The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*

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Japanese macaques reside in large, mixed-sex social groups in which various reproductive strategies of both sexes operate simultaneously. This report represents the first study combining behavioural and genetic data to examine the interaction of male and female reproductive strategies in primates (*N* = 15 adult males, *N* = 15 adult females, Yakushima Island, Japan). During one mating season, socially dominant males monopolized most female matings. Furthermore, the six offspring sired by troop males were more likely sired by higher-ranking males than lower-ranking males. Nontroop males sired three additional offspring in the troop. Lower-ranking troop males avoided direct competition with higher-ranking males by engaging in sneak copulations with females outside of the presence of other males. Also, females expressed mate choice behaviour towards multiple males of various dominance ranks. Thus, the female strategy of attempting to mate with multiple males conflicted with the mate-guarding strategy of high-ranking males. Despite some female mate choice for mid- and low-ranking males and alternative male mating tactics by subordinate males, high-ranking males were able to monopolize most, but not all, within-troop mating and paternity. This result was due in part to the low number of females mating at the same time. The mean number of females displaying mating behaviour per day was 2.42 (range 1–5), and higher-ranking males more successfully monopolized females on days when fewer females were mating. The number of females mating simultaneously influences the outcome of reproductive conflicts between the sexes.

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Animals living in mixed-sex social groups, such as many primates (Dixson 1998), pose a challenge for those studying sexual selection because of the simultaneous operation of many reproductive strategies, such as competition among males, female mate choice, alternative tactics by subordinate males and male sexual coercion of females. Competition among males for access to females is common in animals (e.g. Le Boeuf & Peterson 1969; Clutton-Brock et al. 1982). Among primates, the relationship between male dominance rank and reproductive success is not as straightforward as in other animals (Ellis 1993). Nevertheless, male dominance rank is usually positively correlated with mating success, with various levels of statistical significance, but rarely negatively correlated with mating success (Cowlishaw & Dunbar 1991; Bercovitch 1992a, b; Dunbar & Cowlishaw 1992). Recently, analysis of DNA or immediate gene products has allowed for more accurate assessment of paternity. Similarly, male dominance rank and number of offspring sired are usually positively correlated, with various levels of statistical significance (e.g. nonwild: Smith 1981, 1993; Inoue et al. 1990, 1993; Paul & Kuester 1996; Soltis et al. 1997b; wild: Melnick 1987; Pope 1990; Ohsawa et al. 1993; de Ruiter et al. 1994), but rarely negatively correlated (e.g. nonwild: Shively & Smith 1985).

Male dominance rank does not explain all of the variance in male mating and reproductive success, however. Additional sources of variation in male reproductive success include alternative male mating tactics (Rubenstein 1980) and female mate choice (Small 1993; Andersson 1994). In primates, for example, there is evidence that low-ranking and nongroup males use alternative tactics such as sneak copulations to obtain matings (e.g. Dunbar 1984; Ohsawa et al. 1993; Berard et al. 1994; Manson 1996).
The study of female mate choice in primates has been problematic. Validated measures of female mate choice are only sometimes used (e.g. Manson 1992), distinguishing between behavioural mate choice and underlying preference remains difficult (Soltis 1999), and in only a few species is there evidence for the criteria by which females choose males (e.g. squirrel monkey, Saimiri oeresti; Boinski 1987; brown capuchin monkey, Cebus apella: Janson 1984; vervet monkey, Cercopithecus aethiops: Keddy 1986; Japanese macaques, Macaca fuscata: Soltis et al. 1999; orang-utan, Pongo pygmaeus: van Schaik & van Hooff 1996). In addition, females can re-enforce the male dominance hierarchy by choosing dominant males (e.g. Cox & Le Boeuf 1977), or act in opposition to the male dominance hierarchy by choosing males of other ranks (e.g. Davies 1992; Manson 1992). When male and female strategies are in conflict, there may be sexual coercion (Smuts & Smuts 1993).

Japanese macaques live in bisexual social groups with female philopatry and male dispersal (Pusey & Packer 1987). Direct male–male competition, alternative male mating tactics, female mate choice and male sexual coercion of females are all important in this species. Male dominance rank explains some, but not all, of the variation in male reproductive success. Reported correlations between male dominance rank and (1) mating success and (2) number of offspring sired range from nonsignificant correlations to significant, positive correlations (e.g. mating only: Enomoto 1974; Eaton 1978; Takahata 1982; Perloe 1992; number of offspring: Inoue et al. 1991, 1993; Soltis et al. 1997b).

There is evidence that subordinate Japanese macaque males use sneak copulations as an alternative mating tactic. Nontroop males often invade social groups and mate with resident females (Sprague 1991). Also, in a captive study, low-ranking fathers were less likely to be observed mating with mothers during the ovulatory period than high-ranking fathers (Soltis et al. 1997b).

Female mate choice has also been considered important in Japanese macaques. For example, Huffman (1987, 1991) has shown that females can easily reject male mount attempts, and that dominant males are usually unsuccessful at breaking up mounting series involving females and low-rank males. Furthermore, Soltis et al. (1997b) showed that female mate choice is a stronger predictor than male–male competition of both mating success and number of offspring sired.

Nevertheless, male sexual coercion of females also may be important in Japanese macaques. Male aggression towards females increases in the mating season, and is correlated with high mating frequency (e.g. Enomoto 1981). In addition, male–female aggression may keep females from leaving males once mounting series have begun (Soltis 1999). One study, however, showed that most male–female aggression was a side effect of overall male aggression during the mating season (Soltis et al. 1997a).

This paper comprises the first study combining genetic and behavioural data to answer questions concerning sexual selection in wild, nonprovisioned Japanese macaques. We address the following specific questions.

(1) What is the relationship between male dominance rank and male mating and paternity of offspring? (2) Do subordinate males use alternative mating tactics? (3) How does female mate choice predict male mating and paternity of offspring? (4) How do conflicting male and female strategies interact to produce mating and reproductive outcomes? We compare these results with our previous work on captive Japanese macaques using similar methodology.

### METHODS

#### Study Subjects and Site

This study was conducted on the Nina-A troop of Japanese macaques residing in a broad-leaf evergreen forest on Yakushima Island, Japan, (30°N, 131°E; Maruhashi 1980, 1982). The Nina-A troop consisted of 52 individuals at the beginning of the study (Table 1). Subject animals included all adult males (N=15) and adult females that displayed copulatory behaviour (N=10 non-lactating and N=2 lactating females). All adults could be individually identified by sex, size, facial markings, injuries and scars. In addition, eight of 15 adult males could be identified by unique facial tattoos. The mating season begins in September and can last until February (Maruhashi 1982; personal observations). Troop males are those that were present within the troop at the beginning of the mating season. No males permanently transferred out of or into the Nina-A troop during the study period. Intergroup encounters occurred when one or more nontroop macaques and Nina-A members were observed simultaneously.

#### Behavioural Data Collection

This study represents part of a larger research project in which J.S. and R.T. monitored the Nina-A troop from July 1997 to June 1999. J.S. collected the core behavioural data reported here during the 1997 mating season peak from 27 September to 11 December. Focal samples were conducted on females that displayed copulatory behaviour on the day of or previous to observations (at least 2 mounts, an ejaculatory mount, or copulatory plug observed). J.S. attempted to locate the troop at dawn, and when found, began focal observations on the first such female encountered. Social and sexual behaviours were recorded (see Soltis 1999). Japanese macaques are series mounters (Tokuda 1961), and in this paper mating or

| Table 1. Composition of the Nina-A Troop at the beginning of the 1997 mating season |
|---------------------------------------------|----------|----------|----------|
| **Males** | **Females** | **Total** |
| Adult* (≥4 years) | 15 | 15 | 30 |
| Juvenile (1–3 years) | 10 | 7 | 17 |
| Infant (0 years) | 3 | 2 | 5 |
| **Total** | 28 | 24 | 52 |

*Adult=potentially sexually mature (Takahata et al. 1998).*
ejaculation refer to terminal, ejaculatory mounts. We defined a 'sneak copulation' as a mounting series culminating in ejaculation in which no other adult male was observed from the first mount in the series to the final ejaculatory mount. Focal samples were continued until the female was lost for more than 5 min. Focal samples under 20 min were not analysed. When a focal female was lost, a new focal sample was begun on the next female encountered who met the criteria for observations (even if it was the same female). A total of 198.72 h of focal observations were completed (mean ± SD=16.56 ± 14.87 h/female). The mean focal sample length was 90.99 min (range 20–520 min).

Prior to and during the mating season, J.S. recorded a total of 509 male submissive behaviours (cower, facial grimace, flee) ad libitum. A matrix was formed with losers on one axis and winners on the other. There was a rank reversal between the alpha and beta males midway through the mating season observations. These males were assigned the average of those two ranks combined. The third- through the fifth-ranking males had unstable relationships throughout the season, with bidirectional submission shown among all three males. These three males were each assigned the average of those two ranks combined. Finally, the three lowest-ranking males did not express submission to one another. These three males were assigned the average of the three lowest ranks combined. In the analyses that follow, male dominance rank is expressed as the fraction of other males outranked.

We also arranged males into an attractiveness hierarchy ('attractivity rank') based on female mate choice behaviour directed towards them during female focal samples (Halliday 1983). We used the female Hinde's index (Hinde & Atkinson 1970) as an assay of female mate choice. The Hinde’s index measures responsibility for proximity maintenance within dyads, and is calculated as the proportion of female approaches within the dyad minus the proportion of females leaves within the dyad (we used 1-m leaves and approaches). The index ranges from −1 (where the male is responsible for proximity) to +1 (where the female is responsible for proximity). Only dyads for which there were a total of at least 10 summed approaches and leaves were scored a Hinde’s index (N=79). Twelve males were ranked according to their mean female Hinde’s index. Three males low in dominance rank were excluded because they had only one measurable female Hinde’s index. Males to whom females maintain proximity most have high Hinde’s indices, while males to whom females maintain proximity the least have low Hinde’s indices.

We used the female Hinde’s index as an assay of female mate choice because our previous work shows that this measure is a powerful predictor of both mating and reproductive success in this species (Soltis et al. 1997a, b; Soltis 1999). Even though the female Hinde’s index was negatively correlated with dominance rank, it was a more powerful predictor of mating, ovulatory mating and number of offspring sired than was male dominance rank. Also, female initiation and/or maintenance of proximity are associated with mating in other primate species (rhesus monkey, *Macaca mulatta*; Wallen et al. 1984; Manson 1992; Savanna baboon, *Papio cynocephalus*: Bercovitch 1991).

**DNA Sample Collection and Analysis**

J.S. and R.T. used noninvasive sampling techniques to collect DNA from mothers (N=10), infants born in 1998 (N=10) and potential sires in the troop (N=15). Ejaculate (from masturbation or that issuing from the penis after mating) was collected from 11 males, blood samples collected by previous researchers were used for three males, and a urine sample was collected from the final male. Urine and/or faecal samples were collected from all 10 mothers and for 9 of 10 infants. Muscle tissue was extracted from one infant whose body was recovered after an infanticidal attack (Soltis et al. 2000).

Faecal, urine and ejaculate samples were collected immediately after they were left behind by identified individuals (Hayakawa & Takenaka 1999). A cotton swab was used to scrape the outer surface of faecal samples, and collected faeces was inserted into a tube with 2 ml EDTA and 99.5% ethanol (to 10 ml). Urine samples were collected with plastic pipettes and inserted into tubes with 99.5% ethanol (twice the volume of urine). The coagulated portions of ejaculates were collected with wooden sticks and inserted into tubes with 99.5% ethanol (to 10 ml). All samples were refrigerated at the Kyoto University YakuShima Field Station until DNA extraction at the Primate Research Institute of Kyoto University.

J.S. and O.T. extracted DNA from samples using standard phenol-chloroform procedures, extracts were maintained at 4 °C until polymerase chain reaction (PCR), and amplified DNA was subject to polyacrylamide gel electrophoresis and visualized after silver staining (Inoue & Takenaka 1993; Takenaka et al. 1993; Soltis et al. 1997b; Domingo-Roura 1997; Hayakawa & Takenaka 1999). To relieve amplification inhibition for faecal and urine samples, we included 0.02 μl of T4 gene 32 protein per tube (Kreader 1996), and amplified each sample three separate times using variable amounts of template DNA (0.1, 0.5 and 1.0 μl).

We used nine primers known to be polymorphic in Yakushima macaques (S. Hayakawa, unpublished data). One primer was designed specifically for Japanese macaques (MFGT 21; Domingo-Roura et al. 1997) and eight others originally designed for humans (D1S 550, DS 533, D5S 820, DSS 1457, DSS 1470, D6S 493, D6S 501 and D14S 255; Morin et al. 1997; Nurnberg et al. 1998).

PCR products from noninvasive samples such as faeces and urine can sometimes result in false genotyping, such as allelic drop-out and amplification of nontarget DNA (Taberlet et al. 1999). Methods for overcoming false genotyping include collecting fresh samples combined with good preservation methods, and using trinucleotide or tetrnucleotide microstellites (Taberlet et al. 1999). Samples were always collected immediately after released from the animal and were preserved in ethanol and refrigerated at the end of the day. In addition, seven of nine primers (78%) were tetrnucleotide repeats, while...
only two of nine (22%) were dinucleotide repeats (Domingo-Roura et al. 1997; Morin et al. 1997; Nurnberg et al. 1998).

The most conservative way to overcome these problems is to repeat each DNA amplification (PCR) independently many times for each locus, the so-called ‘multiple-tubes approach’ (e.g. Navidi et al. 1992). But this method is extremely time-consuming and requires large amounts of DNA (Taberlet et al. 1999). We could not follow this most conservative method because of time constraints and the small volume of unreplaceable template DNA from some subjects (small sample amounts combined with high mortality on Yakushima). We did attempt to remove the potential effects of allelic drop-out by excluding all homozygotes derived from noninvasive samples from the data set. The only change in the results was that there were no extra group paternities, so the estimate of the extragroup paternity provided here should be viewed with caution. Associations between independent variables and paternity, on the other hand, were essentially the same with the more conservative approach. Finally, using identical procedures in our laboratory, faecal- and urine-derived PCR products have been cross-validated with blood-derived PCR products from the same individuals (Hayakawa & Takenaka 1999).

### Paternity Determination

After bands for most individuals were visualized for a particular primer, the PCR products from the mother, her offspring and each potential male were run on lanes adjacent to one another (Soltis et al. 1997b). By comparing the mother and offspring genotypes, the paternal genotype was deduced. If the male did not possess the paternal allele(s), he was excluded. If all males in the group were excluded, we considered a nontroop male to have sired the offspring. We considered a male the likely father if (1) the other 14 males in the troop were all excluded, and (2) the male was compatible with the paternal genotype at all examined loci (e.g. Borries et al. 1999). Paternity inclusion probability for likely fathers could not be calculated because allele frequencies are not known on Yakushima Island (Chakraborty et al. 1988).

Ten infants were born in 1998. In nine cases, paternity was resolved according to the above rules (Table 2). Nonfathers were excluded at one to five loci, and likely fathers possessed genotypes compatible with offspring genotypes at seven to eight loci. Paternity could not be resolved for one infant who disappeared, because of the small amount of template DNA that was recovered and a low rate of amplification.

### Statistical Analyses

We used nonparametric statistical tests throughout (SPSS 10.0; two-tailed alpha=0.05). We calculated Wilcoxon matched-pairs signed-ranks tests and partial correlation coefficients according to Conover (1980), and determined for the latter the probability values using a standard table minus one degree of freedom.

### RESULTS

#### Male Reproductive Strategy and Paternity

Nontroop males sired three of nine offspring (33%) for whom paternity could be resolved (Table 2). Twenty-one encounters with neighbouring troops were observed during the study, but only one female was observed to mate with nontroop males. She was a lactating female who mated with two nontroop males during one intergroup encounter, but she did not give birth the following year.

Within the troop, however, dominant males were able to monopolize female mating and paternity. We observed 139 ejaculations by 15 troop males during female focal samples. The number of observed matings was correlated with male dominance rank (Spearman’s rank correlation: \( r_s = 0.700, N = 15 \) males, \( P = 0.004 \); Fig. 1). The number of offspring sired within the troop (6 of 9 offspring, 67%; Table 2) was also positively correlated with male dominance rank (\( r_s = 0.587, N = 15 \) males, \( P = 0.021 \); Fig. 1).

Results were similar after removing males below 7 years of age (mating: \( r_s = 0.595, N = 13 \) males, \( P = 0.032 \); infants sired: \( r_s = 0.551, N = 13 \) males, \( P = 0.051 \)).

Sires were almost never observed mating with the mother during the estimated time of conception, however. We estimated conception periods by counting back

### Table 2. Paternity exclusion analysis for nine mother–infant pairs and 15 males of the Nina-A troop

<table>
<thead>
<tr>
<th>Mother–Infant Pair</th>
<th>Number of group males excluded</th>
<th>Number of loci</th>
<th>Number of males not excluded (compatible)</th>
<th>Number of loci</th>
</tr>
</thead>
<tbody>
<tr>
<td>HOT–HRS</td>
<td>14</td>
<td>2–5</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>TAM–TMK</td>
<td>14</td>
<td>2–4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>NOR–NKR</td>
<td>14</td>
<td>2–4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>YAM–YMS</td>
<td>14</td>
<td>2–4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>WAK–WRB</td>
<td>14</td>
<td>2–4</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>HAM–HCM</td>
<td>14</td>
<td>2–4</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>SKO–5KE</td>
<td>15</td>
<td>2–4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>NAM–NMZ</td>
<td>15</td>
<td>2–4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>YKO–YGI</td>
<td>15</td>
<td>1–4</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
from birth the average gestation length ± 1 SD from observed birthdays (173 ± 7 days; Nigi 1976; Thomsen & Soltis 2000). Nontroop males sired three offspring, but mothers of these offspring were not observed to mate with nontroop males at any time. Of three mothers whose offspring were sired by troop males, one was observed to mate with the sire during the time of her conception period, one was observed to mate with the sire at times other than the conception period, and one was never observed to mate with the sire. In the last three cases, such analyses could not be performed, either because exact birthdays were not known (two cases), or there were no mating season behavioural data for the mother (the case of one lactating female who gave birth).

Dominant males could often monopolize females because there were not usually very many females displaying mating behaviour simultaneously. The mean ± SD number of females displaying mating behaviour per day was 2.42 ± 1.177 (range 1–5). For comparison, in an earlier captive study of Japanese macaques in which males did not monopolize females (N=8 males, N=21 females; Soltis et al. 1997a,b), the mean ± SD number of females displaying mating behaviour was 3.59 ± 1.606 (range 1–8; Mann–Whitney U test: U=1109.50, N₁ =45 days, N₂=85 days, P<0.001). In fact, in this study, 21 of the alpha male’s 61 observed ejaculations (34%; Fig. 1) occurred with one female during an 8-day stretch in which she was either the only female mating or was one of two females mating. During that period, the alpha male secured 84% (21/25) of her matings, although this did not coincide with her conception period, and he did not sire her offspring.

We further tested the priority of access model by calculating, for each observation day, the number of females in the group displaying copulatory behaviour (see Methods), the number of males observed mating during focal samples and the average rank of mating males. The number of males observed mating increased, but not significantly, with the number of females displaying copulatory behaviour (SPSS 10.0 Jonckheere-Terpstra test: JT=336, N=39 days, P=0.099; Fig. 2), but the average dominance rank of males observed mating did decrease significantly with the number of females displaying mating behaviour (JT=190, N=39 days, P=0.029; Fig. 2). This result shows that the larger the number of available females, the greater the mating opportunity for males of various dominance ranks.

Females and males were often observed to run from the central part of the troop and engage in sneak copulations (see Methods) outside of the presence of other troop members. Lower-ranking males were most likely to engage in such sneak copulations (rš = −0.783, N=15 males, P=0.001; Fig. 3).

**Female Reproductive Strategy and Paternity**

The mean ± SD number of 15 males with whom 12 females were observed to mate during focal samples was 5.17 ± 2.855 (range 1–10 males). Although the number of observation hours per female was correlated with the number of observed mating partners (rš =0.883, N=12 females, P<0.001), it was not correlated with the mean rank of females’ mating partners (rš = −0.399, N=12 females, P=0.199), or with the mean female Hinde’s index across males (rš = −0.238, N=12 females, P=0.457). Female Hinde’s indices ranged from −0.692 to +0.909. The mean Hinde’s index for each female, calculated across males, ranged from 0 to +0.533, and the grand mean across all female means was +0.208.

We ordered males into an attractiveness hierarchy based on the Hinde’s index. For each female, we calculated the mean Hinde’s index across males, and males

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**Figure 1.** Relationship between male dominance rank and the number of observed ejaculations (■) and the number of offspring sired (■). The highest-ranking male sired two offspring, and four other males sired one offspring each.

**Figure 2.** For days on which there were one to five females displaying copulatory behaviour in the group, the mean±SE number of males that mated with focal females (○), and the mean±SE dominance rank of males that mated with focal females (■). Dominance rank is expressed as the fraction of other males outranked multiplied by 10. Number of observation days (N) on which one to five females were displaying copulatory behaviour is indicated.
High in attractivity were those with Hinde’s indices above the female’s mean, and males low in attractivity were those with Hinde’s indices below the female’s mean. Female mate choice had only a minimal effect on male mating and no measurable effect on paternity. Males of high attractivity were more likely to become mates than males of low attractivity (Wilcoxon matched-pairs signed ranks test: \(T_{12}=0.018\), \(N=11\) females, \(P=0.044\); Table 3). The absolute number of matings received, however, did not differ between males of high and low attractivity (\(T_{12}=0.474\), \(N=11\) females, \(P=0.636\); Table 3). This is because some females mated many times with a few high-ranking males that were low in attractivity. The dominance rank of males of high and low attractivity also did not differ (\(T=1.423\), \(N=11\) females, \(P=0.182\); Table 3). Group males for whom there was a measurable Hinde’s index sired only four infants. A male of high attractivity sired one offspring, and males of low attractivity sired three (Table 3).

The Interaction of Male and Female Strategies

To compare the effects of male dominance rank with the effects of female mate choice, we ordered males into an attractiveness hierarchy based the their mean female Hinde’s indices (see Methods). Males varied in their attractivity to females, but no male was universally high or low in attractivity across all females. The percentage of troop females to whom males were high in attractivity (definition above) ranged from 25% to 71% (median= 50%). Across males, the mean female Hinde’s index ranged from \(-0.123\) to \(+0.352\) with an overall mean of \(+0.198\). As in the female-centred analysis above, male attractivity rank was not significantly correlated with the number of matings (\(r_S=0.304\), \(N=12\) males, \(P=0.337\)) or number of offspring sired (\(r_S=0.064\), \(N=12\) males, \(P=0.844\)).

Male attractivity and male dominance rank were negatively but nonsignificantly correlated (\(r_S=-0.444\), \(N=12\) males, \(P=0.148\)). That is, females expressed mate choice behaviour to males of various dominance ranks (also see Table 3). We conducted partial correlation analyses to control for the effects of the opposing variables (Table 4). When controlling for the effects of male attractivity rank, the correlations between dominance and mating/number of offspring were stronger. Similarly, when controlling for the effects of male dominance rank, the correlations between attractivity rank and mating/number of offspring also were stronger. In fact, when the effects of male–male competition were removed, the correlation

![Figure 3. The relationship between male dominance rank and the percentage of the total observed matings that were sneak copulations.](image)

<table>
<thead>
<tr>
<th>Females†</th>
<th>% Males mated</th>
<th>Mean number of matings</th>
<th>Mean dominance rank</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High*</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>V</td>
<td>75†</td>
<td>67</td>
<td>1</td>
</tr>
<tr>
<td>F§</td>
<td>67</td>
<td>0</td>
<td>1.67</td>
</tr>
<tr>
<td>D**</td>
<td>50</td>
<td>50</td>
<td>0.5</td>
</tr>
<tr>
<td>S**</td>
<td>80</td>
<td>33</td>
<td>2.2</td>
</tr>
<tr>
<td>T</td>
<td>75</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>G**</td>
<td>50</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>L</td>
<td>100</td>
<td>100</td>
<td>1.5</td>
</tr>
<tr>
<td>Z</td>
<td>67</td>
<td>75</td>
<td>1</td>
</tr>
<tr>
<td>C</td>
<td>50</td>
<td>86</td>
<td>0.5</td>
</tr>
<tr>
<td>W</td>
<td>75</td>
<td>57</td>
<td>2.25</td>
</tr>
<tr>
<td>N</td>
<td>100</td>
<td>33</td>
<td>1.33</td>
</tr>
<tr>
<td>Mean</td>
<td>71.73</td>
<td>45.55</td>
<td>1.314</td>
</tr>
</tbody>
</table>

*For each female, males with a Hinde’s index above the female’s mean across all males were high in attractivity, while those males with a Hinde’s index below the female’s mean were low in attractivity.
†One female who had a Hinde’s index for only one male was excluded.
‡Bold indicates that the sire of the female’s offspring was either high or low in attractivity.
§The sire of this female’s offspring had no Hinde’s index.
**The sires of these females’ offspring were nontroop males.
Male–Male Competition

Nontroop males sired one-third of the offspring born, although this could be an overestimate (see Methods). In only one of 21 intergroup encounters, however, were there observations of a female (who did not give birth) mating with nontroop males. The Nina-A troop was the largest in the area, and other troops usually avoided it. This may have required Nina-A females to mate with nontroop males away from the troop, where observation was particularly unlikely. On the other hand, this result is consistent with previous observations on Yakushima Island, in which mating by nontroop males is extensive (Sprague 1991). Generally, this result adds to a body of evidence that indicates the social group per se is not necessarily predictive of paternity (e.g., Birkhead et al. 1995; Lubjuhn et al. 1999).

Within the troop, however, dominant males were able to monopolize female mating and paternity, thus supporting the priority of access model (Altmann 1962). Only high- and mid-ranking males sired offspring, and the two males that held the alpha position sired 50% (3/6) of within-troop paternity (Fig. 1). More importantly, within- and between-population tests show that the number of females mating simultaneously is associated with the strength of the correlation between male dominance rank and male mating and offspring produced. First, male dominance rank was not correlated with number of offspring sired in a previous captive study where many females mated simultaneously (Soltis et al. 1997b), but was positively correlated with the number of offspring sired in this wild study where fewer females mated simultaneously. Second, in this study, on days when there were more females displaying copulatory behaviour, the average dominance rank of mating males decreased. Taken together, these data provide strong evidence that male–male competition does influence mating and reproductive outcome, but that female mating or ovulatory synchrony can have a strong effect on dominant males’ ability to monopolize mating and paternity (Paul 1997).

In a previous review of primates (Cowlishaw & Dunbar 1991), however, the number of adult group females did not affect the relationship between male dominance rank and mating. This is probably due to the fact that the total number of adult females in a group is a poor measure of the number that actually display mating behaviour at any given time (Emlen & Oring 1977).

Alternative Mating Tactics and Female Mate Choice

Male dominance rank does not explain all the variation in mating and reproductive success, however. First, like other animals (e.g., Gross 1982), male Japanese macaques engage in alternative mating tactics to avoid direct competition with higher-ranking males. In this study, there was a near-linear negative relationship between male dominance rank and the proportion of sneak copulations. Monopolizing females or pursuing sneak ejaculations is probably part of a single conditional strategy, which changes based on relative dominance rank. In this case, such alternative tactics were partially successful. Two mid-ranking males that obtained 63 and 75% of their copulations from sneak copulations (Fig. 3) each sired one offspring, but no low-ranking males did so (Fig. 1).

Second, female mate choice can also dilute the effects of dominance rank. We used a measure of responsibility for proximity maintenance (the female Hinde’s index) as an assay of female mate choice, but found that it did not predict the number of male matings or the number of offspring sired. This is in sharp contrast to our previous work in Japanese macaques, in which the same measure of female mate choice was a strong predictor of mating and number of offspring sired (Soltis et al. 1997b). Again, we believe one reason for this contrast is that in the captive group more females mated simultaneously, allowing more mating opportunities for females and lower-ranking males.

The Interaction of Male and Female Strategies

In this study, male ‘attractivity rank’ was negatively (but not significantly) correlated with male dominance rank. Therefore, when controlling for the effects of the opposing variable, associations with mating and number of offspring became stronger. In particular, when controlling for the effects of male dominance rank, attractiveness and mating became significantly correlated. We interpret these results to mean that females preferred males of many dominance ranks but were monopolized by dominant males, who mostly prevented females from mating with mid- and low-ranking animals. In the absence of male–male competition, therefore, the influence of female mate choice would have been stronger. Likewise, in the absence of female mate choice, the influence of male–male competition would have been stronger (Table 4; see Soltis et al. 1997b for a similar result).

Although the partial correlation between attractiveness rank and mating was significant, the partial correlation between attractiveness and number of offspring was not (Table 4). That is, even when controlling for the effects of

**Table 4. Simple and partial Spearman’s correlation coefficients**

<table>
<thead>
<tr>
<th>Variables</th>
<th>Simple correlation</th>
<th>Partial correlation†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominance and mating</td>
<td>0.700**</td>
<td>0.978**</td>
</tr>
<tr>
<td>Dominance and offspring</td>
<td>0.587*</td>
<td>0.625*</td>
</tr>
<tr>
<td>Attractivity and mating</td>
<td>0.304</td>
<td>0.961**</td>
</tr>
<tr>
<td>Attractivity and offspring</td>
<td>−0.064</td>
<td>0.271</td>
</tr>
</tbody>
</table>

†Attractivity rank was partialled out for dominance rank and mating/offspring, and dominance rank was partialled out for attractiveness rank and mating/offspring.

*P<0.05; **P<0.01.
dominance rank, female mate choice did not predict which males sired offspring. We suspect that female mate choice at ovulation is different from mate choice over the course of the entire mating season, and that we may have missed ovulatory mate choice behaviour due to limited observations. We could not determine the time of ovulation for these study subjects, but in our previous captive work, ovulatory periods were determined based on hormonal profiles. In that study, females directed mate choice behaviour towards multiple males throughout the season, but chose specific males (those who displayed most frequently) during ovulatory periods (Soltis et al. 1997a, b). Thus, females may choose at ovulation, but mate with multiple males throughout the rest of the mating season. We believe that females may benefit from mating with multiple males by decreasing the probability of infant harassment or infanticide (Hrdy 1979). In this study, troop males physically attacked infants eight times more often (including one infanticide) when they had not mated with the mother previously (Soltis et al. 2000).

Males may have used coercion and mate guarding to prevent females from mating with multiple males, however (Smuts & Smuts 1993). In this data set, male aggression was not significantly correlated with frequency of mating (Soltis 1999). On the other hand, 43% of dyads were often characterized in part by high-ranking males successfully monopolizing females. Specifically, male–female aggression, female approach to the male, male grooming the female and prolonged mount series co-occurred within these dyads (Soltis 1999). Male aggression preceded female approaches to the male, indicating that these males may have coerced the females to remain with them. Male grooming of the female and prolonged mount series also may be mate-guarding tactics (Soltis 1999; Manson 1996). Thus, high-ranking male strategies may have prevailed over those of females in part because of successful mate guarding and coercion. Females were often seen attempting to escape from dominant males with whom they were mating, but only 16 of 139 ejaculations (12%) were with low-ranking males (Fig. 1). Again, this contrasts with an earlier study, in which female strategies prevailed over those of males, and male coercion was considered minimal (Soltis et al. 1997a, b).

Future Directions and Conclusions

Several problems with this study point the way towards a better understanding of sexual selection in Japanese macaques and other species. First, we cannot be certain that the female Hinde’s index, or any other behaviour recorded in social groups, is a good measure of underlying female preferences. Only with experimental manipulation can we determine such preferences. Mate choice can be viewed as preferences expressed in a field of constraints, such as male mate guarding, which may inhibit preferences. Future research on mate preferences in primates will benefit from the experimental approach (e.g. Bischoff et al. 1985; Keddy 1986).

Second, paternity inclusion was not performed because the allele frequencies on Yakushima are not known. Thus, ‘likely fathers’ may not be actual fathers. The real fathers could be nontroop males with similar genotypes. We consider this unlikely because genotypes of likely fathers were consistent with those of their presumed infants at seven to eight loci. Nevertheless, when paternity inclusion is possible, more confidence can be put into the results. More paternity studies in the wild would be especially welcome in any case, to avoid the temptation to generalize from this single case from one mating season.

Third, there are other mechanisms of sexual selection that we have not considered, such as female–female competition and sperm competition. Female–female aggression was very rare, although it was sometimes observed in mating contexts. Presently, we are examining aspects of sperm competition and the function of masturbation in these Yakushima macaques, in part to determine whether middle- and low-ranking males increase sperm quality through masturbation to make up for the low quantity of matings.

We make the following conclusions concerning Japanese macaques. (1) Males follow a conditional mating strategy that is dependent on relative rank. At one end of the continuum, high-ranking males primarily guard females and exclude other males, thus avoiding sperm competition, and at the other end, low-ranking males opportunistically engage in sneak copulations, thus increasing sperm competition. (2) Throughout the entire mating season, females attempt to mate with many males of various dominance ranks. Previous work shows that this benefits females by reducing the probability of infant harassment and infanticide (Soltis et al. 2000). During ovulation, on the other hand, females may choose particular males, perhaps those who display most frequently (Soltis et al. 1999). (3) The strategies of females (mating with multiple males) and high-ranking males (monopolizing females) are often in conflict with one another. In this study, male strategies prevailed, while in an earlier study, female strategies prevailed (Soltis et al. 1997a, b). The winning sex is determined, in part, by the number of females mating and/or ovulating simultaneously.

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References


