching for something or someone. Although the target of stalking is seldom evident, the behavior usually terminates in aggression directed towards females. Because of its distinctive quality, stalking was analyzed separately from other aggressive behavior.

Affiliation was measured in terms of the amount of time spent in proximity or in non-aggressive physical contact with unrelated adult females, such as sitting in body contact and grooming. Proximity was scored as affiliative only if the proximity could not be explained by another factor, such as incidental foraging on closely spaced food sources.

The displays performed by each focal male during focal animal data collection were tallied into two separate scores: long-distance displays and courtship displays. Long-distance displays involve the climbing and shaking of a flexible structure, often accompanied by loud guttural vocalizations. These displays are visible and often audible

from great distances. Courtship displays, in contrast, are performed at close range to the target female, and include lip quivering and/or staring at a female, "strutting," "bird dogging," and performing a "whirl-pivot" (see PAVELKA, 1993: 105–106 for full description).

The data were tested and determined to be normally distributed. Tests of two sample means were performed by use of *t*-tests, and three sample means by one-way analysis of variance.

RESULTS

In this study, peripheral males accounted for 58%¹⁾ of all mount-series' observed during scan data collection, which is comparable to SPRAGUE'S (1992) report that non-troop male Yaku macaques (*Macaca fuscata yakui*) account for 41% of all observed matings. With the exception of the two PP3 males, all focal animals were successful in mating. The mean mating scores¹⁾ for the four groups of focal males are as follows: MT=38.28; PP1=29.975; PP2=22.5; PP3=0.

Results of the quantitative comparison of the behaviors of PP1, PP2, and PP3 males are presented in Table 1. The analysis revealed that PP1 males directed significantly more total aggression against unrelated females than did males following PP2 and PP3. PP3 males were the least aggressive toward adult females, which is not surprising given that they were non-interactive in general. The significantly less frequent performance of aggressive

Table 1. Comparison of the behaviors of PP1, PP2, and PP3 peripheral males.

Behavior	PP category	Mean	<i>F</i>	<i>F</i> _i	<i>p</i>
No. of aggressive acts directed at unrelated adult females	PP1/PP2	20.25/8.75	4.348	11.50	< .05
	PP1/PP3	20.25/2.50		17.75	< .01
	PP2/PP3	8.75/2.50		-6.25	ns
Time (in seconds) spent stalking	PP1/PP2	353/8	4.727	344.75	< .05
	PP1/PP3	353/86		-267.25	ns
	PP2/PP3	8/86		-77.50	ns
Time (in seconds) spent affiliating with unrelated adult females	PP1/PP2	5507/2186	7.899	3321.00	< .05
	PP1/PP3	5507/00		5507.00	< .01
	PP2/PP3	2186/00		2186.00	ns
No. of long-distance displays performed	PP1/PP2	2/1.75	2.600	n/a	ns
	PP1/PP3	2/7			
	PP2/PP3	1.75/7			
No. of courtship displays performed	PP1/PP2	7.5/4.25	2.501	n/a	ns
	PP1/PP3	7.5/.05			
	PP2/PP3	4.25/.05			

ANOVAs and Fisher's PLSD post-hoc test where applicable.

1) Based on an adjusted mate score. Not all focal males could be located during all scan sessions, therefore, a proportional mating score was calculated: number of scans in which a focal male was observed mating with a different female divided by the total number of scans during which that male was located.

behaviors by PP2 males may have been part of an attempt to retain a low profile and not draw the attention of main troop males to their presence in the main troop.

The interactions of PP1 males with unrelated females were not always aggressive. In fact, these peripheral males spent significantly more time affiliating with unrelated females than did the other peripheral males. PP2 males affiliated with unrelated adult females significantly less than PP1 peripheral males, and their affiliative interactions occurred almost exclusively while in a consort. The frequency of affiliative interactions of PP2 males with unrelated females did not differ significantly from those of PP3 males, even though PP3 males were not observed affiliating with unrelated females during the focal animal sessions. PP2 males had either little interest in, or little opportunity for associating with unrelated females for purposes other than copulation.

There were no significant differences in either courtship or long-distance display frequencies between the three categories of peripheral males, although some interesting mean differences deserve mention. PP1 and PP2 males had similarly low frequencies of long-distance displays compared to PP3 males. Long-distance displays were probably unnecessary for PP1 and even PP2 males as they were already in proximity to estrous females. PP2 males may have limited their performance of these overt shaking displays in order to avoid drawing the attention of main troop males. Not surprisingly, the distant and solitary PP3 males utilized the long distance display most frequently, although there is no clear evidence from this study that it was successful at enticing females out to them.

The use of courtship displays by the peripheral males directly paralleled the proximity pattern displayed. Although not significant, PP1 males engaged in the highest mean frequency of courtship displays, followed by PP2 and finally PP3 males. The successful adoption of PP1 gave these males the option of using courtship displays more often than those males who were limited by a greater distance between themselves and the females of the main troop.

The results of the quantitative comparison of peripheral with main troop males are presented in Table 2. Main troop males did not direct significantly more aggression toward unrelated females than peripheral males when peripheral males are treated as a group, however when compared with each of the three proximity categories of peripheral males, important differences emerge. Main troop males directed significantly more aggression against unrelated females than peripheral males following PP2 and PP3 but not more than those males following PP1. The results for stalking behavior are comparable to those for other aggressive incidents.

Main troop males spent significantly more time affiliating with unrelated females during the mating season than peripheral males as a whole, but again when peripheral males were divided into PP1, PP2, and PP3, interesting, but perhaps not surprising results emerged. It was the low affiliation scores of PP2 and PP3 males which were responsible for the significantly lower affiliation score of peripheral males as a whole. Both PP2 and PP3 males experienced significantly lower affiliative interactions with unrelated females than main troop males. PP1 males did not differ from main troop males in their affiliative interactions with unrelated females. As with aggressive behavior, males who successfully adopted PP1 closely resembled main troop males in their affiliative behavior.

No significant differences were found between main troop males and the peripheral male group in the frequency with which they performed long-distance or courtship displays even when the proximity pattern of the peripheral males was taken into account. It is interesting to note that PP1 males had the highest frequency of courtship displays, higher even than

Table 2. Comparison of the behaviors of peripheral with main troop males.

Behavior	Sub-group	Mean	<i>t</i> -value	<i>F</i>	<i>F</i> _{<i>i</i>}	<i>p</i>
No. of aggressive acts directed at unrelated adult females	PP/MT	12.10/15.53	-1.189	—	—	ns
	PP1/MT	20.25/15.53		6.038	4.72	ns
	PP2/MT	8.75/15.53			-6.78	< .05
	PP3/MT	2.50/15.53			-8.75	< .01
Time (in seconds) spent stalking	PP/MT	161/237	-0.857	—	—	ns
	PP1/MT	353/237		2.437	n/a	ns
	PP2/MT	8/237				
	PP3/MT	86/237				
Time (in seconds) spent affiliating with unrelated adult females	PP/MT	3077/6032	-2.884	—	—	< .01
	PP1/MT	5507/6032		6.928	-524.67	ns
	PP2/MT	2186/6032			-3845.67	< .01
	PP3/MT	00/6032			-6031.67	< .01
No. of long-distance displays performed	PP/MT	2.90/4.60	-1.267	—	—	ns
	PP1/MT	2.00/4.60		2.018	n/a	ns
	PP2/MT	1.75/4.60				
	PP3/MT	7.00/4.60				
No. of courtship displays performed	PP/MT	4.80/5.13	-0.221	—	—	ns
	PP1/MT	7.50/5.13		2.018	n/a	ns
	PP2/MT	4.50/5.13				
	PP3/MT	0.50/5.13				

t-test for PP/MT comparisons; ANOVAs and Fisher's PLSD post-hoc tests where applicable, for MT with PPI, PP2, and PP3 comparisons.

main troop males. This use of courtship displays by PPI males may have been necessary for them to reassure interested females who may otherwise have been too fearful to approach them because of their aggressive tendencies.

DISCUSSION

Peripheral male subgroups do not occur on Yakushima Island, Japan, where the Japanese macaques have not been provisioned, leading SPRAGUE (1991, 1992) to suggest that these subgroups are the product of provisioning. Provisioning of macaques has been reported to contribute to the formation of large groups with extended and complex matriline and large cohorts of young natal males forming around the troops periphery (HILL, 1991; ASQUITH, 1989; PERLOE, 1992; SPRAGUE, 1992). Most well studied groups of Japanese and rhesus macaques have been provisioned, yet the adaptive significance of the formation of these groups is not understood. Due to their limited social interactions with members of heterosexual troops, peripheral males are generally not considered to be a part of the Japanese macaque mating system. So while males residing in heterosexual troops have been the focus of an abundance of studies, there is little information on the behavior of peripheral males. Peripheral male subgroups may provide insight into the adaptation and evolution of primate social and mating systems.

The present study found that peripheral males were active participants during the mating season, displaying a variety of behavioral patterns. Three initial patterns of increasing proximity to the main troop were recognized early in the mating season, and these

were associated with different behavior and access to mates throughout the rest of the season. Although all peripheral males increased their proximity to the main troop, there was great variation in this behavior, from those who became virtually indistinguishable from the main troop males (labeled Proximity Pattern 1) to those who moved in and out of the main troop in a clandestine fashion (labeled Proximity Pattern 2), to those who had only visual contact, from a distance of 25 m, with the main troop (labeled Proximity Pattern 3). The emergence of these three proximity patterns was obvious to the observer at the beginning of the mating season, and later quantitative analysis showed them to be associated with some important differences in behaviors which may function to increase access to mates: aggressive intimidation, affiliation with unrelated adult females, and courtship display.

Males displaying Proximity Pattern 1 (PPI) deviated most from previous, mostly anecdotal, descriptions of peripheral male mating behavior. These males did not sneak around the main troop and peripheral areas mating in concealed locations, and they rarely engaged in tree shaking displays as a means of enticing females to their locations. Instead, they moved into the main troop area and assimilated themselves into the troop through the use of both aggressive and affiliative behaviors. In most analyses, peripheral males displaying Proximity Pattern 1 showed significant differences in aggression, affiliation, and display with PP2 and/or PP3 peripheral males, but they were not significantly different from main troop males.

Aggressive behaviors directed towards main troop animals accompanied by stalking were described by SPRAGUE (1992) as part of an "alpha-male attitude" characteristic of some non-troop males upon entering a heterosexual troop during the mating season, and his description parallels the observations of the movement of PPI males into the main troop area during this study. PPI males at Arashiyama West also manifest an "alpha-male attitude" which may have facilitated them in joining the main troop during the mating season, as the behaviors characteristic of this 'attitude' were not utilized by males following PP2 or PP3.

The aggressive behavior of PPI males were most prominent during the first month of the mating season, which might indicate that they served as an initial display of the aggressive potential of these males. These initial displays of aggressive behaviors were very noticeable and even the males of the main troop would avoid these 'newcomers' while they were stalking. Perhaps this behavior functioned as sexual coercion to intimidate females, and also to intimidate main troop males, allowing PPI males to remain in the main troop throughout the mating season. PPI peripheral males also used courtship display and affiliation with adult females at higher frequencies than the other peripheral males, and at frequencies comparable to main troop males.

The males who displayed PP2 and PP3 were more consistent in their behavior with what has been anecdotally described for peripheral males in general: opportunistic matings and clandestine movements in and out of the main troop, or tree shaking displays from a distance. Pre-mating season documentation of peripheral males and their activities was necessary for the three proximity patterns to be distinguished. In the absence of pre-mating season documentation, PPI peripheral males would very likely be mistaken as main troop males. This study revealed that there is greater variation in the mating season behavior of peripheral males than has been previously recognized, and that those peripheral males which successfully adopted a pattern of moving into the main troop during the mating season would be indistinguishable from main troop males at that time.

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