# Mating Tactics in Response to Costs Incurred by Mating With Multiple Males in Wild Female Japanese Macaques

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*We investigated the costs of mating with multiple males in terms of feeding time, traveling distances, sexual proceptivity, and male aggression, for wild female* (Macaca fuscata yakui) *on Yakushima Island, Japan. We analyzed all-day focal sampling data from 7 females during the mating season (Sept.-Nov. 1996). On days when estrous females copulated with multiple males, they decreased their feeding time to half that of anestrous days, traveled longer distances, showed more proceptive sexual behaviors and received more aggression from subordinate males than on days when they copulated with only the 1st-ranking male. On days when females copulated with only the 1st-ranking male, they showed no difference in feeding time with that of anestrous days, and expended less effort than the above mating pattern because of short traveling distances, diminished sexual proceptivity and a lower frequency of aggression received. The results suggest that the costs of estrous vary according to female sexual proceptivity and the number and social status of mating partners. Female Japanese macaques exhibit a mixed mating strategy over prolonged estrous periods, which may provide females with opportunities to maximize the benefits of copulating with multiple males and to minimize the costs of estrus by mating with only the 1st-ranking male. During an estrous cycle,*

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*females may be adjusting efforts for reproduction and survival; i.e., mating vs. feeding.*

## INTRODUCTION

The costs and benefits for females of mating with multiple males are currently a lively topic of debate in evolutionary biology (Paul, 2002; Soltis, 2002; Soltis and McElreath, 2001). In many primates, females copulate with more than one male during a single mating season (Dixson, 1997, 1998), because mating with multiple males may provide females with many advantages (Arnqvist, 1989; Hrdy, 1977; Taub, 1980; Parker, 1984; Small, 1988; Smuts, 1987; Soltis, 2002; Soltis and McElreath, 2001; van Noordwijk and van Schaik, 2000; Yasui, 1998).

By contrast, researchers have reported on the costs of mating, such as the expenditure of time and energy (Arnqvist, 1989; Daly, 1978; Matsubara, 2003; Smuts and Smuts, 1993), wounds and parasites (Nunn, 1999), and decreased fertility and lifetime (Chapman *et al.*, 1995). Reynolds and Gross (1990) suggested that females incur high costs of time and energy in the process of assessing multiple mating partners. Costs may differ according to the degree to which females show proceptive, receptive, or attractive sexual behaviors that may be related to the number of males with which they copulate.

Field studies on sexual behaviors during peri-ovulatory periods have compared indicators of mating costs, i.e., sexual activity, feeding time and traveling distance, between forming and not forming consortships (Albert *et al.*, 1996; Aujard *et al.*, 1998; Bercovitch, 1983), between estrus and anestrus states (Matsumoto-Oda and Oda, 1998) and between exhibiting and not exhibiting genital swelling (Aujard *et al.*, 1998). However, the costs of mating with multiple males have seldom been examined directly. A study on the costs of mating with multiple males preferably should be a 3-way comparison for a set of females between contexts when the females were anestrous, mated with a single male, and mated with multiple males. Field researchers have had difficulty in directly comparing contexts when the same females mate with a single male or multiple males because estrous period per female is very short in many species.

Japanese macaques are seasonal breeders and form matrilineal groups with multiple males. The costs and benefits of mating with multiple males should be an especially important problem for female Japanese macaques because they show great variability in the number of male mating

partners during even a single estrous period (Yamagiwa, 1985). Furthermore, female Japanese macaques have prolonged estrous periods in both provisioned and wild conditions (Furuichi, 1987; Huffman, 1987; Okayasu, 1992; review: Nunn, 1999; Takahata, 1980): on average 13.6 days in a cycle of 26.5 days, which repeat 1–4 times in a mating season lasting 4 or 5 mo (Huffman, 1991; Takahata, 1980; Takahata *et al.*, 1999). Highly proceptive females copulate not only with high-ranking but also low-ranking males during the peri-ovulatory period (Huffman, 1992; Mitsunaga *et al.*, 1992; Soltis *et al.*, 1997a,b).

Accordingly, female Japanese macaques can experience, in the same mating season, many days when they mate with only one male or with multiple males, as well as days when they are anestrous. We examined the costs of mating in terms of feeding time, traveling distance, proceptive sexual behaviors, and aggression incurred, by comparing days in the mating season when females mated with only the 1st-ranking male, with multiple males, or with no male. We focus on 2 questions: (1) is there a difference in the cost of mating for females depending on whether they mate with a single partner or multiple partners? and (2) do females choose to mate with multiple partners, and incur the costs of mating with them?

## METHODS

### Study Site and Subjects

The subjects are Macaca fuscata yakui, a subspecies of the Japanese macaque, which inhabits the warm temperate forests of Yakushima Island (30° N, 131° E) in southwest Japan. The site is on the western slope of Mt. Kuniwari between 0 and 200 m above sea level. The macaques characteristically form small groups (mean = 27.1 individuals/group, $N = 17$, range: 13–47) at high densities (mean = 4.8 groups/km$^2$) with a high socionomic sex ratio (number of reproductive males/females within a group; Mean = 0.79, $N = 17$, range: 0.5–1.0) (Yamagiwa and Hill, 1998; Yoshihiro *et al.*, 1999). The study groups have been habituated without provisioning since 1976 (Maruhashi, 1980).

MM collected behavioral data by focal-animal sampling on the females of groups H and B (Table I), the demography of which have been monitored continuously since 1976 and 1992, respectively (Maruhashi, 1982; Sugiura, Personal communication). Because adult and subadult males transferred between groups during the mating season, H varied from 17 to 19 individuals [2–5 adult males (estimated to be >10 yr), 1–3 subadult males (5–9 yr), 5 adult females (>7 yr), 2 subadult females (5–6 yr), 4 juveniles (1–4 yr) and 1 infant

**Table I.** Subjects and sample sizes

| ID | Age | Rank | Troop | Number of samples | | | |
|---|---|---|---|---|---|---|---|
| | | | | Anestrous | Type I | Type II | Total |
| bb | 10 | 2 | B | 1 | 0 | 1 | 2 |
| hk | 11 | 1 | H | 2 | 2 | 2 | 6 |
| kt | 10 | 4 | H | 1 | 2 | 2 | 5 |
| ky | 14 | 3 | H | 2 | 2 | 1 | 5 |
| mt | 5 | 5 | H | 2 | 2 | 1 | 5 |
| sr | 8–9 | 4 | B | 1 | 0 | 1 | 2 |
| sb | 6 | 2 | H | 1 | 2 | 2 | 5 |
| Total | | | | 10 | 10 | 10 | 30 |

(0 yr)] and B varied from 23 to 26 individuals [3–6 adult males, 4 subadult males, 7 adult females, 7 juveniles and 2 infants.

Total focal observation time was more than 2500 h. The mating season may begin in mid-August and continue until January (Yamagiwa, 1985). We analyzed 291 h and 53 min from 55 days of observation on 7 females in the mating season of 1996 from mid-September, when the first estrous female was identified, until the end of November. The females are 3 adult and 2 subadult females in H, and 2 adult females in B that came into estrous during the observation period. Their dominance ranks were 1–3 and 5–6 among H females, and 2 and 4 among B females.

We checked the estrous condition of all females *ad libitum* each day. We considered a female in estrous if she engaged in ≥1 mounting series with ejaculation, during which she was approached and followed by males. All estrous females copulated with multiple males in the 1996 mating season.

## Data Collection

We used the focal-animal method (Altmann, 1974) to obtain continuous behavioral data on 1 female per day. Each day between 08:00 and 16:00 h we monitored a new subject from among the 7 focal subjects making every effort to select for reproductive condition (estrous days, anestrous days) and male partner (the 1st-ranking male, subordinate males).

The data set comprises 30 all-day units, each composed of ≥8 h of observation. Focal samples are all-day samples if we observed a subject for >8 h continuously, and half-day samples if we observed a subject continuously for 4 h in the morning or afternoon. One data point equals one all-day sample ($n = 28$), or the sum of half-day samples in the morning and afternoon of different days within 2 weeks ($n = 4$ half-days). We excluded data collected on rainy days because observation was compromised.

We classified observation days into 3 types: anestrous day: the female did not copulate with any male; type I: an estrous female copulated only with the 1st-ranking male; type II: an estrous female copulated with multiple males including the 1st-ranking male. There was no type II day when the female did not copulate with the 1st-ranking male. Copulation patterns refers to type I and type II days.

We compared sexual proceptivity, receptivity, and attractivity among day-types. We used the frequencies of female approach, looking back and presenting for the index of female sexual proceptivity. We used frequencies mounting series and ejaculation for the index of female sexual receptivity. We used frequencies of male approach for the index of female sexual attractivity (Beach, 1976; Enomoto, 1979).

MM classified general activity patterns into 6 categories: feeding, traveling, resting, grooming, mounting series and other social behaviors. Feeding behavior is searching for dispersed food items, extracting-picking, handling and putting foods into the mouth. A mounting series is continuous multiple mounts, including grooming and resting, near the mating partner between and after mounts. MM measured the duration of one mounting series from the first mount until ejaculation and considered a new mounting series to have begun if the interval between mounts was >5 min. Aggression included chasing, physical attacks—pushing, biting other individuals—and spatial displacement, and flight after receiving aggression from other individuals (Kurland, 1977).

Travel time has been used to indicate energy cost (Taylor *et al.*, 1970). However, travel time does not always correlate with travel distance, which a more direct measure of travel cost (Albert *et al.*, 1996). We measured travel distance by digitizing travel routes into a geographic information system (Arc/Info). Because the research site is extremely mountainous, DS corrected the distances for the influence of topography (Sprague, 1998). Travel distance measured after taking topography into account is on average 10.2% longer than that measured assuming flat topography. We refer to travel distance as the number of m traveled per 10 h of observation. Travel speed is travel distance divided by travel time. Travel and walking time includes time spent feeding on insects on the ground, because travel on the ground often involved foraging.

## Data Analyses

We conducted non-parametric tests to compare behavioral and spatial variables among the 3 day-types. Significance is at 0.05 assuming a 2-tailed distribution. We provide means ±SE. We calculated the Steel-Dwass test

(Dwass, 1960; Steel, 1960)—a non-parametric multiple comparison test—to analyze differences among the day-types via KyPlot 2.0 beta 9 for Windows (http://www.kyenslab.com/en/). We calculated the Kruskal-Wallis, Friedman tests and Kendall's $\tau$ via StatView 5.0 J for Windows.

Sample biases, or correlations with other variables, may potentially affect the results. However, no significant bias exists in the combination of individuals and day-types (Friedman statistic, chi-square $= 0$, NS); all females are represented once or twice in anestrous and type I days, 5 females twice each in type II days. Kruskal-Wallis tests revealed no statistically significant variability among individual females in observation time ($H = 5.92$, NS) or in the variables in the study (Kruskall-Wallis tests, all NS). Kruskal-Wallis tests showed no statistically significant relation with age and rank for the variables in the study.

Of the 27 statistically significant tests, 5 included non-conforming females, i.e. females represented on both sides of a pair-wise comparison that did not follow the trend. The test statistics give the identities of the non-conforming females in the results. Four females (sb, ky, hk, sr) failed to follow the trend once each, and mt failed to follow the trend in 3 tests. We analyzed variation within day-types, to explore whether any study variable might explain some of the variation within day-types and account for the non-conforming females.

## RESULTS

### Number of Male Mating Partners

The number of males copulated with per day varied from 0 to 4 among the 7 females. The numbers of each day-type are: 10 anestrous days, 10 type I, and 10 type II days. Only the 1st-ranking male in H successfully guarded estrous females for an entire day. On type II days, the females copulated with an average of $3.3 \pm 0.26$ males per day, including the 1st-ranking male. The number of estrous females per day ranged from 0–2 in H and 0–1 in B.

### Feeding Time

The feeding times of anestrous and estrous females differ significantly (Fig. 1). Females on type II days invested only half of the time feeding that they did on anestrous days (Steel-Dwass tests, $t = 3.78$, $P < 0.01$). However, feeding time on type I days does not differ from that of anestrous days ($t = 2.12$, NS). Feeding times varied between copulation patterns. On type II
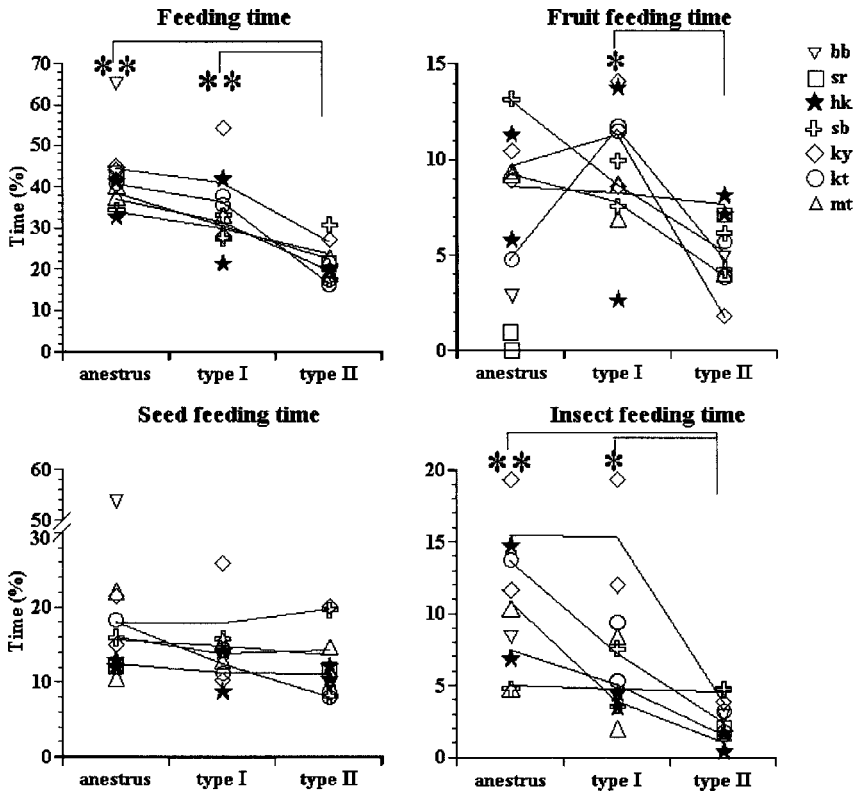
**Fig. 1.** Comparison of activity budgets by mating type. Each symbol indicates an individual, and each line the average for subjects on all 3 day-types. Steel-Dwass tests $*P < 0.05$; $**P < 0.01$.

days, females spent less time feeding than on type I days ($t = 3.33$, $P < 0.01$). Females on type II days spent less time feeding on insects than they did on anestrous days ($t = 3.63$, $P < 0.001$). Feeding times on fruits and insects varied between copulation patterns. Females spent less time feeding on fruits and insects than on type II days on type I days (fruits: I vs. II; $t = 2.80$, $P < 0.05$. insects: I vs. II; $t = 2.72$, $P < 0.05$).

## Travel Distance and Travel Speed

Travel distances per 10 h differed between the copulation patterns (Fig. 2). Those of type II days are significantly longer than those of type I days ($t = -2.48$, $P < 0.05$; sb, ky). However, there is no significant difference in
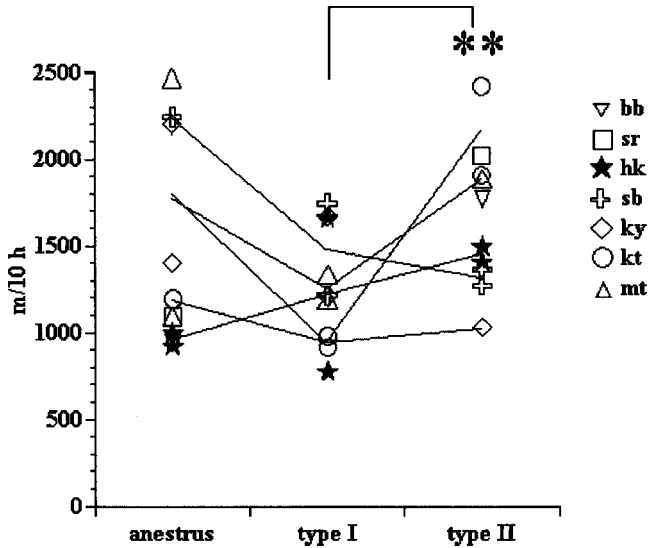
**Fig. 2.** Comparison of traveling distance per 10 h by mating type. Each symbol and line indicates a subject and the averages of groups in each subject in 3 day-types, respectively. Steel-Dwass tests ** $P < 0.01$.

travel distance between anestrous and estrous periods (anestrous days vs. I; $t = 0.23$, NS. anestrous days vs. II; $t = -1.21$, NS). Travel speeds do not differ among the 3 day-types (anestrous days vs. I; $t = 0.45$, NS. anestrous days vs. II; $t = 0.45$, NS. I vs. II; $t = -0.38$, NS). Large variation remains within day-types, and 2 females (sb, ky) did not conform to the trend. Within only Type II days, travel distances correlate with time spent in mounting series, and resting (Kendall's $\tau$, distance vs. mounting series $\tau = 0.60$, $P < 0.05$; distance vs. resting, $\tau = 0.58$, $P < 0.05$) (Fig. 3). The nonconforming females (sb, ky) spent less time in mounting series and resting.

## Agonistic Interactions

During the observation period, we recorded 224 agonistic interactions (58 interactions on anestrous days, 49 on type I, and 117 on type II days). Aggression received differs significantly among day-types (Fig. 4(a)). The total amount of aggression received is higher on type II days than on anestrous days ($t = -3.55$, $P < 0.01$), and higher on type II days than on type I days ($t = -3.10$, $P < 0.01$; hk). However it does not differ between anestrous and type I days ($t = -0.83$, NS). The nonconfirming female (hk) received
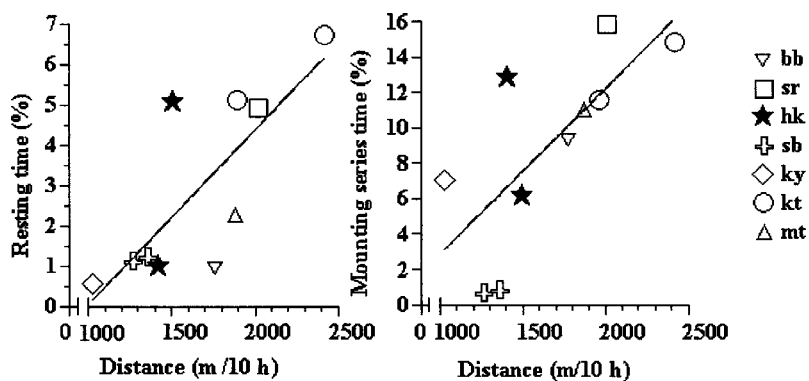
**Fig. 3.** Correlation between travel distance and activity budgets on type II days. Each symbol indicates observed individual.
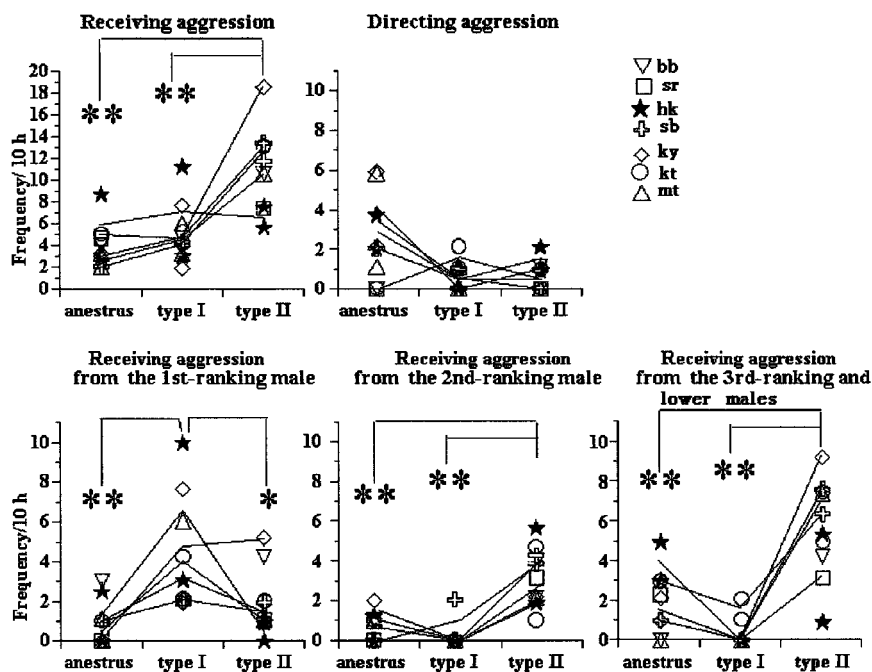


**Fig. 4.** Comparison of frequencies of aggressive interactions by mating type. Each symbol indicates an individual, and each line the average for subjects on all 3 day-types. Steel-Dwass tests $*P < 0.05$; $**P < 0.01$.

aggression from the 1st-ranking male more frequently on type I days than on type II days.

The 1st-ranking male attacked estrous females on type I days more frequently than on anestrous and type II days (anestrous days vs. I; $t = -3.05$, $P < 0.01$. I vs. II; $t = 2.85$, $P < 0.05$). Subordinate males attacked estrous females on type II days more than on anestrous and type I days (2nd-ranking male: anestrous days vs. II, $t = -3.33$, $P < 0.01$, I vs. II, $t = -3.80$, $P < 0.001$; 3rd-ranking male or lower: anestrous days vs. II; $t = -3.07$, $P < 0.01$, I vs. II, $t = -3.75$, $P < 0.01$). However, there is no difference between anestrous and type I days (2nd-ranking male: $t = 2.26$, NS; 3rd-ranking male or lower: $t = 2.32$, NS). The total amount of aggression directed to other individuals does not differ among the 3 day-types (anestrous days vs. I, $t = 1.91$, NS. anestrous days vs. II, $t = 1.78$, NS. I vs. II, $t = 0.00$, NS) (Fig. 4(b)).

## Female Sexual Activity

Female sexual proceptivity increased on type II days (Fig. 5). The frequencies of approach, presenting and looking back—the index of sexual proceptivity—are higher on type II days than on anestrous days (approach: $t = -2.91$, $P < 0.01$, mt; presenting: $t = -3.00$, $P < 0.01$, mt, sr; looking back: $t = -3.72$, $P < 0.001$), while these frequencies except for approach do not differ between type I and anestrous days (approach: $t = -2.48$, $P < 0.05$. presenting: $t = -1.82$, NS. looking back: $t = -2.2$, NS). The frequency of looking back is higher on type II days than on type I days (looking back: $t = -3.32$, $P < 0.01$); however, those of approach and presenting do not differ between type I and type II (approach: $t = -1.98$, NS. presenting: $t = -1.99$, NS).
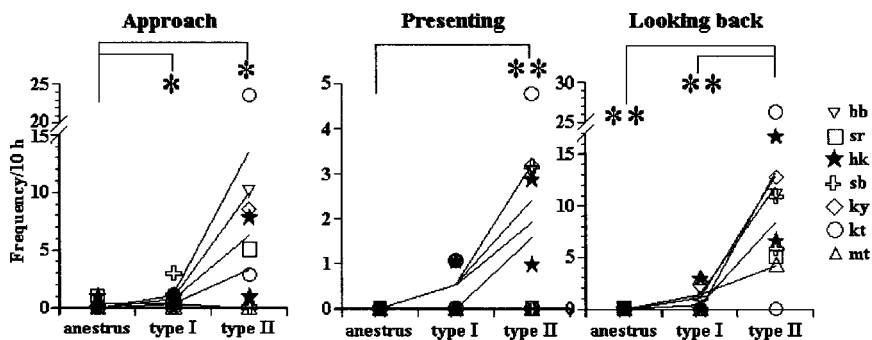


**Fig. 5.** Comparison of sexual proceptivity by day-types. Each symbol indicates an individual, and each line the average for subjects on all 3 day-types. Steel-Dwass tests $^{*}P < 0.05$; $^{**}P < 0.01$.

The frequency of male approach to a female—the index of sexual attractivity—does not differ between type I and type II days ($t = -0.23$, NS). The frequencies of mounting series and ejaculation—the index of sexual receptivity—does not differ between type I and type II days (mounting series: $t = -1.85$, NS. ejaculation: $t = -1.13$, NS).

Two females (mt, sr) failed to follow the trend in proceptivity because they showed zero proceptivity within the respective pair-wise comparisons. They nevertheless copulated with multiple males. Furthermore, a 3-way relation existed between presenting, ejaculation and the number of males copulated with only within type II days (Fig. 6). The frequency of presenting is positively correlated with that of ejaculation (Kendall's $\tau$, $\tau = 0.61$, $P < 0.05$). However, the number of males copulated with is negatively correlated with the other 2 variables (presenting vs. the number of males copulated with: $\tau = -0.68$, $P < 0.05$; ejaculation frequency vs. the number of males copulated with: $\tau = -0.69$, $P < 0.05$).

## DISCUSSION

Our analysis indicates that female Japanese macaques incur costs of mating with multiple males via a decline in feeding time, especially that of insects, energetic expenditure from proceptive behaviors and longer travel distances, and the risk of injury from male aggression. We provides further evidence that the degree of costs varies according to the level of female sexual proceptivity and the number of male mating partners, rather than estrous condition alone. In general, for the 7 focal females, cost variables did not differ between anestrous days and the type I days when they copulated with only the 1st-ranking male. The costs tended to increase on the type II days when they mated with multiple males.
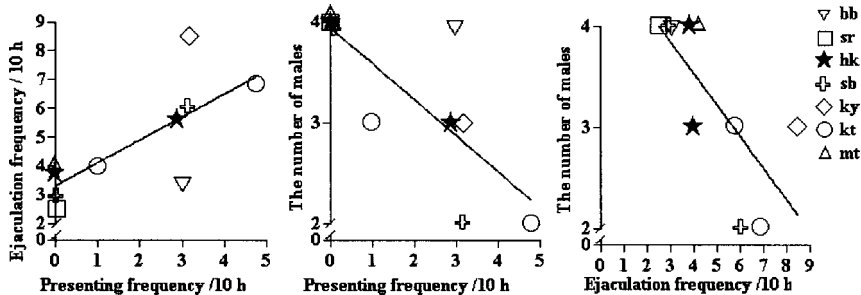


Fig. 6. Correlation among sexual behaviors and the number of males copulated with on type II days. Each symbol indicates a subject.

Feeding time did not differ between anestrous days and type I days, but females shortened feeding time on type II days. In other species, estrous females decrease feeding time to allow for mating behaviors (Bercovitch, 1983; Matsumoto-Oda and Oda, 1998) or social grooming (Aujard *et al.*, 1998). Our results suggest that copulation and other sexual behaviors, including grooming, take priority over feeding when copulating with multiple males, but not when copulating with only the 1st-ranking male. Female Japanese macaques may counterbalance the loss in feeding time incurred while copulating with multiple males via feeding during periods of exclusive copulation with the 1st-ranking male.

Females copulating with multiple males traveled longer distances. Travel distance on type II days was longer than that on the type I days or anestrous days. It is important to measure traveling distance, because distance measures are not equivalent to time budget measures (Alberts *et al.*, 1996). Data analysis should account for topographic effects because topography strongly influences spatial measures in mountainous study sites (Sprague, 1998).

Travel distance may increase because, as reported for other species (Hasegawa, 1990; Wrangham, 1979), consorting estrous females sometimes travel for long periods or distances with their mate. Another reason for longer travel distance may be the avoidance of aggression. Estrous females flee from males that coerce them to copulate and/or hide from the dominant male to mate with more preferred subordinate males and extragroup males (Aujard *et al.*, 1998; Brereton, 1992, 1994; Hasegawa, 1990; Hogg, 1984; Huffman, 1987, 1991; Sprague *et al.*, 1998; Tutin, 1979; Wrangham, 1979). On type II days, the times spent in resting and mounting series are correlated with travel distance probably because estrous females rested before and after mounting series with the males with which they had copulated. Females may travel longer to avoid mate guarding by the 1st-ranking male and to allow enough time to copulate with multiple males.

Dominant males may try to maintain access to estrous females by attacking them (Fedigan, 1983; Bulger, 1993), or by intruding upon their consortships with subordinate males (Furuichi, 1985; Huffman, 1987; Soltis *et al.*, 1997a). The low frequency of aggression on type II days from the 1st-ranking male to females, resulted partly from the long distance traveled by females to avoid coercion by the 1st-ranking male.

The total frequency of aggressive interactions was lower on type I days than on type II days. This is most likely due to the fact that females were in the presence of the 1st-ranking male for most of a type I day and thus were immune from the aggression of subordinate males (Arnqvist, 1989; Smuts and Smuts, 1993). Therefore, we infer that estrous females can reduce energy expenditure and risk of injury via mate guarding of the dominant male.

Females copulating with multiple males exhibited more proceptive sexual behavior than when copulating with only the 1st-ranking male. Estrous females initiate proximity by re-approaching and leading males (Huffman, 1987, 1991; Saayman, 1970), or terminate proximity by leaving them (Manson, 1997; Tutin, 1979). Such active sexual behaviors likely consume more time and energy as females change and keep preferred partners (Daly, 1978; Hausfater, 1975). The other sexual behaviors indicating receptivity and attractivity did not change among mating tactics. Our results and the high frequency of receiving aggression from males in type II days, suggest that male proceptive sexual behaviors, such as male approach to a female and sexual coercion, did not cause female receptivity or female mating with multiple males.

Do females choose to incur the higher costs of mating with multiple males? The behaviors that we used as indices of sexual proceptivity can be interpreted to indicate female choice (Soltis *et al.*, 1997a,b). The higher proceptivity of females on type II days, may indicate their effort to mate with multiple males. However, on type II days, females tended to reduce the frequencies of presenting and copulation when they succeeded in copulating with multiple subordinate males, which suggests that female mating effort is influenced by the mating efforts of subordinate males. Females may not show proceptivity when many males are trying to mate with them, while frequently changing mating partners may reduce ejaculation frequency. By contrast, the high presenting frequency and high ejaculation frequency on days when some females copulated with only 2 males, may be related to female proceptivity towards the 2nd-ranking male.

On type I days, a female has either been coerced into remaining with the 1st-ranking male, or has chosen to mate with him as indicated by the lower but non-zero proceptivity. Females on type I days did not have to work as hard to maintain the consort because of the 1st-ranking male's efforts to approach and follow an estrous female to guard her from the other males. Therefore, the low costs of time and energy on type I days may be the result of female mate choice to allow mate guarding by the 1st-ranking male, instead of coercion by him.

Whether estrous costs are associated with reproductive success cannot be determined directly from our data. Indirect clues are provided by the distribution of proceptive behaviors in the estrous cycle. Female proceptive behaviors correlate positively with estradiol secretion, which reaches a peak before ovulation (Enomoto, 1979; Mitsunaga *et al.*, 1992; Soltis *et al.*, 1997a). The frequencies of female approach, looking back and presenting to males are especially associated with female choice that results in mating (Soltis, 1999). Female feeding time and food intake decrease during the peri-ovulatory period in other primates for which researchers can judge the

ovulation cycle by visual signs of morphology and behavior (rhesus monkeys: Czaja and Goy, 1975; chacma baboons: Bielert and Busse, 1983). Assuming these facts apply to the Yaku macaque females, one can suggest that females pay the costs of copulating with multiple males during peri-ovulatory periods, and minimize the costs of estrus by being spatially proximate to the 1st-ranking male during other periods.

Female Japanese macaques exhibit a mixed mating strategy over prolonged estrous periods, providing them with opportunities to maximize the benefits of copulating with multiple males, or to minimize the costs of estrous by mating with only one male. Mating with multiple males may help to ensure fertilization (Milton, 1985; Small, 1988), to confuse paternity, which may result in the reduced risk of infanticide (Hrdy, 1977; Smuts, 1987; Sugiyama, 1965), and to obtain genetic benefits (Yasui, 1998). However, female reproductive effort includes not only mating and rearing efforts but also survival effort, which is confirmed by the fact that females need to maintain a certain body weight in order to successfully reproduce (Bercovitch, 1987; Bercovitch *et al.*, 1998; Mori *et al.*, 1997; Tardif and Jaquish, 1994; Walker *et al.*, 1983). Japanese macaques also use up accumulated body fat in winter, which overlaps with the mating season (Wada *et al.*, 1975). The estrous Yaku females subjected lost feeding time loss because of their own proceptive sexual behaviors. We suggest that female Japanese macaques seek proximity with the 1st-ranking male partly to avoid aggression from subordinate males and to feed to the exclusion of competitors.

## ACKNOWLEDGMENTS

## REFERENCES

Albert, S. C., Altmann, J., and Wilson, M. L. (1996). Mate guarding constrains foraging activity of male baboons. *Anim. Behav.* 51: 1269–1277.

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour* 49: 227–265.

Arnqvist, G. (1989). Multiple mating in a water strider: Mutual benefits or intersexual conflict? *Anim. Behav.* 38: 749–756.

Aujard, F., Heistermann, M., Thierry, B., and Hodges, J. K. (1998). Functional significance of behavioral morphological and endocrine correlates across the ovarian cycle in semifree ranging female Tonkean macaques. *Am. J. Primatol.* 46: 285–309.

Beach, F. A. (1976). Sexual attractivity proceptivity and receptivity in female mammals. *Horm. and Behav.* 7: 105–138.

Bercovitch, F. B. (1983). Time budgets and consortships in olive baboons (*Papio anubis*). *Folia Primatol.* 41: 180–190.

Bercovitch, F. B. (1987). Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *Am. J. Primatol.* 12: 189–195.

Bercovitch, F. B., Lebron, M. R., Martinez, H. S., and Kessler, M. J. (1998). Primigravidity body weight and costs of rearing first offspring in rhesus macaques. *Am. J. Primatol.* 46: 135–144.

Bielert, C., and Busse, C. (1983). Influences of ovarian hormones on the food intake and feeding of captive and wild female chacma baboons (*Papio ursinus*). *Physiol. Behav.* 30: 103–111.

Brereton, A. R. (1992). Alternative reproductive tactics in stumptail macaques (*Macaca arctoides*). *Folia Primatol.* 59: 209–212.

Brereton, A. R. (1994). Return-benefit spite hypothesis: An explanation for sexual interference in stumptail macaques (*Macaca arctoides*). *Primates* 35: 123–136.

Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 127: 67–103.

Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F., and Partridge, L. (1995). Cost of mating in Drosophila melanogaster females is mediated by male accessory gland products. *Nature* 373: 241–244.

Czaja, J. A., and Goy, R. W. (1975). Ovarian hormones and food intake in female guinea pigs and rhesus monkeys. *Horm. Behav.* 6: 329–349.

Daly, M. (1978). The cost of mating. *Am. Nat.* 112: 771–774.

Dixson, A. F. (1997). Evolutionary perspectives on primate mating systems and behavior. *Ann. N. Y. Acad. Sci.* 807: 42–61.

Dixson, A. F. (1998). *Primate Sexuality*, Oxford University Press, New York.

Dwass, M. (1960). Some k-sample rank-order tests. In Olkin, I. (ed.), *Contributions to Probability and Statistics* Stanford University Press, California, pp. 198–202.

Enomoto, T. (1974). The sexual behavior of Japanese monkeys. *J. Hum. Evol.* 3: 351–372.

Enomoto, T. (1979). On the correlation between sexual behavior and ovarian hormone level during the menstrual cycle in captive Japanese monkeys. *Primates* 20: 563–570.

Fedigan, L. M. (1983). Dominance and reproductive success in primates. Yrbk *Phys. Anthropol.* 26: 91–129.

Furuichi, T. (1985). Inter-male associations in a wild Japanese macaque troop on Yakushima Island Japan. *Primates* 26: 219–237.

Furuichi, T. (1987). Sexual swelling receptivity and grouping of wild pygmy chimpanzee females at Wamba Zaire. *Primates* 28: 309–318.

Hasegawa, T. (1990). Sex differences in ranging patterns. In Nishida, T (ed.), *The Chimpanzees of the Mahale Mountains,* University of Tokyo Press, Tokyo, pp. 99–114.

Hausfater, G. (1975). *Dominance and Reproduction in Baboons (Papio cynocephalus): A Quantitative Analysis*, S. Karger, Basel, Switzerland.

Hogg, J. T. (1984). Mating in bighorn sheep: Multiple creative male strategies. *Science* 225: 526–528.

Hrdy, S. B. (1977). Infanticide as a primate reproductive strategy. *Am. Sci.* 65: 40–49.

Huffman, M. A. (1987). Consort intrusion and female male choice in Japanese macaques (*Macaca fuscata*).*Ethology* 75: 221–234.

Huffman, M. A. (1991). Mate selection and partner preference in female Japanese macaques. In Fedigan, L. M., and Asquith, P. (eds.), *The Monkeys of Arashiyama. Thirty-Five Years of Study in the East and West*, State University of New York Press, Albany, pp. 101–122.

Huffman, M. A. (1992). Influences of female partner preference on potential reproductive outcome in Japanese macaques. *Folia Primatol.* 59: 77–88.

Kurland, J. A. (1977). Kin selection in the Japanese monkey. In Szalay, E. S. (ed.), *Contributions to Primatology*, Vol. 12, S. Karger, New York, pp. 1–145.

Manson, J. H. (1997). Primate consortships. *Curr. Anthropol.* 38: 353–374.

Maruhashi, T. (1980). Feeding behavior and diet of the Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island Japan. *Primates* 21: 141–160.

Maruhashi, T. (1982). An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island Japan. *Primates* 23: 317–337.

Matsubara, M. (2003). Costs of mate guarding and opportunistic mating among wild male Japanese macaques. *Int. J. Primatol.* 24: 1057–1075.

Matsumoto-Oda, A., and Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *Am. J. Primatol.* 46: 157–166.

Milton, K. (1985). Mating patterns of wooly spider monkeys *Brachyteles arachnoides*: Implications for female choice. *Behav. Ecol. Sociobiol.* 17: 53–59.

Mitsunaga, F., Nozaki, M., Inoue, M., Takenaka, A., Takenaka, O., Sakura, O., Sugiyama, Y., and Ohsawa, H. (1992). Steroid hormones and sexual behavior of female Japanese monkeys in an enclosed group. In Itoigawa, N., Sugiyama, Y., Sackett, G. P., and Thompson, R. K. R. (eds.), *Topics in Primatology 2*, University of Tokyo Press, Tokyo, pp. 23–34.

Mori, A., Yamaguchi, N., Watanabe, K., Shimizu, K. (1997). Japanese macaques under poor nutritional conditions and food-enhanced perineal swelling in the Koshima troop. *Int. J. Primatol.* 18: 553–579.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim. Behav.* 58: 229–246.

Okayasu, N. (1992). Prolonged estrus in female Japanese macaques (*Macaca fuscata yakui*) and the social influence on estrus: With special reference to male intertroop movement. In Itoigawa, N., Sugiyama, Y., Sackett, G. P., and Thompson, R. K. R. (eds.), *Topics in Primatology 2*, University of Tokyo Press, Tokyo, pp. 163–178.

Parker, G. A. (1984). Human sperm competition. In Smith, R. L. (ed.), *Sperm Competition and the Evolution of Animal Mating Systems*, Academic Press, Orlando, Tokyo, pp. 601–659.

Paul, A. (2002). Sexual selection and mate choice. *Int. J. Primatol.* 23: 877–904.

Reynolds, J. D., and Gross, M. R. (1990). Costs and benefits of female mate choice: Is there a lek paradox? *Am. Nat.* 136: 230–243.

Saayman, G. S. (1970). The menstrual cycle and sexual behavior in a troop of free ranging Chacma baboons (*Papio ursinus*). *Folia. Primatol.* 12: 81–110.

Small, M. F. (1988). Female primate sexual behavior and conception: Are there really sperm to spare? *Curr. Anthropol.* 29: 81–100.

Smuts, B. B. (1987). Sexual competition and mate choice. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 385–399.

Smuts, B. B., and Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Adv. Stud. Behav.* 22: 1–63.

Soltis, J. (1999). Measuring male–female relationships during the mating season in wild Japanese macaques (*Macaca fuscata yakui*). *Primates* 40: 453–467.

Soltis, J. (2002). Do primate female gain nonprocreative benefits by mating with multiple males? Theoretical and empirical considerations. *Evol. Anthropol.* 11: 187–197.

Soltis, J., and McElreath, R. (2001). Can females gain extra paternal investment by mating with multiple males? A game theoretic approach. *Am. Nat.* 158: 519–529.

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X., and Takenaka, O. (1997a). Sexual selection in Japanese macaques I: Female mate choice and male–male competition. *Anim. Behav.* 54: 725–736.

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X., and Takenaka, O. (1997b). Sexual selection in Japanese macaques II: Female mate choice and male–male competition. *Anim. Behav.* 54: 737–746.

Sprague, D. S. (1998). Topographic effects on measures of monkey habitat-use in a mountainous study site in Japan. *Am. J. Phys. Anthropol.* 26: 207.

Sprague, D. S., Suzuki, S., Takahashi, H., and Sato, S. (1998). Male life history in natural populations of Japanese macaques: Migration, dominance rank, and troop participation of males in two habitats. *Primates* 39: 351–363.

Steel, R. D. G. (1960). A rank sum test for comparing all pairs of treatments. *Technometrics* 2: 197–207.

Sugiyama, Y. (1965). On the social charge of hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates* 6: 213–247.

Takahata, Y. (1980). The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates* 21: 303–329.

Takahata, Y., Huffman, M. A., Suzuki, S., Koyama, N., and Yamagiwa, J. (1999). Why dominants do not consistently attain high mating and reproductive success: A review of longitudinal Japanese macaque studies. *Primates* 40: 143–158.

Tardif, S. D., and Jaquish, C. E. (1994). The common marmoset as a model for nutritional impacts upon reproduction. *Ann. N. Y. Acad. Sci.* 709: 214–215.

Taub, D. M. (1980). Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus*). In Lindburg, D. G. (ed.), *The Macaques: Studies in Ecology, Behavior and Evolution*, Van Nostrand Reinhold, New York, pp. 287–344.

Taylor, C. R., Schmidt-Nielsen, K., and Raab, J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219: 1104–1107.

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 6: 29–38.

van Noordwijk, M. A., and van Schaik, C. P. (2000). Reproductive patterns in eutherian mammals: Adaptations against infanticide? In Schaik, C. P., and Janson, C. H. (eds.), *Infanticide by Males and its Consequences*, Cambridge University Press, Cambridge, pp. 322–360.

Wada, K., Moriya, K., Hara, K., and Ohsawa, W. (1975). On the body fat of Japanese monkeys inhabiting the Shiga Heights (in Japanese with English summary). *Physiol. Ecol. Jpn.* 16: 104–107.

Walker, M. L., Gordon, T. P., and Wilson, M. E. (1983). Menstrual cycle characteristics of seasonally breeding rhesus monkeys. *Biol. Reprod.* 29: 841–848.

Wrangham, R. W. (1979). Sex differences in chimpanzee dispersion. In Hamburg, D. A., and McCown, E. R. (eds.), *The Great Apes*, Benjamin/Cummings Publication, Menlo Park, CA, pp. 481–489.

Yamagiwa, J. (1985). Socio-sexual factors of troop fission in wild Japanese monkeys (*Macaca fuscata yakui*) Yakushima Island Japan. *Primates* 26: 105–120.

Yamagiwa, J., and Hill, D. A. (1998). Intraspecific variation in the social organization of Japanese macaques: Past and present scope of field studies in natural habitats. *Primates* 39: 257–273.

Yasui, Y. (1998). The 'genetic benefits' of female multiple mating reconsidered. *Trends Ecol. Evol.* 13: 246–250.

Yoshihiro, S., Ohtake, M., Matsubara, H., Zamma, K., Hanya, G., Tanimura, Y., Kubota, H., Kubo, R., Arakane, T., Hirata, T., Furukawa, M., Sato, A., and Takahata, Y. (1999). Vertical distribution of wild Yakushima macaques (*Macaca fuscata yakui*) in the western area of Yakushima Island Japan: Preliminary report. *Primates* 40: 409–415.