

Birth timing shift with altitude and its ecological implication for *Macaca thibetana* at Mt. Emei

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Abstract I used cumulative birth rate (CBR) at the middle of the birth season to estimate birth timing in a population of Tibetan macaques in 1992, rather than the periodic survey every 2 or 3 days in 1986 on the same population. In a six day survey (beginning March 18), 11 groups at altitudes between 750-2,400m showed that the CBR significantly decreased with the decline of the groups' range elevations, verifying that infants were born earlier in the season at higher altitudes in the subtropical-temperate transition zone. Considering seasonal changes in body weight and weight dimorphism observed in the macaque, the shift suggests that the reproductive schedule was optimized to ensure the nutrition needed by mating parents, fetuses and newborns, as well as both weaning infants and their mothers in autumn and the coming winter respectively. Accordingly, changes in temperature, photoperiod or rainfall may function as proximate factors of breeding onset to signal food production or availability in different climate zones. **Key words:** adaptation, food, rainfall, reproduction, temperature

Introduction

It has generally been accepted that the birth season of mammals is selected so that young can be produced at the most propitious time of year (Sadleir 1972; Delany 1982). Food abundance is probably the ultimate cause of the breeding season being at any particular time, and the length of day is the proximate factor that stimulates parents to reproduce (Baker 1938, but see Sadleir 1972). This stimulus can be the result of shortening day length for "short-day" species, such as the North American deer which breed earlier further north, or increasing day length for "long-day" species such as voles (Delany 1982).

In macaques, however, there is evidence that factors other than light-dark threshold (van Horn 1980) influence time of onset of breeding. The estimated median conception date is positively related to the onset date of spring rainfall in tropical rhesus (Rawlins and Kessler 1985). Recently, Cozzolino *et al.* (1992)

reported that timing of birth for 25 provisioned groups of Japanese macaques in Japan, Oregon (USA) and Rome (Italy) at temperate zones was not related to latitude, but rather to ambient temperature, i.e. mean conception date was positively related to mean autumn and winter temperatures, and negatively correlated with the magnitude of decrease in mean temperature from August to October. Laboratory studies in Japanese (Nozaki *et al.* 1990) and rhesus macaques (Weherenberg and Dyrenfurth 1983) also offer some data against the photoperiod hypothesis.

Six groups of Tibetan macaques at Mt. Emei showed a mean birth date of March 27 \pm SD 39 days (Zhao and Deng 1988) based on a periodic survey every 2 or 3 days in the 1986 birth season. As with sheep and deer, the macaque is a 'short-day' breeder. Furthermore, timing of birth is negatively correlated with altitude, i.e. infants are born earlier in the season at higher altitudes (Zhao and Deng 1988). The latter result offered a new angle for thinking about the reproductive regulation of macaques.

Few studies on birth timing in primates are made in the field, and no conclusive evidence exists with respect to environmental variables that play the crucial roles in determining the onset of mating activities. This study was designed to confirm the birth timing shift in the same population studied in 1986, using a different survey method, doubling the sample size, and in a much enlarged range of altitudes. As well, this paper reconsidered possible factors influencing reproductive activities in macaques.

Materials and methods

The study site is on the northeast slope of Mt. Emei (103°20'-24'E and 29°32'-35'N), Sichuan Province, southwestern China, in the subtropical-temperate transition zone. Elevations range from 750m to 2,400m. Vegetation consists of subtropical evergreen broad-leaf forest at areas below 1,500m, and temperate forest (deciduous broad-leaf and evergreen broad-leaf mixed forest, and some subalpine evergreen coniferous forest) at higher altitudes. The macaque's favorite food of bamboo, *Chimonobambusa szechuanensis*, mass-appears in the area between 1,600-2,490m. Winters are harsh on macaques, depending as they do mainly on mature leaves; the monthly mean temperature in January was -1.3°C at elevation 2,070m, and 3.4°C at 1,020m (Zhao *et al.* 1989; Zhao *et al.* 1991).

Elevation	High				Middle			Low		
	A	B	D1	D+D2	C	F1	H	E	F	G
Group										
Group size	19	30	21	67	13	15	9	36	30	19
Adult female	6	10	8	26	3	4	5	9	11	7
Yearling	3	3	3	9	1	1	0	5	3	1
Newborn	2	5	3	6	1	1	3	0	1	1
CBR (%)	67	71	60	35	50	33	60	0	13	17

Table 1. Cumulative birth rates (CBR) and related demographic data collected in 11 groups of Tibetan macaques in a six day survey in the middle birth season from March 18 to 23, 1992. $CBR = i / (F - y)$, where i = newborns' number (N), y = yearlings' N, and F = adult females' N (see Zhao and Deng 1988); high = 2,400 - 1,500m, middle = 1,500 - 1,020m and low = 1,020 - 750m; because group D2 was fissioned from group D in the middle of the 1991 mating season, they are treated in combination.

Due to intergroup competition for approaching tourists as potential feeders, the large and dominant groups (Table 1) tended to keep or competitively enter the extremes where tourists enter the area, and only the middle section remained for the small and low ranking groups. Based on data on radio-tracked groups (B, D+D2 and D1, Zhao unpubl. data), the high groups spent about 85% of their time at the trail area. The portion of trail ranging time for groups at the lower extreme was probably the same. Accordingly, the location/elevation where a group was often observed can reasonably represent its activity center in seasons other than winter. For estimation purposes, 11 troops were roughly categorized as high- (troops A, B, D1 and D+D2 at 2,400 - 1,500m), low- (E, F and G at 1,020 - 750m), and middle groups (C, F1 and H at 1,500 - 1,020m).

Based on the interbirth interval of two years, observed earlier at the population level over all altitudes (Table II, Zhao and Deng 1988), it is believed that subtracting the number of yearlings from adult females yields the potential pool of females that could conceive that year in a population experiencing an increase (Zhao 1944b). As such, birth timing in each group can be estimated by the ratio of newborns observed at the survey time to those expected born in the whole season, that is, the cumulative birth rate (CBR) at the survey time:

$$CBR = i / (F - y)$$

where i = newborns' number (N), y = yearlings' N, and F = adult females' N.

The age-sex classes concerned were counted from the high to low groups in six days between March 18-23. Because new births might happen in the higher groups (HG) when I worked on the low groups (LG) in the one-way survey, this method may produce a bias toward lower CBR for HG, and higher CBR for LG.

Results

In 11 groups of Tibetan macaques ranging at the trail area on the slope habitat, with the decline of ranges from high to middle to low elevations (ranked as 3, 2 and 1 respectively), the CBR during March 18-23 significantly progressively decreased [Spearman Rank-Order Correlation: $r = 0.83$, $p < 0.05$, where the critical value (2-tail, 0.05) = 0.63], indicating that birth timing delayed with the lowering of range altitudes (Table 1). Thus, newborns at higher altitudes were exposed to snow for a longer time than those born lower.

Discussion

The birth timing shift observed in 1986 (Zhao & Deng 1988) was confirmed with the CBR. That the birth rates of middle groups (mean = 48%) are very close to the high groups' (mean = 58%) is not in contradiction with this conclusion because much less food supplied by tourists was available in this trail-section than at the two extremes (Zhao 1944b), middle groups were likely to spend more time in forest at the higher parts of their home ranges to harvest the macaque's preferred natural foods (Zhao *et al.* 1989; Zhao *et al.* 1991).

Outwardly, the shift is in keeping with the 'temperature' hypothesis (Cozzolino *et al.* 1992) because the mating season (counting backwards 6 months from the birth season) appears earlier at higher altitudes where autumn-winter temperature is certainly lower than at lower altitudes (Zhao *et al.* 1989).

On the other hand, the effect of nutritional condition on breeding has also been documented. For example, Verme's (1965) experiments with caged white-tailed deer and Scucchi's (1984) work on captive Japanese macaques show that better nutritional conditions

lead to earlier estrus. In keeping with these observations, the macaque body weight measured in the high groups increases to the peak of seasonal fluctuation [16.8kg (F) and 19.5kg (M) in late autumn vs. 11.4kg (F) and 17.0kg (M) in late winter (Zhao 1994a), indicating that mating activity in autumn may also be related to the high nutrient fruits, and bamboo shoots that appear at altitudes above 1600m (Zhao *et al.* 1989; Zhao *et al.* 1991). If the availability of some of high nutrient foods also goes down the slope with change to autumn leaf coloration, it is likely that the reproductive schedule of Tibetan macaques is selected to:

1. increase the likelihood of conception, as recruitment rate increases with better range conditions in deer (reviewed by Sadleir 1972);

2. meet the need of extra energy and nutrients for pregnancy and early stage of lactation (Sadleir 1972) in the harsh winter. The storage and consumption of energy can be measured as a sharper decline of female body weight (-32% vs. -13% seen in males, Zhao 1994a) between late autumn and late winter;

3. start weaning (a bottleneck of infant survival) in the next autumn when infants are about 7 months of age. Weaning at this time also allows the mother to store energy for the coming winter.

It is of theoretical interest to consider the contradictory reports on different environmental factors triggering mating activity in macaques, such as spring rainfall in tropical rhesus (Rawlins and Kessler 1985), temperature in temperate Japanese macaques (Cozzolino *et al.* 1992), and altitude on the slope in the subtropical-temperate transition (this study). Food availability depends on seasonal rainfall in the tropics, whereas, it relies on seasonal changes in temperature in temperate zones (Ricklefs 1973). Thus onset of macaque breeding is very likely to respond to different proximate factors as the 'signal' of production of high nutrient foods in the long-term course of evolution or adaptation. Adams (1960) reported that deer translocated from northern and southern Alabama into the same area showed about one month difference in breeding seasons, responding to difference in photoperiod at their original habitats (also see Bailey 1984). Thus, macaques in captivity may similarly continue to express this trait genetically.

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References

- Adams, W.H. Jr. 1960: Population ecology of White-tailed deer in north-eastern Alabama. *Ecology*, **41**: 706-715.
- Bailey, J.A. 1984: Principles of Wildlife Management. John Wiley & Sons Inc., New York.
- Cozzolino, R., Cordischi, C., Aureli, F. and Scucchi, S. 1992: Environmental temperature and reproductive seasonality in Japanese macaques (*Macaca fuscata*). *Primates*, **33**: 329-336.
- Delany, M.J. 1982: Mammal Ecology. Blackie, London.
- Nozaki, M., Mori, Y. and Oshima, K. 1990: Effects of artificial manipulation of photoperiod on reproductive seasonality of the female Japanese monkey. *Japanese Journal of Animal Reproduction*, **36**: 219-223.
- Rawlins, R.G. and Kessler, M.J. 1985: Climate and seasonal reproduction in the Cayo Santiago macaques. *American Journal of Primatology*, **9**: 87-89.
- Ricklefs, R.E. 1973: Ecology. Chiron Press, New York.
- Sadleir, R.M.F.S. 1972: Environmental effects. In *Reproduction in Mammals* (eds. C.R. Austin and R.V. Short), pp.69-93. Cambridge University Press, London.
- Scucchi, S. 1984: Interbirth intervals in a captive group of Japanese macaques. *Folia Primatologica*, **42**: 203-208.
- van Horn, R.N. 1980: Seasonal reproductive patterns in primates. *Progress of Reproductive Biology*, **5**: 181-221.
- Verme, L.J. 1965: Reproduction study on panned white-tailed deer. *Journal of Wildlife Management*, **29**: 74-79.
- Weherenberg, W.B. and Dyrenfurth, I. 1983: Photoperiod and ovulatory menstrual cycles in female macaque monkeys. *Journal of Reproduction and Fertility*, **68**: 119-122.
- Zhao, Q.-K. 1994a: Seasonal changes in body weight of *Macaca thibetana* at Mt. Emei, China. *American Journal of Primatology*, **32**: 223 - 226.
- Zhao, Q.-K. 1994b: A study on semi-commensalism of Tibetan macaques at Mt. Emei, China. *Revue D'Ecologie*, **49**: 259 - 271.
- Zhao, Q.-K. and Deng, Z.-Y. 1988: *Macaca thibetana* at Mt. Emei, China: II. Birth seasonality. *American Journal of Primatology*, **16**: 261-268.
- Zhao, Q.-K. Deng, Z.-Y. and Xu, J.-M. 1991: Natural foods and their ecological implications for *Macaca thibetana* at Mount Emei, China. *Folia Primatologica*, **57**:1-15.
- Zhao, Q.-K., Xu, J.-M. and Deng, Z.-Y. 1989: Climate, vegetation and topography of the slope habitat of *Macaca thibetana* at Mt. Emei, China. *Zoological Research*, **10** (suppl.): 91-100.

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