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# Male Aggression and the Sexual Behavior of Japanese Monkeys

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ABSTRACT. The factors that regulate male aggressive behavior towards females during the mating season and their relationship to the sexual behavior of Japanese monkeys were investigated. Observations were made on the Shiga A troop in Nagano Prefecture for 132 days during both the non-mating and mating seasons in three successive years. As a result, chasing towards females was observed in males older than 4 years. The frequencies of this type of behavior increased in the mating season. The chasing rank of the individual males did not correlate with the male dominance rank but with the tree-shaking rank. Chasing was directed not only at estrous females but also at non-estrous females. Pairs of both sexes in which chasing was observed, tended to have sexual interactions. Both hormonal and social factors should be considered in the regulation of chasing. The role of aggression in the formation of new male-female bonds is discussed.

## INTRODUCTION

The male-female bond in Japanese monkeys, such as protecting-depending and affinitive relations, is considered to be one of the essential factors constituting the concentric structure of the troop (KAWAI, 1969). Recent studies on the male life history have shown that as a rule the males left their native troop when they were 4 or 5 years old and thereafter joined neighboring troops one after another (ITOIGAWA, 1974; TOKITA & WADA, 1974; FUKUDA, MURAMATSU & TANAKA, 1974; NORIKOSHI & KOYAMA, 1975). The males came to have bonds with females, accompanied by an increasing dominance in the troop (NORIKOSHI, 1975). As the key behavior by which the males establish an affinitive relationship with a female, NORIKOSHI (1976) proposed sexual attack. To examine this hypothesis, analyses should be made of both the determinants of attack and its influence on the social relations between both sexes in the troop.

Based on studies of the sexual behavior of Japanese monkeys, it has been reported that the dominance rank of males correlated with the frequency of copulation (TOKUDA, 1961–2; HANBY, ROBERTSON & PHOENIX, 1971; KAWAI, 1969) and also with that of "check attack" (TOKUDA, 1961–2). However, in some troops the former correlation has not been supported (EATON, 1974). This discrepancy suggests that factors other than the dominance rank of the males, which are in some cases correlated with rank, actually exert an effect on the frequencies of copulation. As such factors, social ones like the tradition of the troop or community, behavioral ones like the displays proposed by MODAHL and EATON (1977) and aggression, or physiological ones might be considered.

The present paper confirms the role of male aggression towards females in connection with the above problems. Behavioral and social determinants of the aggression are presented, and their relations with male dominance rank and sexual behavior are analyzed. The contribution of the aggression towards the formation of male-female bonds is discussed.

## METHODS

This study was based on observations of a Japanese monkey troop in the Yokoyugawa Basin, Nagano Prefecture. The troop, Shiga A, has been fed since 1962 at Jigokudani. Table 1 shows the troop composition. Deliveries peaked from the beginning of April to early May in this troop. The gestation period of the Japanese monkey has been determined by NIGI (1976) as 173±6.9 days. Conceptions, therefore, had occurred mainly from late October to early December. Observations were performed at six periods for a total of 132 days: in the non-mating season, 21 days from July 13 to August 2, 1972 and 17 days from June 15 to July 1, 1973; in the early mating season, 12 days from September 20 to October 1, 1972; and in the middle mating season, 32 days from October 29 to November 29, 1971, 32 days from October 26 to November 26, 1972 and 18 days from November 2 to 19, 1973. The behavior of the monkeys was observed daily for about 9 hr and recorded in pocket notebooks. The classification of the behavior in this troop was as described previously (ENOMOTO, 1974). Female estrus was detected by both the facial redness and the sexual approach by the female towards males.

## RESULTS

Figure 1 shows the mean of the number of estrous females and frequencies of copulation, chasing and tree-shaking by adult males per day in the three seasons of non-mating, early mating and middle mating. During the mating season, the frequencies of both copulation and male chasing increased strikingly, although marked variations were apparent in each year. These types of behavior were observed in 1972 with double the frequencies in 1971. On the other hand, the frequencies of tree-shaking did not show marked elevations even in the mating seasons, although the vocalization which accompanies tree-shaking (ga·ga·ga·; C-5 sound by ITANI, 1963) was characteristically emitted during the mating season. This sound was evocated in 40 out of 92 cases in which males displayed the behavior in 1972. Male chas-

**Table 1.** Composition of the Shiga A troop.

| | 1971 | 1972 | 1973 |
|---|---|---|---|
| Females[1] | 26 | 26 | 27 |
| Adult males[2] | 8 | 8 | 7 |
| Juvenile males[3] | 8 | 9 | 5 |

1) Older than 3 years; 2) older than 6 years; 3) from 3 to 5 years old. Males who left or joined the troop during the study periods are excluded. Members other than these sex-age classes are neglected.

**Table 2.** Frequency of aggressive behavior by a male per day in three age classes in November 1972.

| | Male | | |
|---|---|---|---|
| | Adult | 4-year-old | 3-year-old |
| *N* | 8 | 6 | 3 |
| Attack | 0.11 | 0 | 0 |
| Chasing | 1.25 | 0.03 | 0 |
| Biting | 0.17 | 0.01 | 0 |
| Tree-shaking | 0.36 | 0.02 | 0.01 |
| Tree-shaking with vocalization | 0.15 | 0 | 0 |

No 5-year-old males were present in this troop in 1972.

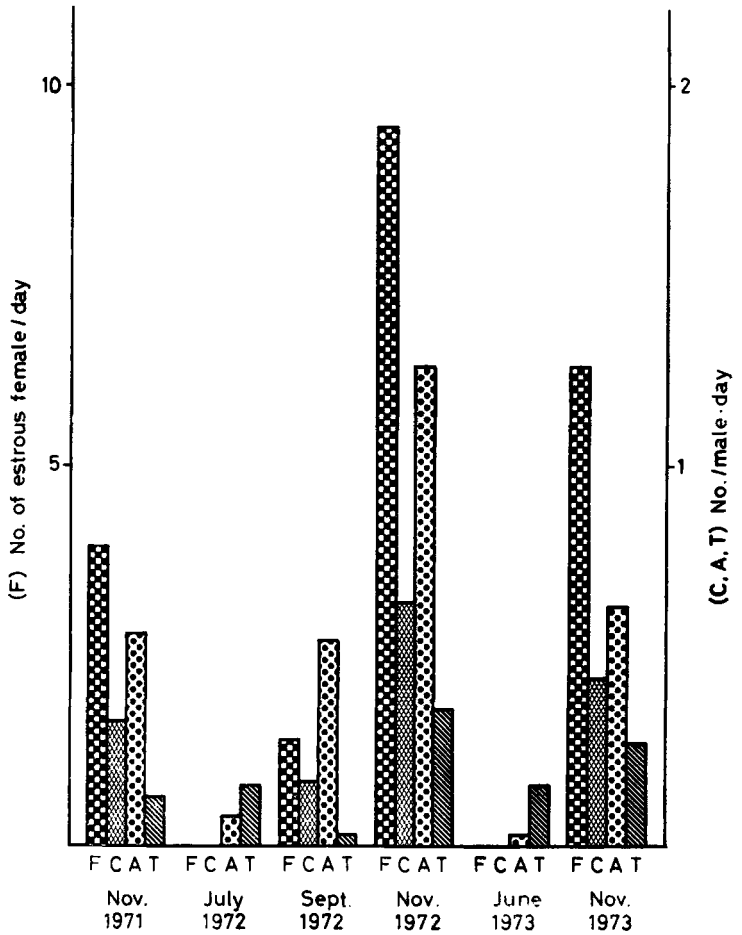


**Fig. 1.** Mean number of estrous females per day and frequencies of copulation, chasing and tree-shaking per day in the non-mating season (July 1972 and June 1973), early mating season (September 1972) and middle mating season (November 1971, 1972 and 1973). F: Number of estrous females per day; C, A, T: frequencies of copulation, chasing and tree-shaking, respectively.

ing and attacks sometimes resulted in serious injury to females. Males also received wounds mainly during this season due to inter-male fighting.

Three-year-old males did not chase females. Four-year-old ones did so but only to a limited extent. Attacks, biting, tree-shaking and chasing were all characteristic in the adult (Table 2).

During the non-mating season, chasing towards females was displayed by dominant males. As the mating season arrived, however, the correlation between chasing and male dominance rank became obscure (Fig. 2). Table 3a shows the frequencies of chasing, tree-shaking and copulation in each adult male. The chasing rank of the individual males did not correlate significantly with their dominance rank (Table 3b), but did with their tree-shaking rank in 1971 and 1972. On the other hand, the rank of the male tree-shaking frequency correlated with both the dominance and copulation ranks. The age and history of the males were not clearly related to the frequencies of these types of behavior.

**Table 3a.** Frequency of chasing, tree-shaking and copulation by adult male Japanese monkeys in the mating season.

| Male | Age[1] | 1971 | | | | 1972 | | | | 1973 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | DR | CH | TS | CO | DR | CH | TS | CO | DR | CH | TS | CO |
| *KN*[2] | 9 | 1 | 22 | 5 | 9 | 1 | 41 | 18 | 14 | 1 | 11 | 4 | 2 |
| *KS*[2] | 7 | 2 | 25 | 11 | 23 | 2 | 39 | 20 | 25 | — | — | — | — |
| *TC*[2] | 7 | 3 | 10 | 1 | 5 | 3 | 23 | 9 | 33 | 2 | 13 | 2 | 6 |
| *A* | — | 4 | 26 | 8 | 20 | 4 | 65 | 20 | 48 | 3 | 13 | 8 | 23 |
| *MT* | — | 5 | 25 | 7 | 20 | 5 | 72 | 18 | 23 | 4 | 15 | 7 | 15 |
| *KB* | — | 6 | 24 | 0 | 3 | 6 | 55 | 3 | 7 | 5 | 21 | 9 | 7 |
| *RK* | — | 7 | 8 | 0 | 4 | 7 | 13 | 2 | 15 | 6 | 11 | 1 | 3 |
| *KR* | — | 8 | 3 | 0 | 1 | 8 | 14 | 2 | 0 | 7 | 18 | 3 | 0 |

DR: Dominance rank; CH: chasing; TS: tree-shaking; CO: copulation. 1) In 1972; 2) males born in this troop. —: Age unknown. A male (*KS*) left and another male joined this troop during the mating season in 1973, but these animals are neglected here.

**Table 3b.** Spearman rank correlation.

| | $r_s$ | | |
|---|---|---|---|
| | 1971 | 1972 | 1973 |
| DR—CH | .470 | .310 | −.473 |
| DR—TS | .714* | .768* | .143 |
| DR—CO | .708* | .500 | .250 |
| CH—TS | .815* | .649* | .634 |
| CH—CO | .804* | .286 | .241 |
| TS—CO | .970** | .744* | .607 |

Abbreviations as in Table 3a. $*p<0.05$; $**p<0.01$.

**Table 4.** Frequencies with which a female mated with a male or received aggressive behavior from a male per day.

| | Copulation[1] | Aggression[2] |
|---|---|---|
| November 1971 | 0.09 | 0.14 |
| September 1972 | 0.12 | 0.39 |
| November 1972 | 0.07 | 0.13 |
| November 1973 | 0.07 | 0.12 |

1) No. of matings per male per day/No. of estrous females per day; 2) No. of instances of chasing per male per day/No. of estrous females per day.

The frequencies of chasing per day correlated positively with the number of estrous females (Fig. 3). The straight regression lines obtained, which were significant at the less than 2.5% level, showed similar patterns in the three years.

The ratio of the frequencies of chasing per day to numbers of estrous females per day during the middle mating season was roughly equal in each year, although the mean numbers of estrous females per day varied markedly (Table 4). This ratio during the early mating season was, however, higher than that during the middle mating season, and chasing towards estrous females was frequently observed.

During the study period from October to November 1972, 16 out of 26 females showed estrus. Each female that once showed estrus received chasing from adult males at a mean frequency of $0.51 \pm 0.33$ (S.D.) times per day throughout the period. When the females showed estrus, they were chased 0.86 times per day, and when they did not show estrus, they were chased 0.14 times per day. Nine of these females received chasing at a significantly higher

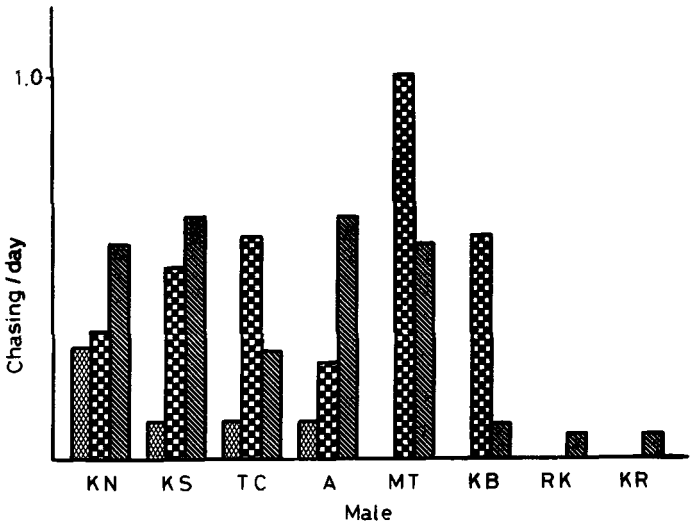


**Fig. 2.** Frequency of chasing per day in each male during the three seasons of non-mating (left column), early mating (middle column) and middle mating (right column) in 1972. See Table 3a for the history, age and dominance rank of the males.

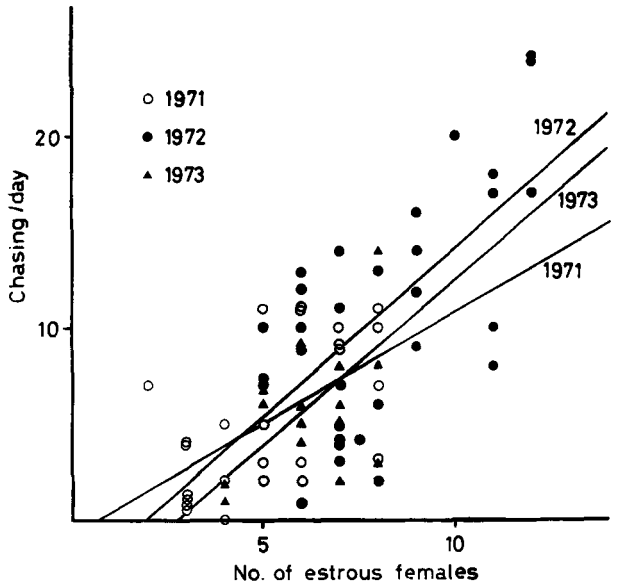


**Fig. 3.** Relationship between number of estrous females and frequency of chasing per day during the mating season in three successive years. Lines represent the straight regression lines for each year. All are significant at the less than 2.5% level.

frequency during their estrous phase, as compared to that at their non-estrous phase ($\chi^2$-test, $p<0.05$). On the other hand, each female that never showed estrus was on average chased by adult males $0.18\pm0.10$ times per day. This value roughly equalled that during the non-estrous phase of the former females, and was significantly lower than that of the former females throughout the survey period ($t = 3.0$, $df = 24$, $p<0.01$). This value of the latter fe-

**Table 5.** Relationship between copulation and chasing in combinations of adult males and females during the mating season.

| | | Copulation 1971[1] | | | Copulation 1972[2] | | | Copulation 1973[3] | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | + | − | Total | + | − | Total | + | − | Total |
| Chasing | + | 30 | 65 | 65 | 38 | 37 | 75 | 25 | 24 | 49 |
| | − | 18 | 45 | 63 | 12 | 25 | 37 | 3 | 46 | 49 |
| | Total | 48 | 80 | 128 | 50 | 62 | 112 | 28 | 70 | 98 |

1) $\chi^2=5.62$, $df=1$, $p<0.02$; 8 males and 16 females; 2) $\chi^2=3.33$, $df=1$, $p<0.1$; 7 males and 16 females; 3) $\chi^2=24.20$, $df=1$, $p<0.001$; 7 males and 14 females. +: Observed; −: not observed. Individuals in which copulation was not observed are neglected.

males, however, was far higher than that during the non-mating season of $0.018\pm0.024$ in 1972 and $0.005\pm0.016$ in 1973. Comparison of the values in the non-mating and mating seasons in 1972 revealed a significant difference ($t = 7.5$, $df = 34$, $p<0.001$). Chasing was mainly observed when the female sat alone, but in 7.8% of the cases the female was chased when she sat with another male.

The relationship between chasing and copulation in combinations of adult males and females was also analyzed (Table 5). A positive correlation was noted between these two types of behavior. On the other hand, grooming in the non-mating season and chasing were negatively correlated (data not shown; $p<0.05$ in 1972 and 1973, and $p<0.1$ in 1971).

## DISCUSSION

During the mating season, males frequently attack and chase females. The present results show that chasing was directed towards not only estrous females but also non-estrous ones. As regards factors affecting this type of behavior, two categories should be considered: physiological and social ones. Among the physiological factors, the increment of androgens in the male circulation during the mating season should be considered. It has been reported in the genus *Macaca* that testosterone affects the sexual behavior of male rhesus monkeys (PHOENIX, 1974) and correlates with the frequency of aggressive behavior (ROSE, HOLADY & BERNSTEIN, 1971). Although a similar report has not yet been presented for the Japanese monkey, NIGI et al. (1980) have stated that male testosterone secretion, testicular size and spermatogenesis were all activated during the mating season in the Japanese monkey. Moreover, they reported that males younger than 3 years old did not show any seasonal fluctuations in these indices, while 4-year-old males did so but very little. These findings coincide with the pattern of chasing frequencies. Although it remains unknown whether androgens directly affect the aggressive behavior, the above findings at least suggest that some factor which has an intimate relationship to testosterone secretion influences the behavior.

The present study also defined a correlation between the frequency of chasing by males and numbers of estrous females. This finding suggests that the chasing may have been activated by the presence of estrous females. Since chasing towards non-estrous females was also frequently observed during the mating season, the behavior does not appear to be released by the stimulus of estrous females, but to have its basis in physiology.

Regarding the second category of factors, social ones, the concentric structure of the troop ceases to function properly in the mating season. At this season, each male follows estrous females somewhere around the troop. The females do not intensively follow higher ranked males, which is in contrast to the situation in the non-mating season. The male-female bonds

such as the protecting-depending relation cease functioning at this time. Estrous females wander in search of preferential males apart from females that are in a genealogical relationship with them. Such weakening of the male-female and female-female bonds which function properly during the non-mating season, brings the wall which separates the central part of the troop from its periphery under the presence of higher ranked males into collapse in the mating season. Even males of lower rank can walk among the females with their tails raised and testes lowered into the scrotum, and they can chase some females. This factor may also have an effect on the appearance of chasing in juvenile males. Males of 4 or 5 years old become dominant over females.

The present study revealed a close correlation between tree-shaking rank and copulation rank in males, although the correlation did appear to fluctuate rather through changes in the male membership. This finding supports the results of MODAHL and EATON (1977), who postulated that displays such as shaking serve as a mechanism of sexual selection and influence the females' choice of males. To test this hypothesis, both the females' reactions to the displays and their effects on the copulatory sequences must be defined. The present results, in contrast to the work of MODAHL and EATON (1977), showed that the tree-shaking rank was also correlated with dominance rank. Tree-shaking is displayed by males of leader class as an expression of their status in some cases (KAWAI, 1969). This situation was typically observed during the non-mating season. On the other hand, the tree-shaking rank was correlated with the chasing rank and accompanied by a vocalization that was also evocated in aggressive interactions. These findings suggest that the correlation between tree-shaking and copulation ranks may not depend on female selection for the sexual partner, but actually represents a relationship between copulation and aggression. In the troop observed by MODAHL and EATON (1977), the absence of exchanges of male members may have affected the female selection for the sexual partner through some social distortion.

The present study showed that pairs in which the male chased the female tended to copulate. However, no aggressive behavior was observed in the sequence leading up to copulation, although appeasement behavior such as hindquarters-display was frequently shown (ENOMOTO, 1974). In this situation, the aggression might be inhibited, even when the female partner threatened the male. If such inhibition does not take place in the copulatory sequence, the mounting series might not be performed. However, sexual behavior is intimately related with the aggression. It is possible that the aggression-inhibiting mechanism has an essential role in the formation of new affinitive bonds between both sexes in the sexual context. After the affinitive bond has once been formed, aggression towards the female of the pair may be strictly inhibited, so that mating between them may be eliminated.

It has been reported that mating between individuals of both sexes in intimate blood relation is inhibited in the Japanese monkey (TOKUDA, 1958; ENOMOTO, 1978; BAXTER & FEDIGAN, 1979), rhesus monkey (SADE, 1968) and olive baboon (PACKER, 1979). It was suggested that both the departure of males from their native troop and certain psychological factors prevent incest. In Japanese monkeys, ENOMOTO (1978) and BAXTER and FEDIGAN (1979) have shown that pairs of both sexes in an affinitive relation tend to avoid sexual interactions with each other, and the avoidance of incest is thought to be related to this mechanism. PACKER (1979) mentioned on the basis of his observations on olive baboons that in natal males, dominance increased with age but reproductive activity decreased; natal males showed interest in the members of other troops, and all males finally emigrated from their natal troop. NORIKOSHI (1975) postulated that in the Japanese monkey, the affinitive bond between both sexes which is

formed through sexual interactions reduces the chance of sexual interaction for the male within the troop, since he stays in the troop and becomes more dominant. The male, therefore, tends to leave the troop, induced by more attractive females in other troops. In this case, instances of father-daughter mating may be reduced as well as son-mother matings. Aggression and its inhibition may play a role in the formation of new male-female bonds, and so participate in the incest-avoiding mechanism.

The appearance of male aggression towards females during the mating season thus depends basically on certain physiological factors and is modified by social factors. This may affect the reconstruction of male-female bonds, through which aggression exerts an influence on the social structure of the Japanese monkey troop.

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