Contrast of Estrus in Accordance with Social Contexts Between Two Troops of Wild Japanese Macaques on Yakushima

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(Received August 17, 2000; accepted March 19, 2001)

Abstract I observed estrus in two adjacent troops (A-troop and M-troop) of wild Yakushima macaques during the 1984 mating season. A-troop females showed short and regularly cycling estrus periods, seldom came into estrus simultaneously, and scarcely failed to mate when they were in estrus. In contrast, females of M-troop, which went through troop takeovers during the mating season, demonstrated mate competition and subsequent estrus prolongation. Early in the mating season, constantly four to seven females of M-troop were in estrus simultaneously, competed for troop males (TMs), and some of them failed to mate. Subsequently many non-troop males (NTMs) approached to the troop, estrous females mated with them frequently, and mating harassments by females decreased. Among those NTMs, one dominated all TMs, which was referred to as a troop takeover. Successively three other NTMs dominated both all TMs and the former dominant NTM, and in total, four troop takeovers occurred in M-troop during this mating season. The females continued to be in estrus during the whole episodes. All the conceived females also showed prolonged postconception estrus, and they were neither inactive nor less attractive to males. It was suggested that M-troop females increased their opportunity to mate with NTMs by estrus prolongation, at the cost of female-female mate competition, to incite active male intertroop movement and subsequent troop takeovers.

Keywords: Japanese macaque, simultaneous estrus, mate competition, troop takeover, estrus prolongation

Introduction

Although female estrus and sexual receptivity in catarrhine are influenced by her menstrual cycles and assure her impregnation (Beach, 1976), they also have greater flexibility in timing than concentrating around ovulation. Females in some macaque species are sexually active both midcycle and perimenstrually (Loy, 1970), and often show prolonged estrus (Takahata, 1980). They also show frequent postconception estrus (e.g., Japanese macaque; Hanby et al., 1971; Takahata, 1980: Rhesus macaque; Loy, 1971: Barbary macaque; Kuster and Paul, 1984), which is not directly related
with reproduction. Hanby et al. (1971) pointed out that receptivity and attractivity of Japanese macaque females who conceived were not different from those who had not conceived, and that neither ovulation nor conception had any discernible effect on the frequency and pattern of sexual activity, nor were female dominance and age related to early conception.

Using this estrus/mating flexibility, female primates seem to manipulate the relationships with males in order to improve their reproductive success. In particular, in recent trend for the studies of sexual selection among macaques, researchers put stress on female reproductive tactics as conflicting against those of males, i.e., female mate choice does not always work in favor of male-male competition, and often affect male reproductive success more than competition among themselves (e.g., Manson, 1995; Bercovitch, 1995; Soltis et al., 1997; Berard, 1999; Takahata et al., 1999). However, the nature of female choice and non-reproductive matings, which often bring the inconsistency between male mating success and his reproductive success, are not yet systematically explained from her own reproductive strategies (Takahata et al., 1999). Although many researchers had been trying to explain such estrus and mating flexibility by functions other than fertilization, those hypothesis mainly propose female tactics to mate with multiple males from making paternity of offspring obscure than avoiding infanticide (Hrdy, 1979; Taub, 1980), which is not really the case of macaque species where infanticide hardly occurs.

Indeed, the flexibility of macaque female estrus and sexual activities are beyond their menstrual cycles, and dramatically heightened when some social changes, e.g., during the process of the entry of the new male (s) into the group, happened (e.g., Japanese macaques; Wolfe, 1976; rhesus macaques; Wilson and Gordon, 1979; long-tailed macaques; Adams et al., 1985). Female estrous conditions seem to be enhanced by those social disturbances and result into prolonged estrus or postconception estrus (Wolfe, 1976). Such “excessive” estrus or sexuality (Small, 1988) may need to be reviewed from those of wild population like Yakushima macaques, where many small-sized troops are distributed continuously and frequent social dynamics take place through the matings between females and non-troop males (NTMs) who visit the troop (Yamagiwa, 1985; Sprague, 1992). Under the circumstances, female sexuality and mate choice may possibly establish relationships with males beyond the troops, thus influence to the sociodemographic dynamism of the local population.

Here I present a case of estrus synchrony and prolongation observed in a wild Japanese macaque (M. f. yakui) troop of Yakushima Island. In the 1984 mating season, I observed female estrus and mating activities in A-troop and M-troop. A-troop females showed short and delimited estrous periods and regularly cycling estrus, which was consistent to their menstrual cycles. No female mate competition was observed in this troop. In contrast, most M-troop females came into estrus simultaneously (estrus synchrony) at the beginning of the mating season. Those females
competed for troop males (TMs) and caused frequent antagonism in the troop, which may have been attracted many NTMs to the troop.

Those NTMs challenged to the alpha male of the troop, and one of them dominated him. Ultimately, four NTMs individually took over the troop in succession during a mating season, which has been rarely reported in multimale troops of Japanese macaques (Sprague, 1992). Females of M-troop kept being in estrus during these troop takeovers (estrus prolongation), and actively mated with NTMs. Their excessive sexuality and high promiscuity seemed to be enhanced by social stimuli, i.e., the influx of NTMs and subsequent troop takeovers. Based on those observations, I investigate how different features of female estrus influence and being influenced by female reproductive tactics in relation to the social dynamics.

**Materials**

The study troops, A-troop and M-troop, lived in a broadleaf evergreen forest on the western slope of Mt. Kuniwari, Yakushima Island, Japan (30°N 130°E). They have been well-habituated to observers since 1976, never being provisioned (Maruhashi, 1982). In this population, mating activities are clearly seasonal (Maruhashi, 1982). Copulations with ejaculation usually occurred from early September to late January (Yamagiwa, 1985). However, since females give birth to from late March to late May with a peak in April (Maruhashi, 1982), they are supposed to conceive only from September to November with a peak in October, if we take the gestation period of 173 ± 6.9 days SD (Nigi, 1976).

During the mating season, many males move among troops. Non-troop males (NTMs) usually begin to appear in October, reaching the maximum number during November (Sprague, 1992). Most of them belong to a certain troop during the non-mating season, since the socionomic sex ratio in Yakushima macaque troops is nearly 0.9 (Maruhashi, 1982). Thus, troop males (TMs) are defined as those who were in either troop at the beginning of the mating season. The same male is sometimes identified both as a TM in one troop and as an NTM for the other troops.

Fig. 1 shows the kin-groups of adult and young adult females and TMs in the study troops during the study. Three females with infants from A-troop (Tm, Hp, and Ma in Fig. 1) showed no physical signs of estrus during the study, and did not copulate with males except one occasion when a TM was observed to mount Tm. None of them gave birth to in the 1985 birth season, so they were also excluded from the analysis. There was no female with infant in M-troop. In summary, there were 11 potentially sexually active females and 6 adult males in A-troop, in the 1984 mating season. The corresponding figures for M-troop were 8 and 2 respectively.

Dominant/subordinate relations were determined from behaviors of each individual during agonistic encounters, approach-retreat, and by submissive behaviors such
Figure 1. Female kin-groups and TM ranking in each study troop.

---: known kin relations; ------: estimated kin relations; +: dead.
Females are shown with one capital and one small, while males with two capitals. Age-classes in parentheses are; A: adult (♀ > 6 years, ♂ > 9); OA: old adult (>20); YA: young adult (♀: 5-6, ♂: 5-9); J: juvenile (1-4). * Natal male; ** Al behaved as a member of Ti kin-group.
as grimaces. There was a linear dominance relationship among three kin-groups of
A-troop (Tt group > Mg group > Hp group) and between two kin-groups of M-troop
(Ak group > It group). All NTMs were individually identified as far as possible.

Methods

All the data were recorded between 1 October and 19 December in the 1984 mat-
ing season. The data on female estrous conditions and copulations collected by T.
Maruhashi, J. Yamagiwa, and D. Sprague were also included in the analysis. The
study period was divided into 6 periods according to the changes of the social con-
texts in M-troop (see Table 1). The combined total observation time of the four re-
searchers on A-troop and on M-troop was 222 h 32 min (44 days) and 264 h 4min
(57 days) respectively. The overlap in days of observation of the troops was 39 days.

Estimation of Estrous Period

On each observation day, I checked estrous conditions with one-zero sampling, by
physical or behavioral signs of estrus, or by copulation. Physical signs of estrus con-
sisted of swelling of sexual skin, redness of facial and sexual skin, or vaginal smell,
which appeared irregularly. Sexual behaviors described by Enomoto (1974), were
used as behavioral signs of estrus (see Okayasu, 1992, for detail). Among 23 behav-
ioral patterns, some like ‘approach’ or ‘walking by’ were regarded as estrous behav-
iors only when a female performed them towards males. Other behaviors, i.e., ‘re-
ceiving sexual behaviors from males,’ ‘branch-shaking displays with barking,’ ‘ha-
rassment of mating pairs,’ and ‘masturbation’ were observed only in the sexual con-
texts, therefore adapted to determine female estrous conditions when the observation
was too brief to recognize her other sexual behaviors.

I observed females by focal animal sampling which varied in length from 15-min
to 8 hrs per day. Estrous conditions of non-focal females were checked as well by ad
lib. sampling. Females sometimes moved away from the troop whole day, making
observations on them impossible. Females were assumed to have continued to be in
estrus during those days, if they showed estrous signs either on the day before or
after the observation gaps. Copulations which occurred around the focal animal were
recorded by ad lib. sampling.

Female estrous periods were determined by the cessation of her sexual behavior,
since I could not confirm her menstrual cycles neither by hormonal changes nor by
virginal breeding. The frequency distribution among the different lengths of cessa-
tion decreased between 9 and 11 days (Fig. 2). This suggested that when a female
had a period of less than 9 days with no sexual behavior, I could regard it as a tempo-
rary cessation of her sexual activities within one estrous spell, while when it lasted
more than 11 days, I should regard the sexual periods before and after this cessation
### Table 1. The social incidents occurred in M-troop and the observation time in each period

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<td>Changes of the social contexts</td>
<td>Simultaneous estrus in females</td>
<td>First NTM appeared</td>
<td>Oct.26 NR defeated MA (1st takeover)</td>
<td>Oct.31 GA dominated TMs (2nd takeover)*</td>
<td>Nov.8 KK defeated GA (3rd takeover)</td>
<td>Dec.8 DL defeated KK (4th takeover)</td>
<td>Total</td>
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The study period was divided into six periods in accordance with social incidents in M-troop. A-troop observation period was also divided because the home range of the two troops overlapped each other and the number of NTMs visited both troops during the study.

* Observation time was that of total focal troop-hours of four researchers.

** Mating harassment was recorded in episode for each harassing female and regarded as successful if the copulation was terminated without ejaculation.

* NR disappeared before GA showed up, and the alpha male (MA) who was injured severely dropped out from the troop during this period.
as two separate estrous periods.

Estrus after the days of conception, counted back from the dates of parturition using Nigi (1976)'s gestation period of 173 ± 6.9 days SD, was recognized as post-conception estrus. Four and three parturitions were observed in A-troop and in M-troop respectively.

Definitions

Copulation was defined as male mountings on a female with insertion, terminated either with ejaculation, or a period with no mountings lasted longer than 5min, or departure of one of the participants towards other individuals.

Female Harassment of mating was defined an approach (es) by a female within touch of a mating pair, accompanied by her solicitation towards the mating male (often the case when the subordinate harassed the dominant) or by her aggression towards the mating female. It often was not as severe as “interference” described by Niemeyer and Anderson (1983), but a harassing female could seriously impair the mounting series of a copulating pair. Such approaches were recorded in sequence sampling (Altmann, 1974), and were counted for one harassment if they occurred in one copulation of the pair. The harassment was regarded as successful for the harassing female, if the copulation was terminated without ejaculation. The harassment

![Figure 2. Distribution of the cessation of sexual behavior in each study troop. Observation gaps were excluded from the analysis.](image-url)
was counted on each female, if more than one female harassed the same pair at the same time.

**Results**

**Characteristics of Estrus in Wild Yakushima macaques**

In the 1984 mating season, females of A-troop and M-troop showed quite different estrus (Fig. 3). Duration of estrus and the relationships between estrus and conception were compared between the troops, in order to investigate how estrus prolongation of M-troop females affected to their reproduction.

In A-troop, non-estrous females with infants showed no interest toward the males nor mating pairs. All the other females, except Ts, showed plural estrous period with cyclicity (Fig. 3). The mean length of estrous cycle between the day of an estrous period and that of the next was $26.2 \pm 1.3$ days ($n=15$; range; 16–35 days). Such estrus cyclicity agreed with the previous reports from caged Japanese macaques ($26.3$ days; Nigi, 1975) and from a provisioned troop ($26.5$ days; Takahata, 1980).

All four females of A-troop who conceived during the study had a single conception estrous period, with only one (Hm) of them showing postconception estrus for only one day (Fig. 3). Fertile estrus in A-troop females suggested their estrus cyclicity being consistent with their menstrual cycles, and they were in estrus during their midcycle.

On the other hand, most M-troop females, except It and Sm, were in estrus throughout the study (Fig. 3). All the Ak kin-group females had at least one prolonged estrous period of nearly 60 days or more, suggesting that they were continuously in estrus over 3 menstrual cycles, counting the estrus cyclicity of 26 days in A-troop as their menstrual cycles. This was also the case with Sk in It group, and the mean cumulative duration of estrous periods for each female in M-troop ($55.6 \pm 6.0$ days; $n=8$; range; 22–71 days) was longer than in A-troop ($12.6 \pm 4.1$ days; $n=11$; range; 1–40 days: Mann-Whitney; $Z=4$, df = 10, $p < 0.01$, two-tailed).

M-troop young adults were in estrus as long as the adults, whereas A-troop adults were in estrus significantly longer than the young adults (Table 2). In either troop, however, there was no significant difference in cumulative duration of estrus among the kin-groups (Table 2).

As for M-troop, prolonged estrus and heightened sexual activities of females made no contribution to their conception rate: the conception rate among females without surviving offspring from the previous year was the same for the two troops (0.36 for A-troop and 0.38 for M-troop). All three M-troop females who came to be pregnant were estimated to have conceived by 23 October (Fig. 3), before showing estrus prolongation over their menstrual cycles.

All the three conceived females in M-troop showed postconception estrus (Fig. 3),
Figure 3. Estrous periods of females in each troop.

Because estrous conditions of females changed within a day, and also they were likely to be in estrus while being absent from the troop (Okayasu, 1992), I did not distinguish between the day a female was absent and she was not in estrus. The estrous periods were estimated only from the days the female was confirmed to be in estrus.

○ Estrous period; ←——→: Estimated conception period.
+ A day the female copulated or engaged in copulatory sequence with her partner.
* Females who had surviving infants.
** Females who gave birth to during the 1985 birth season.

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and their mean cumulative duration of postconception estrus was $40.3 \pm 11.5$ days. Nor were they noticeably less active in sexual behaviors, and frequently copulated during their postconception estrus (Fig. 3).

High-ranking females did not have higher rate of conception than those of middle-or low-ranking in either troop. In the 1985 birth season, one of four (25%) high-ranking females who showed estrus during the 1984 mating season gave birth to in A-troop. On the other hand, one of five (20%) middle-ranking, and two of two (100%) low-ranking females gave birth to in A-troop. In M-troop, one of four (25%) high-ranking and two of four (50%) low-ranking females gave birth to. Between 1974 and 1993, the rank was not correlated with reproductive parameters among the kin-groups (Takahata et al., 1998).

### Difference of Female Mating Activities According to the Social Contexts

Female mate competition and troop takeovers, which were rarely reported in Japanese macaques living in multimale troops, were observed in M-troop during the study. Those two incidents took place in consequence of simultaneous estrus early in the mating season, then female estrus in M-troop prolonged under those social stimuli (Fig. 3). Female mating activities during the incidents were examined in compar-

### Table 2. Differences of cumulative duration of estrus between age-classes and between kin-groups

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<tr>
<td>Adult</td>
<td>$56.2 \pm 7.1$</td>
<td>Not significant</td>
</tr>
<tr>
<td>Young Adult</td>
<td>$54.0 \pm 16.0$</td>
<td></td>
</tr>
<tr>
<td>$Ak$ kin-group</td>
<td>$63.5 \pm 2.5$</td>
<td>Not significant</td>
</tr>
<tr>
<td>$It$ kin-group</td>
<td>$47.8 \pm 11.0$</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>$55.6 \pm 6.0$</td>
<td></td>
</tr>
</tbody>
</table>

* It tests the difference of each age-class or kin-group.

* Between $Tt$ and $Mg$ kin-groups.

* Between $Mg$ and $Hp$ kin-groups.

* Between $Tt$ and $Hp$ kin-groups.
ison with those of A-troop females.

**Simultaneous Estrus and Female Mate Competition**

In A-troop, females showed short and delimited estrous periods which scarcely overlapped with those of others (Fig. 3), and an average of two or fewer females were in estrus simultaneously (Table 1). Female harassments of matings were not observed in the troop. Therefore, estrous females consistently gained their partners when they showed clear estrous signs. Te, for example, was observed to be with her partner on seven out of eight days of her estrus during the study (Fig. 3).

In contrast with A-troop, four females of M-troop were already in estrus at the beginning of the study and the number increased up to seven on 17 October (Fig. 3). Two adult and two young adult TMs, however, were available for their mating partners at that time.

Both adult TMs tended to form consort relationships with only adult females like Ak, Sk, or Sd which lasted whole day. As a result, intense harassments of matings over young adult males occurred among other estrous females, lasting 10–30 min, often resulting in the mating pair separated before or during the mounting series (Table 1). Three to four estrous females were gathered around a TM, presenting to him or threatening another estrous female, thus creating a lot of antagonism among themselves. Hence females like Ks or Si failed to mate during this period even if they showed active behavioral estrous signs (Fig. 3), and the copulation frequency in M-troop did not increase correspondingly to the increase of the number of estrous females (Table 1). On 4 October, for example, persistent harassments of matings among Ks, Si, and Sm lasted for 1 h 9 min. Three females presented to an young adult male PC by turns, but he tried to mate only with Si. Ks, however, kept threatening the other two so that none of them could mate. At last, when Si presented to PC and Ks chased and mounted Si, he began to move, leaving them.

Such antagonism accompanied by peculiar sounds or screams of estrous females seemed to draw males’ attention in neighboring troops. The first two NTMs appeared around M-troop on 18 October with increasing numbers as days progressed.

Mating harassments by females decreased after 20 October, when estrous females in M-troop eventually gained 6 NTMs for possible mating partners and each female began to copulate with males (Table 1). Harassments were observed 1.3 episodes per observation day during 1–20 October, while 0.3 during the rest of the study period.

In total, I observed 24 episodes of female harassments (Table 1) in 15 female-female dyads of M-troop, of which 11 were directed from the dominant to the subordinate, while 13 were in the opposite direction. Thirteen episodes were between non-kin dyads, while 11 were between kin dyads. Estrous females harassed the dominants or kin females as well as the subordinates or non-kin females, although the sample size was too small for the statistical analysis.
Although mating harassments by females decreased drastically after the appearance of NTMs, it did not entirely diminish even after they got enough number of NTMs for their partners (Table 1). Different from early in the mating season, an estrous female with her partner harassed another pair in those cases. On 22 November, for example, Ab repeatedly approached to a mating pair, Si and K2 (an NTM) from 20 m away, while she was grooming another NTM SS. Ab presented to K2 (or less likely threatened Si), then went back to SS to restart grooming. K2 kept ignoring Ab until Si escaped from him. Hence K2 chased Ab in aggressive manner and moved away from her, following Si. Ab fled away then went back to SS.

In those cases, the harassing female seemed more to reveal her ‘heat’ or sexual hyperactivity by harassing the mating pair than to compete for her partner. Or else, she might try to gain an extra mating partner by going back and forth between two males, to assure her mating promiscuity. Those attempts, however, often encountered the harassed male’s aggressive rejection and did not contribute to her immediate mating success. Rather, her primary matings prolonged and delayed while she was engaged in harassments, which seemed not to contribute to her mating success neither.

**Troop Takeovers**

A total of 28 NTMs approached A-troop but none of them dominated TMs, i.e., troop takeovers did not occur during the study.

Females of A-troop did not copulated with NTMs as often as with TMs throughout the study. There were few chances for estrous females to mate with NTMs unless they stay away from the troop, since NTMs were chased away by multiple TMs if they tried to mate with females along the troop. Under the circumstances, only six of 28 NTMs (21.4%) were observed to copulate with one or two A-troop females (from one to four times), except an NTM who copulated 11 times with four partners. The copulations with NTMs occupied 17.5% (21/120) of all the observed copulations in A-troop.

On the contrary, most of the 47 NTMs who approached M-troop attempted to mate along the troop from the beginning. Cooperative attacks by TMs successfully prevented them from coming into the troop until the first troop takeover took place on 26 October. Nevertheless, TMs could not prevent all the estrous females from mating with NTMs, since there were constantly more estrous females than adult TMs (Table 1) and those who were not with their partner tended to be away from the troop in order to find NTMs as their mating partners (Okayasu, 1992). Lots of aggressive encounters occurred between TMs and each NTM.

Table 1 illustrates approaches of NTMs to M-troop and process of troop takeovers. In M-troop, the ratio of copulations with NTMs reached 68.8% (132/192) after the first takeover by NR, compared with 28.6% (4/14) before the takeover (18–
25 October). In total, 47 NTMs appeared, 24 (51.1%) were observed to copulate, and the copulations with NTMs occupied 62.7% (136/217) of the total observed copulations.

**Discussion**

Females of wild Yakushima macaques exhibit short and well-defined estrous periods and consistently mate with TMs as seen in A-troop, unless conspicuous social incidents occurred in the troop. Their behavioral estrus cyclicity of 26.2 ± 1.3 days closely conform to those of 26.3 days for caged Japanese macaques (Nigi, 1975) or 26.5 days for a provisioned troop (Takahata, 1980). Females rarely come into estrus simultaneously due to the small number of females in each troop and to the short estrous periods of individual female.

However, most females in M-troop came into estrus simultaneously from the early part of the 1984 mating season. This unusual estrus synchrony seemed to bring up social incidents and dynamics, then consequently female estrus might have prolonged. These estrus synchrony and prolongation are discussed from the female reproductive strategies in wild Japanese macaques.

**Simultaneous Estrus, Female Mate Competition, and Troop Takeovers in M-Troop**

Since there was no apparent social stimuli to bring about estrus synchrony in M-troop, simultaneous estrus at the beginning of the study (Fig.3) might have occurred by coincidence. By October 17, up to seven females were in estrus in one day. However, there were only two adult and two young adult males in the troop as mating partners. This shortage of TMs might have led to an unusual degree of female competition over acquisition of mates. As a result, intense harassments of matings seemed to occur among estrous females, and mating pairs were often disrupted even before they started mounting series.

Harassments of matings are caused more by males than by females (Niemeyer and Anderson, 1983), thus have been mainly discussed in the context of male-male competition and female mate choice along the primate reproductive biology (e.g., Huffman, 1991; Berard et al., 1994; Chism and Rogers, 1997; Soltis et al., 1997; Berard, 1999). However, some authors (Bercovitch, 1995; Soltis et al., 1997) pointed out that the females-female competition could also effect in the reproductive scene, for example, during agonistic interactions among female savanna baboons over access to a male (Seyfarth, 1978).

To a lesser extent, estrus synchrony itself can operate as female mate competition (Wasser, 1983; Bercovitch, 1995). As for this study, since simultaneous estrus in females occurred in M-troop where only two adult males were available, female-
female competition became pronounced up to the level of intense harassments of matings.

The particular reproductive feature of Yakushima macaque population is the high intertroop mobility of males during the mating season (Maruhashi, 1982; Yamagiwa, 1985; Sprague, 1992). Taking this social context into account, estrus synchrony in M-troop seemed to have resulted in enlarging the number of mating partners by inciting male intertroop movement, even if M-troop males became temporally “limited” resources for females to compete. They gained NTMs (including TMs from neighboring troops) as additional partners fairly soon, and once NTMs began to appear around M-troop, the number reached as many as estrous females within a day.

Note that high degree of harassment and interruptions of matings did not appear to have negative effects on conception rate among females in M-troop. The proportion of M-troop females conceived in the 1984 mating season was similar to that of A-troop females. The average birth rate of 0.27 between 1974 and 1993 (Takahata et al., 1998) also suggested that the conception rate in M-troop during the study was not low at all. All the three females who gave live births in the next birth season became pregnant by 23 October, which agreed with the tendency that Yakushima macaque females conceive in early half of the mating season, i.e., between September and November with the peak in October. Those aspects indicated that the fertility of M-troop females might not have changed irrespective of social contexts during the mating season.

Intensity of harassment did not prevent females from conception, and all the three females who gave live births in the next birth season became pregnant while female harassments of matings were most frequent and intense. They might not have been as serious or stressful as those between males, which sometimes derive the physical fights. Or females might harass the others more because of their sexual hyperactivity (Takahata, 1980) than for competing mates, as seen in Ab’s case. Therefore, the harassments were not severe enough to influence female conditions, and the subordinates harassed the dominants as often as the other way around, or they often harassed each other within their kin-group.

**Excessive Sexuality in Female Japanese Macaques**

Throughout the 1984 mating season, the conditions of M-troop females seemed to be kept hypersensitive (Okayasu, 1992). All the three females continued to be in estrus even after they conceived, in contrast with A-troop in which no postconception estrus was recognized except Hm for only one day (Fig. 3). The mean cumulative postconception estrus in M-troop reached excessively long for over 40 days.

Estrous conditions of those M-troop females might be heightened by the appearance of many NTMs and the consequent troop takeovers, which occurred soon after or at the end of their fertile estrus. The dominant adult female, Sd, for example, had
been in estrus for 56 days after her conception (Fig. 3) and observed to copulate 36 times during her postconception estrus. She copulated more with NTMs (22 times with 13 partners) than with TMs (14 times with 3 partners) during that time. Also another adult female, Sk, being in postconception estrus for 48 days (Fig. 3), copulated more with NTMs (28 times with 11 partners) than with TMs (4 times with 3 partners) during her postconception estrus (Okayasu, in prep.).

Other females in M-troop, except an old adult, It, also showed prolonged estrous periods of more than 40 days, much longer than A-troop (Fig. 3). Their estrous duration was considerably longer than any of those reported so far (13.6 days [Takahata, 1980] or 8.9 days [Huffman, 1991] among Japanese macaque females in a provisioned troop; 9.2 days [Carpenter, 1942], 11.0 days [Kaufmann, 1965], or 5.2 days [Loy, 1971] among rhesus macaque females of Cayo Santiago). They showed estrous signs throughout the menstrual cycle, in “runs” as reported in a provisioned troop of Japanese macaques (Wolfe, 1984).

M-troop female conditions seemed to be kept hypersensitive even out of their midcycle, therefore coming into estrus immediately when some social antagonism occurred in the troop, e.g., troop encounter, as reported elsewhere (Okayasu, 1992). In patas monkeys, there is also some evidence that an enhanced level of social excitement may bring female monkeys into estrus (Rowell and Hartwell, 1978). Rowell (1978) called this enhancement of female sexual activities as ‘Hoo Haa Effect,’ following social disturbance such as a novel male entry to the group. Prolonged estrus in M-troop females may be one of the case of ‘Hoo Haa Effect’ or social-context-dependent estrus as Wolfe (1976) suggested in the mentioned Japanese macaque troop, being facilitated by the constant presence of unfamiliar NTMs and by the frequent troop takeovers. The effect becomes more evident in comparison with short and delimited estrus in A-troop, in which no conspicuous social incident occurred while NTMs appeared.

M-troop females did neither fail to conceive during the social antagonism at the beginning of the mating season, nor achieve higher conception rate with such social-context-dependent estrus or “excessive sexuality” (e.g., prolonged estrus, postconception estrus; Small 1988) in later two third of the mating season. Although Yakushima macaque females tended to have less fertility in the later half of the mating season, the reason why M-troop females in prolonged estrus did not conceive remained uncertain.

However, there is some evidence that male rhesus macaques who formed long term consort relationships have greater reproductive success than those with sneaky tactics (Berard et al., 1994). In other words, in order to conceive, females may also need to form consort relationships with males during their fertile estrus. All the three females of M-troop who became pregnant formed consort relationships with TMs during their fertile estrus, responding to his constant follow (Okayasu, unpublished
data). Hence, female choice of NTMs with extreme mating promiscuity during their prolonged estrus (Okayasu, in prep.) might have affected to their conception. In contrast, A-troop females tended to form consort relationships with TMs (Okayasu, in prep.) during their delimited estrous periods.

Yakushima macaque females may develop excessive sexuality to attract many NTMs and so enlarge the range of potential partners in the mating season. Moreover, simultaneous and prolonged estrus in M-troop females did not only attract individual NTMs, but also incited male-male competition beyond the troop by encouraging the confrontation between NTMs and TMs. Non-estrous females tended to avoid NTMs or even tried to exclude them with TMs, whereas estrous females showed active proceptivity toward NTMs (Okayasu, 1992). The mating attempts by NTMs in M-troop eventually caused troop takeovers in succession (Sprague et al., 1996).

Such tactics of females may need to be considered from a long term reproductive strategy. The frequent male transfers in Yakushima population produce sociodemographic variation within a troop over time and sociodemographic diversity among troops in a local population (Suzuki et al., 1998), which may influence female reproductive status over time. Although NTMs scarcely contribute to the immediate reproduction for the next birth season, they often cause the troop takeovers or troop fission when immigrating into the troop (Maruhashi, 1982, 1991; Yamagiwa, 1985, Sprague et al., 1996). Those social dynamics may require females to reorganize troop integration or intratroop social relationships, but may also give them a chance to improve the quality or quantity of their home range by dominating adjacent troops with newly immigrated male(s) (Maruhashi, 1982, 1991; Takahata et al., 1999). On the other hand, if females failed to manipulate the situation, their troop itself may extinct in the extreme cases, which actually happened to M-troop (Takahata et al., 1994).

Takeovers of the alpha-male (or a harem male) status had been reported mainly from species which live in one-male groups (e.g., redtail monkey; Cords, 1984; blue monkey; Cords et al., 1986). The male influx into groups of these species coincided with female estrus synchrony, as observed in this study. Cords et al. (1986) speculated the relation between female estrus synchrony and male influx as the reciprocal stimulation both between and within the sexes, producing a cascade of sexual activity. Females of these species have no conspicuous changes in coloration or the presence of sexual swellings indicating their ovulation, similar to Japanese macaque females (Enomoto, 1974), who are living in multimale troops, and their social-context-dependence of estrus and characteristics of mating show similar tendency irrespective of their social organization.
Acknowledgment

I am grateful to Drs. D. S. Sprague, T. Maruhashi, and J. Yamagiwa, who encouraged me throughout my field research in Yakushima, and allowed me to use their unpublished data. I also express my thanks to Prof. T. Nishida and the members of the Lab. of Human Evolution Studies, for their helpful comments and suggestions. I am also grateful to Drs. Y. Takahata, T. Enomoto, D. A. Hill, and H. Takasaki, for their help in writing this manuscript. Special thanks are accorded to Mrs. A. Kozono and Mrs. H. Watanabe, for their help in my staying in Yakushima. This study was supported in part by the Cooperative Research Fund of the Primate Research Institute, Kyoto University, by a Grant-in Aid for Special Project Research on Biological Aspects of Optimal Strategy and Social Structure from the Ministry of Education, Science and Culture, Japan, and also by the Research Fellowship Division, Japan Society for the Promotion of Science.

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Estrus in Wild Japanese Macaques


Editor-in-Charge: Masanaru Takai