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Influence of Fluctuation in the Operational Sex Ratio to Mating of Troop and Non-troop Male Japanese Macaques for Four Years on Kinkazan Island, Japan

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ABSTRACT. Taking advantage of a marked yearly fluctuation in the number of estrous females, I studied the differences in mating success between troop males and non-troop males in an unprovisioned group of Japanese macaques. Fluctuation in the defendability of estrous females by troop males, as predicted by the operational sex ratio (the number of estrous females per troop male), strongly affected the mating with ejaculation (successful mating) per observation day of both troop and non-troop males. When operational sex ratio was low, troop males monopolized successful mating inside the troop. No successful mating of non-troop males was observed inside the troop. In contrast, both troop and non-troop males were able to mate often inside the troop when operational sex ratio was high. These findings suggest that troop males obtained the benefit of secured successful mating in the troop because troop males could mate successfully even in mating seasons with a low operational sex ratio, and the chance of successful mating for non-troop males will increase as the ability of troop males to monopolize estrous females decreases.

Key Words: Japanese macaques; Mating; Defendability of estrous females; Troop males; Non-troop males; Operational sex ratio.

INTRODUCTION

In primate species with male dispersal and female bonding, males either become troop or non-troop males after their natal and/or secondary transfer (PUSEY & PACKER, 1987). Non-troop males have been observed to gain access to troop females and mate with them, suggesting that males have alternative mating strategies corresponding with different periods in their life history (Japanese macaques: NISHIDA, 1966; SUGIYAMA, 1976; YAMAGIWA, 1985; FURUICHI, 1985; SPRAGUE, 1991; SUZUKI et al., 1998; rhesus macaques: LINDBURG, 1969; BERARD et al., 1994; hanuman langurs: LAWS & LAWS, 1984; red-tailed monkeys: CORDS, 1984; JONES & BUSH, 1988; blue monkeys: CORDS et al., 1986; HENZI & LAWES, 1987; patas monkeys: HARDING & OLSON, 1986; OHSAWA et al., 1993). Therefore, primatologists must reformulate theories of male mating success to incorporate mating by non-troop males (SPRAGUE, 1991).

The defendability of estrous females by troop males affects the mating success of both troop and non-troop males. When the number of females simultaneously in estrus is relatively small compared to the number of troop males, and these troop males are able to dominate non-troop males, then troop males are expected to defend estrous females from non-troop males and thus monopolize mating success. Moreover, according to the female defense polygyny theory, dominant males attain high mating success in many primate groups through interference competition for access to estrous females. Male dominance rank is assumed to predict male mating success (BERENSTAIN & WADE, 1983). Also, the priority of access to estrous females model (ALTMANN, 1962) proposes that male dominance rank maintains the precedence of access to estrous females, allowing dominant males to attain high mating success. In contrast, when the number of females simultaneously in estrus is relatively large compared to the number of available males, then non-troop males are predicted to mate more often, because it is difficult for troop males to control all estrous females. Consequently, the ability to defend estrous females is predicted by the number of estrous females per troop male.

However, socio-demographic parameters of a troop tend to fluctuate considerably (ALTMANN & ALTMANN, 1979; DUNBAR, 1987). In some seasonal breeding species, such as Japanese and rhesus macaques, the number of estrous females in a troop fluctuates not only during a mating season (TAKAHATA, 1980; YAMAGIWA, 1985) but also from year to year (BERARD, 1999). This suggests that an evaluation of relative mating success between troop and non-troop males based on data collected in only one mating season may be misleading. To analyze the effect on male mating success of fluctuations in the number of estrous females per troop male, research should cover at least several successive years.

This study took advantage of marked yearly fluctuations in the number of estrous females in a troop of Japanese macaques over a 4-year period. I first review yearly fluctuations in the number of estrous females, troop males, non-troop males, and the number of estrous females per troop male. Second, to measure defendability of estrous females, I describe the agonistic interference of non-troop males by troop males. Third, I analyze the effect of fluctuations in the number of estrous females per troop male on the mating success of troop and non-troop males.

METHODS

I conducted this study on Kinkazan Island, Miyagi Prefecture (38°16'N, 141°35'E), Japan. This island has a total area of about 10 km^2, and it is covered with cool temperate zone deciduous forests (NAKAGAWA, 1990). Six unprovisioned Japanese macaque troops, whose home ranges overlapped widely, inhabited the island (IZAWA, 1998; MARUHASHI et al., 1998). I chose one of them, the Kinkazan A troop, as the subject of this study. This troop has been habituated, and individuals have been identified since 1984 (SATO, 1988). On this island, the mating season usually lasts from late September to early December, with a peak in mating activity around October to November. Yearly fluctuation in the number of births has been reported in the Kinkazan population (IZAWA, 1992, 1995). These fluctuations are suggested to be related to differences in fruiting patterns during the conception-pregnancy period from year to year (SUZUKI et al., 1998).

Males were defined as follows: (1) troop males (TMs): non-natal and immigrated males, at least 5 yr old, found ranging with females during the non-mating season; (2) non-troop males (NTMs): males who were observed at the periphery or interacting with the subjects of the study troop after the start of the mating season when I had first observed an estrous female in the study troop. During the study period, I observed no young troop males aged 6 to 9 yr old. However, I did observe NTMs ranging in age between 6 and >15 yr old. In the Kinkazan population, the youngest solitary males or males in all-male groups were 3 yr old. Solitary males made up 61.7% (552/895) of records between 1982 and 1993, and the sizes of all-male groups ranged from 2 to 17 individuals (SPRAGUE et al., 1998). Although there were no data available for body weights of either TMs or NTMs, males within the same age classes seemed to be similar in size.

The numbers of TMs, NTMs, and estrous females (EFs) were recorded daily while I observed the study troop. Estrus was judged from observations of mating, the presence of vaginal plugs, and the degree of red coloration of the faces and genital regions. Operational sex ratio (OSR: EMLEN & ORING, 1977) was defined as the number of EFs per TM. All NTMs were monitored and identified daily during the study period. No NTMs remained in the study troop after the mating season had ended in any of the study periods. No natal males were observed mating during the study periods. In the Yakushima study population, TMs were observed to visit other troops as NTMs and mate during the mating season (SPRAGUE, 1992); in contrast, no TMs of my study troop were observed to visit other troops during the study period. When encounters between groups were observed, matings between individuals of different troops were recorded in the Yakushima study population; in contrast, no intergroup mating was recorded in Kinkazan population (SAITO et al., 1998).

Mating was defined as a series of mountings between a male and a female, terminated by: (1) cessation of mounting for at least 5 min; (2) separation of consort pair animals by at least 15 m; or (3) ejaculation (HANBY & BROWN, 1974). A mating with ejaculation was defined as a successful mating.

The location of mating was divided into two areas : (1) *inside the troop*, in a place where I could observe any number of other TMs and other estrous and/or anestrous females; (2) *outside the troop*, in a place where I could not see other TMs and anestrous females. I only used data from observations within the troop to make comparisons between TMs and NTMs unless otherwise stated, because matings outside the troop potentially involved not only estrous females of the study troop, but also estrous females of other troops.

I used two sampling methods to record mating. Kinkazan Island has good visibility because grazing pressure of Shika deer (*Cervus nippon*) has suppressed the growth of ground cover. Furthermore, there are no cliffs, except along the shoreline (NAKAGAWA et al., 1991). Nevertheless, NTMs were difficult to follow, and some of them were observed for only a few days. Thus, in order to record as many matings as possible, the mating of both TMs and NTMs were recorded by all-occurrence sampling. To investigate the mating frequency of TMs and NTMs, I compared the number of successful matings per observation day for each male. Second, to measure their mating frequency, all TMs were followed and observed for 10 hr each using focal animal sampling (ALTMANN, 1974) during the study years. The focal sampling time of a TM in one day was no more than 1 hr. After completing 30 min of focal sampling of a TM, I switched to a different focal TM or restarted focal sampling of the same individual after a 30-min interval. The total number of focal sampling hours was 130. When all mating observation data by both methods are pooled, they may be biased towards troop males; thus, to eliminate this possibility, I excluded all matings observed by focal sampling of TMs from the analyses when I compared the mating behaviors of TMs to NTMs. The numbers of observation days in each year were 32 (1992), 20 (1993), 28 (1994), and 17 (1995). The numbers of available observation days inside the troop for comparative analysis between TMs and NTMs were 16 (1992), 15 (1993), 13 (1994), and 13 (1995), and the total observation time was 372 hr 43 min for the entire four years.

Agonistic interference was defined to have occurred when one or more males aggressively approached the dyad of a male and an EF. Agonistic interference was recorded during all observations irrespective of whether focal animals were involved. All statistical tests used were non-parametric (Kruskal-Wallis, Wilcoxon matched pairs signed rank tests, and Kendall's rank correlation coefficient) and two-tailed unless otherwise stated.

RESULTS

YEARLY FLUCTUATION IN THE NUMBER OF EFS, TMS, AND NTMS

Relatively small numbers of estrous females were recorded in 1992 and 1994, whereas large numbers were observed in 1993 and 1995, when almost all females came into estrus (Table 1). The percentage of estrous females among all adult females was 25% (5/20) in 1992, 95% (19/20) in 1993, 15% (3/20) in 1994, and 94% (17/18) in 1995. The number of EFs per observation day was 1.1 in 1992, 5.9 in 1993, 1.5 in 1994, and 6.4 in 1995. Differences in the number of EFs per observation day among the study years were significant (Kruskal-Wallis test, $df=3$, $H=45.3$, $p<0.0001$). The number of TMs in the mating season decreased from 5 in 1992 to 2 in 1995 (Table 1). No TM was observed mating outside of the troop during the study period.

The mean daily OSR was 0.21 in 1992, 1.9 in 1993, 0.48 in 1994, and 3.1 in 1995; these differences were significant ($df=3$, $H=50.05$, $p<0.00001$). This fluctuation predicted that the defensibility of EFs was high in the 1992 and 1994 mating seasons when the OSR was low. In contrast, defendability of EFs was predicted to be low in the 1993 and 1995 mating seasons, when the OSR was high.

The total number of non-troop males recorded during the mating season increased from 8 in 1992 to 18 in 1995 (Table 1). The number of NTMs per observation day in the mating season was 1 in 1992, 4.1 in 1993, 4.9 in 1994, and 6.6 in 1995 (Table 1). Differences in the number of NTMs per observation day among the study years were significant ($df=3$, $H=38.3$, $p<0.0001$).

Whether NTMs assessed the possibility of mating based on the OSR of a troop on a daily basis was unclear. A significant correlation was found between the daily OSR and the daily number of NTMs in 1992 (Kendall's rank correlation coefficient, $N=16$, $\tau=0.415$, $p<0.05$) and 1993 ($N=15$, $\tau=0.38$, $p<0.05$), but was not found in 1994 ($N=13$, $\tau=0.336$, $p>0.1$) and 1995 ($N=13$, $\tau=0.377$, $p<0.1$).

The number of observed days per NTM was 2.0 (8 NTMs, 16 observation days, s.d.=1.0, range, 1 – 4) in 1992, 4.4 (14 NTMs, 15 observation days, s.d.=4.2, range, 1 – 14) in 1993, 4.2 (15 NTMs, 13 observation days, s.d.=3.5, range, 1 – 11) in 1994, and 4.7 (18 NTMs, 13 observation days, s.d.=4.6, range, 1 – 13) in 1995. I found no significant differences in the number of observation days of each NTM among the study years ($df=3$, $H=1.64$, $p>0.6$).

AGONISTIC INTERFERENCE

No agonistic interference between TMs and NTMs was observed in 1992. Only one episode of agonistic interference of a NTM by a TM was observed in 1994. The NTM had been mating when the interference occurred, and this interference inhibited his ejaculation. In contrast, 4 cases of agonistic interferences of a NTM by a TM were observed in 1993, and 11 cases in 1995. These findings suggest that TMs made stronger efforts to interfere in the mating between NTMs and EFs when defendability of EFs decreased. In fact, agonistic interferences by TMs inhibited the successful matings of 2 NTMs in 1993 and 3 NTMs in 1995. Nevertheless, TMs failed to inhibit most successful matings by NTMs in 1993 and 1995, when the OSR was high (see below). Of 24 agonistic interferences between TMs and NTMs, only 2 NTMs behaved in a dominant way over TMs. However, they were unsuccessful in inhibiting the TMs. This suggests that TMs dominated almost all NTMs and that defendability of EFs decreased as the OSR increased.

During focal animal sampling of TMs, the frequency of all agonistic interactions including agonistic interferences from TMs to NTMs was 0.06 (3 times/50 observation hours) in 1992, 0.3 (10 times/30 observation hours) in 1993, 0.26 (8 times/30 observation hours) in 1994, and 0.35 (7 times/20 observation hours) in 1995. NTMs seemed to attempt to intrude into the troop and approach EFs irrespective of OSR. However, low frequencies of agonistic interactions from TMs to NTMs in low OSR years suggests that it was difficult for NTMs to approach when the troop contained only a few estrous females.

Table 1. Socio-demographic parameters in Kinkazan A troop from the 1992 to 1995 mating seasons.

		Number of adults			Estrous females				Operational sex ratio[2]				Non-troop males			
					Overall	Per observation day			Overall	Per observation day			Overall	Per observation day		
Study years	Troop size	Males	Females[1]	Total	number	Number	s.d.	Range	ratio	Ratio	s.d.	Range	number	Number	s.d.	Range
1992	46	5	20(5)	25	5	1.1	0.2	1 - 2	1	0.21	0.05	0.2 - 0.4	8	1	1.1	0 - 4
1993	38	3	20(2)	23	19	5.9	2.4	3 - 12	6.3	1.9	0.79	1.0 - 4.0	14	4.1	1.6	2 - 8
1994	51	3	20(14)	23	3	1.5	0.5	1 - 2	1	0.48	0.17	0.3 - 0.7	15	4.9	1.8	2 - 8
1995	43	2	18(0)	20	17	6.4	1.9	2 - 8	8.5	3.1	0.9	1.0 - 4.0	18	6.6	1.2	5 - 8

1) Numbers in parentheses show the number of females who gave birth in the year and remained with their infants in the mating season; 2) Operational sex ratio was defined as the number of estrous females per troop male.

Table 2. Successful mating of troop males observed by focal and all-occurrence sampling.

	1992 mating season			1993 mating season			1994 mating season			1995 mating season		
Rank	Troop male	Focal sampling	All-occurrence sampling	Troop male	Focal sampling	All-occurrence sampling	Troop male	Focal sampling	All-occurrence sampling	Troop male	Focal sampling	All-occurrence sampling
1	*AR*	1	0	*PR*	12	13	*PR*	4	5	*CR*	9	10
2	*IS*	3	3	*CR*	6	2	*CR*	3	0	*NT*	8	27
3	*PR*	0	0	*NT*	4	2	*NT*	1	1			
4	*CR*	0	0									
5	*NT*	0	0									

RELATIONSHIP BETWEEN OSR AND MATING SUCCESS OF TMs AND NTMs

The number of successful matings by TMs recorded using all-occurrence sampling was similar to the number recorded using focal sampling. I found a significant correlation between the all-occurrence and the focal sampling methods (Kendall's rank correlation coefficient, N=13, τ=0.788, p<0.01, Table 2), and no significantly different distribution resulted from using pooled data (Wilcoxon matched pairs signed rank test, z=−0.354, p>0.7). Therefore, I used the matings recorded by all-occurrence sampling for the analyses of successful mating.

Overall, 125 successful matings were observed by all-occurrence sampling (Table 3), of which 63 (50.4%) involved TMs and 62 (49.6%) involved NTMs. The number of observation days for each NTM ranged widely, so pooled data of the number of matings was a poor predictor of whether a NTM performed in successful matings within the troop. Therefore, I used the number of successful matings per observation day of each TM and NTM to analyze mating success.

In 1992 and 1994, when a low OSR was recorded, no mating of NTMs was observed, and TMs monopolized successful matings inside the troop. This supports the hypothesis that TMs succeed in defending EFs inside the troop when the number of EFs is relatively small compared to that of TMs. In 1994, however, I did observe one successful mating by a NTM with an estrous troop female outside of the troop.

TMs mated more often in years with higher OSRs. The number of successful matings of TMs among each study year recorded by focal sampling was significantly different (Kruskal-Wallis test, df=3, H=9.6, p<0.05, Table 2). This suggests that the chance of successful mating for TMs increased as the OSR increased.

In contrast, NTMs mated both inside and outside of the troop in 1993 and 1995, when a large number of EFs were recorded (Fig. 1). With the exception of younger (6- to 7-yr-old) individuals, NTMs were able to mate with females of all ranks. In addition, successful mating by a NTM with an estrous troop female was observed outside of the troop once in 1993, and successful matings by 2 NTMs with two estrous troop females were observed outside of the troop six times in 1995 (Table 3). These observations suggest that the chance of successful mating of NTMs increased as the ability of troop males to monopolize EFs decreased.

DISCUSSION

This study showed that defendability of EFs was a good predictor of the difference of successful mating inside the troop between TMs and NTMs. In fact, when the number of EFs was relatively small compared to that of TMs, TMs monopolized successful mating inside the troop.

Table 3. Successful mating by troop and nontroop males by all-occurrence sampling during study years.

Study	Number of successful matings	
year	Troop males	Non-troop males
1992	3(0)	0(0)
1993	17(0)	13(1)
1994	6(0)	0(1)
1995	37(0)	49(6)
Total	63(0)	62(8)

Numbers in parentheses show the matings observed outside of the study troop.

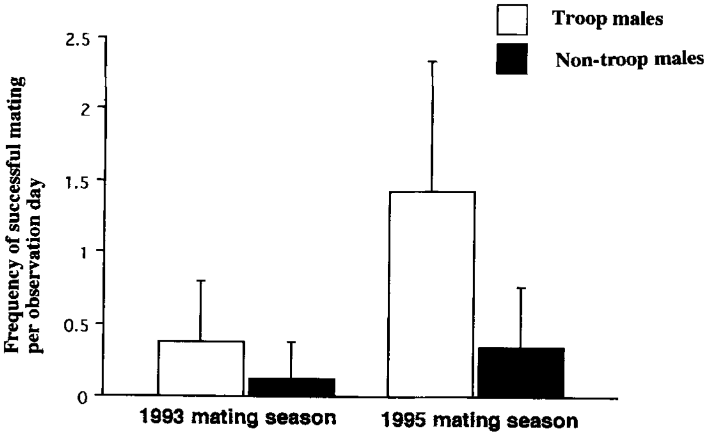

Fig. 1. Mean frequency of successful mating per observation day with standard deviation by troop and non-troop males in the 1993 (3 troop males and 14 non-troop males) and 1995 (2 troop males and 18 non-troop males) mating seasons.

This suggests that most TMs dominated over NTMs. On the other hand, both TMs and NTMs mated often when the number of EFs was relatively large compared to that of TMs. This indicates that fluctuations in the OSR strongly affect defendability of EFs by TMs and influence the mating success of males. The chance of successful mating of NTMs will increase as the ability of TMs to monopolize EFs decreases.

Males display two basic mating strategies. They secure successful mating by either attempting to monopolize estrous females or by trying to mate with as many different females as possible (SUGIYAMA, 1990). SMUTS (1987) summarized alternative male competitive tactics in several non-human primates. In redtail monkeys, patas monkeys, langurs, and Japanese macaques, one tactic is for males to become long-term residents in a mixed group, and the other is for males to invade groups when females are in estrus and to copulate with them. These alternative tactics correspond to those used by TMs and NTMs, respectively, as described in this study, where TMs pursued the strategy of securing successful matings. They obtained the benefits of securing successful matings in the troop because they were able to mate successfully inside the troop even in mating seasons with low OSR. However, this study could not clarify whether the strategy of NTMs to mate with as many females as possible was in fact successful. In a troop with a low OSR, TMs may monopolize mating success inside the troop because EFs are easy to defend. Under such circumstances, it may be preferable for NTMs to search for EFs in other troops or mate outside troops. To confirm this speculation, it is necessary to follow NTMs for an entire mating season.

In species with a multi-male social structure, defendability of EFs tends to be weak in populations with a high socionomic sex ratio (i.e. the number of females per troop male) since the OSR is potentially related to the socionomic sex ratio. In Japanese macaques, NTMs were often observed in populations with high socionomic sex ratios (SUGIYAMA, 1976; YAMAGIWA & HILL, 1998; SPRAGUE et al., 1998). This suggests that for males in populations with such socio-demographic characteristics, the preferable alternative mating tactic may be to become a non-troop individual. On the other hand, in populations with a low socionomic sex ratio, defendability of EFs by TMs should be high, and becoming an NTM may be an unprofitable mating tactic. The Yakushima macaque study population had a low socionomic sex ratio, and NTMs were rarely observed (YAMAGIWA & HILL, 1998; SPRAGUE et al., 1998). Here, TMs intruded into other troops and mated as NTMs (SPRAGUE, 1992), and frequent matings by NTMs were observed (FURUICHI, 1985; YAMAGIWA, 1985; SPRAGUE, 1991). Therefore, males may have been improving their mating tactics in response to fluctuation in the OSR.

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