BEHAVIOURAL DOMINANCE AND REPRODUCTIVE SUCCESS IN FEMALE JAPANESE MONKEYS (MACACA FUSCATA)

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Abstract. Eight years of reproductive data (including 248 births) from a translocated troop of Japanese monkeys (Macaca fuscata) living in a 42-ha enclosure provided three measures of female reproductive success: fecundity, survival of infants to 1 year of age, and age at first parturition. No significant relationship was found between social dominance and these measures. Social dominance was considered with respect to both matrilineal and individual female rank. Additional data on female dominance ranks over four generations of adult females revealed no significant concordance over time. The finding that ranks may not be stable over the lifetime of a female is a significant one because the variation in reproductive success among the females of a group is likely to be further diminished by any instability. For 34 females that were adults for the 8-year period considered, there was no significant correlation between the average rank of a female and either fecundity or survivorship of infants to 1 year of age. These data considered along with the results of other studies of female dominance and reproduction suggest that any effect of female social dominance on reproductive success is probably dependent upon resource availability, with significant benefits accruing to high-ranking individuals only during subsistence periods. It is suggested that dominance competition among female macaques may be a behavioural strategy with a variable payoff.

Introduction

Behavioural dominance is a widespread, though irregularly distributed, characteristic of both vertebrate and invertebrate species. Its ecological significance lies partly in the ability of some animals to obtain first access to limited resources such as food (Gauthreaux 1978). In many vertebrate species, high agonistic dominance rank is associated with breeding success, particularly among males (e.g. bighorn sheep, Ovis canadensis: Geist 1971; laboratory mice: DeFries & McClearn 1970; numerous galliform species: Wiley 1973; Ballard & Robel 1974; Rippin & Boag 1974; elephant seals, Mirounga angustirostris: LeBoeuf 1974), but also among the females of some species (e.g. wolves, Canis lupus: Rabb et al. 1967; dwarf mongoose, Helogale parvula: Rood 1980; elephant seals, M. angustirostris: Reiter et al. 1981).

The proximate function and evolutionary consequences of social dominance in non-human primate species have been the source of much debate (Bernstein 1970, 1976, 1981; Deag 1977; Rowell 1974; Dunbar 1980; Wilson et al. 1978; toque, M. sinica: Dittus 1979; gelada, Theropithecus gelada: Dunbar & Dunbar 1977; Dunbar 1980). However, only limited data exist for two questions that relate directly to the evolutionary significance of primate female behavioural dominance.

First, it is not known at what levels of relative resource abundance subordinate females are, in fact, at a reproductive disadvantage. While dominance relationships among the individuals of a group may determine access to actual or potentially limiting resources of all kinds, the energetic demands of reproduction make competition over food especially important for females. Subordinate group members are often depicted as having to weigh the consequences of being out-competed for food against the benefits
of group-living (e.g. the exploitation of resources unavailable to solitary, predator defence, defense of quality food patches; Brown & Orians 1970; Brown 1975; Wrangham 1980). The notion that populations are usually food-limited may have created a misleading set of expectations, particularly with reference to rank and reproduction (Morse 1980). The omnivory of macaques and baboons may be an adaptation that, in effect, reduces the consequences of intraspecific competition for food resources (Hamilton et al. 1981; Hausfater et al. 1981): an eclectic diet and the potential to use alternative foods may minimize the losses that low-ranking individuals might otherwise suffer when displaced from preferred but limited items. Thus it is necessary to determine if differential reproduction based on rank exists when low-ranking females receive adequate nutrition, as Sade et al. (1976) and Silk et al. (1981) have suggested.

A second question concerns the stability of female dominance rank over time, as well as its mode of transmission to offspring. High-ranking females may have higher reproductive success than low-ranking females, but the occurrence of significant variation among the individuals of a group will depend on the length of time animals remain at particular dominance ranks. Further, if individuals are to reap ultimate benefits from high rank, those of their offspring that survive to sexual maturity must themselves enjoy the benefits of high rank at breeding age. The mechanism of female rank acquisition in macaques is well documented: ranks are socially inherited matrilineally with female offspring assuming ranks just below those of their mothers. Younger siblings rank over older ones such that the rank order among sisters is the inverse of their birth order (Kawai 1965a, b; Sade 1972). While it is clear that, relative to those of males, the dominance relationships of females are stable (Sade 1972; Hausfater et al. 1982), they may not be permanent over an individual's lifetime (Koyama 1967, 1970; Gouzoules 1980; Hausfater 1981; Bramblett et al. 1982).

Both male and female Japanese macaques (M. fuscata) exhibit social dominance in the direction of agonistic encounters. Nearly linear dominance hierarchies, stable over periods of as long as several years, have been documented (Koyama 1967, 1970), and these hierarchies can influence the priority of access to various resources, such as food (Kawai 1965a, b; Koyama 1967; Eaton 1976). Thus the traditional model of female dominance rank and reproductive success can be logically extended to female Japanese monkeys. If the ability to acquire essential resources, which are assumed to have fitness-related effects, is determined by competition among individuals living in the social group, then it can be suggested that increased fitness should accrue to individuals of high rank. Mori (1979) recently found that, in a food-stressed population of Japanese monkeys, more offspring of high-ranking females survived than did those of low-ranking females.

We report here the results of a long-term study of female Japanese monkey social dominance and three measures of reproductive success: fecundity, survival of infants to 1 year of age, and age at first parturition. Additionally, we present data that demonstrate a discordance of dominance ranks considered over four generations of adult females. On the basis of our results we suggest that a revised model of primate female dominance and reproduction is required, employing a life-history approach, and incorporating demographic and social factors.

**Methods**

The study group was a natural troop of Japanese monkeys translocated virtually intact (150 of 158 members) in February 1972, to a 42-ha enclosure near Laredo, Texas. Prior to this move, the monkeys had been studied intensively by researchers at Arashiyama, near Kyoto, Japan, resulting in known dominance relationships and maternal genealogies dating back to 1954. Population dynamics of the Arashiyama monkeys, including details of the group fission in 1966, are well documented (Koyama 1967, 1970; Koyama et al. 1975). Demographic data on the Arashiyama West group in Texas are presented elsewhere (Clark & Mano 1975; Fedigan et al., in press).

Human intervention at the Texas site was minimal, and although given supplemental food provisions, the monkeys foraged on indigenous vegetation for much of their food (Clark & Mano 1975). The nature of the supplemental food provided was not uniform over the 8 years in Texas. Two periods (each 4 years in length) occurred and, although the nutritional composition of the food in these periods differed to some extent, level of digestible energy as well as gross amounts of provisioned food, remained constant (S. Gouzoules et al., unpublished data). More importantly, none of the measures of female reproductive success reported here differed with respect to rank across the two feeding periods (fecundity: Kolmogorov–Smirnov two-
Data on the direction of dyadic agonistic encounters were continuously monitored by on-site investigators. During the period 1972 to 1979, 248 infants were born into the troop. The social group was also partially provisioned but, like the Arashiyama West group, also foraged for food. The Arashiyama West birth rate was substantially higher than the rate for the Koshima group (20.9%) during a food-stressed period, but lower than that for the same group during a very heavy feeding regime (62.5%) (Mori 1979). Moreover, it was well below the rate of almost 1 infant per reproductive year for rhesus macaques under a heavier provisioning regime on Cayo Santiago (R. Rawlins, personal communication). More extensive descriptions of the enclosure and habitat are found elsewhere (Gouzoules et al. 1975; Gouzoules et al. 1981).

During the period 1972 to 1979, 248 infants were born into the troop. The social group was continuously monitored by on-site investigators. Data on the direction of dyadic agonistic encounters were used to assess dominance relationships in the troop. An unambiguous submissive response (fleeing, fear grimacing, avoiding, clear supplantation) directed by one monkey to another served as the criterion for assessing the loser of such encounters. Ordering the data on these encounters, so that winners ranked over losers, produced the dominance hierarchy. Individuals were arranged in the rank order that produced the fewest reversals. With a group as large as the study troop it was not possible to witness every potential combination of dyadic encounters. Since transitivity of relationships held for all known dominance relations, transitivity of relationships was assumed in a very few cases. In order to present long-term assessments of hierarchical consistency, our dominance data were compared with those previously published for the Arashiyama monkeys (Koyama 1967, 1970). Japanese researchers employed high-incentive foods such as peanuts to induce dyadic interactions from which dominance assessments were made. Though this technique differs from our own in that only data from uninduced interactions were collected by us, the dominance hierarchies produced by these two techniques in 1972 proved to be the same.

**Results**

**Female Age**

Before an analysis of female dominance rank and reproduction could be performed, it was necessary to account for the possible effects of female age on fecundity and infant survival. Wolfe & Noyes (1981) reported that females of the Arashiyama West group aged 18 years and older had a lower birth rate than that of younger females assessed during one birth season (but see below: analyses based on long-term data on the same population revealed no statistically significant differences). Also, some studies have reported that young females do not reproduce as successfully as do older females (Drickamer 1974; Hird et al. 1975). Theoretical predictions (Barash 1976), as well as empirical evidence from laboratory studies (Seay 1966; Mitchell & Stevens 1969), suggest differences may exist between, for example, younger and older mothers in terms of the parental care given offspring. We first considered a null hypothesis that females of different reproductive ages did not vary in terms of fecundity. If the null hypothesis were correct, then the distribution of births among females of different ages could be predicted from the numerical distribution of females of different ages over the years. Thus, since 5-year-old females made up 12.3% of the over-all-years population, they would be expected to have produced 12.3% of the 248 total number of infants, or 30.5 infants. No significant difference between these two distributions (Fig. 1) was found (Kolmogorov–Smirnov one-sample test, two-tailed: \( D = 0.068, P > 0.05 \)). In our population, females of different reproductive ages did not vary significantly in fecundity.

An analysis of maternal age and infant survival to 1 year of age tested a null hypothesis that, over all years, infants of mothers of various
ages did not differ from the population mean rate of survival to 1 year. (The mean and median rate of survival to 1 year were only fractionally different.) Again, no significant difference between the two distributions (Fig. 2) was found (Kolmogorov–Smirnov one-sample test, two-tailed: $D = 0.123, P > 0.20$). We conclude that maternal age did not significantly influence infant survival to 1 year. Based on these two analyses, the postulated influences of maternal age could be ignored for the purposes of assessing dominance and reproduction in our study population.

Genealogical Rank and Reproduction

Following the example of Sade et al. (1976) we performed an analysis on the relationship between genealogical rank and infant production, survival to 1 year of age, and age at first par- turition (Table I). In Sade et al.'s analysis, however, it was unnecessary to consider genealogical rank shifts since only two years of data from Cayo Santiago were used. Although relatively infrequent, such changes in female dominance rank have been observed in Japanese monkeys (Koyama 1967, 1970), in wild baboon populations (Hausfater 1981), and in a captive vervet monkey (Cercopithecus aethiops) group (Bramblett et al. 1982). We have documented their occurrence in our study troop as well, where shifts in the female dominance hierarchy were precipitated by the illness of the highest ranking female (Gouzoules 1980). The six major matrilines of our group shifted ranks with respect to one another during the period considered here and contributed data to a particular rank based on their length of tenure at that rank. For example, the Rhesus genealogy, which was highest ranking from 1972 to 1974, contributed the 13 infants born into it during that period to the rank 1 total. However, this genealogy ranked second in the troop for the re-

<table>
<thead>
<tr>
<th>Genealogical rank</th>
<th>Infants produced (1972–1979)</th>
<th>Expected</th>
<th>Infants surviving to 1 year (1972–1978)</th>
<th>Expected</th>
<th>5-year-old female births</th>
<th>Expected</th>
<th>$\bar{X}$ age of first birth</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>46</td>
<td>45.01</td>
<td>33</td>
<td>33.6</td>
<td>9</td>
<td>4.51</td>
<td>5.7</td>
</tr>
<tr>
<td>2</td>
<td>58</td>
<td>51.86</td>
<td>40</td>
<td>41.3</td>
<td>5</td>
<td>3.86</td>
<td>6.0</td>
</tr>
<tr>
<td>3</td>
<td>36</td>
<td>38.65</td>
<td>27</td>
<td>25.0</td>
<td>1</td>
<td>3.54</td>
<td>6.4</td>
</tr>
<tr>
<td>4</td>
<td>16</td>
<td>18.10</td>
<td>13</td>
<td>12.9</td>
<td>1</td>
<td>0.97</td>
<td>5.5</td>
</tr>
<tr>
<td>5</td>
<td>30</td>
<td>31.80</td>
<td>21</td>
<td>20.7</td>
<td>1</td>
<td>2.25</td>
<td>5.6</td>
</tr>
<tr>
<td>6</td>
<td>41</td>
<td>41.58</td>
<td>27</td>
<td>27.5</td>
<td>2</td>
<td>3.86</td>
<td>6.4</td>
</tr>
</tbody>
</table>

$\chi^2 = 1.29$  \quad P > 0.90

$\chi^2 = 0.226$  \quad P > 0.99

$D = 0.296$  \quad P > 0.05

$r_s = 0.058$  \quad P > 0.05
mainder of the study period, during which it produced 45 infants. These infants were included in the rank 2 total. Three small genealogies (Blanche, Shiro and Deko)-consisting of one or two females each were deleted from the following analysis so as not to confuse genealogical and individual rank relationships.

Table I contains expected values for infant production calculated under the null hypothesis that genealogical ranks did not differ, and that the summed reproductively-active years for the members of each genealogical rank, alone, determined the number of infants produced. In the study population the earliest age of first parturition was 5 years; thus 5 years was considered the first reproductively-active year. The product of the average number of reproductively-years per infant born for the population during this period (1.96 reproductively-years/infant) and the summed reproductively-active years for a genealogical rank yielded the expected infant production for that rank. No significant differences were apparent (χ² = 1.29, P > 0.90) and we concluded that genealogical rank did not affect infant production. Nor did genealogical rank have a significant influence on infant survival to 1 year of age (χ² = 0.266, P > 0.99; expected values shown in Table I).

Also examined was the possibility that high-ranking genealogies had a higher proportion of first parturitions at the earliest age of 5 years. We first established that there was no statistically significant variation in the proportion of 5-year-olds to give birth among the cohorts from 1972 to 1979. Observed values for the number of 5-year-olds giving birth among genealogies of different ranks did not differ from expected values based on the mean population figure and the number of 5-year-old females in each genealogical rank class (Kolmogorov-Smirnov one-sample test, two-tailed: D = 0.296, P > 0.05, Table I). A further analysis of both rank and age at sexual maturation demonstrated no correlation between genealogical rank and the mean age at first birth for each genealogy (r = 0.058, P > 0.05, N = 6, Table I). Ages at first birth for 49 of 50 females born between 1967 and 1973, who reached 5 years of age between 1972 and 1978, ranged between 5 and 8. One low-ranking female who did not give birth until 11 years of age (4 SD above the mean) was not included in this and subsequent analyses.

Individual Female Rank and Reproduction
While Sade et al. (1976) assumed that all the adult females of one genealogy were either dominant or else subordinate to all adult females of another genealogy, our dominance data, and the long-term genealogical records available on our study group, indicated that such linear ranking was not always the case. Individual females or subsets of a genealogy sometimes had disparate ranks relative to their kin, meaning that a more accurate assessment of female dominance rank and reproduction was necessary at the level of individual females. We performed two analyses using individual females rather than genealogies as subjects.

First, the reproductive data were recast into three rank categories: high, medium, and low, dividing the dominance hierarchy into thirds, with females contributing data to a category for the duration of their tenure at that rank (Table II). No significant relationship between dominance class and either fecundity or infant survival to 1 year was found (fecundity: χ² = 2.43, P > 0.25; infant survival: χ² = 0.69, P > 0.50). Similarly, we found no significant trend for rank

### Table II. Individual Rank: Infant Production, Survivorship and Age at First Reproduction

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>94</td>
<td>82.7</td>
<td>64</td>
<td>59.7</td>
<td>11</td>
<td>6.23</td>
</tr>
<tr>
<td>Medium</td>
<td>79</td>
<td>82.7</td>
<td>59</td>
<td>59.7</td>
<td>6</td>
<td>8.86</td>
</tr>
<tr>
<td>Low</td>
<td>75</td>
<td>82.7</td>
<td>55</td>
<td>59.7</td>
<td>4</td>
<td>5.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>248</td>
<td>179</td>
<td>21</td>
<td>21.0</td>
</tr>
<tr>
<td>χ² = 2.43</td>
<td></td>
<td></td>
<td>χ² = 0.69</td>
<td></td>
<td>χ² = 5.19</td>
<td></td>
</tr>
<tr>
<td>P &gt; 0.25</td>
<td></td>
<td></td>
<td>P &gt; 0.50</td>
<td></td>
<td>P &gt; 0.05</td>
<td></td>
</tr>
</tbody>
</table>
to influence the proportion of females giving birth at 5 years of age ($\chi^2 = 4.42, P > 0.10$); this relationship approached significance. Furthermore, an analysis of all ages (5–8) at which females first gave birth revealed that dominance rank and age at first birth were independent ($G = 5.2, P > 0.20$, Sokal & Rohlf 1969, Table III).

We next calculated a Spearman rank correlation on female dominance rank and infant production (Fig. 3). For each birth a female was assigned a value equal to the proportion of adult females over whom she was dominant at the time she gave birth. Rank changes over the years were thus incorporated into this analysis (e.g. female B5865 dominated 21% of the adult females when she gave birth in 1974 but, following rank shifts, she dominated 96% of the females when she gave birth in 1975). Although a significant level of correlation was achieved ($r_s = 0.491$, $P < 0.05$, $N = 20$, one-tailed), the variance in fecundity accounted for by rank was not great ($r^2 = 0.241$). More importantly, the rank classes did not differ significantly from expected values based on the mean value ($\chi^2 = 15.78, P > 0.50$, $df = 19$). Further lessening the significance of the correlation between high rank and number of infants produced was a significant correlation between high dominance rank and infant mortality ($r_s = 0.588$, $P < 0.05$, $N = 10$), with rank accounting for about 35% of the variance in infant mortality among females (Fig. 4).

Since the mean rate of infant survival to 1 year in the study group, over all years, was 90%, the effect of the higher rate of infant mortality among high-ranking females was not strong enough to change the correlation between high rank and infant production (but see below—'Mean rank and reproduction'). An analysis of the correlation between rank and number of females to give birth at the earliest age of 5 years was non-significant ($r_s = 0.548$, $P > 0.05$, $N = 10$, Fig. 5a). Nor was there a correlation between rank and the number of five-year-old females ($r_s = 0.327$, $P > 0.05$, $N = 10$). Although there was a significant correlation between female rank and the average age at first birth ($r_s = 0.681$, $P < 0.05$, $N = 10$), there was no significant difference in the average age at first birth for the rank classes considered in that analysis (Kruskal-Wallis one-way analysis of variance: $H = 4.03$, $P > 0.90$, corrected for ties, Fig. 5b).

**Genealogical ranks.** Table IV provides an analysis of the concordance of genealogical ranks.

![Genealogical ranks](image1.png)

**Table III. The Independence of Rank and Age at First Birth**

<table>
<thead>
<tr>
<th>Individual female rank</th>
<th>Female age at first birth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>High</td>
<td>10 (6.6)</td>
</tr>
<tr>
<td>Medium</td>
<td>6 (7.0)</td>
</tr>
<tr>
<td>Low</td>
<td>3 (5.4)</td>
</tr>
</tbody>
</table>

$G = 5.2, P > 0.2, df = 4$.

Expected frequencies, in parentheses, calculated from marginal totals, assume independence of rank and age at first birth.

![Genealogical ranks](image2.png)

**Fig. 3.** Female dominance rank and number of infants born (1972–1979). Individual females were assigned values equivalent to the proportion of adult females over which they were dominant at the time each gave birth. Since the number of adult females in the group varied in each birth season (due to sexual maturation and death), dominance assessed in this manner yielded comparable data.

![Genealogical ranks](image3.png)

**Fig. 4.** Female dominance rank and number of infant deaths before 1 year of age (1972–1978). Dominance assessed as in Fig. 3.
over time. (Data prior to 1972 were provided by Koyama 1967, 1970.) The matrilineal genealogies of the study troop were represented in 1957 by the oldest living females, or 'matriarchs', of each genealogy. In other years rankings among the descendants (as a group) of these females are given: thus four generations are represented in the 22-year period, as great-great-grandchildren of the 1957 matriarchs were present in 1979. In 1966 a fission of the troop produced two sister-groups, one of which became the translocated Arashiyama West troop. Ranks in this table show genealogies of the Arashiyama West troop only and illustrate rank changes with respect to one another. Group fission as one cause of female rank changes is discussed in the text. Analysis of the ranks of the genealogies indicated no agreement over the years (Kendall’s coefficient of concordance, $W = 0.314$, $P > 0.05$).

**Mother–adult daughter ranks.** Table V presents correlations between mother–daughter pairs

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nose</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Rheus</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Betta</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Pelka</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Petitemon</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Matsu</td>
<td>6</td>
<td>1</td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>

*Rankings (in order of descending dominance) among the matrilineal genealogies of the study group are represented in 1957 by rankings among the oldest living females, 'matriarchs', of each genealogy. In other years rankings among the descendants (as a group) of these females are given: thus four generations are represented in the 22-year period, as great-great-grandchildren of the 1957 matriarchs were present in 1979. In 1966 a fission of the troop produced two sister-groups, one of which became the translocated Arashiyama West troop. Ranks in this table show genealogies of the Arashiyama West troop only and illustrate rank changes with respect to one another. Group fission as one cause of female rank changes is discussed in the text. Analysis of the ranks of the genealogies indicated no agreement over the years (Kendall’s coefficient of concordance, $W = 0.314$, $P > 0.05$).

**Table V. Dominance of Adult Females and their Offspring at Maturity**

<table>
<thead>
<tr>
<th>Genealogy</th>
<th>1957</th>
<th>First daughter</th>
<th>First grand-daughter</th>
<th>First great-grand-daughter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nose</td>
<td>0.93</td>
<td>0.67</td>
<td>0.53</td>
<td>0.35</td>
</tr>
<tr>
<td>Rheus</td>
<td>0.86</td>
<td>0.78</td>
<td>0.81</td>
<td>0.72</td>
</tr>
<tr>
<td>Betta</td>
<td>0.79</td>
<td>0.57</td>
<td>0.45</td>
<td>0.91</td>
</tr>
<tr>
<td>Pelka</td>
<td>0.57</td>
<td>0.88</td>
<td>0.06</td>
<td>0.76</td>
</tr>
<tr>
<td>Petitemon</td>
<td>0.50</td>
<td>0.60</td>
<td>0.63</td>
<td>—</td>
</tr>
<tr>
<td>Matsu</td>
<td>0.36</td>
<td>0.94</td>
<td>0.29</td>
<td>0.10</td>
</tr>
<tr>
<td>Rakushi</td>
<td>0.29</td>
<td>0.31</td>
<td>0.26</td>
<td>—</td>
</tr>
<tr>
<td>Blanche</td>
<td>0.00</td>
<td>0.20</td>
<td>0.78</td>
<td>—</td>
</tr>
</tbody>
</table>

Correlations: between 1957 female and first daughter: $r_s = -0.262$, $P > 0.05$; between first daughter and first grand-daughter: $r_s = -0.262$, $P > 0.05$; between first grand-daughter and first great-grand-daughter: $r_s = -0.10$, $P > 0.05$.

Dominance of offspring assessed at maturity (5–10 years of age). Dominance assessed as in Fig. 3.
Mean rank and reproduction. Although the 8-year duration of our study did not permit the comparison of mean ranks and reproduction over females' entire lifetimes, it was possible to compare reproduction among females whose ranks could be averaged over the 8-year period. For this analysis only the 34 females that were adults (5 years or older) in 1972 and that survived the entire 8-year period were considered. Each female's yearly ranks (in terms of proportion of adult females dominated) from 1972 to 1979 were averaged to yield a mean rank. Mean ranks ranged between 0 and 89% of adult females dominated. Correlation analyses between mean rank and fecundity (Fig. 6) and between mean rank and infant survivorship (Fig. 7) revealed no significant relationship between female mean rank and either fecundity ($r_s = 0.28$, $P > 0.05$) or infant survivorship ($r_s = 0.155$, $P > 0.05$).

Discussion
On the basis of our results, we suspect that under conditions of relative food abundance, low-ranking females may be able to successfully compete reproductively with high-ranking females. In our study population, provisioned food was not provided ad libitum, but in limited quantities once daily (S. Gouzoules et al., unpublished data), and the monkeys foraged heavily on native vegetation for much of their diet. The monkeys exhibited rank-related differences in access to both provisioned food and indigenous vegetation, and the majority of our dominance data were collected in these contexts. Thus, despite clear hierarchical behavior patterns, no significant reproductive differential among females occurred. As noted above, p. 1140, the average yearly reproductive rate in our study group was considerably below the highest reported for Japanese and rhesus macaques; therefore, a potential for rank-related differences in reproduction existed but was not realized.

While our results apparently conflicted with those from other studies of provisioned macaques (Drickamer 1974; Sade et al. 1976; Wilson et al. 1978), some of these differences can be resolved by a reconsideration of those studies. For example, most of the rank-related differences in female rhesus monkey reproduction reported by Drickamer (1974) were not accompanied by statistical tests of significance. Our re-analysis of the La Parguera data yielded the following results:

1. Infant production by females partitioned into high, medium and low rank classes did not differ significantly from expected values based on the mean birth rate for the entire population ($\chi^2 = 1.24$, $P > 0.50$, $df = 2$).

2. No significant difference existed among the three rank classes in terms of infant survival; mortality of infants less than six months of age

Fig. 6. Female mean rank and number of infants born (1972–1979). Yearly ranks, in terms of proportion of adult females dominated from 1972 to 1979 were averaged to yield mean ranks for 34 females.
for mothers of the three rank classes did not differ from the mean mortality rate for the entire population ($\chi^2 = 3.55, P > 0.10, df = 2$).

(3) The time of the year that an infant was born did not influence infant mortality within 1 year of age ($\chi^2 = 7.53, P > 0.10, df = 5$, with expected mortality per month based on the proportion of infants born in that month). This result has a bearing on the claim that daughters of high-ranking females produced their first infants at an earlier age than did those of low-ranking females. The differences between the high and low-ranking group in average age at first parturition was 6 months, and since the birth season over the years considered had a duration of approximately 6.6 months (p. 68), it is unclear whether there were more first parturitions per birth season (the relevant criterion for seasonally breeding species, Rowell 1977) for high-ranking females. Without differential mortality according to time of the year of birth, the 6-month difference may be demographically meaningless (Trussell 1978).

Wilson et al. (1978) reported that, in the Yerkes Field Center's rhesus colony, middle and low-ranking females had more sterile years than did high-ranking females; also, low-ranking females lost more infants due to mortality within 1 month of birth than did high and middle-ranking females. The statistical significance of these findings apparently depended upon an inconsistent combining of the rank classes (high, middle, and low), which reduced the degrees of freedom when there appeared to be no combining requirement, e.g. small expected frequencies. Re-analysis of these data indicated that high-, middle- and low-ranking females did not differ from expected values based on the mean number of sterile years ($\chi^2 = 4.28, P > 0.05, df = 2$), nor did they differ significantly from expected values based on mean infant mortality within one month ($\chi^2 = 4.42, P > 0.05, df = 2$).

More difficult to reconcile are differences between our results and those of Sade et al. (1976) who analysed the intrinsic rate of increase for genealogies of different ranks on Cayo Santiago. Comparisons are complicated by the fact that, in calculating the intrinsic rates of increase from a life table based on 2 years of data, group J (with by far the highest group intrinsic rate of increase) was excluded from the analysis because of problems with rank classification. Recently, Silk et al. (1981) reported that in a captive colony of bonnet macaques (M. radiata), where food was available ad libitum but where the mean infant mortality rate was 48%, low-ranking females experienced lower rates of infant survival to 6 months of age than did high-ranking females (although, curiously, females in the lower half of the hierarchy produced more infants that actually survived, $N = 37$, than did females in the top half, $N = 23$; Fig. 3, p. 1112). Therefore, considering all the available evidence on provisioned macaque groups, we conclude that our finding of a non-significant relationship between female dominance rank and several reproductive parameters is probably not unique.
Natural primate populations are known to be subject to environmental fluctuations that influence resource availability (see Hausfater 1975; Dittus 1979; Altmann 1980, page 15). Some of these fluctuations are likely to be predictable, e.g. seasonal changes in resource availability, while others are probably quite unpredictable, for example, the cyclical changes in the Amboseli ecosystem described by Western & Van Praet (1973). We suggest that a relationship between female dominance rank and reproductive success might be strongest during subsistence periods. At other times a trend in the direction of this relationship may persist, but variation among females of different ranks will probably not be significant. This suggestion is supported by the direction of our data, as well as that from La Parguera and the Yerkes colony. Dunbar (1980) also reported a positive correlation between rank and reproduction, but did not demonstrate long-term significant differences in reproductive success in his expanding gelada baboon population. A consistent trend in the direction of high rank across several such samples should not be interpreted as evidence for differential reproductive success without consideration of the statistical significance of the rank-related differences for each case. While a consistent trend in the direction of high rank may exist, a relationship showing significant heterogeneity (Sokal & Rohlf 1969, page 581) is suggested by the non-significant differences: the trend is not uniform in magnitude.

Dittus (1979) and Mori (1979) reported that juveniles of high-ranking female macaques had a higher rate of survival during periods of population decrease, but recent studies on yellow baboons (*Papio cynocephalus*) and vervet monkeys (Altmann 1980, page 39; Cheney et al. 1981), conducted in Amboseli, have failed to show a relationship between female rank and several reproductive parameters. Thus, even under relatively harsh conditions rank-related access to scarce resources may not, in and of itself, promote variation in female reproductive success (Cheney et al. 1981; but see Wrangham 1981). Cheney et al. (1981) have pointed out that, at all of the sites where rank-related female reproductive success has been reported, there were few or no predators present. If their finding that high-ranking vervet monkeys suffer heavier losses from predation holds over time and is supported at other sites, another factor in elucidating the relationship between dominance and reproductive success will have to be considered.

In summary, our results in conjunction with those from a re-evaluation of data from other provisioned macaques, suggest that in expanding non-human primate populations, the relationship between female dominance rank and reproductive success will not be a significant one. Moreover, our finding that ranks may not be stable over the course of a female’s lifetime further complicates evaluations of the evolutionary consequences of female behavioural dominance. In addition to reports of genealogical rank shifting in Japanese monkey and baboon groups (see Results above), other well documented demographic processes such as group fissions (Koyama 1970; Furuya 1960, 1969; Chepko-Sade & Oliver 1979; Chepko-Sade & Sade 1979) and even group fusions (Altmann 1980) result in a re-ordering of female dominance ranks. (See Chepko-Sade & Oliver 1979, for a discussion of the effects of group fissions on the fitness of formerly low-ranking females.) Events such as illness and death and social alliances may also alter rank relationships (Seyfarth 1977; Gouzoules 1980). If, as we suggest, the effect of female dominance on reproductive success varies depending, at least to some extent, upon resource availability, then the fact that a female’s dominance rank in the group is likely to fluctuate during her lifetime will further diminish the variation in reproductive success among females. In our correlational analysis of rank and fecundity, females contributed birth data to more than one rank category if their ranks varied over the 8-year period. The significant correlation between rank and reproduction thus produced was not sustained, however, when infant production was analysed with respect to the mean rank of each female over the 8-year period.

On the basis of these findings we speculate that low-ranking females are not inherently less fit individuals behaving in a fashion that minimizes an ineluctable disadvantage. As Bernstein & Gordon (1980) have determined experimentally with male rhesus monkeys, dominance rank in a group is dependent upon social context and is not determined by innate attributes of the individual.

Social relationships among females are not structured so that individuals, or their descendants, remain permanently at a particular dominance rank. Shifts in the hierarchy will depend upon the occurrence of fortuitous and unpre-
dictable asymmetries in the social alliances of the group. Existing alliances may be disrupted by death, disease, or other demographic processes, or can be altered via social interactions. Benefits will indeed accrue to dominant individuals, but only, we suspect, during subsistence level periods of high competition for resources, and any long-term benefits stemming from these periods are subject to the consequences of rank shifts. At other times dominance interactions among females may have little or no significance in terms of differential reproduction. We speculate that all individuals share a similar behavioral tendency to engage in competitive interactions over resources: the subordinate or dominant role is irrelevant to the strategy. In effect, participants gamble that they, or their close kin, will be in a favorable position regarding alliance asymmetries at a critical time. Adherence to this system could be explained by a model of developmentally or culturally stable strategies (Dawkins 1980).

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