

Population Dynamics of Arashiyama West Japanese Macaques

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Demographic data have been collected on the Arashiyama Japanese macaque population from 1954 until the present, through the fissioning of the original group into two parts in 1966, and through the translocation of one of the two groups to Texas in 1972. Population dynamics are reported for the Arashiyama West group in Texas during 1972 to 1979 and then compared to data from Japan. After a short period of adjustment for the translocated group, during which time natality rates were relatively low and mortality rates were relatively high, many aspects of population structure, birth rates, and survivorship showed trends similar to those observed in Japan. This suggests that both long-term homeostatic processes and shorter-term responses to environmental fluctuations are significant to the study of nonhuman primate demography.

KEY WORDS: demography; *Macaca fuscata*; environmental responses; homeostatic processes.

INTRODUCTION

The study of many aspects of ecology and behavior requires knowledge of demographic parameters, including details of reproduction, birth, and death, of the individuals in populations. Although a few early reports, such as Carpenter (1962), Rowell (1969), Southwick and Siddiqi (1968), and Koford (1965, 1966), began the description of long-term changes in nonhuman primate groups, the longitudinal data covering the

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species life expectancy period, important for determining life history patterns, are only now becoming available. This paper concerns population dynamics in one such longitudinally studied group of monkeys, the Arashiyama West Japanese macaques (*Macaca fuscata*). Our analysis of demographic trends takes advantage both of the many years of research on this population and of the unique experiment in altering environmental parameters that resulted from the translocation of one of the groups from Japan to Texas.

A number of groups of Japanese macaques have been studied since the early 1950s, and the recording of individual births, life histories, and deaths, as well as population censuses, has resulted in extensive demographic information on this species. Itani *et al.* (1963, 1975) and Masui *et al.* (1975) have reported on the best known of the Japanese monkey groups, the Takasakiyama population, while Furuya (1968) described long-term changes in the Gagyusan group, and Mori (1979) analyzed population changes in the Koshima group. The Arashiyama Japanese macaques have been studied from 1954 until the present, through the fissioning of the original group into two parts in 1966, and through the translocation of one of the two groups to Texas in February 1972. When the group fissioned into two, they were called the "A" and "B" groups, and after the translocation of Arashiyama A to Texas, the two groups were renamed Arashiyama West and East, respectively. The population dynamics of Arashiyama, and Arashiyama East, monkeys in Japan were described by Koyama (Koyama, 1970; Koyama *et al.*, 1975, 1980; Norikoshi and Koyama, 1974).

METHODS

The Arashiyama West group of Japanese monkeys was translocated to a site near Laredo, Texas, in February 1972, where they were released into a 42.4-ha enclosure of native brushland, surrounded by an electrified fence. Throughout this study, the animals were minimally provisioned with animal feed,³ minimally disturbed by humans, and free to range over the large enclosure, foraging for a major portion of their diet on the native vegetation and encountering the local fauna. Descriptions of the south Texas en-

³During feeding regime 1 (Feb. 1972–Aug. 1975) the group was provisioned at a maximum rate of approximately 16.3 kg of food per day of whole grains, fruits, and commercial cattle food (Wayne Creep Feed), an average of 112 g of food per animal per day. During feeding regime 2 (Sept. 1975–Aug. 1979) the group received 22.7 kg per day of commercial monkey food (Wayne Monkey Diet), or approximately 107 g per monkey per day.

vironment and comparisons with the Japan habitat are given by Gouzoules *et al.* (1975, 1981) and Clark and Mano (1975).

This report presents 8 years of data on the population dynamics of the Arashiyama West monkeys at Laredo, from February 1972 to August 1979. Researchers recognized all individuals in the group. All animals were marked with permanent tattoos. Daily recordings of births, deaths, and other significant life history events were made, in addition to regular censusing of the group. The age of each individual in the group, except for two of the nonnatal males, was known to the day of birth.

While the recording of births and the calculation of natality rates are relatively straightforward, the determination of mortality rates is more open to interpretation because of the difficulties of distinguishing between death and emigration of an individual that simply ceases to appear in the group. Since one of the objectives of this report is a comparison with Arashiyama records from Japan, Koyama's interpretation (personal communication) of mortality is followed here: disappearance at less than 2 years is recorded as "death," while disappearance at a later age is recorded as "emigration."⁴

Because the electrified fence functioned only intermittently, Texas monkeys were in fact able to emigrate. Of the 23 individuals older than 2 years that disappeared, all were mature males, except for a small group of females ($N = 6$) that disappeared together on 1 day immediately following the 1972 release. We presume that some of these immigrant males subsequently died in this dry, remote area of south Texas. However, some males were sighted on neighboring ranches and were subsequently trapped to be sent to zoo colonies; two males were shot by local people, and one was reported run over on a highway. In addition, 38 members of the group were captured to form fledgling zoo groups; almost all of these captures took place in the last year of our study, and population data for those individuals are not used from that point on to calculate demographic trends in this report.

The objectives of the present paper are to summarize the patterns of population growth and decline for Arashiyama West monkeys in their first

⁴Clearly deaths of some mature individuals may be misclassified as emigrations using this system, but the converse error of misclassifying emigrations as deaths is unlikely, since individuals less than 2 years old are unknown to emigrate in Japanese macaques. Following a "disappearance" a careful search was always made for a cadaver, and these were found easily enough that we assume we did not misclassify very many deaths. Only if no body was found was the disappearance classified as an emigration. On several occasions following a disappearance, reports of monkey sightings were received from neighboring ranches, confirming the emigration. Thus, because some interpretation of disappearance is necessary to pursue the demographic analysis, and for the reasons given above, we chose to follow Koyama's system.

8 years in Texas and to compare Arashiyama West data with Japanese data collected during two periods: the 18 years prior to translocation and the 8 years since 1972. For the latter time period, comparison is made between the sister group remaining in Japan and the translocated group.

RESULTS AND DISCUSSION

Four of the major processes which determine group size and composition are birth, immigration, death, and emigration (the "BIDE" model; see Cohen, 1969). In Fig. 1, these four principal population processes are diagrammed and compared for the Arashiyama West and East groups over the years 1972 to 1979. Beginning with similar population sizes in 1972, the Arashiyama West group experienced somewhat fewer births, somewhat more deaths, and the same number of emigrations, compared to Arashiyama East. Given the radically altered environmental circumstances for Arashiyama West in Texas, these population profiles were surprisingly similar. Using the evidence presented in the following figures, we suggest that most of the differences observed in overall natality and mortality patterns between the two sister groups in Texas and Japan were concentrated in the first 2 years following translocation. After these initial years of adjustment, the Texas population was an expanding one, similar in its demographic patterns to other groups of Japanese monkeys, especially Arashiyama East.

When the Arashiyama population was first contacted in 1954, 34 group members were identified (Fig. 2). The population increased steadily from 1954 until 1966, when the 163 member group fissioned into two parts.

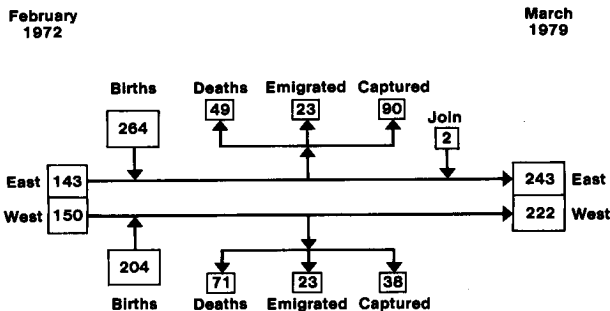


Fig. 1. Comparative flow chart of population events in Arashiyama West and East, 1972-1979. The format of Fig. 1 and the Japanese data for Figs. 1-7 are courtesy of N. Koyama, and re-graphed from Koyama *et al.* (1980).

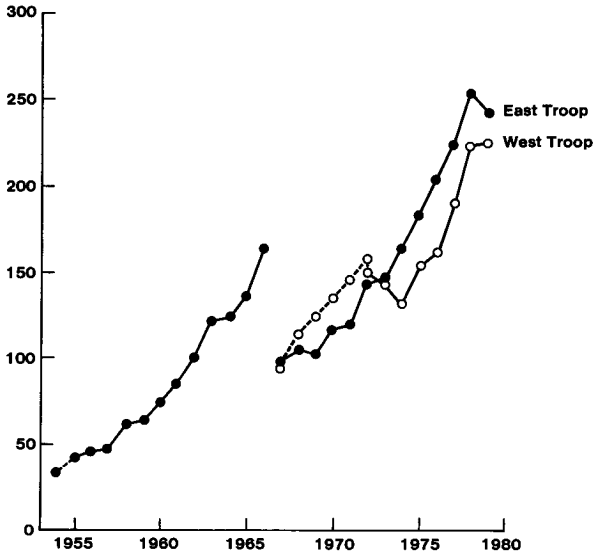


Fig. 2. Changes in Arashiyama population size, 1954–1979.

Both groups then continued to expand until 1972, when 150 of the 158 members of Arashiyama A were moved to Texas. From 1972 to 1979, in Texas, the mean annual rate of population growth was 8.6%, whereas it had been 13.7% in Japan. However, as can be seen in Fig. 2, the Arashiyama West population declined sharply in its first 2 years following translocation (annual decreases of 5 and 7%), before it regained its Texas arrival size of 150 individuals in 1975 and began to expand again. The mean annual growth rate in Texas, excluding the first 2 years (and excluding 1979, when captures reduced group size), was 14.12%, very comparable to the rate from Japan.

Following a halt in provisioning of the Koshima group of Japanese monkeys, Mori (1980) reported a population decline, which he attributed in part to a drop in the birth rate and an increase in infant mortality. These same two factors clearly played an important role in the Arashiyama West population decline following translocation. In February of 1972 the Arashiyama West females arrived pregnant from Japan, and the birth rate in the 1972 spring birth season was comparable to birth rates in Japan. However, Fig. 3 shows the relatively low natality rates for Arashiyama West in 1973 (4.9%) and 1975 (14.2%). The mean annual birth rate (natality per 100 monkeys) in Texas was 17.7% during this study, while it was 20.1% for Arashiyama East during the same time period. Further, Fig. 4 shows a

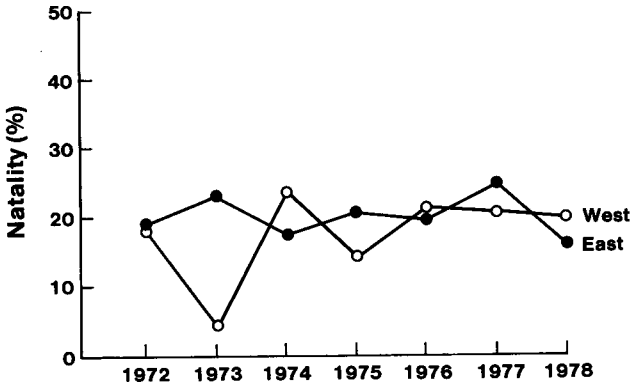


Fig. 3. Natality in the Arashiyama West and East groups (births per 100 monkeys), 1972-1978. Natality for Arashiyama West was expressed per 100 animals, that is, the "crude birth rate," rather than per 100 adult females, in order to make the comparison to the data and the published graphs available for Arashiyama East in Japan.

sharp rise in infant mortality in 1972 and 1973. The infant mortality (death before 1 year of age) was 11.8% in Arashiyama West, compared to 9.1% in Arashiyama East, during the 1972 to 1978 time period. However, the mean annual infant mortality dropped from a high of 36.3% in the first 2 years following translocation to a low of 6.7% in the latter 5 years.

It might be expected that the translocation of the Arashiyama West monkeys would have affected not only group size but also group composi-

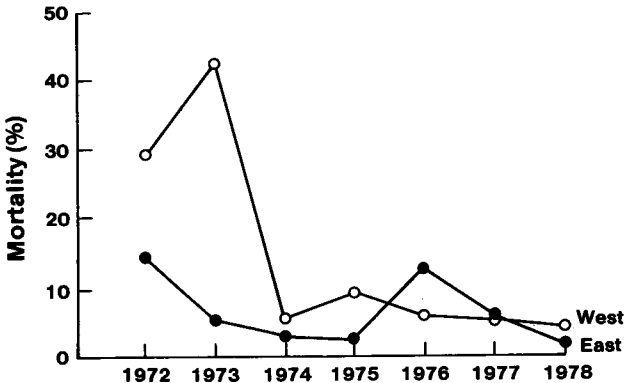


Fig. 4. Infant mortality in the first year of life: comparison of Arashiyama West and East (mortality per 100 live births), 1972-1978.

tion. In February 1972, the group arrived in Texas with 37% males and 63% females in the population (a 1:1.7 sex ratio), and 3% of the population were classified as "old" (> 18 years), while 42% were classified as "young" (or < 4 years). Two years later, in February 1974, after the impact of the move and the new environment had had time to affect the group composition, the ratio of males to females in the population (1:2) and the percentage of old individuals (3%) were very little changed, but the young category (infants and juveniles) was down to 29%. By February 1978, 6 years after the translocation, this young age class had recovered its former representation of 42% of the population.

While the overall sex ratio of the Arashiyama West group was little altered by the move to Texas, the ratio of adult males to adult females was changed (Fig. 5), albeit temporarily. Over the 18 years that the group was followed in Japan, there were many fluctuations in the adult sex ratio, from a 1956 high of 1 male to every 1.5 females to a 1959 low of 1:4.2. A peak in adult male representation had preceded the translocation of the troop, and during the first year in Texas the ratio dropped to a value close to the 1959 low in Japan but then subsequently increased. Because the adult sex ratio has varied over the years that the Arashiyama population has been studied, we do not conclude that the translocation resulted in a uniquely low adult male representation in the population. This contradicts Wolfe (1979), who claimed that a "scarcity" or "shortage" of adult males existed following the translocation. The adult sex ratios were at all times comparable to values reported from Japan and, by 1973 and 1974, had returned to the average ratio in Japan. Over the 18 years in Japan the mean sex ratio for adults was 38% (1:2.6), and over the 8 years in Texas it was 37%.

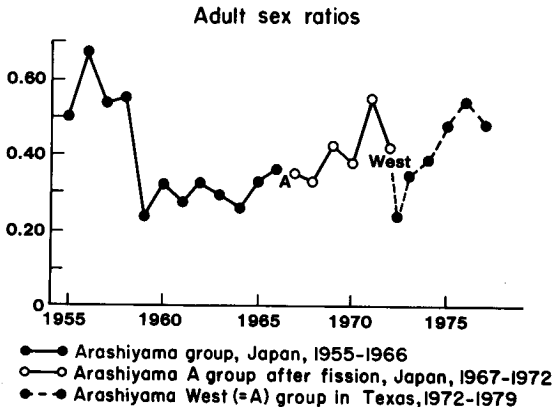


Fig. 5. Annual fluctuations in ratio of adult males to adult females for Arashiyama monkeys in Japan and Texas.

Life tables have now been constructed for several primate species (e.g., Dittus, 1975; Teleki *et al.*, 1976; Masui *et al.*, 1975; Sade *et al.*, 1977; Altmann *et al.*, 1977), and survivorship (l_x) can be calculated as the number of individuals observed alive in the population at the earliest age of each age interval or from the analysis of age-specific mortality rates (see Dittus, 1981). The patterns to be expected are concave survivorship curves, indicating a heavier mortality earlier in life (with the individuals that survive to adulthood having a relatively high expectation of further life) and a lower survivorship for adult males than for adult females (Deevey, 1947). Survival patterns for Arashiyama West are inferred in this paper from proportionate age distribution curves. Census data were used to generate these curves, in order to make the comparison with the data available from Japan; and c_x was calculated because of the limitations on calculating l_x for an expanding population. Table I presents the age struc-

Table I. Age Structure and Distribution for the Arashiyama West Population of Japanese Monkeys, 1974-1978^a

Age interval (yr.)	Average No. observed ^b				Proportionate age distribution c_x	
	FF	(SD)	MM	(SD)	FF	MM
0	12.8	(4.5)	13.8	(3.3)	1.000	1.000
1	11.6	(5.8)	12.8	(3.8)	0.906	0.928
2	9.6	(4.7)	9.4	(3.1)	0.750	0.681
3	9.6	(4.5)	7.4	(3.1)	0.750	0.536
4	8.6	(5.1)	6.6	(3.0)	0.672	0.478
5	8.2	(4.4)	5.2	(3.1)	0.641	0.377
6	8.2	(4.3)	5.0	(2.2)	0.641	0.362
7	8.0	(3.8)	4.6	(2.2)	0.625	0.333
8	6.6	(3.3)	3.0	(1.6)	0.531	0.202
9	7.0	(3.3)	1.4	(0.5)	0.531	0.101
10	5.6	(2.2)	1.4	(0.5)	0.438	0.101
11	5.4	(1.5)	1.0	(0.6)	0.422	0.072
12	4.0	(1.3)	1.0	(0.6)	0.313	0.072
13	3.2	(1.4)	0.8	(0.7)	0.250	0.058
14	2.8	(1.4)	0.8	(0.7)	0.218	0.058
15	1.8	(1.1)	0.4	(0.4)	0.141	0.029
16	1.6	(0.4)	0.4	(0.4)	0.125	0.029
17	1.2	(0.7)	0.4	(0.4)	0.094	0.029
18	0.8	(0.5)	0.4	(0.4)	0.063	0.029
19-25	4.4	(1.4)	1.8	(0.4)	0.049	0.021
(7-yr interval)	(0.63/yr of life)		(0.26/yr of life)			

^aDuring this time period the mean rate of population increase (\bar{r}) was 14.12 (SD = 5.5), very comparable to the \bar{r} in Japan of 13.7 (see also Fig. 2).

^b \bar{X} number observed in each age interval, averaged over census years, 1974-1978.

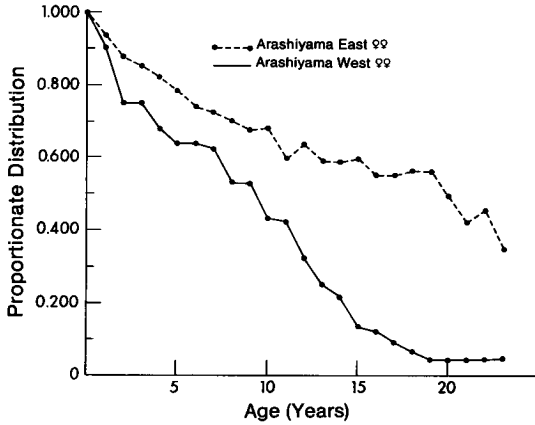


Fig. 6. Comparative age distribution curves (c_x) for Arashiyama West and East female monkeys.

ture and proportionate age distribution for the Arashiyama West population, averaged over census years with a relatively constant rate of population growth. Proportionate age distribution curves for Arashiyama monkeys (Figs. 6 and 7) indicate that females had an overall higher survival in the group than males, with female survival approximating a diagonal curve, while that of males exhibited the concave curve. The diagonal curve for females indicates a fairly steady decrease in survival rate for all age intervals, while the male curve indicates a lower survival in the group,

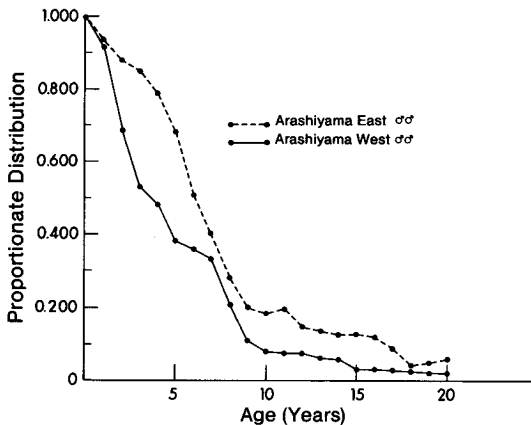


Fig. 7. Comparative age distribution curves (c_x) for Arashiyama West and East male monkeys.

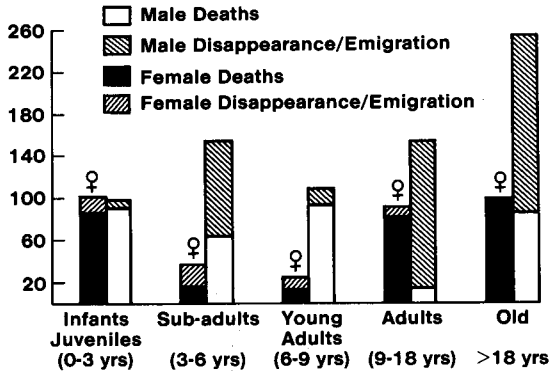


Fig. 8. Deaths and emigrations per 1000 monkeys in each age/sex class, Arashiyama West, 1972-1979.

especially between 5 and 10 years, the pubertal and young adult phases. Comparing Japan and Texas, Arashiyama East females exhibited higher survival rates (55% survival of females to 18 years) than Arashiyama West females, while the curves for males were very similar in both groups. From these data, it appears that the pattern of survivorship was similar for males in Japan and Texas, plummeting during the adolescent years, while female survivorship was higher in Japan.

For the Arashiyama West group, known deaths and emigrations, calculated for the various age/sex classes and expressed per 1000 animals, are shown in Fig. 8 and Table II. Males and females showed similar rates only when immature, that is, the infant and juvenile category. The open columns indicate that known deaths (cadavers found) are differentially high for subadult and young adult males and for adult and old adult females. However, if emigrations, as represented by the hatched columns, are also

Table II. Deaths and Emigrations, February 1972-March 1979

Age interval (yr)	Deaths		Disappearance/emigrations		Deaths per 1000 ^a		Deaths/disappearance/emigrations per 1000 ^a	
	FF	MM	FF	MM	FF	MM	FF	MM
0-3	19	21	2	1	84	93	101	98
3-6	3	6	1	9	18	62	29	154
6-9	2	6	1	1	15	92	22	106
9-18	9	1	2	4	80	13	88	152
> 18	3	1	0	2	100	83	100	250

^aRaw frequencies are expressed per 1000 monkeys in each age/sex class.

considered, it is evident that a much larger proportion of mature males than mature females was lost to the population. At Arashiyama East more males emigrated while in the subadult and young adult phases, however, it is not at all uncommon in Japan for adult and old adult males also to leave the group. In Texas, adult and old adult males exhibited the highest rate of emigration.

From their arrival in Texas in 1972 until August 1979, when this study terminated, 96 monkeys either died or emigrated from the group. Of the original 150 monkeys that came over from Japan, 74 were still alive at the end of this study. Texas offered some unique causes of mortality for Japanese macaques, including local poisonous plants, predators, and parasites. However, mortality also occurred in Texas as it did in Japan, from neonatal death due to unknown causes, from illnesses such as heart disease and pneumonia, and occasionally from human interference.

The causes of group loss during the 8 years of the study can be summarized as follows. In 21% of the cases, cadavers were recovered, but autopsies were not possible. Many of these deaths (13% of the total loss) were neonatal. In other cases, immediate recovery of bodies allowed autopsies to be performed. Thus it is known that 10% of the losses resulted from management-related stress such as heat exhaustion during handling and release and electrocution on the fence. Almost all of the latter deaths occurred during and immediately after the 1972 release into the new enclosure. Another 10% were due to illness and pregnancy complications, 9% to demyelination resulting from toxins in the local plant, *Karwinskia humboldtiana* (see Joiner *et al.*, 1975), 8% from predation by bobcat and domestic dog (see Gouzoules *et al.*, 1975), 5% from infestation by screw-worm fly larvae (*Cochliomyia hominivorax*; see Clark and Mano, 1975), and 4% from wounding or trauma, sources unknown. Finally, in 33% of the cases, individuals simply ceased to appear at the study site. Five percent were less than 2 years of age and presumed dead, 4% represent the females that disappeared on the day after the release, and 24% were mature males, presumed to have emigrated.

CONCLUSIONS

In one of the few theoretical discussions of nonhuman primate demography, Altmann and Altmann (1979) concluded that demographic processes affect group size and composition, which in turn affect behavior and social relationships. To complete the cycle of effects, behavior itself can alter demographic parameters. The Altmanns considered, in particular, demographic "constraints" on behavior and social organization. They argued that many social phenomena assumed to be widespread (such as ex-

tensive kinship networks) are, in fact, dependent on large, expanding populations and that expanding populations are more characteristic of *provisioned* primate groups than nonprovisioned ones. However, Dunbar (1979, 1980) proposed that most primate field studies report *expanding* populations associated with group fission. His own study population of nonprovisioned geladas (*Theropithecus gelada*) increased at a rate of 12% per annum, a figure comparable to the population growth reported for many provisioned groups of monkeys (Drickamer, 1974; Koford, 1966).

In fact, nonprovisioned primate populations have been described in the literature as declining [e.g., Amboseli baboons and vervets (Hausfater, 1975; Struhsaker, 1976)], as stationary [e.g., toque macaques in Sri Lanka (Dittus, 1975, 1977, 1979, 1980)], and as expanding [e.g., geladas in Ethiopia (Dunbar, 1979, 1980) and baboons at Gilgil (Strum and Western, 1982)]. Rather than arguing that *most* primate populations exhibit any one of these trends, recent theoretical works, such as Caughley (1977), would suggest that natural populations experience phases of all three. Indeed, the groups of toque macaques studied by Dittus (1977, 1979, 1980) are reported to have shown all the phases of population growth, although the net growth of the population as a whole was zero.

As a result of its translocation from Japan to Texas, the Arashiyama West group experienced a temporary decline in population in the 2 years immediately following the move. This decline was brought about largely through lower natality and higher infant mortality. Caughley (1977) has suggested that lowered fecundity and higher infant mortality may be general indicators of declining populations in ungulates, and Mori (1980), Altmann *et al.* (1977), and our results indicate that this might also be true of Old World monkeys. That the stresses of the new environment⁵ had their greatest impact on the young is perhaps not surprising. However, the minimal impact of the translocation on other age/sex classes is noteworthy in light of the common assumption⁶ that peripheral adolescent males as well as the "elderly" of both sexes are the age/sex classes most expendable (in terms of reproductive potential) as well as vulnerable to environmental stresses, such as predation, lack of access to water, etc. Caughley has argued that what happens to the most vulnerable age group under different environmental conditions is the key factor in unraveling population processes. Thus, determining the most vulnerable age group in a population is an important step in predicting population dynamics.

⁵Climatic changes and new flora and fauna, including poisonous, predatory, and parasitic species.

⁶Especially in explanations of adult sex ratios; see, for example, Carpenter (1965), DeVore and Hall (1965), and Crook (1972).

Equally remarkable as the period of decline, however, is how quickly the population began to expand again and to return to demographic parameters similar to those reported from Japan. This is evident both in comparison to the 18 years of demographic data on the same group prior to its translocation and in comparison to the demographic trends reported for the sister group in Japan over the same time period. This indicates some consistency in the demographic patterns of the Arashiyama groups, even though the population experienced declining, expanding, and stationary phases. As Cohen *et al.*, 1980, pp. x, xvi) have noted,

... we would expect mechanisms and systems of population regulation to be fairly specific to particular populations or species.

... when observations in sufficient depth and detail are possible, it becomes evident that the actual population history of any species is a complex mix of homeostatic tendencies and of disruptive influences of the environment.

A characteristic demographic profile for a primate population or even a primate species could be related to endogenous mechanisms of population regulation, such as genetic and/or social factors, as well as to exogenous mechanisms. The impact of nutritional factors on female reproductive parameters in the Arashiyama West population will be explored in a separate paper (Gouzoules, S., *et al.*, in preparation). Interestingly, the Arashiyama West group has displayed stability in another aspect of its population biology—the timing of its mating and birth seasons (Gouzoules *et al.*, 1981). In the latter paper it was suggested that a phenomenon akin to social drift, enhanced by genetic separation, might lead to group-specific timing of the mating season. Some resistance of this group-specific timing to the immediate disruptive effects of environmental change was indicated by the fact that the onset and termination of birth seasons did not change significantly following the translocation from Japan.

It seems important to separate the two sets of processes that population biologists look for in animal populations, long-term processes tending to create and maintain stability (of which a stationary condition is but a special case) and short-term responses to environmental changes (which are no less significant for their brevity). The translocation of the Arashiyama West group to Texas has allowed us to begin to see, at least in part, how this population responded to a sudden and intense environmental change and then, by its return to previous patterns, to glimpse the longer-term processes at work.

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