PRIMATES, 33(1): 49 – 68, January 1992

Demography and Reproductive Parameters of a Free-ranging Group of Japanese Macaques (*Macaca fuscata*) at Katsuyama

N. ITOIGAWA, T. TANAKA, N. UKAI, H. FUJII, T. KUROKAWA, T. KOYAMA,
A. ANDO, Y. WATANABE, and S. IMAKAWA
Osaka University

ABSTRACT. Demographic and reproductive data were analyzed for a period of 28 years in the females of a free-ranging group of Japanese macaques at Katsuyama, Okayama Prefecture, Japan. The overall mean, age-specific fecundity rates were 5.43% for 4-year-olds and 41.86% for 5-year-olds, increasing to a peak of 66.67% for 13-year-olds. Fecundity remained relatively high (52.31 – 54.24%) in 16 – 19-year-olds, but decreased sharply (45.45 – 17.86%) in 20 – 23-year-olds, and became very low in 24 – 26-year-olds. Females aged 27 years or more did not produce infants. The average age at first birth was 5.41 years. Births peaked in mid-May. The timing of the first births each year remained essentially unchanged during the study period, whereas the timing of the median and last births shifted towards the later part of the season. The mean interbirth interval for all females was 1.56 years. The value was 1.54 years for multiparous females and 1.29 years for females following infant loss. These intervals were significantly shorter than those for primiparous females, and females with surviving infants. The overall mean infant mortality within the first year of life was 10.2%. The value was 8.6% for 10 – 14-year-olds, and 7.5% for 15 – 19-year-olds. The timing of birth differed among the four female matrilineal dominance rank-classes. The female fecundity rates increased as a function of matrilineal dominance rank. It is suggested that all demographic and reproductive data should be analyzed in detail with respect to the group's history.

Key Words: Demography; Reproductive parameters; Free-ranging group; Japanese macaques.

INTRODUCTION

The demography of a primate group can be studied, firstly, from the life-history processes of the group members including births, maturation, reproduction, emigration and/or deaths, and secondly, from the group's size and composition in terms of the age/sex-classes of the group members. Reproductive parameters denote factors which determine the rates at which the group's size and composition change primarily through the life-history processes of the group members. Demography and reproductive parameters have been studied in many primate species such as black spider monkeys (*Ateles paniscus chamek*) by MCFARLAND SYMINGTON (1988), rhesus macaques (*Macaca mulatta*) by DRICKAMER (1974) and SMITH (1982), Barbary macaques (*Macaca sylvanus*) by PAUL and THOMMEN (1984), olive baboons (*Papio anubis*) by STRUM and WESTERN (1982) and SMUTS and NICOLSON (1989), yellow baboons (*Papio cynocephalus*) by ALTMANN et al. (1977), hamadryas baboons (*Papio hamadryas*) by SIGG et al. (1982), gelada baboons (*Theropithecus gelada*) by DUNBAR (1984), hanuman langurs (*Presbytis entellus*) by BORRIES et al. (1990), and chimpanzees (*Pan troglodytes*) by GOODALL (1983). One of the controversial issues arising from these studies is the determination of female reproductive success as a function of age, parity, and social variables such as dominance rank. In this connection, long-term studies of the demography and reproductive parameters of free-ranging groups of Japanese macaques (*Macaca fuscata*) are important. Studies on population dynamics have been conducted in several groups of provisioned Japanese macaques whose members could be individually identified (ITANI et al., 1963; KAWAI et al., 1967; KOYAMA et al., 1975; TAKAHATA, 1980; SUGIYAMA & OHSAWA, 1982).

In this paper, we present 28-year data on the demography and reproductive parameters of the females of a free-ranging group of Japanese macaques at Katsuyama, Okayama Prefecture, Japan. The following seven major areas of data analysis are considered, with the aim of achieving a comprehensive understanding of the population dynamics and reproductive parameters of the Japanese macaque group: (1) the demographic composition of the group; (2) age-specific fecundity rates; (3) sex of infants; (4) timing of births; (5) interbirth intervals; (6) infant mortality; and (7) female matrilineal dominance rank in relation to reproductive success.

STUDY GROUP AND ITS HISTORY

Members of the free-ranging Katsuyama group of Japanese macaques formed the subjects of our study. The group lives in a mountainous area in the northern part of Katsuyama (35°05′N, 133°42′E). Its home range size averages about 3 km^2, with seasonal and long-term variations. The vegetation in the group's home range includes deciduous and evergreen forests, planted coniferous forests, grass-bush fields, and cultivated land. Provisioning of the Katsuyama group was initiated by the first author in January 1958 and has been continued until the present time by researchers from Osaka University and staff of the town office of Katsuyama. Food is provided in an open area measuring about 610 m^2 in the Kamba valley, which is located approximately at the center of the group's home range. Provisioning is normally conducted twice a day, provided that the group comes to the feeding area. The provisions consist mainly of soybeans and wheat in amounts ranging from approximately 20 to 150 g per day per animal.

The group members were individually identified during the initial stage of provisioning in 1958. There were 36 adult and subadult females estimated to be 4 or more years old, and 16 adult males estimated to be 5 or more years old in the group in March 1958. One of the subadult females was identified as being the daughter of a particular adult female. Concerning the remaining 35 adult and subadult females, and three of the five juvenile females estimated to be 3 years old, mutual blood relationships could not be assigned. Thus, each of these 38 females was designated as the matriarch of an independent matrilineage as from March 1958. The remaining juveniles and infants of both sexes were then classified into each matrilineage. It has been possible for a large majority of the offspring born to each matriarch during and after 1958 to be individually identified by researchers from Osaka University. As regards the 16 adult males and 6 subadult males estimated to be 4 years old and juvenile males estimated to be 2 or 3 years old, membership of a specific matrilineage was not assigned. These 22 males, together with other males born after 1958 whose matrilineages were not identified, including non-natal males, were therefore each given a name that was different from the names of the original 38 matrilineages. A total of 18 matrilineages became extinct between April 1958 and May 1973, because of death, disappearance or capture of matrilineal members, and the group's fission in April 1973. There were 20 matrilineages remaining in the group as of 1986.

When the group was observed in February 1958, the alpha male was *M43*Romeo*

(M: male; 43: 1943, year of birth; *: estimate; *Romeo*: identification name). His tenure ended with his sudden death in June 1964. He was shot by a farmer as the group was foraging across cultivated land. The beta male, *M42*Gabo*, became the new alpha male. His tenure ended in February 1970 at the estimated very old age of 28 years, when he became subordinate to the beta male, *M62Rika'58'* (*Rika'58'*: the *Rika* matriarch's daughter born in 1958, was his mother). *M62Rika'58'* thus became the new alpha male.

The group split in April 1973, chiefly because of social conflicts between the adult females of high-ranking matrilineages, including the alpha male's mother and grandmother, and those of middle-ranking matrilineages, including the alpha male's mating partners. The fission produced two groups, i.e. a major group and a minor one. The members of the major group have been our subjects of study since the fission in 1973. The alpha male of the major group, *M62Rika'58'*, disappeared in August 1976. He may have died as a result of an unaccountable debility at the age of 14 years. The beta male, *M65Rika'60'*, a cousin of *M62Rika'58'*, became the new alpha male. His tenure has continued since August 1976.

RESULTS

DEMOGRAPHIC COMPOSITION OF THE GROUP

The group's size was 104 individuals when it was observed in January 1958. The size was perhaps less than 100 in 1957. A group population census has been conducted each year since 1958 at the beginning of September, approximately three months after the peak of the birth season. Table 1 summarizes the changes in demography of the group between 1958 and 1972, up to the period preceding the group's fission (hereafter termed the pre-fission period). Table 2 gives data for the period from 1973 to 1986 (hereafter termed the post-fission period). The group's size increased from 112 individuals in 1958 to 235 in 1972, but it decreased to 185 individuals in 1973 because of the group's fission. The group's size increased to more than 200 individuals during the post-fission period.

Figure 1 shows the changes in adult sex ratio defined as the number of adult females per adult male (adults being defined as 5 or more years old in both sexes). The sex ratio was generally low in the early period of provisioning, but increased to its highest ratio of 3.89 in 1967, remaining relatively high during the 1968 – 1972 period but fluctuating during the 1973 – 1986 period.

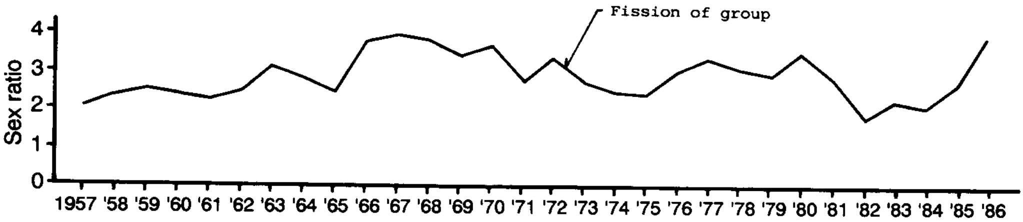

Fig. 1. Yearly changes in adult sex ratio between 1958 and 1986. The sex ratio was defined as the number of adult females per adult male, with adult age being defined as 5 or more years old in both sexes. The ratio for 1957 was estimated.

Table 1. Demographic composition of the Katsuyama group during the pre-fission period (1958 – 1972).*

	1958		1959		1960		1961		1962		1963		1964		1965		1966		1967		1968		1969		1970		1971		1972	
Age in years	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0	4	9	10	11	9	13	10	12	9	19	14	8	17	13	12	14	20	25	13	11	19	24	20	15	23	16	15	22	15	25
1	8	9	4	9	10	11	9	13	9	12	8	16	15	8	15	12	12	14	20	23	13	10	17	24	17	14	23	16	14	20
2	6	11	8	8	4	9	10	11	7	13	10	12	8	16	13	8	13	11	12	13	18	17	13	9	14	20	16	14	20	14
3	4	4	5	10	8	8	4	9	10	11	7	11	10	11	8	15	9	8	10	9	8	10	12	13	11	8	13	16	11	10
4	2	5	4	4	5	9	8	8	4	8	9	10	6	11	8	11	5	12	9	5	5	8	6	7	9	10	9	5	7	12
5	2	4	2	5	4	4	4	8	7	8	4	7	9	10	7	11	6	9	3	8	6	4	2	6	4	6	8	9	5	4
6	2	6	2	4	2	5	4	4	2	7	5	7	3	7	8	10	1	10	5	7	1	8	5	2	2	6	4	5	3	8
7	2	5	2	4	1	4	2	5	3	3	0	6	4	7	3	7	2	10	1	9	3	7	1	6	3	2	2	5	4	5
8	2	2	2	4	1	4	1	4	1	5	2	3	0	6	4	7	2	6	2	10	1	6	3	6	1	5	3	2	1	5
9	1	2	1	2	2	4	1	4	0	4	1	5	2	3	0	5	4	5	2	6	0	8	1	6	1	4	1	5	3	2
10	1	1	1	2	1	2	1	4	0	3	0	4	1	4	2	3	0	5	3	4	2	6	0	8	1	6	1	4	1	5
11	1	1	1	1	1	2	1	2	1	4	0	3	0	4	1	4	2	3	0	5	2	3	1	5	0	6	0	6	0	4
12	0	1	1	1	1	1	0	2	0	2	1	4	0	3	0	4	0	4	1	3	0	3	2	3	2	4	0	6	0	6
13	1	2	0	1	1	1	1	1	0	1	0	2	1	4	0	3	0	4	0	4	1	3	0	2	2	3	2	4	0	6
14	1	1	1	2	0	1	1	1	1	1	0	1	0	2	1	3	0	3	0	4	0	4	1	3	0	2	3	3	1	4
15	1	2	0	1	1	2	0	1	1	1	1	1	0	1	0	2	1	3	0	3	0	3	0	3	0	3	0	2	2	3
16	1	1	1	2	0	1	1	2	0	1	1	1	0	1	0	1	0	2	1	2	0	2	0	3	0	3	0	3	0	2
17	0	1	1	1	1	2	0	1	1	2	0	1	0	1	0	1	0	1	0	2	1	2	0	2	0	3	0	3	0	3
18	0	1	0	1	1	1	1	2	0	1	0	2	0	1	0	1	0	1	0	1	0	2	1	1	0	2	0	3	0	3
19	0	1	0	1	0	1	1	1	1	2	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	0	2	0	3
20	0	1	0	1	0	0	0	1	1	0	1	2	0	1	0	2	0	1	0	1	0	1	0	0	0	1	0	1	0	2
21	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	1	0	1
22	0	1	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0
23	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
24	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0
25	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1
26	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
27	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Total	39	73	46	79	53	90	60	100	58	110	65	109	77	118	83	127	78	141	83	135	81	137	86	129	90	127	100	139	87	148
Grand total	112		125		143		160		168		174		195		210		219		218		218		215		217		239		235	

*Annual census as of the beginning of September. M: Male; F: female.

Table 2. Demographic composition of the Katsuyama group during the post-fission period (1973 – 1986).*

	1973		1974		1975		1976		1977		1978		1979		1980		1981		1982		1983		1984		1985		1986	
Age in years	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0	14	16	14	17	19	8	17	16	22	17	13	19	30	21	11	18	14	20	15	13	17	25	18	24	13	21	9	9
1	11	17	13	15	14	15	19	5	17	15	22	16	12	18	26	18	10	17	12	19	13	12	17	21	15	23	10	18
2	9	11	11	16	12	15	13	9	15	5	13	15	17	11	10	16	24	18	10	15	10	16	13	12	17	20	13	21
3	10	9	9	11	10	16	11	12	10	6	11	4	10	9	15	9	9	16	21	16	5	13	10	15	13	9	14	17
4	8	6	7	8	8	8	7	13	7	9	8	6	10	4	8	8	15	9	8	13	20	15	5	12	9	13	12	9
5	6	9	6	4	7	6	5	7	4	11	5	8	6	6	7	4	8	8	15	6	7	10	12	13	4	9	9	11
6	5	4	6	8	4	2	4	6	4	7	3	10	4	7	3	6	5	4	8	6	9	6	5	7	6	7	3	8
7	1	4	3	4	3	7	2	2	4	6	4	6	3	9	2	7	3	6	4	3	2	6	6	5	3	6	3	7
8	4	3	1	4	1	2	2	7	2	2	3	5	3	6	1	9	2	6	3	6	3	3	2	5	3	5	1	6
9	1	2	3	3	1	4	1	2	1	7	2	2	3	5	1	5	1	9	2	6	5	5	2	2	2	5	2	3
10	1	2	1	2	2	2	1	4	1	2	1	6	1	2	2	5	1	5	1	9	1	6	5	4	1	2	0	5
11	1	5	1	2	1	2	1	2	0	4	1	2	0	6	0	2	2	3	1	5	1	8	1	5	3	4	1	1
12	0	2	1	5	1	2	1	2	1	2	0	4	1	2	0	6	0	1	2	3	1	5	0	8	0	4	1	4
13	0	3	0	2	1	4	1	1	1	2	1	2	0	4	1	2	0	6	1	1	2	3	1	4	0	8	0	4
14	0	5	0	3	0	2	0	4	1	1	1	2	1	2	0	4	1	2	0	6	1	1	2	3	1	4	0	6
15	0	2	0	5	0	3	0	2	0	4	1	1	1	2	1	2	0	4	1	2	0	6	1	1	2	3	1	4
16	1	2	0	2	0	4	0	3	0	2	0	4	1	1	1	2	1	2	0	4	1	2	0	6	1	1	2	3
17	0	1	1	2	0	2	0	4	0	3	0	2	0	4	1	1	1	2	1	2	0	3	1	2	0	6	1	1
18	0	2	0	1	1	2	0	2	0	4	0	3	0	2	0	4	1	1	1	2	1	2	0	3	1	2	0	6
19	0	2	0	2	0	1	1	2	0	1	0	4	0	3	0	2	0	4	1	1	0	2	1	2	0	3	1	2
20	0	2	0	2	0	2	0	1	1	2	0	1	0	4	0	3	0	2	0	4	1	1	0	2	1	1	0	2
21	0	2	0	2	0	2	0	2	0	1	1	2	0	1	0	4	0	3	0	2	0	4	1	1	0	2	1	1
22	0	1	0	2	0	2	0	2	0	2	0	1	1	2	0	1	0	3	0	2	0	2	0	4	1	1	0	0
23	0	0	0	1	0	1	0	2	0	2	0	2	0	1	1	0	0	1	0	3	0	2	0	1	0	3	0	1
24	0	0	0	0	0	1	0	0	0	2	0	2	0	2	0	1	1	0	0	1	0	2	0	1	0	1	0	1
25	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0	1	1	0	0	1	0	2	0	0	0	1
26	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	1	0	0	0	0	1	0	0
27	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
28	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Total	72	113	77	124	85	116	86	112	91	119	90	131	104	136	91	141	99	156	108	153	101	163	103	166	96	165	84	151
Grand total	185		201		201		198		210		221		240		232		255		261		264		269		261		235	

*Annual census as of the beginning of September. M: Male; F: female.

Table 3. Changes in age-specific fecundity rates* during the pre-fission period (1958 – 1962, 1963 – 1967, 1968 – 1972).

	1958 – 1962					1963 – 1967					1968 – 1972				
	No. of animals					No. of animals					No. of animals				
Age in years	Adult females (A)	Infants Male	Infants Female	Total (B)	Rate: (B/A %)	Adult females (A)	Infants Male	Infants Female	Total (B)	Rate: (B/A %)	Adult females (A)	Infants Male	Infants Female	Total (B)	Rate: (B/A %)
4	34	3	2	5	14.71	49	3	2	5	10.20	42	0	0	0	0.00
5	29	4	10	14	48.28	45	10	8	18	40.00	29	12	10	22	75.86
6	26	4	3	7	26.92	41	5	11	16	39.02	29	3	10	13	44.83
7	21	4	9	13	61.90	39	14	6	20	51.28	25	6	10	16	64.00
8	19	2	8	10	52.63	32	7	4	11	34.38	24	8	7	15	62.50
9	16	3	3	6	37.50	24	5	8	13	54.17	25	7	7	14	56.00
10	12	2	6	8	66.67	20	3	10	13	65.00	29	12	9	21	72.41
11	10	1	6	7	70.00	19	7	2	9	47.37	24	8	7	15	62.50
12	7	4	1	5	71.43	18	3	6	9	50.00	22	7	6	13	59.09
13	6	2	2	4	66.67	17	5	3	8	47.06	18	6	6	12	66.67
14	6	3	3	6	100.00	13	2	2	4	30.77	16	4	3	7	43.75
15	7	2	4	6	85.71	10	2	3	5	50.00	14	2	8	10	71.43
16	7	4	0	4	57.14	7	1	1	2	28.57	13	6	1	7	53.85
17	7	0	3	3	42.86	6	2	1	3	50.00	13	2	6	8	61.54
18	6	1	2	3	50.00	6	1	2	3	50.00	11	3	5	8	72.73
19	6	2	1	3	50.00	6	3	0	3	50.00	8	3	3	6	75.00
20	3	0	0	0	0.00	7	0	1	1	14.29	5	1	2	3	60.00
21	3	0	1	1	33.33	4	1	1	2	50.00	4	1	1	2	50.00
22	4	1	0	1	25.00	3	0	0	0	0.00	2	1	1	2	100.00
23	4	0	0	0	0.00	2	1	0	1	50.00	2	0	0	0	0.00
24	4	0	0	0	0.00	1	0	0	0	0.00	3	0	0	0	0.00
25	2	0	1	1	50.00	1	0	0	0	0.00	3	0	0	0	0.00
26	1	0	0	0	0.00	1	1	0	1	100.00	2	0	0	0	0.00
27	0	0	0	0	0.00	1	0	0	0	0.00	0	0	0	0	—
Total	240	42	65	107	44.58	372	76	71	147	39.52	363	92	102	194	53.44

*The fecundity rates were obtained each year as of the beginning of September, approximately 3 months after the peak of the birth season.

Table 4. Changes in age-specific fecundity rates* during the post-fission period (1973 – 1977, 1978 – 1982, 1983 – 1986).

Age in years	1973 – 1977					1978 – 1982					1983 – 1986				
	No. of animals					No. of animals					No. of animals				
	Adult females (A)	Infants			Rate: (B/A %)	Adult females (A)	Infants			Rate: (B/A %)	Adult females (A)	Infants			Rate: (B/A %)
		Male	Female	Total (B)			Male	Female	Total (B)			Male	Female	Total (B)	
4	44	3	1	4	9.09	40	0	0	0	0.00	49	0	0	0	0.00
5	37	9	12	21	56.76	32	4	3	7	21.88	43	1	7	8	18.60
6	27	4	3	7	25.93	33	9	7	16	48.48	28	6	5	11	39.29
7	23	6	9	15	65.22	31	7	9	16	51.61	24	6	5	11	45.83
8	18	5	2	7	38.89	32	5	9	14	43.75	19	3	7	10	52.63
9	18	6	8	14	77.78	27	10	8	18	66.67	15	4	3	7	46.67
10	12	4	5	9	75.00	27	6	6	12	44.44	17	5	4	9	52.94
11	15	8	2	10	66.67	18	6	5	11	61.11	18	9	6	15	83.33
12	13	4	3	7	53.85	16	5	5	10	62.50	21	4	6	10	47.62
13	12	5	5	10	83.33	15	5	5	10	66.67	19	3	11	14	73.68
14	15	5	4	9	60.00	16	4	3	7	43.75	14	1	5	6	42.86
15	16	4	7	11	68.75	11	5	3	8	72.73	14	4	3	7	50.00
16	13	6	0	6	46.15	13	3	5	8	61.54	12	4	3	7	58.33
17	12	5	3	8	66.67	11	0	7	7	63.64	12	1	3	4	33.33
18	11	5	2	7	63.64	12	2	4	6	50.00	13	4	1	5	38.46
19	8	2	2	4	50.00	14	6	2	8	57.14	9	0	3	3	33.33
20	9	3	1	4	44.44	14	2	8	10	71.43	6	1	1	2	33.33
21	9	1	4	5	55.56	12	1	0	1	8.33	8	1	2	3	37.50
22	9	2	0	2	22.22	9	1	2	3	33.33	7	0	2	2	28.57
23	6	0	1	1	16.67	7	1	0	1	14.29	7	0	2	2	28.57
24	3	0	0	0	0.00	6	1	0	1	16.67	5	0	0	0	0.00
25	0	0	0	0	—	5	0	0	0	0.00	4	0	0	0	0.00
26	1	0	0	0	0.00	4	0	0	0	0.00	1	0	0	0	0.00
27	1	0	0	0	0.00	2	0	0	0	0.00	0	0	0	0	—
28	1	0	0	0	0.00	1	0	0	0	0.00	1	0	0	0	0.00
29	0	0	0	0	—	1	0	0	0	0.00	0	0	0	0	—
30	0	0	0	0	—	0	0	0	0	—	1	0	0	0	0.00
31	0	0	0	0	—	0	0	0	0	—	1	0	0	0	0.00
32	0	0	0	0	—	0	0	0	0	—	1	0	0	0	0.00
Total	333	87	74	161	48.35	409	83	91	174	42.54	369	57	79	136	36.86

*The fecundity rates were obtained each year as of the beginning of September, approximately 3 months after the peak of the birth season.

Table 5. Overall mean age-specific fecundity rates* during 1958 – 1986 and a comparison between the pre- and post-fission periods.

	1958 – 1972					1973 – 1986					Total (1958 – 1986)				
	No. of animals					No. of animals					No. of animals				
		Infants					Infants					Infants			
Age in years	Adult females (A)	Male	Female	Total (B)	Rate: (B/A %)	Adult females (A)	Male	Female	Total (B)	Rate: (B/A %)	Adult females (A)	Male	Female	Total (B)	Rate: (B/A %)
4	125	6	4	10	8.00	133	3	1	4	3.01	258	9	5	14	5.43
5	103	26	28	54	52.43	112	14	22	36	32.14	215	40	50	90	41.86
6	96	12	24	36	37.50	88	19	15	34	38.64	184	31	39	70	38.04
7	85	24	25	49	57.65	78	19	23	42	53.85	163	43	48	91	55.83
8	75	17	19	36	48.00	69	13	18	31	44.93	144	30	37	67	46.53
9	65	15	18	33	50.77	60	20	19	39	65.00	125	35	37	72	57.60
10	61	17	25	42	68.85	56	15	15	30	53.57	117	32	40	72	61.54
11	53	16	15	31	58.49	51	23	13	36	70.59	104	39	28	67	64.42
12	47	14	13	27	57.45	50	13	14	27	54.00	97	27	27	54	55.67
13	41	13	11	24	58.54	46	13	21	34	73.91	87	26	32	58	66.67
14	35	9	8	17	48.57	45	10	12	22	48.89	80	19	20	39	48.75
15	31	6	15	21	67.74	41	13	13	26	63.41	72	19	28	47	65.28
16	27	11	2	13	48.15	38	13	8	21	55.26	65	24	10	34	52.31
17	26	4	10	14	53.85	35	6	13	19	54.29	61	10	23	33	54.10
18	23	5	9	14	60.87	36	11	7	18	50.00	59	16	16	32	54.24
19	20	8	4	12	60.00	31	8	7	15	48.39	51	16	11	27	52.94
20	15	1	3	4	26.67	29	6	10	16	55.17	44	7	13	20	45.45
21	11	2	3	5	45.45	29	3	6	9	31.03	40	5	9	14	35.00
22	9	2	1	3	33.33	25	3	4	7	28.00	34	5	5	10	29.41
23	8	1	0	1	12.50	20	1	3	4	20.00	28	2	3	5	17.86
24	8	0	0	0	0.00	14	1	0	1	7.14	22	1	0	1	4.55
25	6	0	1	1	16.67	9	0	0	0	0.00	15	0	1	1	6.67
26	4	1	0	1	25.00	6	0	0	0	0.00	10	1	0	1	10.00
27	1	0	0	0	0.00	3	0	0	0	0.00	4	0	0	0	0.00
28	0	0	0	0	—	3	0	0	0	0.00	3	0	0	0	0.00
29	0	0	0	0	—	1	0	0	0	0.00	1	0	0	0	0.00
30	0	0	0	0	—	1	0	0	0	0.00	1	0	0	0	0.00
31	0	0	0	0	—	1	0	0	0	0.00	1	0	0	0	0.00
32	0	0	0	0	—	1	0	0	0	0.00	1	0	0	0	0.00
Total	975	210	238	448	45.95	1111	227	244	471	42.39	2086	437	482	919	44.06

*The fecundity rates were obtained each year as of the beginning of September, approximately 3 months after the peak of the birth season.

AGE-SPECIFIC FECUNDITY RATES

The age-specific fecundity rates were obtained each year as the percent of females of a given age producing viable infants which survived to approximately 3 months of age. Tables 3 and 4 summarize the changes in age-specific fecundity during the group's pre-fission and post-fission periods, respectively. Table 5 shows the mean age-specific fecundity rates for 305 adult and subadult females between 1958 and 1986. The following four aspects of the age-specific fecundity remained essentially unchanged during the entire study period: (1) a sharp rise in fecundity rates was observed in 5-year-old females; (2) the highest rate was in females between the ages of 10 and 15 years; (3) the fecundity rates remained relatively high in females between the ages of 16 and 19 years; and (4) a decrease in rate occurred in females aged over 20 years.

The mean fecundity rate for the period between 1958 and 1986 was 44.06%, ranging from 36.86% (1983 – 1986) to 53.44% (1968 – 1972). A gradual decreasing trend during the post-fission period (1973 – 1986) was noted. Overall, 5.43% of all 4-year-old females gave birth to their first infant. The corresponding pre- and post-fission means were 8.00% and 3.01%, respectively. The overall mean fecundity rate increased sharply to 41.86% for the 5-year-old females, and then gradually increased to its highest level, 66.67%, for the 13-year-olds and to its second highest level, 65.28%, for the 15-year-olds, with fluctuations occurring as a function of increasing age. The fecundity rates remained relatively high for females which ranged in age from 16 (52.31%) to 19 years (52.94%), but decreased to 17.86% for 23-year-olds, and finally dropped to 0% for 27-year-olds. The oldest female ever documented in the Katsuyama group was 32 years old.

SEX OF INFANTS

Among a total of 919 infants recorded during the study period, 437 were males and 482 were females. The sex ratio was thus 1 : 1.10. Table 6 lists the numbers of infants of each sex according to their mother's age-class. There were no significant differences in number of infants of each sex in relation to the age-classes of the mothers.

AGE OF FEMALES AT FIRST BIRTH

Table 7 shows the age at first birth for 111 females born in the pre-fission period (1958 – 1972) and for 45 females born in the post-fission period (1973 – 1980). The average age at first birth was 5.30 years for the females born in the pre-fission period, 5.69 years for the females born in the post-fission period, and 5.41 years for all 156 females combined.

Table 6. Sex of infants according to age-class of mother during the 1958 – 1986 period.

	Number of infants	
Age-class of mother (yrs.)	Male	Female
4	9	5
5 – 9	179	211
10 – 14	143	147
15 – 19	85	88
20 – 25	21	31
Total	437	482
Grand total	919	

Table 7. Number of females by age at first birth according to year of birth: pre-fission (1958 – 1972) and post-fission periods (1973 – 1980).

Age of female at first birth (yrs.)	Females born 1958 – 1972			Females born 1973 – 1980			Total females born 1958 – 1980		
	M	F	Total	M	F	Total	M	F	Total
4	8	3	11	1	1	2	9	4	13
5	37	32	69	9	11	20	46	43	89
6	10	9	19	6	8	14	16	17	33
7	6	5	11	4	4	8	10	9	19
8	1	0	1	1	0	1	2	0	2
9 or more	0	0	0	0	0	0	0	0	0
Total	62	49	111	21	24	45	83	73	156
Mean age at first birth (yrs.)			5.30[a)]			5.69[b)]			5.41

M: Male infant; F: female infant. a) vs. b): K-S test, $p=0.05$.

The difference in age at first birth between the pre- and post-fission periods was significant [$p=0.05$; Kolmogorov-Smirnov test (K-S test), two-tailed], indicating a tendency for older age at first birth among females born in the post-fission period.

TIMING OF BIRTH

The monkeys of the Katsuyama group have a birth season which begins in March and ends generally in July. Figure 2 illustrates the monthly trisectional distribution for a total of 914 births, including neonatal deaths, during the entire study period. Some of the 919 births analyzed in Tables 5 and 6 were omitted from the analysis due to difficulties in determining the exact timing of birth. The birth peak (189/914 births) was in mid-May, with

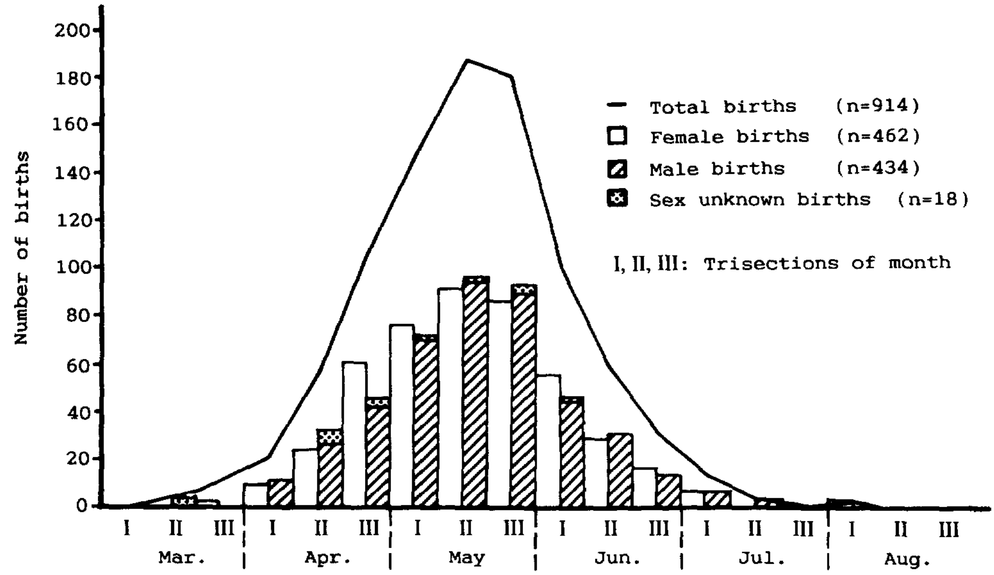

Fig. 2. Monthly trisectional distribution of births recorded between 1958 and 1986.

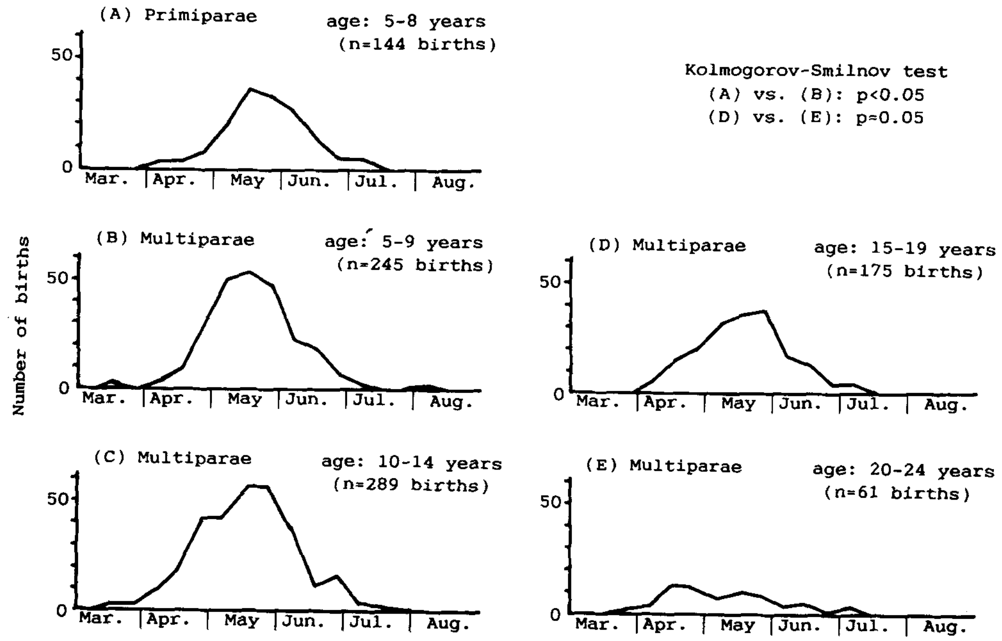

Fig. 3. Monthly trisectional distribution of births recorded during the 1958 – 1986 period, according to parity and mother's age-class.

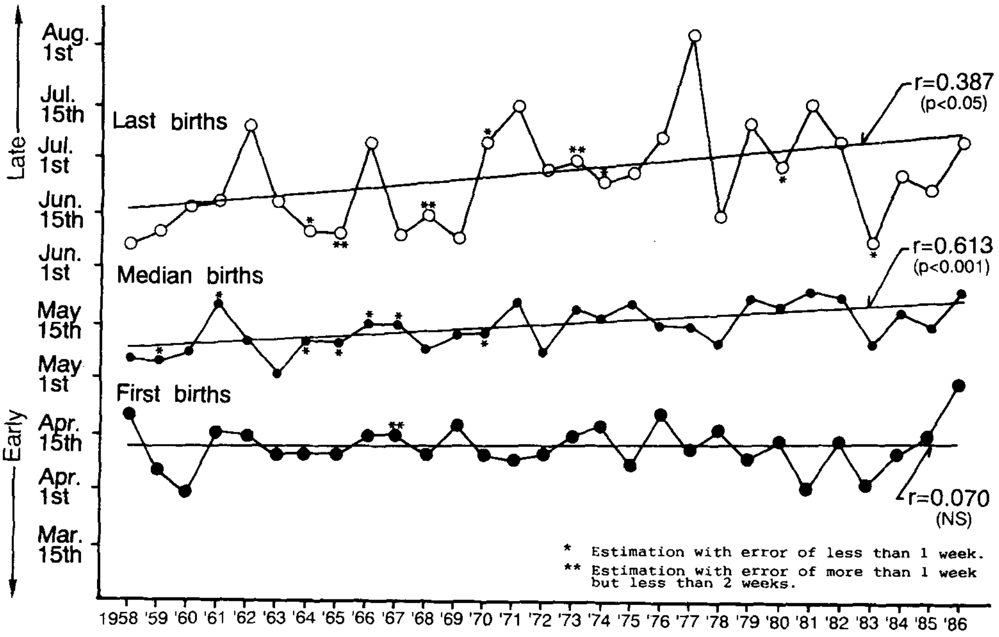

Fig. 4. Yearly changes in the timing of birth between 1958 and 1986, according to the yearly first, median, and last infants born which survived beyond approximately 3 months of age.

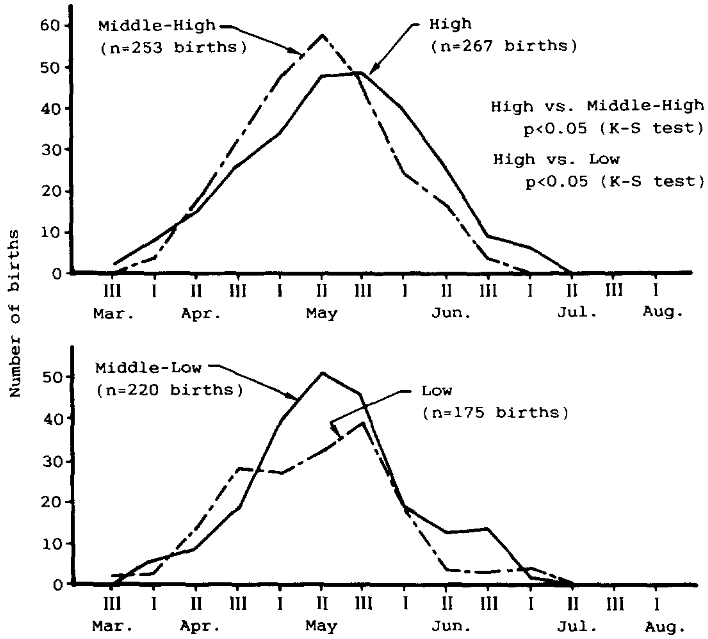

Fig. 5. Differences in birth timing among four matrilineal dominance rank-classes during 1958 – 1986.

20.02% of all births occurring in April, 56.78% in May, and 21.12% in June. There was no significant difference in timing of birth in relation to infant's sex.

Figure 3 shows the monthly trisectional distribution of the 914 births according to the female's parity and age-class. The 5 – 8-year-old primiparous females gave birth significantly later than did the 5 – 9-year-old multiparous females ($p<0.05$; K-S test, two-tailed). There were no significant differences in timing of births among the four age-classes of multiparous females, except that the 20 – 24-year-old females gave birth significantly earlier than did the 15 – 19-year-old females ($p=0.05$; K-S test, two-tailed).

The yearly changes in timing of birth with respect to the first, median, and last births of infants surviving for at least the first three months are illustrated in Figure 4. The timing of the yearly first births ranged from March 29, 1960 to April 29, 1986 and remained essentially unchanged during the entire study period. In contrast, the timing of the yearly median births ranged from May 1, 1963 to May 24, 1981 and shifted towards a significantly later period of the season ($p<0.001$; correlation coefficient, $r=0.613$). The timing of the yearly last births ranged from June 6, 1958 to August 9, 1977 and shifted towards a significantly later period of the season ($p<0.05$; correlation coefficient, $r=0.387$).

Figure 5 shows the differences in timing of births among the four matrilineal dominance rank-classes during the entire study period. The distribution of timing of births for the high ranking class females differed significantly from those for the middle-high- and the low-ranking class females ($p<0.05$; K-S test, two-tailed, for each comparison). The birth peak occurred in late-May for the high-ranking class females and in mid-May for the middle-high-ranking class females. The latter distribution was shifted towards an earlier period of the birth season. The timing of births for the low-ranking class females exhibited a plateau-type distribution with two peaks, one occurring in late-April and the other in late-May.

Table 8. Length of interbirth intervals in years according to age-class of mother over time.

	1958–1962			1963–1967			1968–1972			1973–1977			1978–1982			1983–1986			Total		
Age-class of mother (yrs.)	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.
5–9	13	1.42	2	15	1.52	2	17	1.41	2	14	1.81	3	15	1.95	3	4	1.33	2	78	1.59	3
10–14	12	1.45	2	21	1.58	3	32	1.54	2	21	1.59	2	29	1.54	2	24	1.78	2	139	1.57	3
15–19	7	1.48	2	11	1.72	3	14	1.44	2	22	1.42	2	11	1.58	2	23	1.46	2	88	1.49	3
20–23	2	2.00	2	3	1.38	2	5	1.55	4	7	1.41	2	13	1.60	3	9	1.87	3	39	1.59a)	4
24–26	2	2.40	3	2	1.50	2	2	1.50	2	3	1.50	2	3	1.50	3	7	2.13	4	19	1.83b)	4
Total	36	1.51	3	52	1.58	3	70	1.50	4	67	1.53	3	71	1.61	3	67	1.65	4	363	1.56	4

a) vs. b): U-test, $0.05 < p < 0.1$.

Table 9. Length of interbirth intervals in years according to parity and infant loss or rearing by year-block periods between 1958 and 1986.

Parity and Infant loss or rearing	1958–1962			1963–1967			1968–1972			1973–1977			1978–1982			1983–1986			Total (1958–1986)		
	N	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.	*N*	Mean	Max.
Parity:																					
Primiparous	17	1.65	2	21	1.48	2	34	1.71	2	20	1.90	3	29	1.83	3	16	1.81	2	137	1.73a)	3
Multiparous	32	1.51	3	51	1.56	3	68	1.46	4	70	1.50	2	73	1.55	3	69	1.66	4	363	1.54b)	4
Following:																					
Infant loss1)	11	1.27	3	8	1.50	2	8	1.00	1	10	1.30	2	4	1.50	2	9	1.22	3	50	1.29c)	3
Surviving infant2)	36	1.54	3	52	1.59	3	70	1.52	4	67	1.55	3	71	1.61	3	67	1.68	4	363	1.58d)	4

1) Infant died within the first 3 months of life; 2) Infant lived beyond the first 3 months of life. a) vs. b): U-test, $p < 0.05$; c) vs. d): U-test, $p < 0.05$.

INTERBIRTH INTERVALS

Table 8 presents the lengths of the interbirth intervals, in years, for 363 mothers according to age-class by year-block periods between 1958 and 1986. The overall mean length of the interbirth interval was 1.56 years, and ranged from 1 to 4 years. The mean length for mothers aged 24 to 26 years was longer than that for mothers aged 20 to 23 years at an almost significant level ($0.05 < p < 0.1$; Mann-Whitney U-test, two-tailed). On the other hand, there were no significant differences in mean lengths of the interbirth intervals between the age-classes of 5 – 9, 10 – 14, and 15 – 19 years. No uniform increasing or decreasing trend was noted in the mean length of the interbirth intervals across the year-block periods.

Table 9 presents the lengths of the interbirth intervals for 363 females according to parity and infant loss or survival by year-block periods between 1958 and 1986. A female could be classified as multiparous and primiparous, and as having reared and lost an infant within the time span of one year-block period. The mean length of the interbirth interval was 1.73 years for primiparous females following the birth of the first infant. This was significantly longer than the 1.54 year interval found for multiparous females ($p < 0.05$; Mann-Whitney U-test, two-tailed). The mean length of the interbirth interval was 1.29 years for females following infant loss within the first 3 months of the infant's life. This was significantly shorter than the 1.58 years for females following infant survival beyond the first 3 months ($p < 0.05$; Mann-Whitney U-test, two-tailed).

INFANT MORTALITY

A total of 949 births, including neonatal deaths of unknown sex, were analyzed for infant mortality in relation to the mother's age-class (Table 10). Within the first 12 months after birth, 10.2% (97/949) of all infants died. The infant mortality was high within 1 month after birth (6.1%), but decreased during the first 1 – 3-month period (1.1%), and remained at a relatively low level during the remaining 3 – 12-month period (3.1%). In relation to the mother's age-class, the infant mortality was highest for mothers aged 20 – 26 years old (14.6%), relatively high for those which were 4-year-olds (13.3%) and 5 – 9-year-olds (11.9%), relatively low for 10 – 14-year-olds (8.6%), and lowest for 15 – 19-year-olds (7.5%). The infant mortality in 10 – 19-year-old mothers differed from that in 20 – 26-year-old mothers at an almost significant level ($0.05 < p < 0.1$; $\chi^2 = 2.87$). The male infant mortality (8.8%) was higher than the female infant mortality (6.3%) at an almost significant level ($0.05 < p < 0.1$; $\chi^2 = 2.83$).

Table 11 shows the infant mortality in relation to the parity of the mother. The female infant mortality for primiparous females (11.9%) was significantly higher than that for multiparous females (5.1%) ($p < 0.05$; $\chi^2 = 5.42$). For multiparous females, the male infant mortality (9.3%) was significantly higher than the female infant mortality (5.1%) ($p < 0.05$; $\chi^2 = 5.11$).

DOMINANCE RANK AND REPRODUCTIVE SUCCESS

It was found that the female fecundity rates increased as a function of matrilineal dominance rank. Figure 6 plots the fecundity rates of adult females aged 5 or more years old for 23 matrilineages during the 1958 – 1973 period as a function of matrilineal dominance rank. The fecundity rate for each matrilineage was defined as the percent of

Table 10. Infant mortality according to mother's age-class (1958–1985).

			Infant mortality						Total infant mortality within 12 months of age	
Age-class of mother (yrs.)	Sex of infant	No. of births	0–1 months of age		1–3 months of age		3–12 months of age			
			N	%	N	%	N	%	N	%
4	Male	9	0	0	0	0	0	0	0	0
	Female	6	2	33.3	0	0	0	0	2	33.3
	Unknown	0	—	—	—	—	—	—	—	—
	Total	15	2	13.3	0	0	0	0	2	13.3
5–9	Male	185	9	4.9	1	0.5	6	3.2	16	8.7
	Female	206	5	2.4	3	1.4	10	4.9	18	8.7
	Unknown	14*	14*	—	—	—	—	—	14*	—
	Total	405	28	6.9	4	1.0	16	4.0	48	11.9
10–14	Male	149	8	5.4	3	2.0	6	4.0	17	11.4
	Female	147	2	1.4	2	1.4	1	0.6	5	3.4
	Unknown	4*	4*	—	—	—	—	—	4*	—
	Total	300	14	4.7	5	1.7	7	2.3	26	8.6a)
15–19	Male	82	1	1.2	1	1.2	0	0	2	2.4
	Female	86	3	3.5	0	0	2	2.3	5	5.8
	Unknown	6*	6*	—	—	—	—	—	6*	—
	Total	174	10	5.7	1	0.6	2	1.2	13	7.5b)
20–26	Male	20	0	0	0	0	4	20	4	20
	Female	31	0	0	0	0	0	0	0	0
	Unknown	4*	4*	—	—	—	—	—	4*	—
	Total	55	4	7.3	0	0	4	7.3	8	14.6c)
Total	Male	445	18	4.0	5	1.1	16	3.6	39	8.8d)
	Female	476	12	2.5	5	1.1	13	2.7	28	6.3e)
	Unknown	28*	28*	—	—	—	—	—	28*	—
	Total	949	58*	6.1	10	1.1	29	3.1	97	10.2

*Infants of unknown sex died within 1 month of age. a) & b) combined vs. c): $\chi^2=2.87$, $0.05<p<0.1$; d) vs. e): $\chi^2=2.83$, $0.05<p<0.1$.

Table 11. Infant mortality by parity of mother (1958–1985).

			Infant mortality						Total infant mortality within 12 months of age	
	Sex of infant	No. of births	0–1 months of age		1–3 months of age		3–12 months of age			
Parity			N	%	N	%	N	%	N	%
Primiparous	Male	69	2	2.9	0	0	2	3.0	4	5.8
	Female	84	4	4.8	0	0	6	7.5	10	11.9a)
	Unknown	6*	6*	—	—	—	—	—	6*	—
	Total	159	12	7.5	0	0	8	5.2	20	12.6
Multiparous	Male	376	16	4.3	5	1.3	14	3.7	35	9.3b)
	Female	392	8	2.0	5	1.3	7	1.8	20	5.1c)
	Unknown	22*	22*	—	—	—	—	—	22*	—
	Total	790	46	5.8	10	1.3	21	2.6	77	9.7
Total	Male	445	18	4.0	5	1.1	16	3.6	39	8.8
	Female	476	12	2.5	5	1.1	13	2.7	30	6.3
	Unknown	28*	28*	—	—	—	—	—	28*	—
	Total	949	58	6.1	10	1.1	29	3.1	97	10.2

*Infants of unknown sex died within 1 month of age. a) vs. c): $\chi^2=5.42$, $p<0.05$; b) vs. c): $\chi^2=5.11$, $p<0.05$.

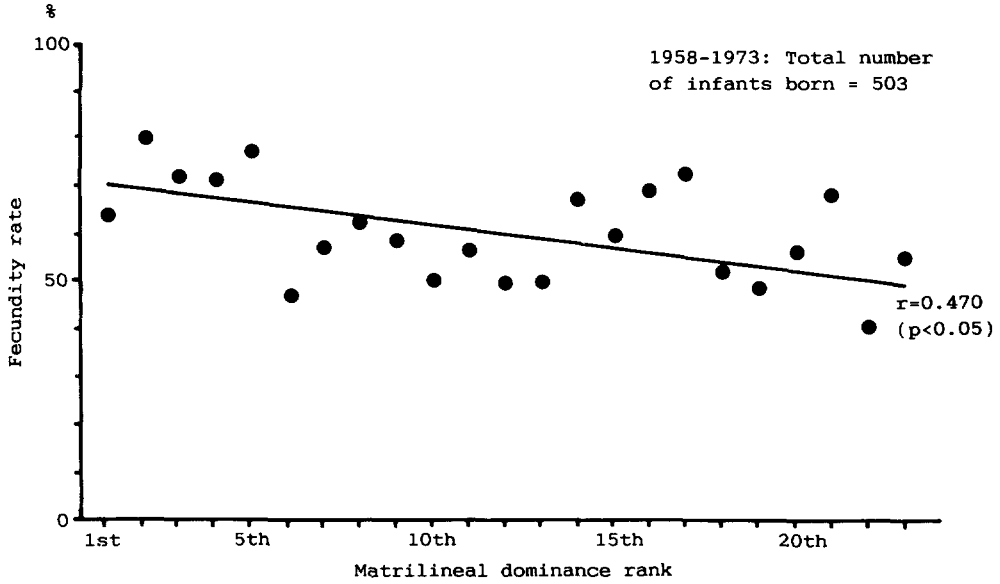

Fig. 6. Fecundity rates of adult females aged 5 or more years old during 1958–1973, as a function of dominance rank of 23 matrilineages.

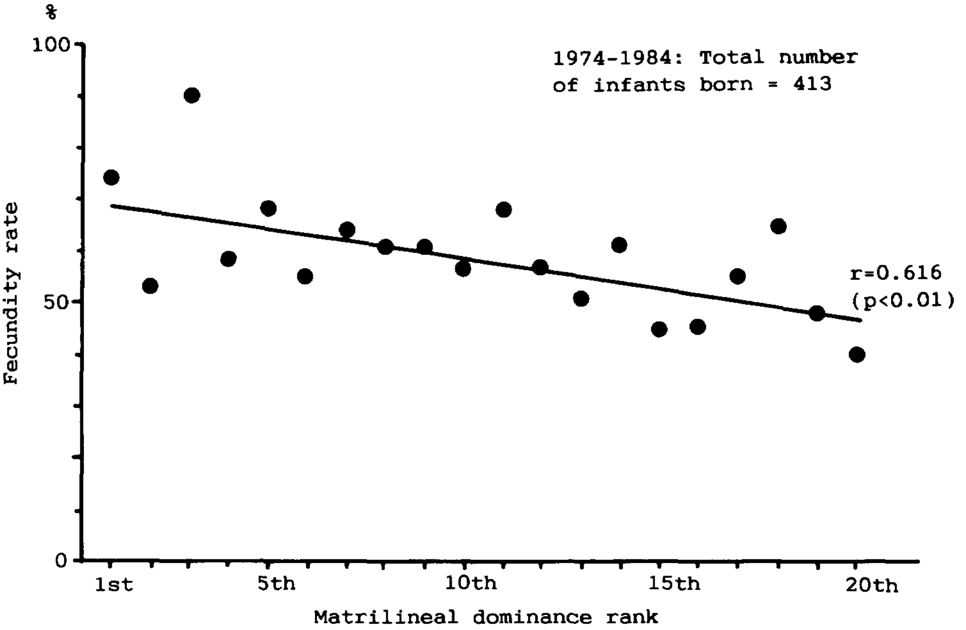

Fig. 7. Fecundity rates of adult females aged 5 or more years old during 1974–1984, as a function of dominance rank of 20 matrilineages. The data analysis was conducted only up to 1984.

adult females producing viable infants during potential breeding years. The matrilineages were ranked according to their dominance rank as of March 1973, one month prior to the group's fission. The fecundity rates increased significantly in relation to rise in the matrilineal dominance rank ($p < 0.05$; correlation coefficient, $r = 0.47$), ranging from 41% for the 22nd ranking matrilineage to 80% for the 2nd ranking matrilineage. However, there were deviations from this trend, such as a low rate (47%) for the 6th ranking matrilineage and a high rate (73%) for the 17th ranking matrilineage. Figure 7 plots the fecundity rates for 20 matrilineages during the 1974 – 1984 period. The matrilineages were ranked according to their dominance rank as of March 1984. A significant correlation was again found between increase in the fecundity rate and rise in the matrilineal dominance rank ($p < 0.01$; correlation coefficient, $r = 0.616$). The fecundity rates during the 1974 – 1984 period ranged from 90% for the 3rd ranking matrilineage to 40% for the 20th, with smaller converse variations than during the 1958 – 1973 period.

DISCUSSION

The changes in the group's size and age-sex composition with time were influenced by several complex factors including the female fecundity, infant mortality, emigration/death of group members, the social dynamics such as group fission, environmental conditions such as food resources and climatic changes, and human intervention/interference via food supply, hunting, and capture. As an outcome of these complex factors, the group's size increased more than two-fold during the 28-year study period, with year-to-year variations in the total size and age-sex composition.

Female reproductive parameters such as the overall fecundity, age at birth of the first infant, and length of the interbirth intervals did not reveal an increment in reproductive activities during the study period. Conversely, the female age at first birth appears to have risen. This could indicate a decrement in reproductive activities for young adult females over the course of the group's history. In contrast to the young adult females, the old adult females probably improved in their reproductive activities. Further analysis is needed on the detailed relationships between the reproductive and mortality parameters and long-term changes in the group's social organization and environment.

Four-year-old females seldom gave birth, but 41.86% of all 5-year-old females did. The fecundity rate reached a peak (66.67%) in females aged 13 years. According to the findings of KOYAMA et al. (1975) for the Arashiyama group of Japanese macaques, 55.4% of all 5-year-old females gave birth and the peak fecundity rate (65.9%) occurred in females aged 11 years. Our data showed that the fecundity rates remained relatively high for females which ranged in age from 16 (52.31%) to 19 years (52.94%), but decreased to 17.86% for 23-year-olds, and finally dropped to 0% for 27-year-olds.

The following characteristics of the adult female age-classes are suggested on the basis of the overall mean age-specific fecundity rates shown in Table 5: (1) 4-year-olds, few bear infants: (2) 5 – 9-year-olds, the fecundity rates increase substantially; (3) 10 – 15-year-olds, the fecundity rates are at their highest levels; (4) 16 – 19-year-olds, the fecundity rates decrease but remain relatively high; (5) 20 – 23-year-olds, the fecundity rates decrease sharply; (6) 24 – 26-year-olds, few bear infants; and (7) 27 plus-year-olds, none produce infants. Thus, the age-class of 4-year-olds can be termed as subadult, that of 5 – 9-year-olds as adult-I, that of 10 – 15-year-olds as adult-II, that of 16 – 19-year-olds as adult-III, that of 20 – 26-year-olds as old adult, and that of 27 plus-year-olds as senile.

Our results agree with the findings of TANAKA et al. (1970) for Japanese macaques, and of PAUL and THOMMEN (1984) for a semifree-ranging population of Barbary macaques, in terms of the significantly longer interbirth intervals for primiparous females than for multiparous females. On the other hand, our observation of shorter interbirth intervals following infant loss within the first three months of life compared to those following infant survival, does not agree with the findings of PAUL and THOMMEN (1984) who reported that death of an infant had no apparent influence on the length of the interbirth interval. This discrepancy could reflect a difference in breeding strategies between the two species (ALTMANN et al., 1978): Barbary macaques have a normal birth interval of one year, whereas Japanese macaques have one of two years.

The infant mortality within the first year of life was 10.2% for our population, which was approximately equal to that of 9.1% for the Barbary population studied by PAUL and THOMMEN (1984). The infant mortality in our population was the lowest for mothers aged 15 – 19 years. The mothers of this age-class are perhaps the most experienced in rearing infants, despite their slightly lower rates of producing infants as compared to mothers aged 10 – 14 years. SUGIYAMA and OHSAWA (1982) found in another population of Japanese macaques, that the infant mortality was higher for primiparous mothers than for multiparous mothers. This result is in agreement with our findings for the female infant mortality.

The Katsuyama group has a birth season which begins in March and lasts normally until July. The timing of each year's first births did not change essentially during the 28-year study period, whereas the timing of the yearly median and last births shifted to a later period of the season, with considerable variations. This indicates that the period of the birth season has become extended through a shift in the terminal period of breeding, but not its onset, due probably to changes in the environmental conditions associated with provisioning.

Reproductive success in adult females can be evaluated from a number of parameters, among which the timing of births, infant mortality, and fecundity in relation to female matrilineal dominance rank are important. We found that the 5 – 8-year-old primiparous females produced their infants later in the first season than did the 5 – 9-year-old multiparous females. A delay in timing of births in young primiparous females has also been reported for other populations (PAUL and THOMMEN, 1984; SILK et al., 1981). In our population, the 20 – 24-year-old multiparous females produced their infants earlier in the season than did the 15 – 19-year-old multiparous females. Furthermore, the timing of births differed among the four female matrilineal dominance rank-classes. For example, the timing of births in the low-rank-class females displayed a plateau-type distribution with two peaks, one occurring at the early stage and the other at the late stage of the season. Our results may indicate how disadvantageous females in terms of reproductive activities, such as young primiparous, old multiparous, and low-ranking females, differentiate their breeding activities with time in order to achieve reproductive success in competition with reproductively advantageous females.

DRICKAMER (1974) found that infants born to high-ranking females of a rhesus macaque colony had a higher rate of survival than did the young of low-ranking females. We did not observe such a significant difference in infant mortality in relation to matrilineal dominance rank of the mothers. Deaths in infants may result from various causes, such as predation and hunting in addition to incomplete development of the infants and maltreatment by mothers. Thus, the infant mortality appears to be subject to more complex influences from the environment than is the female fecundity. This could be one reason why no correlation between infant mortality and matrilineal dominance rank of the mothers was found in our population.

Our data demonstrate that female fecundity rates increase as a function of matrilineal dominance rank. Several studies have reported a correlation between reproductive success and dominance rank in females (DRICKAMER, 1974; DUNBAR, 1984; SMUTS & NICOLSON, 1989). On the other hand, some other studies have reported an absence of such a correlation (TAKAHATA, 1980; WOLFE, 1984; FEDIGAN et al., 1986). Complex factors must be involved in producing these discrepancies, among which access to food resources is considered possibly important. A linear correlation between fecundity and dominance rank in females may not occur in environments of the type where females are not highly competitive for food, or conversely, where only the most dominant females have access to the major food resources. Thus, the results obtained in our population could be attributable, among other causes, to a moderate level of competition among the females for food resources.

We found that the correlation between female fecundity and matrilineal dominance rank involved a considerable degree of variability among the matrilineages. Complex factors must have produced these variations, among which several inter-individual relationships during the course of the group fission in 1973 should be included, as follows. The mating partners of the alpha male expelled the alpha male's adult female kin during the course of the group fission. The matrilineal dominance ranks of these mating partners rose considerably (ITOIGAWA, 1988), but their fecundity rates were relatively low despite the rise in their dominance rank. The low fecundity rates might be partly attributable to their excessive aggression towards the adult female kin of the alpha male which appeared to inhibit their sexual interactions with the alpha male. In order to clarify such complex factors influencing female reproductive success, all data must be subjected to detailed analysis in relation to the group's history.

Acknowledgements. We are greatly indebted to Professors T. AMANO, Y. MAEDA, A. SAWADA, I. KAWAGUCHI, and T. MINAMI of Osaka University for their helpful guidance, to Professor S. I. PERLOE of Haverford College for his invaluable comments and assistance in correcting the English of our manuscript, to Professor M. YOSHIDA of Osaka University for offering us the program for statistical analysis, to Dr. M. NAKAMICHI of Osaka University for his constructive comments, to Dr. M. KAWAI of the Japan Monkey Centre for his encouragement and advice, and to Dr. Y. TAKAHATA of Kyoto University for his helpful suggestions. We sincerely thank to our colleagues at Osaka University, particularly, J. OKI, T. YASHIMA, H. SOGABE, K. NEGAYAMA, A. YOSHIDA, S. MACHIDA, and A. SAKAI, and the people of Katsuyama for their invaluable assistance over many years.

REFERENCES

ALTMANN, J., S. A. ALTMANN, & G. HAUSFATER, 1978. Primate infant's effect on mother's future reproduction. *Science*, 201: 1028 – 1029.

————, S. A. ALTMANN, G. HAUSFATER, & S. A. MCCUSKEY, 1977. Life history of yellow baboons: physical development, reproductive parameters and infant mortality. *Primates*, 18: 315 – 330.

BORRIES, C., V. SOMMER, & A. SRIVASTAVA, 1991. Dominance, age, and reproductive success in free-ranging female hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.*, 12: 231 – 257.

DRICKAMER, L. C., 1974. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatol.*, 21: 61 – 80.

DUNBAR, R. I. M., 1984. *Reproductive Decision: an Economic Analysis of Gelada Baboon Social Strategies*. Princeton Univ. Press, New Jersey.

FEDIGAN, L. M., L. FEDIGAN, S. GOUZOULES, H. GOUZOULES, & N. KOYAMA, 1986. Lifetime reproductive success in female Japanese macaques. *Folia Primatol.*, 47: 143–157.

GOODALL, J., 1983. Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Z. Tierpsychol.*, 61: 1–60.

ITANI, J., K. TOKUDA, Y. FURUYA, K. KANO, & Y. SHIN, 1963. The social construction of natural troops of Japanese monkeys in Takasakiyama. *Primates*, 4(3): 1–42.

ITOIGAWA, N., 1988. Life histories of Japanese monkeys in a free-ranging group. Proceedings, IXth Biennial Meetings of the International Society for the Study of Behavioural Development. Center of Developmental Education and Research, Tokyo, pp. 222–230.

KAWAI, M., S. AZUMA, & K. YOSHIBA, 1967. Ecological studies of reproduction in Japanese monkeys (*Macaca fuscata*). I. Problems of the birth season. *Primates*, 8: 35–74.

KOYAMA, N., K. NORIKOSHI, & T. MANO, 1975. Population dynamics of Japanese monkeys at Arashiyama. In: *Contemporary Primatology*, S. KONDO, M. KAWAI, & A. EHARA (eds.), Karger, Basel, pp. 411–417.

MCFARLAND SYMINGTON, M. 1988. Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *Amer. J. Primatol.*, 15: 45–67.

PAUL, A. & D. THOMMEN, 1984. Timing of birth, female reproductive success and infant sex ratio in semifree-ranging Barbary macaques (*Macaca sylvanus*). *Folia Primatol.*, 42: 2–16.

SIGG, H., A. STOLBA, J.-J. ABEGGLEN, & V. DASSER, 1982. Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates*, 23: 473–487.

SILK, J. B., C. B. CLARK-WHEATLEY, P. S. RODMAN, & A. SAMUELS, 1981. Differential reproductive success and faculative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Anim. Behav.*, 29: 1106–1120.

SMITH, D. G., 1982. A comparison of the demographic structure and growth of free-ranging and captive groups of rhesus monkeys (*Macaca mulatta*). *Primates*, 23: 24–30.

SMUTS, B. & N. NICOLSON, 1989. Reproduction in wild female olive baboons. *Amer. J. Primatol.*, 19: 229–246.

STRUM, S. C. & J. D. WESTERN, 1982. Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *Amer. J. Primatol.*, 3: 61–76.

SUGIYAMA, Y. & H. OHSAWA, 1982. Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatol.*, 39: 238–263.

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

TANAKA, T., K. TOKUDA, & S. KOTERA, 1970. Effects of infant loss on the interbirth interval of Japanese monkeys. *Primates*, 11: 113–117.

WOLFE, L. D., 1984. Female rank and reproductive success among Arashiyama B Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 5: 133–143.

—— Received *December 7, 1990*; Accepted *November 13, 1991*

Authors' Names and Present Addresses: NAOSUKE ITOIGAWA, *Department of Comparative and Developmental Psychology, Faculty of Human Sciences, Osaka University, Yamada-oka, Suita, Osaka, 565 Japan*; TOSHIYUKI TANAKA, *Faculty of Low and Letters, Kagoshima University, Korimoto, Kagoshima, 890 Japan*; NOBUYUKI UKAI, *Department of Social Education, Faculty of Education, Bukkyo University, Kita-ku, Kyoto, 603 Japan*; HISANORI FUJII, *Faculty of Letters, Shokei College, Shimizu, Kumamoto, 860 Japan*; TAKAKO KUROKAWA-NEGAYAMA, *Fushimidai, Inagawa-cho, Kawabe-gun, Hyogo, 666-02 Japan*; TAKAMASA KOYAMA, *Faculty of Liberal Arts, Kawamura Gakuen Woman's University, Sageto, Abiko, Chiba, 270-11 Japan*; AKITO ANDO, *Department of Human Relations, Faculty of Letters, Mukogawa Women's University, Ikebiraki-cho, Nishinomiya, Hyogo, 663 Japan*; YOSHIO WATANABE, *Faculty of Domestic Science, Mimasaka Women's College, Tsuyama, Okayama, 708 Japan*; SHINJI IMAKAWA, *Department of Comparative and Developmental Psychology, Faculty of Human Sciences, Osaka University, Yamada-oka, Suita, Osaka, 565 Japan.*