

Japanese Monkey Group Translocation: Effects on Seasonal Breeding

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*A 150-member troop of Japanese monkeys (*Macaca fuscata*) was translocated from its temperate native habitat, near Kyoto, Japan, to a 42-ha enclosure near Laredo, Texas, in February 1972. The seasonal timing and distribution of 430 births recorded over the period 1954–1971 were compared to those of 186 births recorded in Texas from 1973 to 1979. Despite striking climatological and environmental differences between the pre- and the posttranslocation sites, the timing of the birth season remains unchanged, although the distribution of births was altered. These findings, considered in light of other published data on the seasonality of mating in macaques, suggest that a phenomenon akin to social drift may account for much of the intertroop variation that occurs.*

KEY WORDS: troop translocation; seasonal breeding; *Macaca fuscata*.

INTRODUCTION

Primate species that breed seasonally are particularly interesting to the reproductive biologist, and much research has been devoted to discovering what combination of internal and environmental factors serves to coordinate the members of a breeding population. The principal model en-

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visioned has involved an internal physiological rhythm synchronized by such environmental factors as photoperiod, temperature, and rainfall, as well as social factors in some species. The present paper concerns the translocation of a social group of 150 Japanese monkeys (*Macaca fuscata*) from its home range near Kyoto, Japan, to a 42-ha enclosure near Laredo, Texas, in February 1972. This geographic transfer provided the opportunity to examine the reproductive patterns of the group in two very different environments.

Of particular interest are a number of studies which suggest the existence of an annual rhythm in sexual potency that is, at least to some extent, independent of major environmental variables (Michael and Keverne, 1971; Michael and Wilson, 1975; Michael *et al.*, 1975; Michael and Bonsall, 1977, 1979). A persistence of the annual androgen rhythm in males subjected to constant laboratory conditions of photoperiod, temperature and food has been demonstrated to occur for up to three years (Michael and Bonsall, 1977). Michael *et al.* (1975) report that annual rhythms may, however, occur independently of changes in plasma androgen in laboratory experiments in which photoperiod was controlled, and they suggest that under appropriate environmental stimulation these rhythms "would be expected to be entrained to enhance the male's fertility" (p. 172). Males were tested in the latter experiments with ovariectomized females treated with estrogen. The significance of such social stimulation to the maintenance of endogenous rhythms was demonstrated by Gordon and Bernstein (1973), who found that males living in outdoor enclosures, but deprived of females, failed to show increased hormonal or sexual behavior levels at the appropriate time of the year. Also, Vandenberg and Drickamer (1974) were able to bring males in a free-ranging group into a sexually active and fertile condition by introducing into the group females that were made sexually receptive out of season by estradiol benzoate implants.

Vandenberg (1973) has suggested that "a primary timing influence from the environment only sets the stage for mating and social factors act as proximal stimuli to initiate the actual onset of mating" (p. 16). Environmental factors, particularly photoperiod, act upon neuroendocrine mechanisms to induce an overall synchrony to the mating season, and within that season, "social stimuli acting through behavioral and endocrine mechanisms" effect a coordination within a particular breeding population. Photoperiod seemed the most likely major environmental factor operating in this model; a number of other fluctuating variables such as temperature, vegetation changes, and rainfall were considered and rejected.

Evidence cited in support of even photoperiod as the significant environmental factor in coordinating macaque breeding is, in fact, sparse.

Michael and Bonsall (1979, p. 283) argued that since rhesus monkeys (*Macaca mulatta*) in the Southern Hemisphere (in Australian zoos and on an island near Rio de Janeiro, Brazil) show a 6-month shift in the breeding season, photoperiod is implicated. However, Vandenberg (1973) reviewed the available evidence on this point and concluded that the data are actually too few to substantiate the contention. The Ilha do Pinheiro reference concerns Koford's 5-day visit to the colony in 1962 and was based on the incidence of pregnancy and the ages of young in the population, not birth data. The Australian zoo data come from a 1930s survey by C. G. Hartman: Vandenberg (1973) observed that "a six month reversal from the peak in the northern hemisphere" was revealed in the survey data, although the sample size was small ($N = 39$) and births were recorded in every month of the year but one. Vandenberg went on to note that an argument against photoperiod is supported by observations on two Puerto Rican colonies, Cayo Santiago and La Parguera, which, although at the same latitude, breed with a 90-day difference in birth season peak.

Japanese monkeys also manifest a distinct mating and birth season. Kawai *et al.* (1967) have provided the most detailed examination of the annual reproductive cycle in this species. Intergroup differences in the timing of the birth season were apparent from birth data collected on 25 groups, ranging through much of Japan between latitude $31^{\circ}22'N$ and latitude $41^{\circ}15'N$. Precise causal relationships between the timing of the birth season and environmental factors such as latitude, rainfall, temperature, nutrition, and social factors were not obvious from the data. The different groups of monkeys did seem to fall into three birth season temporal patterns (Fig. 1), with birth peaks in April, May, and June.

Van Horn (1980) performed a regression analysis on the data of Kawai *et al.* (1967) and concluded that the results were consistent with a photoperiod hypothesis of reproductive regulation. Additionally, he presented data collected over a 7-year period by G. G. Eaton on the Oregon troop of Japanese monkeys (another translocated group) located at latitude $45^{\circ}N$, at least 8° further north than the most northerly troop for which reliable data from Japan exist. According to Van Horn's regression analysis, the season of conceptions at Oregon should come significantly earlier than those of the Japanese troops. However, the mean conception date for the Oregon troop did not fall as early as the regression line for the data from Japan predicted. Van Horn nevertheless proposed that, taken as a whole, the birth season data suggested a regulatory relationship between annual photoperiod cycles and reproductive activity; outliers, such as the Shodoshima troops, were assumed to be genetically distinct, with different thresholds to environmental stimuli than the majority of troops. He thus advocated a more direct link to photoperiod than have previous investigators.

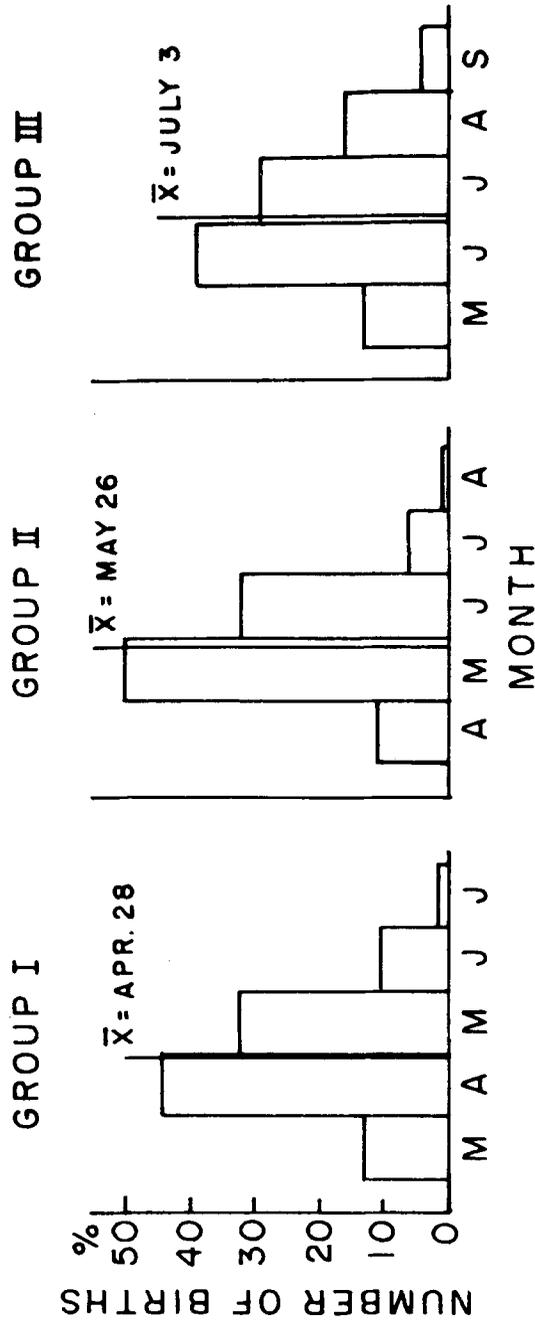


Fig. 1. Birth season temporal patterns of Japanese monkeys [from Kawai *et al.* (1967)].

METHODS

The Arashiyama population of Japanese monkeys was studied for 18 years by a number of Japanese scientists prior to the translocation of one of the two social groups to Texas. Koyama *et al.* (1975) have presented data on the distribution of 430 births over the period 1954-1971 for the Arashiyama monkeys (Fig. 2). These data provide information on a relevant aspect of Japanese monkey reproduction: the timing and distribution of births within the season of the year during which parturition occurs. The large number of births recorded, as well as the period of time over which the data were collected, provides a firm set of population data against which similar data from the translocated group of monkeys can be compared.

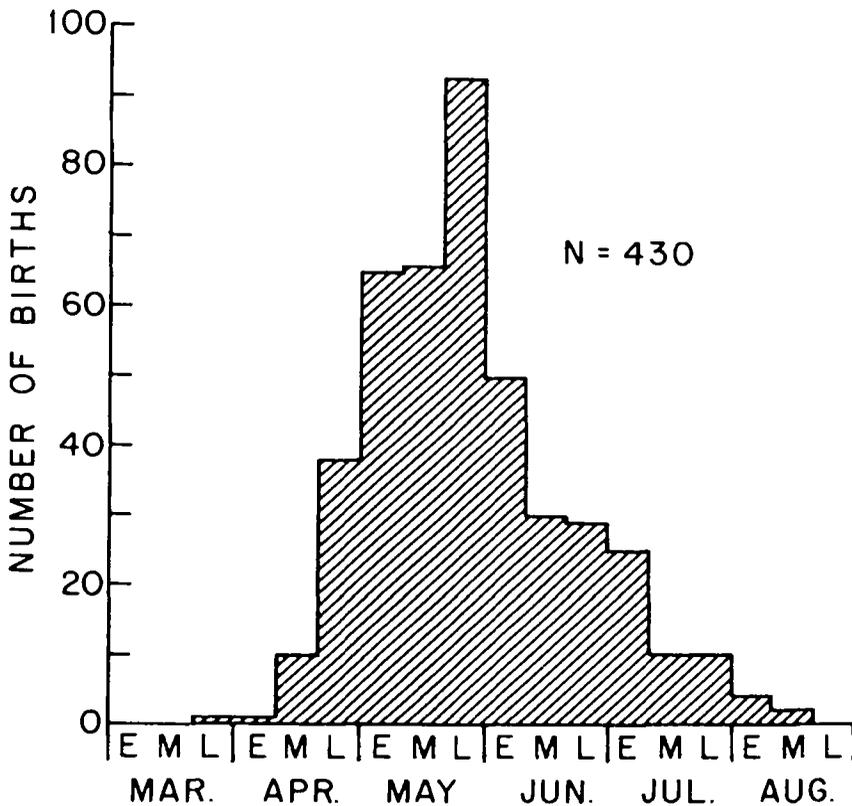


Fig. 2. Distribution of Arashiyama births, 1954-1971 [from Koyama *et al.* (1975)].

A comparison of certain aspects of the monkeys' pre- and postranslocation habitats is useful. Arashiyama is a mountain which lies on the outskirts of Kyoto, Kyoto Prefecture, Japan (latitude 35°00'N and longitude 135°40'W). The translocation site is located about 48 km northwest of Laredo, Texas, at latitude 28°05'N and longitude 99°23'W, thus falling about 5° south of the most southern point in the range of *Macaca fuscata fuscata*. Physiographically, the pre- and postranslocation sites differ considerably, and the striking contrast in weather patterns between the two sites is highlighted in the comparative climatograph in Fig. 3. The Laredo area clearly presents a much hotter and drier environment at all times of the year. Arashiyama mean monthly temperatures never exceed 30°C, and daily highs exceed 30°C only in July and August. Laredo mean monthly temperatures exceed 30°C during June through September, and daily maximum temperatures exceed 30°C from April through October. Arashiyama experiences a peak period of precipitation in June and July, following the birth peak which occurs in May. Laredo receives most of its annual precipitation (nearly 40%) in 2 months, September and May, and in these 2 months the mean monthly precipitation barely exceeds that of the driest months in Arashiyama.

In Texas, from 1972 to 1980, the monkeys ranged over a 42-ha enclosure surrounded by an 8-ft electric fence. Human intervention was minimal, and although given supplemental food provisions (as the monkeys of Arashiyama have received since 1954), the monkeys foraged on local plants and animals for much of their food.

In the present analysis, the first infants born in Laredo, in the spring of 1972 following translocation, are not included as they were conceived in Japan. This paper considers six birth seasons for which exact birth dates for 186 infants were recorded during the period 1973–1979. The distribution of the 186 births recorded after translocation is compared to a theoretical expected distribution calculated from the distribution of births at Arashiyama ($N = 430$) recorded prior to translocation (Fig. 2).

As noted above, simple, direct cause-and-effect relationships have not been established between any particular environmental factor and reproductive timing in macaques. Decreasing day length probably sets the stage for mating activities, but other factors, including social influences, are likely determinants of the finer timing. Predictions regarding the troop's mating and birth season patterns in Laredo would thus be tenuous at best, given the complex biological causality involved. However, to facilitate discussion of the data from the transplant site, we offer the following considerations:

(1) Is the temperature critical to conception? Kawai *et al.* (1967) reported that the maximum temperature at which conception first occurs is

always below 30°C. Thus the start of the birth season in Laredo should be delayed. Daily maximum temperatures there exceed 30°C from April through October, and at Arashiyama, Japan, conceptions occurred as early as September.

(2) Does photoperiod serve to fine-tune the timing? Laredo is about 5° south of the most southern point in the range of *Macaca fuscata*. The timing of the birth season might thus shift toward that of the more southerly troops on Kyushu, i.e., shift from a Group II pattern to a Group III (later) pattern (Fig. 1).

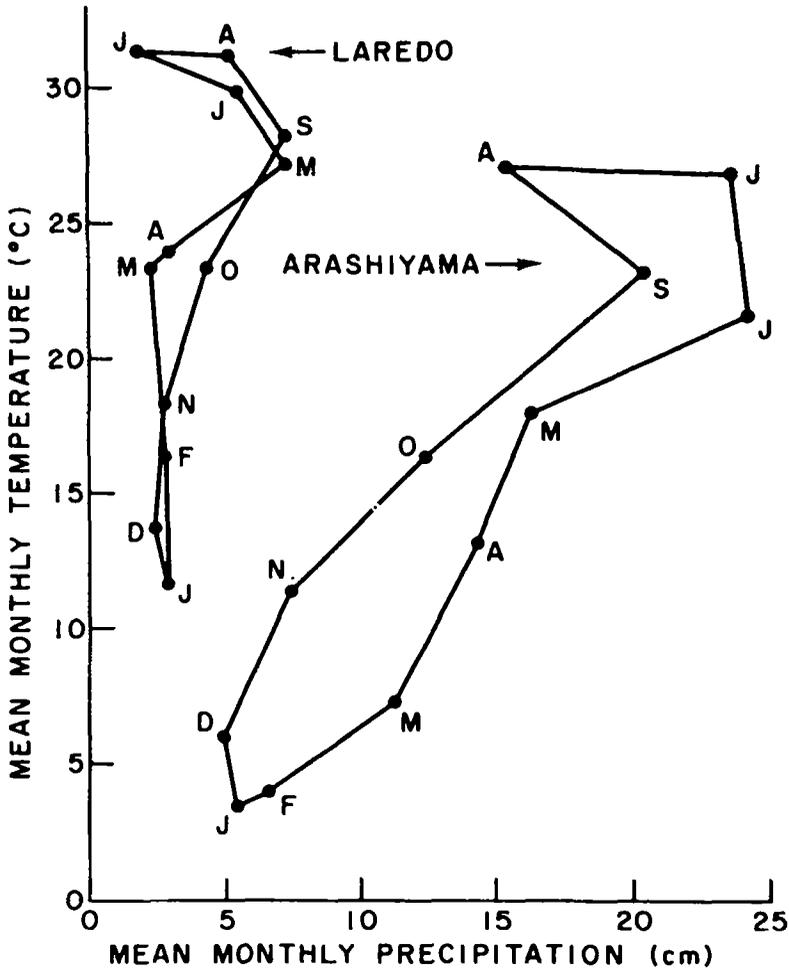


Fig. 3. Comparative climatograph of Arashiyama and Laredo.

(3) Does peak rainfall serve as a timing cue? The earliest conceptions at Arashiyama, Japan, occur in late August and early September, following the 2 wettest months of the year. July is the driest month at Laredo, but August and September show increases (see Fig. 3). The resulting prediction would have the birth season delayed at Laredo, as would predictions 1 and 2 above.

These predictions involve a temporal shifting of the onset and termination of the birth season, and not the possibility of distributional changes within a constant temporal pattern.

RESULTS

The distribution of the 186 births recorded after translocation, along with the expected distribution of births calculated from the 430 births recorded for the troop in Japan, is presented in Fig. 4. The onset of the birth season has continued to be in late March. At Arashiyama the birth season tended to decline from a peak in late May and terminate by the middle of August; while no births have been recorded in August in Laredo, one early September birth (September 1) did occur. In Laredo, 41.4% of the births have come in May, compared to more than 50% ($N = 222$) at Arashiyama. A chi-square goodness-of-fit test of the two birth distributions shows a significant difference ($\chi^2 = 42.3$, $P < 0.01$) (small frequencies at the tails of the distributions combined). Apparently there has not been a shifting of the birth season in terms of onset and termination dates; instead, a flattening of the peak has occurred, producing a more platykurtic distribution of births. May continues to be the peak month of births in Laredo, as it was at Arashiyama, but the peak is less sharp. The Arashiyama birth season peak was well defined and fell in late May, with 41.9% of the births coming prior to this time and 36.9% after. In Texas, with the late-May peak less well defined, 45.2% of the births occurred prior to late May and 39.2% after that time. Thus, a larger proportion of the births has taken place earlier in the birth season in Texas than had been the case at Arashiyama.

The patterns observed at the Laredo translocation site therefore do not confirm the predictions considered above, all of which suggested a delayed onset and termination to the birth season. Despite the similarity in the direction of these predictions, which were based on hypotheses involving several environmental factors (temperature, photoperiod, and peak rainfall), no such trend was detected, either by a consideration of all 186 births (cumulative distribution) or by a year-to-year assessment (Table I).

These conclusions are relevant only in reference to the onset and termination of the birth season. The statistically significant change in the

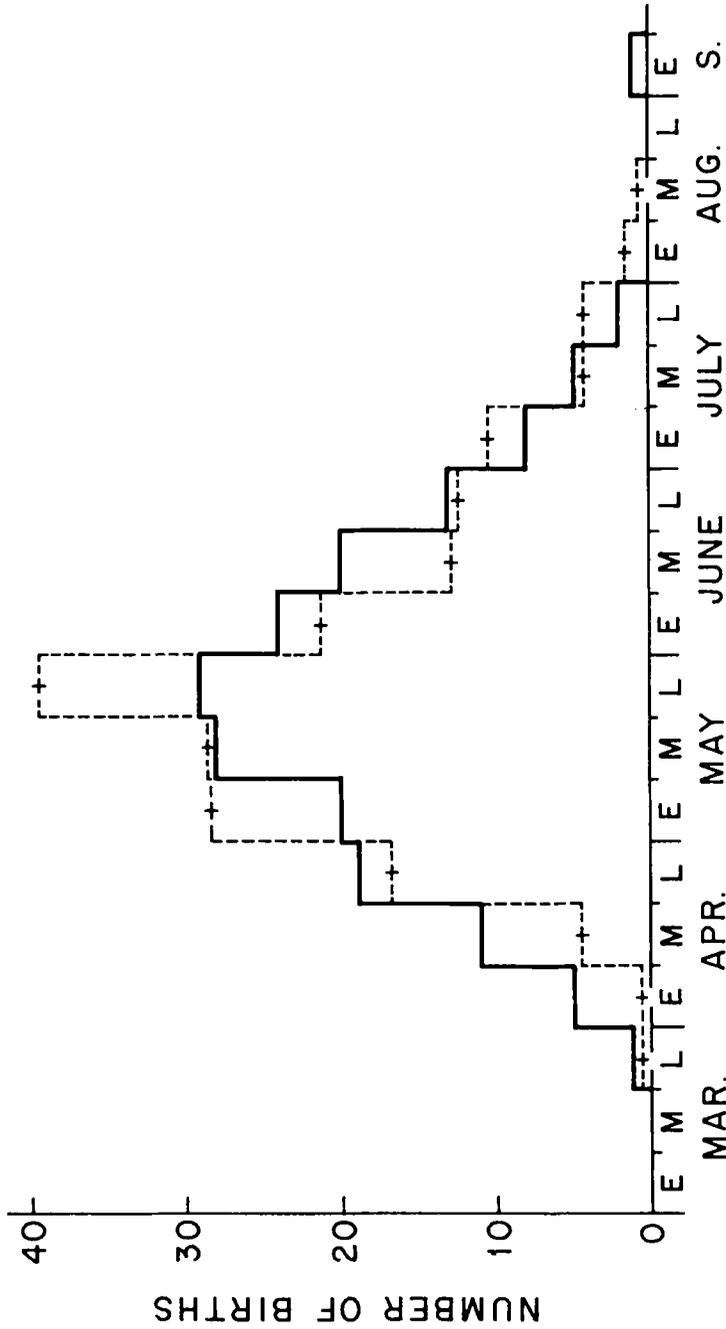


Fig. 4. Distribution of recorded Laredo births and the expected distribution from Arashiyama data. (-----) Expected; (—) observed.

Table 1. Monthly Distribution of Births in Texas for Each Year (1973-1979).

MAR.	APR.			MAY			JUNE			JULY			AUG.			SEPT.			TOTAL	
	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L		
			1	1	2		1	2											1973	7
				1	3		6	5	4	7	3	2							1974	31
		1		3	4		2	2										1	1975	22
				4	3		2	3	2										1976	33
				9	7	6	3	7	1		1								1978	47
				4	6	11	11	4	2	1	1								1979	46
				20	28	29	24	20	13	8	5	2							OBS.	186
EXP:	.37			16.4	4.3		21.6	12.8	12.5	10.8	4.3	4.3				0.7		0		

distribution of births reported above did not involve this type of temporal shift.

DISCUSSION

Vandenbergh (1973) argued that a decreasing day length and an as yet unknown complex of extrinsic and intrinsic factors serve to coordinate mating activities within a particular period of the year (autumn and early winter), but that differences between populations may be a matter of more immediate factors. Social factors were suggested as possibly significant determinants at this level. Observations following the translocation of 31 rhesus monkeys from Cayo Santiago to La Parguera (Varley and Vessey, 1977) supported this hypothesis. As noted above, these two populations, though at the same latitude, show birth seasons that differ in their peaks by 90 days. The translocated Cayo Santiago monkeys shifted to the La Parguera pattern in the course of 2 years.

No such dramatic shift occurred with the Laredo Japanese macaques, perhaps because there were no external social forces to promote a change. With this speculation in mind, it is perhaps worthwhile to reconsider the intertroop variability seen among different groups of Japanese monkeys in terms of the temporal patterning of the birth season. Kawai *et al.* (1967) found no causal relationships between various environmental factors and the three temporal patterns (Fig. 1) that were apparent from their data on 25 troops. Temporal patterns of the birth season did seem to relate most strongly to geographic locations: the groups on the island of Kyushu exhibited pattern 3; those on Shodoshima Island, pattern 1; and those on Honshu, pattern 2. This relationship is even stronger if groups that had been translocated or artificially formed ($N = 6$) are excluded from the classification. Furthermore, if only groups for which four or more birth seasons had been recorded are used, a very strong argument for "regional differences" in the timing of the birth season can be made. Social and possibly even genetic separation of populations may contribute to this phenomenon.

Support for the latter hypothesis comes from research by Nozawa *et al.* (1975) on genetic variation within and between troops of *M. fuscata*. Their study used genes controlling blood-protein polymorphisms as markers. Analyses of correlations between geographic and genetic distances among troops revealed that the gene constitutions of two troops separated by more than 100 km could be regarded as virtually independent of one another. These results suggested that the populations of Japanese macaques studied had split into a number of local demes in which random genetic drift could prevail. Perhaps the regional differences seen among Japanese monkey groups in terms of mating season timing are due to a phenomenon akin to

social drift (Wilson, 1975), enhanced also by the genetic separation known to exist.

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