

Determinants of reproductive seasonality in the Arashiyama West Japanese macaques

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Introduction

Reproductive seasonality has been well documented in Japanese macaques (*Macaca fuscata*) (Tokuda, 1961-2; Kawai, Azuma & Yoshiba, 1967; Nigi, 1976; Eaton *et al.*, 1987; Gouzoules, Gouzoules & Fedigan, 1981). A number of possible influences on the timing of annual cycles have been identified, for example photoperiod, temperature, rainfall patterns, endogenous circannual rhythms, social synchrony and social drift. General reviews of primate seasonal reproduction (Lancaster & Lee, 1965; Van Horn, 1980; Lindburg, 1987) all refer in some detail to the data on Japanese macaques, which show that the exact timing of birth seasons, and by inference mating seasons, in different populations varies along a latitudinal gradient. The further south a monkey group is located in Japan, the later in the calendar year its mean dates of conception and parturition. Each group has a characteristic timing that is relatively consistent over the sampled years (Kawai *et al.*, 1967). One inference that may be drawn from this relationship between reproductive timing and latitude is that various seasonal, environmental factors that also vary along a latitudinal cline (e.g. photoperiod and, to a lesser extent, daily minimum/maximum temperatures and rainfall patterns) may act as necessary proximate cues to modulate endocrine and reproductive functions. A second inference, however, which may be drawn from these data showing that regional populations in Japan characteristically conceive and deliver young at different mean dates, is that seasonal environmental factors have exerted their effects over evolutionary time by altering gene frequencies in the separated populations.

This chapter compares the seasonal timing of births in the Arashiyama population in Japan (at latitude 35° 00' N) during a 15-year period to that of the descendant Arashiyama West population in Texas (at latitude 28° 05' N) over a subsequent 15-year period. The fundamental question

addressed is whether the birth season (and inferentially, the breeding season) has shifted in time in the Texas habitat. The translocation of the Arashiyama West group from Japan to Texas and the ongoing data collection at both sites offer a unique opportunity to examine the effects of extrinsic and intrinsic factors on seasonal reproduction. No other primate population has been studied over many annual breeding cycles in its native habitat and then moved as an entire group to a new location that differs extensively in the environmental cues for reproductive seasonality.

A distinction between the proximate and ultimate effects of environmental factors is made in most descriptions of seasonality in animals (e.g. Baker, 1938; Sadleir, 1969; Jones, 1981; Bronson, 1989). Ultimate effects refer to environmental factors (such as food availability) that exert selective pressure to restrict reproductive activities to a particular time of the year, whereas proximate effects refer to the 'fine tuning' of reproductive seasonality within a narrower time frame, primarily through the immediate impact of extrinsic factors on physiological processes. In species, such as monkeys, that exhibit long periods of gestation and lactation, the proximate cues will be separate in time, and different in nature, from the 'optimal season factors' that select for annual cyclicity.

In addition, Gwinner (1981, 1986) has noted that some species may evolve emancipation, or 'uncoupling' from all extrinsic effects by incorporating seasonal timing into an endogenous circannual rhythm. The presence of an internal circannual 'clock' has been demonstrated through experimental research on many vertebrate species (see references in Gwinner, 1986). Furthermore, some captive studies of rhesus macaques (e.g. Michael & Bonsall, 1977; Michael & Zumpe 1978; Wickings & Nieschlag, 1980) have found that male monkeys maintain seasonality of reproductive functions over several years even under constant and controlled laboratory conditions. Finally, Nozaki, Oshima & Mori (1990) concluded that individually caged Japanese monkeys (both intact and chronically estradiol-treated ovariectomized females) exhibited striking circannual variations in endocrine levels, appropriate to the breeding and non-breeding seasons.

Of the several environmental factors that have been suggested to modulate annual patterns, photoperiod has received the most empirical support (e.g. Sadleir, 1969; Immelman, 1973; Herbert, 1977; Hoffman, 1981; Gwinner, 1981, 1986). Seasonal change in daylength is the meteorological variable that is most correlated with latitude and is the most consistent, and thus reliable, from year to year. Observational research on mammals that occur over wide geographical areas, such as hamsters, deer

and lagomorphs, has often found that the timing of breeding seasons follows a latitudinal gradient, and thus a photoperiod cline. In addition, a large body of experimental research has demonstrated that alterations of light/dark cycles in the laboratory can affect the endocrine status of a variety of vertebrates (Sadleir, 1969; Hoffman, 1981; Bronson, 1989). However, the relationship between light and reproductive cycles is a complex one and varies from species to species. Several hypotheses, such as the 'hourglass' system and the 'Bunning model', have been proposed to explain how photoperiod might act as a proximate cue for the onset of mating. It is sometimes argued that monkeys inhabiting the tropics would experience very little seasonal change in daylength. However, many organisms exhibit a very precise 'critical photoperiod' and one interpretation is that they are sensitive, and can respond, to very small changes in daylength. Furthermore, the 'Bunning' model, proposes that neither changes in daylength nor the changing ratio of light to dark are the cueing factors: rather the critical photoperiod occurs when light coincides with a particular phase of the intrinsic rhythm of sensitivity in the organism.

In terms of primates, support for the hypothesis that photoperiod regulates annual breeding seasons comes from the six-month reversal found in rhesus macaques living in zoos in the southern hemisphere (e.g. Bielert & Vandenberg, 1981). Also, Van Horn (1980) reanalyzed data from Kawai *et al.* (1967) on Japanese macaques, as well as data from a variety of sources on lemurs and rhesus monkeys, to argue that photoperiod cycles are the primary regulatory factor ('zeitgeber') in the reproductive seasonality of anthropoids. He further concluded that Japanese macaques respond to a critical daylength of slightly less than 12 hours.

In contrast, Rawlins & Kessler (1985) argued that changes in photoperiod at the latitude of Cayo Santiago (18° N) are not sufficient to bring about seasonality in the rhesus monkeys found there, and reiterated that two groups, located at the same latitude but on different islands, exhibit different timing. These two researchers analyzed eight years of rainfall and temperature data and concluded that Koford's (1965) original hypothesis was correct. Koford postulated (and see also Vandenberg & Vessey, 1968) that the onset of spring rains triggers the onset of the mating season in the Cayo Santiago rhesus monkeys. Building on this postulate, Rawlins & Kessler (1985) suggested that photoperiod sets the temporal limits of annual seasonal reproduction, while the onset of annual spring rains regulates reproductive activity *within* that range.

Kawai *et al.* (1967) also considered a number of environmental variables correlated with latitude in their survey of Japanese monkey groups, and

concluded that the relationship between extrinsic factors and reproductive timing was not simple. However, they did note that conceptions did not begin until the daily maximum temperatures dropped below 30 °C in all of the 25 groups studied across Japan. They also grouped 25 populations into three patterns of reproductive timing: northerly, middle range and southerly group patterns.

We suggest that if environmental factors act primarily as proximate cues for the onset of spermatogenesis, ovulatory cycles and conception, then the breeding and birth seasons should have shifted in Texas as compared to the Japanese pattern in accordance with the altered environmental cues (i.e. to a more southerly pattern). Conversely, if the environmental factors that vary according to latitude in Japan have acted primarily to select for stable, endogenous circannual rhythms in geographically and genetically separated populations of monkeys, then the timing of reproductive seasonality in the Arashiyama West group should have remained consistent with the pattern of origin, even after the monkeys were moved to a new habitat.

Gouzoules *et al.* (1981) previously compared the timing of the birth seasons in Arashiyama, Japan to birth dates from six of the first years in Texas, and found that the onset and termination of the seasons remained unchanged in the new habitat, although the distribution of births was altered. Their finding of a characteristic and stable group-timing for reproductive seasonality, which was maintained in the population even as the habitat changed, led the authors to suggest that the regional differences seen among Japanese monkey groups in terms of the birth season are due to a phenomenon akin to 'social drift', enhanced by the genetic separation known to exist between groups. Some researchers have argued that when seasonal animals maintain their circannual rhythms under new conditions it may be due simply to 'refractoriness' (e.g. Sadleir, 1969; Hoffman, 1981; Jones, 1981), and that experimental studies which transport seasonal organisms to new conditions must be conducted over many breeding cycles. The present paper extends Gouzoules *et al.* (1981) by comparing 15 years of data from Texas with 15 years from Japan, and by examining daily rainfall, temperature and photoperiod patterns in relation to various aspects of reproductive timing in Texas.

Methods

The study subjects were the breeding age females in the Arashiyama and descendant Arashiyama West (AW) populations of Japanese macaques that have been studied by Japanese and Western primatologists from 1954

to the present (for details, see Fedigan & Asquith, 1991). This population, which numbered 34 on first contact, fissioned into two daughter groups in 1966; these were named Arashiyama A and B. Six years later, in 1972, one of these two daughter groups (Arashiyama A) was translocated almost in its entirety (150 out of 158 group members) to a large ranch in southern Texas and renamed the Arashiyama West group. Most of the breeding females in the early years in Texas had previously given birth in Japan, and thus constitute a cohort that was sampled, and then translocated and sampled again. However, over the years, younger females who were born in Texas reached reproductive maturity and became part of the sample.

For the past 38 years, with the exception of 1977, the exact birth dates and identity of the mothers of virtually all infants born into the Arashiyama groups have been recorded. This paper analyzes 30 of these birth seasons, those from 1957–71 in Japan, and 1974–89 in Texas. The first three years of data from Japan were deleted due to small sample sizes and missing data points. In the Texas data set, the 1972 birth season was deleted because the monkeys arrived from Japan already pregnant, 1973 was deleted due to an unusually small sample size of births ($n = 7$), and 1977 was not included because exact birth dates were not available. Birth dates for 416 infants born in Japan and 790 infants born in Texas were used in the analyses.

The timing of a birth season has at least six components: the dates of onset, termination, mean birth and median birth, the length of the season and the frequency distribution of birth dates. Since the median birth date (and inferred median conception date) is the least affected by outlying observations, we focused primarily on it. Earlier studies of seasonally breeding macaques, such as that of Drickamer (1974), have shown that any female's exact date of parturition in a given year may be affected by her recent reproductive history (e.g. when she last gave birth, and whether the infant survived). On the assumption that the median conception/birth date is the measure of the group's reproductive timing least affected by such individual life history variables, we use it to best-represent the 'core timing' of the season. (See also Lindburg's (1987) comments on the preferability of the median over the mean or onset dates.) Conception dates were calculated by counting back 173 days from birth dates (Nigi, 1976), and all dates are presented as consecutive days in the Julian calendar (1–365). Descriptive data on all six components are presented; standard parametric and non-parametric tests (analyses of variance, *t*-tests, Kolmogorov–Smirnov tests, regression analyses), from the SPSS PC package, were used to compare the results from Japan and Texas. Daily maximum and minimum

temperatures and daily rainfall patterns between 1974 and 1989 in Laredo and San Antonio, Texas, were obtained from the National Climatic Data Center. Daylength was calculated by Dr D. Hube of the University of Alberta, by interpolating from data provided in the *Observers' handbook*, Royal Astronomical Society of Canada, and checked against sunrise/sunset charts provided by the US Naval Observatory.

Results

Components of reproductive timing in the Arashiyama monkeys in Japan and Texas

To control for the possibility that the timing of the birth season was more variable in one location than another, F_{\max} tests were run. When the variances were homogeneous ($p > 0.05$) a pooled variance t -test was carried out; when variances were heterogeneous ($p < 0.05$) a separate variance t -test was used. Only one of the variables, mean birth date, proved to be heteroscedastic.

Table 17.1 displays descriptive data for five components of the birth season: dates of mean and median births, and onset, termination and length of the season. It can be seen that the mean birth date shifted slightly forward in Texas. Thus, day 148 (28 May) was the mean birth date for the 15 years in Japan as compared to day 143 (23 May) in Texas. However, the difference was not significant ($t = 1.74$; $df = 22.27$; $p = 0.095$).

The median birth date was nearly the same in both locations: day 143 in Japan, day 142 in Texas ($t = 0.53$; $df = 28$; $p = 0.602$). Table 17.1 also shows that the mean date for the onset of the birth season in Japan (day 113, 20 April) shifted forward by 20 days to the mean onset date in Texas (day 91, 31 March), which was a significant difference ($t = 4.23$; $df = 28$; $p = 0.000$), but the termination dates were similar (day 206, 25 July, in Japan, and day 207, 26 July in Texas; $t = -0.24$; $df = 28$; $p = 0.810$).

The mean length of the birth season was significantly longer in Texas, having increased from 92 days in Japan to 117 in Texas ($t = -2.39$; $df = 28$; $p = 0.024$). However, there were, on average, nearly twice as many infants born in a Texas season (52.7) as compared to a Japanese birth season (27.7), and regression analysis showed that the length of the season was related to the number of infants born ($r^2 = 0.57$; $F_{1,28} = 13.31$; $p = 0.001$). Furthermore, an analysis of co-variance demonstrates that the relationship between the length of the season and the number of births was not significantly different in the two locations ($F_{1,27} = 0.15$; $p = 0.703$).

Table 17.1. *Timing of the birth seasons*

Site	Year	Mean	Median	Onset	Termination	Length	No. births
Japan	57	152.0 ^a	145	121	201	80	13
Japan	58	147.7	146	121	183	62	11
Japan	59	147.2	145	118	215	97	15
Japan	60	153.0	149	127	177	50	22
Japan	61	152.0	149	130	179	49	16
Japan	62	154.9	150	126	192	60	21
Japan	63	146.2	142	108	212	104	25
Japan	64	142.9	142	99	215	116	27
Japan	65	141.4	135	101	252	151	35
Japan	66	149.3	143	114	203	89	40
Japan	67	159.3	149	120	211	91	38
Japan	68	148.8	144	118	210	92	32
Japan	69	142.0	137	85	224	139	45
Japan	70	143.1	133	105	198	93	28
Japan	71	137.9	136	107	218	111	48
Mean		147.9	143	113.3	206	92.3	27.7
Texas	74	172.9	172	137	205	68	31
Texas	75	144.4	139	84	247	163	22
Texas	76	133.9	129	99	190	91	35
Texas	78	135.0	131	93	201	108	43
Texas	79	147.2	150	100	200	100	43
Texas	80	130.6	129	67	196	129	40
Texas	81	131.5	129	93	180	87	56
Texas	82	137.1	136	81	183	102	52
Texas	83	139.2	143	88	193	105	57
Texas	84	147.9	149	71	233	162	79
Texas	85	144.3	146	96	224	128	57
Texas	86	140.6	145	73	194	121	78
Texas	87	145.7	144	99	244	145	70
Texas	88	143.1	142	87	204	117	46
Texas	89	145.5	145	94	223	129	86
Mean		142.6	142	90.8	207.8	117	53

^aDates are expressed as days in the Julian calendar (1-365).

Thus, the seasons were the 'same' length in Japan and Texas when adjusted for the number of births.

There was also a significant relationship between the onset date and the number of births per season, when all 30 years are considered ($r^2 = 0.423$; $F_{1,28} = 20.59$; $p = 0.0001$), but there was no significant relationship between the termination date and the number of infants born. This indicated that, as more infants were born, the likelihood increased of an

Table 17.2. Cumulative proportions of births in different intervals of the season

Period	Month	Japan	Texas	Difference
Early	March	0.00	0.10	-0.10
Middle	March	0.00	0.40	-0.40
Late	March	0.20	1.20	-1.00
Early	April	0.50	4.80	-4.30
Middle	April	2.90	11.40	-8.50
Late	April	11.80	22.50	-10.70 ^a
Early	May	27.20	35.60	-8.40
Middle	May	43.80	47.20	-3.40
Late	May	65.40	64.90	0.50
Early	June	76.90	78.00	-1.10
Middle	June	83.90	86.30	-2.40
Late	June	90.40	91.60	-1.20
Early	July	94.70	96.20	-1.50
Middle	July	96.90	98.30	-1.40
Late	July	98.60	99.10	-0.50
Early	August	99.50	99.40	0.10
Middle	August	99.80	99.60	0.20
Late	August	99.80	99.70	0.10
Early	September	100.00	100.00	0.00

^aLargest unsigned difference (D) = 10.70.

earlier birth date and thus of a longer season. However, an analysis of co-variance showed that the relationship between the onset dates and the number of births was marginally significantly different in the two locations ($F_{1,27} = 3.87$; $p = 0.059$). Thus, even when adjusted for the number of births per season, the onset of reproduction could be said to be somewhat earlier in Texas than Japan.

The sixth component of seasonal timing, the distribution of birth dates, was compared for Japan and Texas with a Kolmogorov-Smirnov test (Sokal & Rohlf, 1981). Birth dates were divided into 19 intervals, three time periods per month (early, middle and late), from early March to early September, and the cumulative proportions of births in each consecutive time period were calculated. Table 17.2 shows that there was a significant difference (D) between the distribution of birth dates in Japan and Texas ($D = 10.7$, $p < 0.01$).

To further examine the comparative distributions, the 416 births in Japan and 790 in Texas were plotted as percentages per month of the season (Fig. 17.1). Again, each month was divided into early, middle and late periods. From Fig. 17.1 it can be seen that the peak period of births in both Japan and Texas was in late May. However, in Japan, the late May birth

peak was greater than the one in Texas (53.6% of all births occurred in May in Japan, compared with 42.4% in Texas). Also, a smaller percentage of births occurred in April in Japan (11.5%) than in Texas (21.3%). The percentages of infants born in June and July were quite similar in both locations (June: 25% vs 26.7%; July: 8.2% vs 7.5%), and there were very few births in March, August or September in either location. Thus, the significant difference that was found in the overall distributions of birth dates in Japan and Texas (Table 17.2) can be attributed primarily to differences occurring in the months of April and May. Although similar proportions of births had taken place in both locations by the median birth dates of 23 May (Japan) and 22 May (Texas), a higher proportion of births were distributed in May in Japan and April in Texas. This may indicate a slight shift forward into April of the birth season in Texas, a shift forward that was also suggested by the somewhat earlier onset and mean birth dates in Texas as compared to Japan.

Comparison of the Arashiyama monkeys with other populations of Japanese macaques

Overall, the two distributions of birth dates in Fig. 17.1 look very similar. However, the Kolmogorov-Smirnov test is highly sensitive to sample size and it is, perhaps, not surprising that significant differences were found between the 416 birth dates from Japan and 790 from Texas. A more revealing question might be how the patterns of Arashiyama and AW birth dates compare to the timing of the birth season in other populations of Japanese macaques. Kawai *et al.* (1967) presented birth data for 25 groups in Japan, located at latitudes ranging from 31° N to 41° N. From these data, they concluded that each group has a characteristic timing of its birth season that is more or less fixed. Some of these 25 groups were sampled for fewer than 4 birth seasons or 10 birth dates, however, and several groups had been translocated from their original sites. Thus, for his subsequent analysis, Van Horn (1980) chose only those 11 of the 25 groups that were adequately sampled and still living in their original locations. With this sample, he was able to demonstrate a highly significant correlation between latitude and mean birth dates.

Following Van Horn, we also selected birth data from these 11 groups and plotted the mean conception date of the groups as a function of latitude (Fig. 17.2). As reported previously by Van Horn (1980), we found that there is a significant linear relationship between the latitudinal location of these Japanese macaque groups and the timing of their birth seasons ($r^2 = 0.79$,

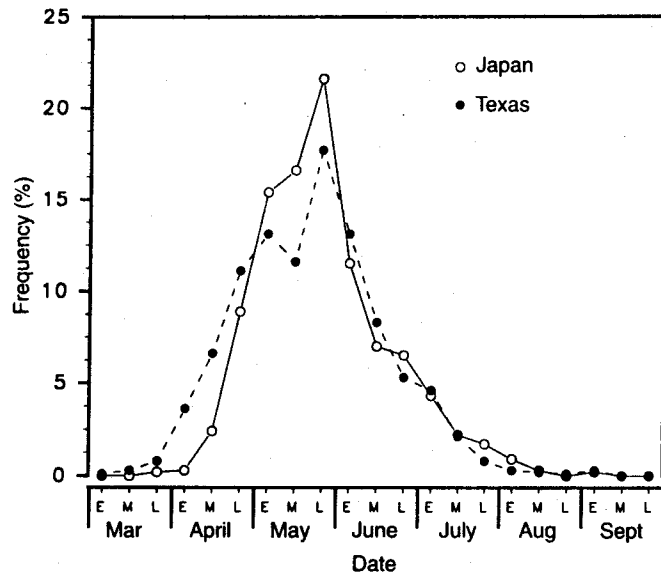


Fig. 17.1. Distribution of birth dates in Japan (1957-71, $n = 416$) and Texas (1974-76, 1978-89, $n = 790$), plotted as percentages per month of the season. Each month is divided into early (E), middle (M) and late (L) periods.

$F_{1,9} = 33.7, p = 0.0003$). Figure 17.2 also displays the mean birth date from AW according to its Texas location at 28°N ; this group falls far off the regression line for Japanese macaque groups. However, if plotted according to its 'site of origin', rather than transfer site, the AW group falls appropriately on the regression line.

Environmental factors and the timing of reproductive events in Texas

It has already been demonstrated that the study group did not shift to a later breeding season when translocated to a more southerly location (as predicted by the hypothesis that photoperiod, or some aspect of the correlation of seasonal light/dark ratios with latitude, is a proximate determinant of reproductive timing), therefore comparative daylength data at the two sites are presented here simply for descriptive purposes. Table 17.3 shows daylight hours in Kyoto, Japan and Laredo, Texas, calculated as the interval between sunrise and sunset. From this it can be seen that, during the longest day of the year, 21 June, daylength in Kyoto is 34 minutes longer than in south Texas, and during the shortest day of the year, 21 December, daylength in Kyoto is 25 minutes shorter than in south

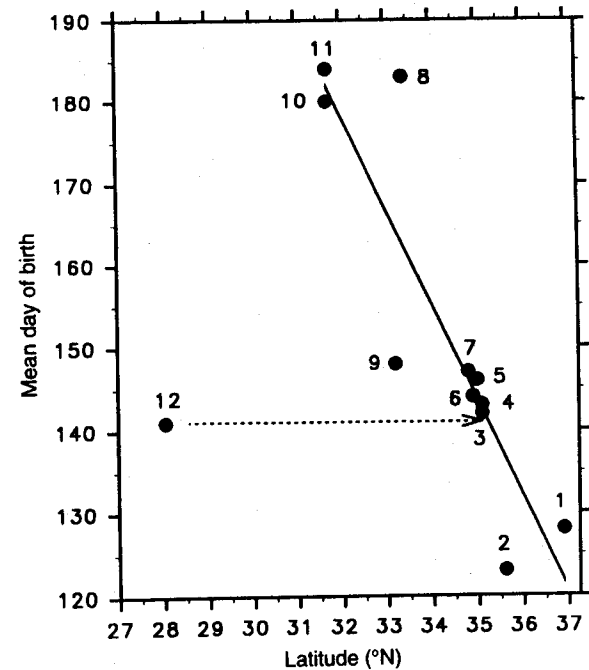


Fig. 17.2. Mean birth date of the population as a function of latitude, for 12 groups of Japanese macaques. Arashiyama West population is group no. 12, which is plotted according to its current location at approximately $28^\circ 05' \text{N}$ in Texas, and also according to its site of origin at $35^\circ 00' \text{N}$, near Kyoto, Japan.

Texas. For arguments that photoperiod may regulate the timing of conception in Japanese macaques, the crucial time period would presumably occur between the fall equinox of 23 September (when daylength is equal to approximately 12 hours at all latitudes) and the late December median conception dates of the Arashiyama monkeys. During this time period, daylength is decreasing by a mean of approximately 2 min per day (rate of 0.3%) in Kyoto, and a mean of less than 1 min per day (rate of 0.1%) in south Texas.

Apart from photoperiod, the two climatic factors that have been identified as possibly regulating the reproductive seasonality of Japanese monkeys (and other seasonal macaques) are rainfall and temperature patterns. Gouzoules *et al.* (1981) presented a comparative climatograph, which showed that rainfall and temperature patterns vary considerably between Kyoto and south Texas. For example, in Japan, June and July are the most rainy months, whereas in south Texas, rainfall since 1974 has occurred mainly in May-June and September-October (National Climatic

Table 17.3. Monthly changes in daylength at the different Arashiyama sites

Date	Daylight hours ^a		Difference (min)
	Kyoto	Laredo	
1 January	9:51	10:22	-31
1 February	10:28	10:51	-23
1 March	11:23	11:32	-9
1 April	12:32	12:27	5
1 May	13:35	13:14	21
1 June	14:19	13:49	30
21 ^b June	14:31	13:56	35
1 July	14:29	13:55	34
1 August	13:56	13:28	28
1 September	12:55	12:46	9
23 ^c September	12:00	12:00	0
1 October	11:51	11:53	-2
1 November	10:46	11:05	-19
1 December	10:00	10:30	-30
21 ^d December	9:48	10:13	-25

^aDaylength calculated as the interval between sunrise and sunset, which depends on latitudes, but not longitude. No corrections for refraction or altitude have been made. (Calculations made by Dr D. Hube of the University of Alberta, by interpolating data from the *Observer's handbook*, Royal Astronomical Society of Canada.)

^b21 June is the summer solstice and the longest day of the year in the northern hemisphere.

^c23 September is the autumnal equinox and daylength is 12 hours in all parts of the world.

^d21 December is the winter solstice and the shortest day of the year in the northern hemisphere.

Data Center data). To examine the possibility that relatively heavy rainfall in the months immediately preceding the mating season might 'trigger' the requisite endocrine changes, we focused on the pattern of rainfall in August, September and October in Texas (mean onset of conceptions in Texas is 10 October). We also calculated the time period when maximum temperatures dropped below 30°C.

Table 17.4 summarizes daily rainfall and temperature data for Laredo, between 1974 and 1979, and similar climatic data for San Antonio, Texas, between 1980 and 1989. It should be noted that weather patterns in San Antonio may be slightly wetter and cooler than those prevailing in Dilley (approximately 156 km to the south), but San Antonio is the closest weather station for which daily records are available from the National Climatic Data Center. Also presented in Table 17.4 are the relevant

Table 17.4. Climatic variables and conception in Texas

Year	Rain onset ^a	Rain total ^b	Temp. <30°C ^c	1st Con. interval ^d	1st Con. date ^e	Onset interval ^f	Median/con. interval ^g	Median/con. date ^h
74	1	21.79	8	12	330	12	15	365
75	4	9.85	11	7	277	11	12	332
76	7	10.12	7	8	292	9	11	322
78	4	10.32	9	8	286	9	11	324
79	0	1.15	10	8	293	10	13	343
80	1	8.78	9	4	260	8	11	322
81	2	12.38	9	8	286	8	11	322
82	7	4.26	8	7	274	10	12	329
83	1	7.50	6	7	281	9	13	336
84	2	10.04	6	5	264	10	13	342
85	6	9.16	6	8	289	9	13	339
86	3	11.27	8	6	264	9	13	338
87	4	3.01	8	8	292	9	13	337
88	2	3.43	9	7	280	9	13	331
89	7	7.83	8	8	287	10	13	338

Data from 1974-79 are for Laredo, and from 1980-89 are for San Antonio.

^aFirst interval in which 1.5 inches fell. Each month was divided into 3 intervals, beginning with the month of August.

^bTotal accumulated rainfall in August, September and October, in inches.

^cFirst interval in which daily maximum temperatures (temp.) dropped to <30°C.

^dInterval during which the first conception (con.) took place.

^eFirst conception date (Julian calendar date out of 365).

^fFirst interval of the season by which 10% of the conceptions had occurred.

^gInterval during which the median conception date occurred.

^hMedian conception date (Julian calendar day).

conception dates for the Arashiyama monkeys in Texas. Regression analyses were run comparing three climatic variables (rainfall onset, total rainfall (August, September and October), and maximum temperatures $<30^{\circ}\text{C}$) to three aspects of the timing of the mating season (first conception, first 10% of conceptions, and median conception date). None of the nine regressions resulted in significant relationships (or even approached significant relationships) between these climatic variables and the timing of the breeding season. Unlike the conclusion of Kawai *et al.* (1967), who found that conceptions did not begin until the temperature dropped below 30°C , we found that the onset of conception in Texas occurred during periods when daily maximums were still regularly reaching 33°C .

Discussion

Many discussions of annual reproductive cycles in primate populations do not identify which components of the timing of reproductive seasons are at issue. In our presentation, six aspects of the timing of reproductive seasonality were distinguished, and only one of these was shown to vary significantly between the Arashiyama groups in Japan and Texas; that is, the distribution of birth dates. A frequency plot of the distribution of birth dates showed that proportionally more infants were born in April in Texas and in early and mid-May in Japan, but by late May equal proportions had been born in both locations.

The median and terminal birth dates were virtually identical in the two locations and the mean birth dates were similar. Differences between Japan and Texas in the length and onset of the birth seasons were accounted for largely by the increasing number of infants born per season over the years of the study. A comparison of AW with other groups of Japanese monkeys showed that the timing of the AW season was consistent with their original location (Kyoto, 35°N) and was different from that of groups found in other parts of Japan.

We interpret these results to indicate that the AW monkeys have maintained a stable, group-specific, circannual rhythm of seasonal reproduction over many years under environmental conditions different from those found in their native habitat. Thus, it seems unlikely that the environmental factors traditionally linked to seasonality are currently acting as proximate cues to regulate endocrine and reproductive processes in our study population.

However, since proximate effects are often said to 'fine-tune' the season,

we also tested to see whether daily changes in rainfall and temperature might be related to the variation that does exist in the onset and median dates of conception in Texas; no relationships were found. According to the latitudinal cline found in Japan, if proximate cues were 'fine-tuning' the seasons, we would have expected AW to move toward later dates in the calendar year. However, if we have any evidence for a shift at all (and this is a matter of interpretation of marginally significant differences), they could be said to have shifted toward an earlier season.

Further evidence for the stability of reproductive timing in the AW monkeys can be obtained from an examination of the dates of 21 births that have occurred in a small subgroup of AW monkeys that was transported to Montreal, Canada in 1985. The median birth date in this subgroup, living at $45^{\circ}30'\text{N}$, is day 140, 20 May, and the mean birth date is day 143, 23 May (calculated from data provided by Dr B. Chapais). These values are virtually identical to the characteristic timing of the Arashiyama population from which the Montreal monkeys originate and, therefore, different from the timing of Japanese macaque groups that occur at more northerly latitudes in Japan. Nozaki *et al.* (1990) found that artificial manipulations of photoperiod in the laboratory, or chronic implantation of melatonin, had no effects on the timing of ovulatory cyclicity, which also suggests that photoperiod is not acting as a proximate effect.

If the timing of AW mating and birth seasons is not reliant on the proximate environmental cues that have been traditionally proposed, but remains consistent over many years in a new habitat, what *does* regulate the timing of reproductive seasonality in this group? We will suggest and examine a number of possible answers to this question, many of which are not mutually exclusive. Firstly, a characteristic circannual rhythm may persist in the AW group simply as an example of a very lengthy refractory period (i.e. a period when the environmental stimuli that normally regulate reproduction are not effective). However, refractory periods in laboratory tests are normally very brief, and then the animals adjust their timing to the current environmental cues. Even for long-lived animals such as macaques, 15 years would be a long time to maintain an annual pattern that is not modulated by either intrinsic rhythms or extrinsic cues. In any case, the monitoring of the birth season in Texas continues, so this hypothesis could be further tested in the future.

Secondly, it might be argued that the proximate cues, such as photoperiod changes, in south Texas are not sufficiently different from the conditions near Kyoto to bring about a change in reproductive timing. This seems unlikely, given the latitudinal gradient of reproductive timing in the

different Japanese macaque groups that was demonstrated by Kawai *et al.*, (1967) and Van Horn (1980). There is not a great deal of difference between the latitudinal locations in Japan of the 11 groups included in the analyses ($36^{\circ} 90' - 31^{\circ} 70' = 5^{\circ} 20'$ of difference), but the mean birth dates of the most northerly and southerly groups differ by approximately 60 days. These different mean dates of birth and their significant correlation with latitude would indicate that Japanese monkeys should be capable of responding to very small or precise differences in photoperiod, if that is the mechanism involved. The AW monkeys were moved 7° south of their original habitat and yet their mean birth date differs by only five days from that of the Arashiyama group in Japan. The timing of AW reproduction continues to fit clearly into the 'middle range' group identified by Kawai *et al.* (1967), even though the south Texas habitat exhibits quite different temperature and rainfall patterns.

That being said, it is still possible that the AW monkeys rely on some proximate cues (such as magnetic fields) that may occur similarly in Texas and Japan, but have not yet been considered here. As one example, if the monkeys had some way of 'measuring' the number of days subsequent to the autumnal equinox, this proximate cue would remain the same anywhere in the world. Perhaps all groups in Japan are ultimately selected to mate in the fall and give birth in the spring, but each group has its own 'critical day', or critical period of days, for the onset of spermatogenesis and ovulatory cycling, as calculated from the fall equinox. However, no such mechanism has been described for any other species, and one wonders why the characteristic 'critical days' for each group would fall along a latitudinal gradient.

Another proximate factor that has remained similar in the new habitat, and has not yet been discussed, is the social environment. For a number of species, social stimuli, especially pheromones, exchanged between females have been shown to be the proximate cause of reproductive synchrony (reviewed by Ims, 1990; see also Herndon, 1983). The AW group was translocated intact from Japan to Texas, and that may have played a role in the maintenance of their characteristic reproductive timing. It is possible to envision that one individual's reproductive status may have a stimulatory influence on her fellow group members, and thus enhance reproductive synchrony in the group. It is less easy to envision the mechanism that would continue to couple this synchronized group of females to some precise calendar date in the year. In a group with such consistent circannual rhythms, such as the Arashiyama monkeys, who is the primary keeper of the annual clock? If social stimuli alone were responsible for maintaining

reproductive synchrony in a new habitat, we might expect that females of the group would coordinate the timing of their ovulatory cycles but that the mating season itself would become uncoupled from its temporal location in the calendar. Most discussions of social cues (e.g. Lindburg, 1987; Bronson, 1989; Ims, 1990) seem to accept that either environmental or intrinsic factors set the timing of the reproductive seasons, and then social cues act to 'cluster' the conceptions or births within that season.

It is also important to note here two constraining characteristics of the AW group that may have an impact on reproductive seasonality. The first characteristic is that the AW group is provisioned (and indeed, almost all the groups in the Kawai *et al.* (1967) study have been provisioned since the early 1950s.) Such food supplementation may have largely ameliorated the selective pressure of seasonal food availability over the past 40 years. It could be argued that if the monkeys in Texas were forced to rely more extensively on native resources, then the mating and the birth seasons would shift in accordance with local patterns of food availability. The second characteristic is that the AW group has not experienced the immigration of new males since its translocation to Texas, although it has exhibited high rates of male emigration. If the timing of mating seasons in Japan remains consistent over the years, even as males transfer groups, one would assume that the philopatric females are the 'keepers of the circannual rhythm' and that males adjust to the timing of the group into which they have immigrated. However, the real situation may be more complicated, and perhaps the mating season in Texas would shift with the introduction of new breeding males.

Finally, we would like to suggest the possibility that reproductive seasonality in Japanese macaques relies on an endogenous circannual clock that has become emancipated from extrinsic factors, and is set to initiate reproductive events differently in each of the genetically distinct groups in Japan. It is possible that the precise timing found in the different groups is the result of genetic and/or social drift (Gouzoules *et al.*, 1981) and, thus, has no necessary functional explanation. However, the strong correlation between reproductive timing and latitude in Japan seems unlikely to be entirely fortuitous or due to chance differences between populations, especially as such correlations are found in other vertebrate species. We have argued that photoperiod, in spite of its relationship to latitude, is unlikely to be operating as a proximate cue for seasonality in our study group. But photoperiod may well have been involved in the evolutionary selection for circannual clocks with different 'critical days' in different genetic populations of Japanese monkeys. Once the clock was 'set' it would

continue to follow the same temporal pattern as long as the group remains socially and genetically intact.

From the results of the 'Arashiyama translocation experiment', and from the evidence on seasonal rhythms in other animals, we suggest that reproductive seasonality in this group relies primarily on an endogenous circannual clock that has become emancipated from the traditionally examined climatological cues, but which may be affected by the social environment and by other proximate cues that have yet not been identified.

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