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## Lifetime Reproductive Success in Female Japanese Macaques

Linda Marie Fedigan<sup>a</sup>, Laurence Fedigan<sup>b</sup>, Sarah Gouzoules<sup>c</sup>, Harold Gouzoules<sup>c,d</sup>,  
Naoki Koyama<sup>e</sup>

<sup>a</sup>Department of Anthropology, and <sup>b</sup>Faculté Saint-Jean, University of Alberta, Edmonton, Alta., Canada;

<sup>c</sup>Yerkes Regional Primate Research Center, Field Station, Lawrenceville, Ga., USA;

<sup>d</sup>Department of Psychology, Emory University, Atlanta, Ga., USA;

<sup>e</sup>Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan

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**Abstract.** Lifetime reproductive success, measured by the number of offspring surviving to age five, varied from 0 to 10 in a group of 33 provisioned female Japanese macaques. Of the three contributors to reproductive success, the number of reproductive years, fecundity per year and survivorship of offspring to reproductive age, the first accounted for two-thirds of the variation. Fecundity per year and survivorship were negatively correlated, indicating reproductive costs of reducing interbirth interval. No other demographic measure used, nor the behavioral measure 'dominance rank', significantly correlated with lifetime reproductive success or its components. Age-specific changes in fecundity and infant survival were not found for this sample, neither could cessation of reproduction, even in very old females, be demonstrated.

### Introduction

Despite speculation concerning the relationship between life span and other life history traits [e.g., Calwell, 1983; Comfort, 1961; Gadgil and Bossert, 1970; Hamilton, 1966; Medawar, 1955; Rose, 1983; Shiao-Yen and Botkin, 1980; Stearns, 1976, 1983; Tuomi et al., 1983], few empirical studies of individual life histories are available for longer-lived species, especially mammals. Data on total lifetime reproductive success are critical to the evaluation of several as-

sumptions in modern interpretations of sexual selection theory, e.g., the premise that female variance in reproductive success is negligible in comparison to that of males [Bateman, 1948; Daly and Wilson, 1978; Wilson, 1975] or the wide-spread assumption that short-term evaluations of competitive success adequately reflect lifetime patterns of reproductive success. However, because of the many years of study required to measure reproductive parameters over the life span of individuals in long-lived, slowly reproducing species, there are as yet few

published studies measuring lifetime reproductive success and its components in vertebrate species [but see Clutton-Brock et al., 1982; McGregor et al., 1981; Smith, in press]. For primates, several studies of differential individual reproductive success over a 5- to 10-year period have recently become available [e.g. Clarke and Glander, 1984; Drickamer, 1974; Fairbanks and McGuire, 1984; Gouzoules et al., 1982; Silk et al., 1981; Wilson et al., 1978]. But there have been as yet no reports on differential lifetime success for any primate species. In this paper we present data and analyses on the reproductive records of 33 female Japanese monkeys (*Macaca fuscata*) followed from birth to death.

Our goals are to describe the variability in lifetime reproductive success of female Japanese monkeys, measured by offspring survival to reproductive maturity, and to calculate the contribution of major life history variables to differential success. Our analyses seek to answer the following questions.

*How can variation in lifetime reproductive success be apportioned among its major demographic components of fecundity, reproductive life span and offspring survival rate?* All three of these measures are known to vary between individuals in the same social group [e.g., fecundity: Clarke and Glander, 1984; lifespan: Koyama et al., 1975; offspring survival: Dittus, 1977] but no study of primates has yet examined the relative and multiplicative contributions of these components to variation in lifetime reproductive success.

*What are the effects of starting to reproduce earlier or later than the mean age at first birth?* Some studies of primates [e.g., Drickamer, 1974] use age at first birth as a measure of reproductive success, the implication

being that those females who start to reproduce earlier gain a long-lasting competitive edge over those who start later. However, no one has looked at the relationship of differential age at first birth to the pacing of reproduction (interbirth intervals or its inverse, fecundity per year), to the costs of reproduction (offspring survival, maternal survival) and to the total picture of lifetime reproductive success in a long-lived species such as Japanese macaques.

*Are there different phases or rates of reproduction in a female's lifetime, that is, are there age effects on female reproduction?* Previous research on the effects of age on female reproductive success in primates has produced mixed results. Some studies have found that older females exhibit significantly lowered fecundity and/or greater infant mortality [e.g., Hrdy and Hrdy, 1976; Strum and Western, 1982; Wilson et al., 1978], whereas other studies, sometimes of the same species, do not find evidence for reproductive senescence in older females [e.g., Dolhinow et al., 1979; Gouzoules et al., 1982]. If older females do produce fewer infants and/or lose more of their offspring, this would reduce the advantages of long life span to lifetime reproductive success.

*Does the sex ratio of offspring bear any relationship to lifetime reproductive success in this cohort?* If either male or female offspring have a significantly higher rate of mortality before reaching maturity, then sex ratio of offspring should be reflected in lifetime reproductive success. Further, it has been suggested that females can facultatively adjust the sex ratio of their offspring to produce more of the sex that offers the greatest reproductive advantages to the mother [e.g., Altmann, 1980; Meikle et al., 1984; Silk et al., 1981; Simpson and Simpson, 1982].

*Does dominance rank affect reproductive success or the various components of lifetime reproductive success?* In primatology, the majority of the research on reproductive success has focused upon the association between dominance rank and reproduction. The results of some studies indicate that dominant females are more successful than subordinate females, either because rank determines differential access to critical resources [Dittus, 1977; Whitten, 1983] or because lower-ranking females suffer harassment from high-ranking females which reduces their fecundity or offspring survivorship [Dunbar, 1977, 1980; Silk et al., 1981]. In contrast, other studies have not found a clear relationship between rank and measures of reproductive success [e.g., Cheney et al., 1981; Dolhinow et al., 1979; Gouzoules et al., 1982; Takahata, 1980]. No study of primates has yet examined the relationship of dominance to the totality of a female's lifetime reproductive success, rather than to a restricted phase of her life.

Finally, we asked the question: What are the attributes of the most successful female in the Arashiyama cohort, and what is the best strategy for a female Japanese macaque to enhance her lifetime reproductive success?

## Methods

### *The Study Population*

The Arashiyama group of Japanese macaques was first contacted, provisioned, and studied by primatologists near Kyoto, Japan in 1954. Koyama [1967, 1970], Norikoshi and Koyama [1975] and Koyama et al. [1975] have published detailed demographic data on the Arashiyama population in Japan. In 1966 the group fissioned into two daughter groups (A and B, later renamed West and East), and in 1972 one of these (West) was transferred intact into a 42-ha enclou-

sure in Texas, while the sister group (East) remained in its native habitat.

In Texas, the monkeys were free to range over the large enclosure, and human intervention was kept to a minimum. These Arashiyama West monkeys were given supplemental provisions as they had been in Japan, however, they foraged on indigenous vegetation for much of their food. Several studies [Clark and Mano, 1975; Gouzoules et al., 1975, 1981; Fedigan et al., 1983] document in detail the responses of the population to the new habitat. Comparative studies have demonstrated extensive demographic similarities between Arashiyama West and East, after a short period of perturbation in which mortality rates rose and natality rates dropped in Arashiyama West following the transfer. Eight years of comparative data show striking similarities in population growth, mortality, emigration, natality and birth seasonality patterns between the two groups [Fedigan et al., 1983; Gouzoules et al., 1981; Koyama et al., 1980].

### *The Study Sample*

For the present study of lifetime reproductive success, we examined the life history records of all females born to the Arashiyama West (= A) lineages between 1950 and 1963. All births and deaths of this female cohort and their offspring are known to the day with the exception of three females who were small juveniles at the onset of Japanese record-keeping. Birth dates for these three females are estimates. Of the 41 females born into this cohort, all have died except eight. The latter were excluded from the analyses because they are still mating and reproducing, and because they have offspring that have not yet reached the age of five (our measure of reproductive success). However, these 8 were compared to the rest of the females for all appropriate measures to determine if and how they differ from the rest of the cohort. In addition, 6 of the 33 dead females in the cohort died before giving birth to any offspring. In analysing the variation in lifetime reproductive success, the proportion contributed by the 6 females who failed to reproduce is first calculated, and then the components of variation in success for the remaining 27 females are analyzed.

### *The Measures*

Each of our subjects was scored for 7 original variables: number and sex of offspring born, interbirth interval, offspring survivorship, age at first birth, age

at death, sex ratio of offspring and dominance rank. These variables are measured as follows. Number of offspring born is the total number of live births over a female's lifetime (Japanese macaques are seasonal breeders, females produce one offspring at a time, with few exceptions, and a maximum of one infant per year whether or not the previous infant survives). Interbirth interval is the actual time in years between live births for each female. Mean lifetime interbirth interval is calculated as the total number of reproductive years divided by the number of live births. Subjects giving birth to less than two viable infants are not included in analyses of interbirth intervals. The number and sex of offspring surviving is measured each year up to age five (the average age at reproductive maturity). Emigration is not a confounding variable in the analysis of male offspring survival to 5 years, since very few males emigrated before the age of five, and the location of those few that did was known; they were not counted as dead.

Age at first birth and age at death are measured in years. Longevity is the age at death. Sex ratio of offspring is the number of male per female offspring alive at each age (birth, 1 year, 5 years). Each female in the cohort is assigned a mean lifetime dominance rank. Between 1967 and 1980, six complete dominance hierarchies (based on direction of agonistic signals) for Arashiyama West females are available, with intervals of 2-3 years between them. A subject is ranked in each of the dominance hierarchies for which she is alive and reproductively mature at the time, and these scores are averaged to produce the final lifetime rank. Because the total number of individuals in the hierarchies changes over time, the raw dominance ranks are adjusted to a value equal to the proportion of females over whom the subject is dominant in each hierarchy [percent of cohort dominated, see Cheney et al., 1981, and Gouzoules et al., 1982, for detailed description of this method of standardizing ranks].

### *The Analyses*

*Components of Variability in Lifetime Reproductive Success.* The rationale and the Fortran program for computer analysis of variability in lifetime reproductive success were designed by Clutton-Brock and Brown [personal comment]. The program was modified for use on the University of Alberta Amdahl computer by Caroline Lanigan. All other analyses use programs from the 1983 SPSSx Users' Guide.

Lifetime reproductive success of any animal that has reproduced at least once and completed its reproductive life can be measured by the number of its offspring which have themselves lived to reproductive age, 5 years in the case of Japanese macaques. The latter variable can be thought of as the product of reproductive life span ( $l = \text{longevity} - \text{age at first birth}$ ), fecundity per year ( $f = \text{total number of births divided by reproductive life span}$ ) and the proportion of offspring born which survive to age five (s). That is, LRS (number surviving to age 5) =  $l \times f \times s$ .

The program is designed to first calculate that part of total variance in lifetime reproductive success due to animals who die before reproducing ( $l \times f \times s = 0$ ) and then to analyze the contribution of the three components,  $l$ ,  $f$  and  $s$ , to the remaining variance due to the reproducing part of the cohort.

The variable  $s$ , proportion surviving to reproductive age, can be broken down into several components representing different periods in survival from birth to maturity. In the present study, we broke survival to age five into two components,  $s_1 = \text{proportion surviving from birth to age one}$  and  $s_2 = \text{proportion surviving from age one to age five}$ . After running the program with the original variables,  $s$ , we reran it using  $s_1$  and  $s_2$  in order to determine the relative contribution to variable survivorship of the two periods, birth to age one and age one to age five.

*Age-Specific and Sex Ratio Effects.* Age-specific survivorship by sex from birth to age five was plotted for the 177 infants born to the 27 females who had completed their reproductive lives. For the same group of females, age-specific interbirth interval and infant survival was plotted using four maternal age classes: 4-8, 9-13, 14-18 and 19+ years. As well, age at first birth and sex ratio at birth 1 and 5 years were examined for correlations with reproductive success, its three components ( $l$ ,  $f$ ,  $s$ ) and with dominance.

*Dominance and Reproductive Success.* The sociological variable, dominance, was tested for correlations with lifetime reproductive success, its three components ( $l$ ,  $f$ ,  $s$ ) as well as age at first birth and infant sex ratio. In addition, the sample ( $n = 27$ ) was divided into two groups, above and below the median dominance rank, and used in a one-way analysis of variance (Kruskal-Wallis) in which the components of lifetime reproductive success, age at first birth and infant sex ratio were the dependent variables.

*Costs of Reproduction.* Two types of costs were examined, maternal survival and infant survival. Costs to maternal survival were calculated by dividing the sample of females who produced at least one infant before dying ( $n = 27$ ) above and below the median value for  $f$  and testing for a difference in mean age at death. Costs to infant survival were analyzed by dividing the sample in the same manner and comparing the two groups for differences in mean proportion of infants surviving to age five.

## Results

### *The Cohort*

Life history data for the 27 females comprising the main sample in the following analyses are presented in table I. The cohort was made up of 41 females, divided into 3 categories: those that died without reproduc-

Table I. Summary of life history data on 27 female Japanese macaques

Female No.	Offspring born, $n$	Offspring surviving to		Age at first birth years	Age at death years	Mean birth interval years	Sex ratio ( $n > 4$ )		Mean dominance %
		1 year	5 years				at birth	at 5 years	
1	8	6	6	7	22	2.00	1.00	1.00	66
2	13	11	9	7	22	1.23	1.60	1.25	20
3	13	11	10	6	21	1.23	1.16	1.00	82
4	8	8	8	4	18	1.88	1.67	1.67	5
5	14	8	8	5	25	1.50	3.67	2.00	42
6	8	5	4	4	16	1.63	0.60	0.33	56
7	9	8	7	5	15	1.22	0.80	0.75	66
8	9	8	7	4	17	1.56	1.25	1.33	7
9	4	4	4	5	22	4.50	0.33	0.33	73
10	6	5	3	5	16	2.00	0.50	0.50	32
11	5	4	4	5	14	2.00	1.50	1.00	75
12	4	3	2	6	12	1.75	1.00	-	68
13	7	6	6	6	19	2.00	2.50	2.00	28
14	4	3	3	5	10	1.50	1.00	0.50	87
15	7	4	4	5	17	1.86	0.40	0.33	18
16	3	2	2	5	9	1.67	-	-	89
17	10	7	6	4	14	1.10	0.25	0.20	52
18	11	9	9	6	27	2.00	0.38	0.50	30
19	3	3	3	5	9	1.67	-	-	92
20	2	1	1	5	7	2.33	-	-	12
21	4	2	0	4	9	1.50	3.00	-	50
22	1	1	1	5	9	5.00	-	-	44
23	1	1	1	5	6	2.00	-	-	32
24	1	1	1	6	9	4.00	-	-	65
25	9	9	7	6	21	1.78	0.80	0.75	54
26	9	8	6	4	13	1.11	1.25	2.00	42
27	4	2	1	5	9	1.25	3.00	-	39
Mean	6.56	5.19	4.56	5.15	15.11	1.98	1.32	0.97	49
SD	3.80	3.16	2.98	0.86	5.88	0.98	0.97	0.62	26
Range	1-14	1-11	0-10	4-7	6-27	1.10-4.50	0.25-3.67	0.20-2.00	5-92

No sex ratio is given (-) when the number of offspring is lower than 4.

**Table II.** Components of LRS in Japanese macaques

**(a) Mean and variance of l, f, s and their products for 27 reproductive females**

	Original		Standardized
	mean	variance	
l	10.963	31.499	0.262
f	0.602	0.029	0.081
s	0.712	0.059	0.117
lf	6.591	14.013	0.321
ls	7.980	25.375	0.417
fs	0.410	0.023	0.126
lfs	4.630	8.598	0.389

**(b) Percentage contributions to variation in LRS [ $V(lfs)/(lfs)^2$ ] among 27 reproductive females**

	l	f	s
l	67.33		
f	-5.50	20.76	
s	9.62	-18.43	30.09
lfs	-3.87		

**(c) Inclusion of 6 nonreproductive females**

Proportion of reproducing females 0.82  
 Overall variance (OV) 10.27  
 Percent OV due to nonreproducing females 32.00  
 Percent OV due to reproducing females 68.00

**(d) Percentage contributions to variation in LRS [ $V(lfs)/(lfs)^2$ ] among all animals born and died**

	l	f	s
l	45.78		
f	-3.74	14.12	
s	6.54	-12.53	20.46
lfs	-2.63		

ing ( $n = 6$ ), those that produced at least one offspring before dying ( $n = 27$ ), and those still alive ( $n = 8$ ). All three parts of the cohort were compared for dominance rank (Kruskal-Wallis one-way analysis of variance) and showed no significant differences.

Those females that reproduced (the 27 who are dead and the 8 still alive) were compared for differences in age at first birth, sex ratio at birth and (using present age for the females still alive) for differences in l and f. No significant differences were found for age at first birth or for sex ratio at birth. The 8 living females had a significantly higher mean number of reproductive years ( $t = -4.27$ ,  $p < 0.001$ ) and a nonsignificant trend towards lower fecundity per year (i.e., longer interbirth intervals). Since these 8 females represent a longer-lived portion of the cohort, the importance of the number of reproductive years is likely to be underestimated in the following analyses.

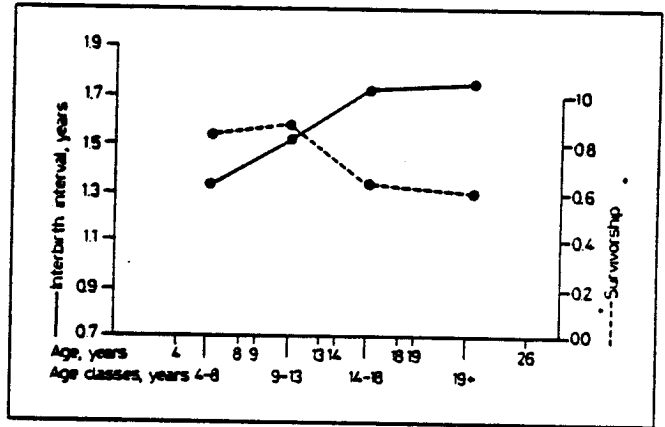
*Components of Lifetime Reproductive Success*

Results from the analysis of components of lifetime reproductive success are shown in table II. Of the sample of 33 females followed from birth to death, 27 (82%) produced offspring. The overall variance was 10.27, of which 32% is due to those who produced no offspring, while 68% is due to variation among the 27 who reproduced. In turn, the 68% of the overall variance in lifetime reproductive success due to the 27 can be broken down into 45.78% attributable to variation in the number of reproductive years, 14.12% due to variation in f, and 20.46% to variation in s.

In addition, -12.53% of the overall variance can be attributed to simultaneous variation in f and s, 6.54% to simultaneous vari-

**Fig. 1.** Maternal age-specific inter-birth intervals and infant survivorship for 27 Japanese Macaque females.

$$\text{Survivorship} = \frac{\text{Number of infants surviving to one year per age class}}{\text{number of infants born to that age class}}$$



ation in  $l$  and  $s$ , and  $-3.74\%$  to simultaneous variation in  $l$  and  $f$ . Negative signs indicate reduction of the contribution of the separate variables and indicate variables that are negatively correlated in the sample. The contribution of the threefold simultaneous variation is  $2.63\%$ .

Only the simultaneous variation in  $f$  and  $s$  ( $-12.53\%$ ) would appear to be an important contribution to the overall variance in lifetime reproductive success; the negative correlation between  $f$  and  $s$  suggesting a trade-off between interbirth interval and survival of successive offspring.

When survival was broken down into  $s_1$  and  $s_2$ ,  $s_1$  contributed  $7.6\%$  overall variance in reproductive success of the 27 females and  $s_2$   $10.8\%$ . Thus mortality between 1 and 5 years contributed approximately  $35\%$  more to the total variance in survival of offspring than did survival through the first year of life.

#### *Maternal Age-Specific Interbirth Interval and Infant Survivorship*

Figure 1 shows age-specific interbirth intervals and infant survivorship to one year of age for mothers in four age classes, 4-8,

9-13, 14-18 and 19 years. Interbirth interval increased during the first three age classes, then leveled off in older adult females. Infant survivorship decreased between the second and third age classes, then the line flattened out. More importantly females of the different age classes did not differ significantly from the population mean for either interbirth intervals (Kolmogorov-Smirnov one-sample test, two tailed,  $D = 0.52$ ,  $p > 0.20$ ) or for offspring survivorship ( $D = 0.54$ ,  $p > 0.20$ ). As a final check on age-specific effects, we found that mothers classified by individual years of age did not vary significantly in fecundity ( $D = 0.054$ ,  $p > 0.20$ ).

#### *Infant Age and Sex Specific Survivorship*

Figure 2 shows infant male and female survivorship from birth to age five. Mortality in both sexes was highest in the first year of life, with both curves leveling off after age one. More male infants died, especially in the first year of life (nonsignificant difference,  $28\%$  as compared to  $18\%$  for females). There was a trend for females giving birth to more female than male infants to have

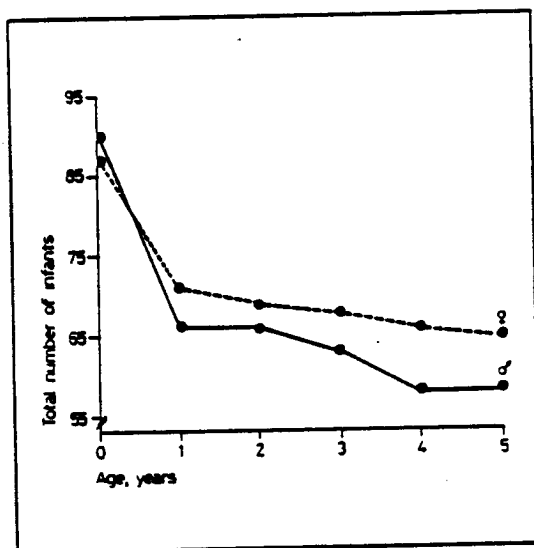


Fig. 2. Male and female offspring survivorship from birth to age five for 177 infants born to 27 Japanese macaque females.

greater lifetime reproductive success, but the trend did not reach significance in this cohort ( $r = 0.40$ ,  $p = 0.08$ ).

### Correlation Matrix

The negative relationship between fecundity per year ( $f$ ) and proportion of infants surviving to age five ( $s$ ), first seen in the analysis of components of variability in LRS, is also shown in table III ( $r = -0.478$ ,  $p = 0.012$ ). Neither  $f$  nor  $s$  were significantly correlated with  $l$ .

Age at first birth was not significantly correlated with any of the other variables. Sex ratio at birth showed no significant correlation with any of the other variables except sex ratio at age five ( $r = 0.898$ ,  $p < 0.000$ ). Dominance rank showed no significant correlation with any other variables in the matrix.

Table III. Spearman rank correlation matrix between three components of lifetime reproductive success,  $l$ ,  $f$  and  $s$ , age at first birth, sex ratio at birth and at 5 years and dominance

	$l$	$f$	$s$	Age at first birth	Offspring at 5 years $n$	Sex ratio at birth	Sex ratio at 5 years	Dominance
$l$ ( $n = 27$ )	1.000							
$f$ ( $n = 27$ )	-0.110	1.000						
$s$ ( $n = 27$ )	0.134	-0.478*	1.000					
Age at first birth ( $n = 27$ )	0.239	-0.308	0.216	1.000				
Number of offspring surviving to 5 years ( $n = 27$ )	0.846**	0.314	0.277	0.249	1.000			
Sex ratio at birth ( $n = 21$ ; ≥ 4 offspring)	-0.136	0.202	-0.142	-0.028	0.009	1.000		
Sex ratio at 5 years ( $n = 18$ ; ≥ 4 offspring)	0.115	0.191	0.278	0.127	0.423	0.898**	1.000	
Dominance ( $n = 27$ )	-0.128	0.004	0.111	0.165	-0.160	-0.227		1.000

\*  $p < 0.05$ ; \*\*  $p < 0.01$ .



### *Dominance*

After being tested as a correlate of the other measures used in the study (table III), dominance was tested as the independent variable in a Kruskal-Wallis one-way analysis of variance. The sample of 27 females was divided into two groups, above and below the median dominance score, and the two groups were tested for differences in  $l$ ,  $f$ ,  $s$ , age at first birth and sex ratio at birth. No significant differences were found between the groups for any of the variables.

### *Costs of Reproduction*

To clarify the costs of reproduction, the low correlation of  $s$  to  $l$  and the significant negative correlation of  $s$  to  $f$ , we asked: (a) whether females with longer interbirth intervals (i.e., low  $f$ ) lived significantly longer than females with shorter interbirth intervals, and (b) whether females with longer interbirth intervals had significantly higher  $s$  values than females with shorter interbirth intervals.

To answer the first question, we divided the sample above and below the median value for  $f$  and tested (Mann-Whitney U test) for a significant difference in mean age at death. Females in the group with lower  $f$  had an older mean age at death than the higher-fecundity females (16.7 years at death as compared to 14 years at death), but the difference was not significant ( $U = 61$ ,  $p = 0.254$ ).

To further test the trade-off between interbirth interval and  $s$  (see negative correlation for  $f$  and  $s$ , table III) we divided the sample into two groups for fecundity and compared them for a difference in mean  $s$ . Females in the group with lower values (longer interbirth intervals) had a significantly

higher  $s$  value than those in the group with higher fecundity (Wilcoxon Rank Sum W test  $W = 214.5$ ,  $p = 0.0065$ ).

### Discussion

The lifetime reproductive success of Japanese macaque females depends most strongly on their reproductive lifespan, which contributed nearly 70% of the variability in the females of our cohort. The survival of offspring to maturity is the second largest contributor to variation in success, and fecundity the third. Further, offspring survival and fecundity are in a negative relationship to each other (table II and III), which suggests that there are measurable costs to reproduction. Although the shape of a trade-off function between reproduction and mortality has not been measured for any primate species, studies of baboons have shown that reproduction can be associated with increased mortality [Berger, 1972] and delayed subsequent reproduction [Altmann et al., 1978]. The present analysis shows clearly the cost to infant survival of reducing the interbirth interval too much; females with short interbirth intervals lost significantly more of their offspring before age five than those with longer intervals. The potential cost to maternal survival is not clearly demonstrated; however, there is an indication here that females who space their births over longer intervals have slightly longer reproductive lives. High fecundity per year can thus be said to have clear costs for the survival of the infant and may, in some situations, have costs to the mother as well.

Given the large range in age at death (6–27 years) for females that reached maturity,

and the relatively small range in age at first birth (4–7 years, 96% of the females began between 4 and 6 years), it is not surprising that age at first birth failed to correlate significantly with lifetime reproductive success, or the components thereof, or with dominance (table III). This indicates that the long-term advantages to a female macaque of starting to reproduce earlier than the average (5.1 years) are minor, [see also the findings of Wilson et al., 1984, for rhesus macaques] and that the benefits which accrue from a longer reproductive life span are due to extension of reproduction into old age.

The benefits of living longer and continuing to reproduce into old age would be reduced if older females suffered significantly higher offspring mortality or produced very few infants. For example, Wilson et al. [1978] found that older rhesus macaques experienced more sterile years and more infant losses, whereas Small [1984] found for the same species that older females had longer interbirth intervals (a nonsignificant difference) and they experienced significantly greater infant survival. In our sample of Japanese macaque females, neither survivorship nor interbirth intervals were significantly different between the four age classes. Interbirth interval lengthened slightly and survivorship fell somewhat during adult life, then both remained fairly constant in old age. Furthermore, out of the 27 females who reproduced, 22 died within one year of their last parturition (range of ages at death = 6–25 years). The remaining five experienced a cessation of parturition lasting three or more years prior to death (ages at death = 9, 14, 17, 22 and 27 years). At least two of these five females were known to be seriously ill in the last years of their lives. Thus there is no evidence for an age-specific cessation of re-

production or for lowered fecundity and survivorship in old females for this cohort of Japanese macaques [cf. Graham et al., 1979; Wolfe and Noyes, 1981; but see also Gouzoules et al., 1984].

Most theories of the evolution of life span have hypothesized that high levels of reproductive output early in life are selected for at the expense of deleterious effects later in life, for example reproductive senescence or even 'early death' [Hamilton, 1966; Lamb, 1977; Medawar, 1955; Williams, 1957, 1966]. As we have seen, Japanese macaque females have a very limited capacity to accelerate rates of reproduction, and thus there is little possibility for a trade-off between 'bursts' of reproduction early in life and senescence or foreshortened lifespan. Steady production until death, with adequate interbirth intervals to enhance offspring survival, and the accumulation of many reproductive years would seem to be the key to reproductive success in this species.

Variation in lifetime reproductive success may also be affected by the sex ratio of offspring born, if one sex experiences greater mortality or reproductive variation than the other. In our sample, more male than female offspring died, and thus there was a nonsignificant trend for mothers giving birth to more female than male infants to have greater reproductive success. In contrast to some other studies of macaques, there was no trend for dominant females to give birth to more daughters [Silk et al., 1981; Simpson and Simpson, 1982] or to more sons [Meikle et al., 1984], although rank did achieve the highest correlation with sex ratio of any of the variables in this study (table III). In sum, differential survivorship of male and female offspring was only a very minor contributor to lifetime reproductive success.

The one social variable which could have an impact on all other variables tested in this study is dominance rank. Thus, other studies of primates have argued that dominance is related to fecundity [e.g., Wilson et al., 1978], offspring survivorship [e.g., Dittus, 1977], age at first birth [Drickamer, 1974] and sex ratio of offspring [e.g., Altmann, 1980]. In this cohort of Japanese macaques dominance rank showed no significant relationship with the other measures used in the study. This result supports our earlier finding on a larger sample of females followed over 8 years [Gouzoules et al., 1982] and corroborative findings by Takahata [1980] and Wolfe [1984], which suggest that dominance may not be related to reproductive success in the Arashiyama population of Japanese macaques. If competitive hierarchies affect reproductive success through differential access to resources, it is not surprising that dominance should bear little relationship to reproductive success in a cohort of females which is not food-limited. Neither are these females stressed by the confinement of cage life, in which dominant females may have unchecked ability to harass the subordinates who cannot escape.

The evaluation of effects of provisioning (or high resource levels) on dominance is problematic. Mori [1979] argued that dominance has more of an effect on female Japanese macaque reproduction when food conditions are poor (e.g., after provisioning of his study group had ceased), whereas Sugiyama and Oshawa [1982] found that dominance effects were more evident during times of provisioning than not. Neither of the studies tested for statistical significance of any of the differences found under provisioned versus nonprovisioned conditions, and neither of them presented comparable

measures of dominance. The comparison of dominance effects in the two studies is confounded by the fact that Mori [1979] did not state how he measured dominance, and Sugiyama and Ohsawa [1982] used the terms dominant and subordinate synonymously with central and peripheral, without demonstrating that there was a correspondance between 'spatial distance from the alpha male' [their measure of social status; Sugiyama and Ohsawa, 1982, p. 241] and the dominance hierarchy of the group, which is normally defined and measured by agonistic interactions.

These are the only two studies available comparing reproductive patterns in Japanese macaques under provisioned and non-provisioned conditions, and their findings suggest that provisioning leads to population growth through generally increased fecundity and infant survivorship, and possibly through faster maturation and earlier age at first birth. Neither study found that provisioning had an effect on survival rates of individual over two years of age and thus it should not alter measures of longevity.

If high resource levels tend to attenuate rank-related reproductive differences between females, then it is all the more remarkable that substantial variation in reproductive success still occurs in our cohort, which ranges from 0 to 14 live births per female ( $\bar{x}$  = 6.56; SD = 3.8) and 0 to 10 offspring surviving to maturity ( $\bar{x}$  = 4.56; SD = 2.98). Recently, some authors [Hrdy and Williams, 1983; Wasser, 1983] have questioned the assumption that variation in female reproductive success is negligible, and in particular that it is always substantially less than male variation in reproductive success.

Paternity in primates is notoriously difficult to ascertain, in part because females of

many species mate with multiple partners and do not restrict mating to the time of ovulation. Almost all studies of male reproductive success have relied on weak behavioural inferences from the quantity of male mating to the biological success of males in impregnating females [see Fedigan, 1983, for review of studies of rank and reproduction in primates]. In many primate societies, males transfer between groups and thus experience a very different life history pattern from that of females who remain in the natal group and likely produce offspring steadily over their lifetimes. In the Arashiyama population, nonnatal males have on average a reproductive tenure in the group of 4 years [unpubl. data] and may spend the rest of their lives as solitaires or peripherals to other groups, or they may simply die young. The maximum number of infants which a male could father during this average tenure of 4 years is unknown, but such a 'burst' of reproduction, followed by little to no reproductive activity, may not carry him as far beyond the range of maximum female production as has been commonly assumed. For example, Meikle et al. [1984] estimated the variance in male rhesus macaque lifetime reproductive success to be threefold that of females, and following their methods, we estimate the variance of reproductive success for a matched cohort of Japanese males to be approximately 2.5 times the variance in females. Meikle et al. [1984] calculated for each birth season the average number of offspring born per mature male (natal and nonnatal) that was censused in the group for at least 3 months during the previous breeding season. Then for each male the average number of offspring/male was summed for all breeding seasons during which he was resident in the group. Using their method, we

estimated lifetime reproductive success for 43 Japanese macaque males born 1950-1963 and followed until death or solitarization. The mean number of offspring produced per male over his reproductive tenure was 7.78 (cf. mean number of offspring born per female: 6.56) and the male variance was 36.82 (females: 14.44).

However, the method of Meikle et al. does minimize male variance and it is obvious that the question cannot be conclusively settled until the advent of widely-applicable techniques for the determination of genetic paternity.

In the provisioned Arashiyama West group, females do vary considerably in lifetime reproductive success. The more successful ones can be said to come from all dominance ranks, to have relatively long interbirth intervals, high infant survival rates and long reproductive lives, with no signs of reproductive cessation. Clearly, length of reproductive lifespan is the key to high reproductive success in this cohort. Equally clearly, there is nothing in the present analyses which 'predicts' longevity. Why some of our sample lived long lives, others died young and still others in middle age, presently can only be 'explained' on an anecdotal level. With the detailed and close knowledge we have of these individuals, we often find ourselves explaining away the life history of any particular female: 'she was sickly from birth..... she had just delivered an infant when the screwworm infestation climaxed..... she broke a leg and never seemed to recover.....' and so on. And although some degree of resistance to disease or immunity is expected to be inherited, for any individual being in the right or wrong place at the right or wrong time is important to its survival. We would not suggest that chance is

the explanation of variable reproductive success in this cohort, though chance should have its place in the equation. But we do feel that we will be unlikely to find a single heritable trait of greater longevity in simple association with an environmental one.

Is longevity heritable? We tested age at death for 12 mother-daughter pairs in our cohort and found no indication of it; however, some of the mothers have offspring who are still living, so we may be dealing with a truncated sample. A thorough test of such a heritable trait would require a much bigger sample and will be difficult to achieve. Nevertheless, it should be an important focus of attention for animals whose life expectancy is long and for whom longevity may be more important than any other environmentally or socially mediated effect.

### Summary

In this study of the life histories of 33 Japanese macaque females, we attempted to determine the contributions to lifetime reproductive success of a number of demographic and environmental variables. Lifetime reproductive success, measured as the number of offspring surviving to age five, varied from 0 to 10 for this cohort. Analysis of the contributions to this variation of the three components of lifetime reproductive success, the number of reproductive years, fecundity per year and the proportion of offspring surviving to age five, showed that the number of reproductive years was by far the largest component, accounting for some two thirds of the variation among the 27 females who reached reproductive age. The other two components, fecundity per year and survivorship were negatively correlated, imply-

ing a trade-off between rate of reproduction and offspring survival. The reproductive cost of reducing interbirth interval was clearly demonstrated for this sample.

None of the other measures used in the study, age at first birth, sex ratio or lifetime dominance rank were correlated significantly with lifetime reproductive success or its components. Neither were significant age-specific changes in fecundity or infant survival found for this group of females and cessation of reproduction could not be demonstrated, even in very old females. We tested for heritability of lifespan in our sample by correlating age at death for 12 mother-daughter pairs. As was to be expected with such a small sample, there was not a significant correlation.

Although in this group, environmental variables had little or no effect on lifetime reproductive success, clearly there are situations, especially limiting ones, where they would do so. Equally clearly, the determinants of longevity in potentially long-lived animals are not apparent and require further study.

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L.M. Fedigan, PhD  
 Department of Anthropology,  
 University of Alberta,  
 Edmonton, Alta. T6G 2E1 (Canada)