Environmental change and housing conditions result in disappearance and return of reproductive seasonality in rhesus macaques (*Macaca mulatta*)

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Rhesus macaques in their natural environments, as well as in the free-ranging colony at Cayo Santiago, Puerto Rico are highly seasonal breeders. Many animal species lose breeding seasonality when brought under captive conditions. The present study that covers a period of 25 years between 1985 and 2010 reports a quick loss of reproductive seasonality in Group O of rhesus macaques after the group was shifted from Cayo Santiago to German Primate Centre at Gottingen, Germany in 1984, and maintained indoors with controlled temperature and day-length periods for about four years. We divided the study period of 25 years into five time-periods of five years each for analysis of the data. Over the subsequent years, births started to concentrate within only a few months indicating an increasing trend towards return of reproductive seasonality. This increase coincided with the increasing number of births in groups with outdoor facilities. Because other factors such as food, water, etc. were similar in indoor and outdoor conditions, we infer that the recovery of seasonality in the outdoor groups was due to the variations in temperature and photoperiod. We report here the presence of reproductive seasonality, its disappearance and return in the same colony and its descendents.

Keywords: Outdoors, return of seasonality, reproductive seasonality, rhesus macaques.

MANY animal species show some degree of seasonality of reproduction in their natural habitats. Primates are considered highly seasonal and moderately seasonal breeders if over 67% births and 33–67% births respectively, occur within three months[1]. A species could be regarded as a non-seasonal breeder if births are more or less equally spread over months. The factors that influence reproductive seasonality include rainfall and photoperiod[2] not only in females, but also through hormone production in males[3]. In the temperate region, it is photoperiod and environmental temperature, and in the tropics, it is cyclic rainfall that results in cycles of food availability which determine reproductive seasonality[4]. However, in certain cases, photoperiodicity may not show any effect on conception and food availability alone may be the main factor for reproductive seasonality[5–7].

A few general patterns of reproductive seasonality are described and discussed in the literature; births may occur at the time of resource abundance enhancing the survivorship of the mother[8], or such that resource abundance coincides with weaning enhancing survivorship of the offspring[9]; frugivorous primates are more seasonal breeders than folivorous primates as fruit availability is more seasonal than leaves[10]; species in the temperate region are more seasonal than those in the tropics where day length does not significantly vary over months[11]. Even in the tropical regions, rainforest-dwelling primates are less seasonal or show no seasonality compared to deciduous forest-dwelling primates. For example, in the case of macaques, some species are strictly seasonal breeders, whereas others are non-seasonal breeders[12,13].

Macaques including *Macaca silenus*, *M. nemestrina*, *M. nigra*, *M. tonkeana*, *M. maurus* and *M. arctoides* are largely non-seasonal and all these species inhabit rainforests. On the other hand, *M. sylvanus*, *M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*, *M. fascicularis*, *M. mulatta*, *M. fuscata* and *M. cyclopis* are seasonal breeders and primarily inhabit deciduous forests. The tropical rainforests remain wet and provide some food throughout the year, whereas food and rainfall vary significantly over the year in the deciduous forests thus inducing reproductive seasonality[14].

When brought under captivity, a number of species which are seasonal breeders in their natural environments, tend to become year-round breeders due to changes in light–dark cycles affecting endocrine status[15,16]. The controlled indoor conditions which are also usually accompanied by irregular social environment may also disrupt the annual seasonal rhythms[17,18]. Rhesus macaques kept in semi-captive conditions in the southern hemisphere showed birth seasonality during October–March as opposed to April–September in the natural habitats of the northern hemisphere, as the temperatures during these two periods would be more or less similar being on opposite sides of the equator[19].

Whereas cyclic food availability is the ultimate factor in determination of reproductive patterns in nature, environmental factors such as onset of rainfall, temperature and photoperiodicity act as proximate factors for fine-tuning reproduction to coincide with food availability[20]. However, a single factor such as onset of rainfall may not be sufficient to explain seasonality that seems to be regulated by a variety of factors[21]. Referring to the observation that under captive conditions, patterns of seasonal

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reproduction disappear, we ask whether a species has the capacity to revert to the evolved patterns if it is provided with the relevant proximate factors again. Here we report in the same colony of rhesus macaques, the patterns of birth in a free-ranging environment, under indoor captive conditions, and again when the animals were provided with outdoors facilities.

The subjects for this study included the rhesus macaques of Group O transferred from Cayo Santiago, Puerto Rico (lat. 18.16, long. 65.73, day-length variation 2 h 17 m) to the German Primate Centre (DPZ) (lat. 51.53, long. 9.93, day-length variation 9 h 11 m), Gottingen, Germany in 1984, and its descendents till 2010. The group initially comprised 86 individuals (age-class 0–2: 15 males and 30 females; age-class 3, 4: 2 males and 9 females; age-class > 5: 8 males and 22 females). For the origin of Group O on Cayo Santiago, see Rawlins[22]. After arrival at DPZ, the group was subdivided along matrilines and kept in several separate subgroups, the number of which increased from six to nine between 1984 and 1989.

Over the first four years, the monkeys were housed in indoor keeping units only. Between 1988 and 1989, three large groups were moved to outdoor enclosures that also included the availability of indoors facilities to the animals. During the later years till 2010, more groups were moved to the outdoor enclosures. The indoor keeping was arranged such that each group could use 2–4 adjacent rooms (12 m^2 ground space each). Light schedule, temperature, humidity and air pressure in the indoor keeping units were controlled and kept constant over the years (12–12 h; 23°C; 55% and –0.1 mbar). After the movement of groups into the outdoors facilities, the feeding schedules remained the same as under indoor conditions.

In the present post facto study we obtained birth data from records on life-history events of the DPZ rhesus population and the former Group O at Cayo Santiago. For analysis purposes, we divided the entire duration of the study into six time-periods. Time-period 1 refers to the time when the animals were at Cayo Santiago. In order to cover a long period and for easy comprehension, we divided the period between 1985 and 2010 into five time-periods of five years each. During the rest of the time periods (2 to 6), the animals were at DPZ: 2, 1985–1990; 3, 1991–1995; 4, 1996–2000; 5, 2001–2005 and 6, 2006–2010. In order to study seasonality in reproduction, we used the records of the number of births occurring in groups kept indoors or outdoors during each month of each time-period. Likewise, we also recorded the total number of births occurring in groups indoors or outdoors for each time-period. A total of 1097 births that occurred during the study period are included in the analysis.

In order to answer the question whether reproductive seasonality can disappear and can also return, we related the number of births occurring during a short period of time of the year with that occurring in groups with outdoor facilities. We present the observations on distribution of births during different months (Figure 1) and the births in indoor and outdoor housing conditions of the animals (Figure 2).

In the case of time-period 1 (at Cayo Santiago), nearly 86% of the births occurred during a period of three months, March to April, with no births during several months, indicating strong seasonality. For time-period 2, though there was a slightly higher concentration of birth during November–December ($\chi^2 = 27.24$, d$f = 11$, $P < 0.004$), births were distributed over all months with considerable percentage in each month indicating a trend towards non-seasonality. During time-period 3, births were spread almost equally over all months ($\chi^2 = 18.34$, d$f = 11$, $P < 0.07$). For time-period 4, over 72% births concentrated during a period of five months from April to August ($\chi^2 = 70.96$, d$f = 11$, $P < 0.001$), now indicating a trend towards seasonality. In the case of time-period 5, over 80% births occurred during a five-month period between February and June, with no births during November. Over 92% births in time-period 6 were concentrated during a period of five months from February to June, with no births during October and November. The results, therefore, clearly indicate a disappearance of birth seasonality during time-periods 2 and 3, and a slow return of seasonality during the later time-periods. However, whereas the birth season at Cayo Santiago was during January–March, it was during February–May at DPZ.

During time-period 1 when the macaques were at Cayo Santiago, all births occurred under free ranging conditions (Figure 2). During time-period 2, over 75% births were in the animals kept indoors. During time-period 3, the number of births indoors and outdoors was about 50% under each condition. During time-period 4, when more animals were shifted to outdoor enclosures, over 67% births occurred in these groups. The number of births occurring outdoors was over 85% and nearly 100% during time-periods 5 and 6 respectively.

As the number of births occurring in outdoor facility increased (Figure 2), the number of births occurring within a period of four months (February–May: period decided post facto on the basis of data; Figure 1) also significantly increased (Pearson product–moment correlation: $r = 0.95$, d$f = 5$, $P < 0.01$) demonstrating an increasing trend towards seasonality.

The results of the present study reveal some important changes in birth patterns in rhesus macaques under different keeping conditions. The group that was highly seasonal at Cayo Santiago quickly lost seasonality when kept under indoor conditions at DPZ. However, it regained seasonality, though slightly later than at Cayo Santiago, when provided with outdoor facilities.

When the animals were provided with outdoor facilities, other important features such as food and water availability remained the same as under indoor condition. The outdoor and indoor facilities, therefore, differed markedly in terms of temperature and day length. In

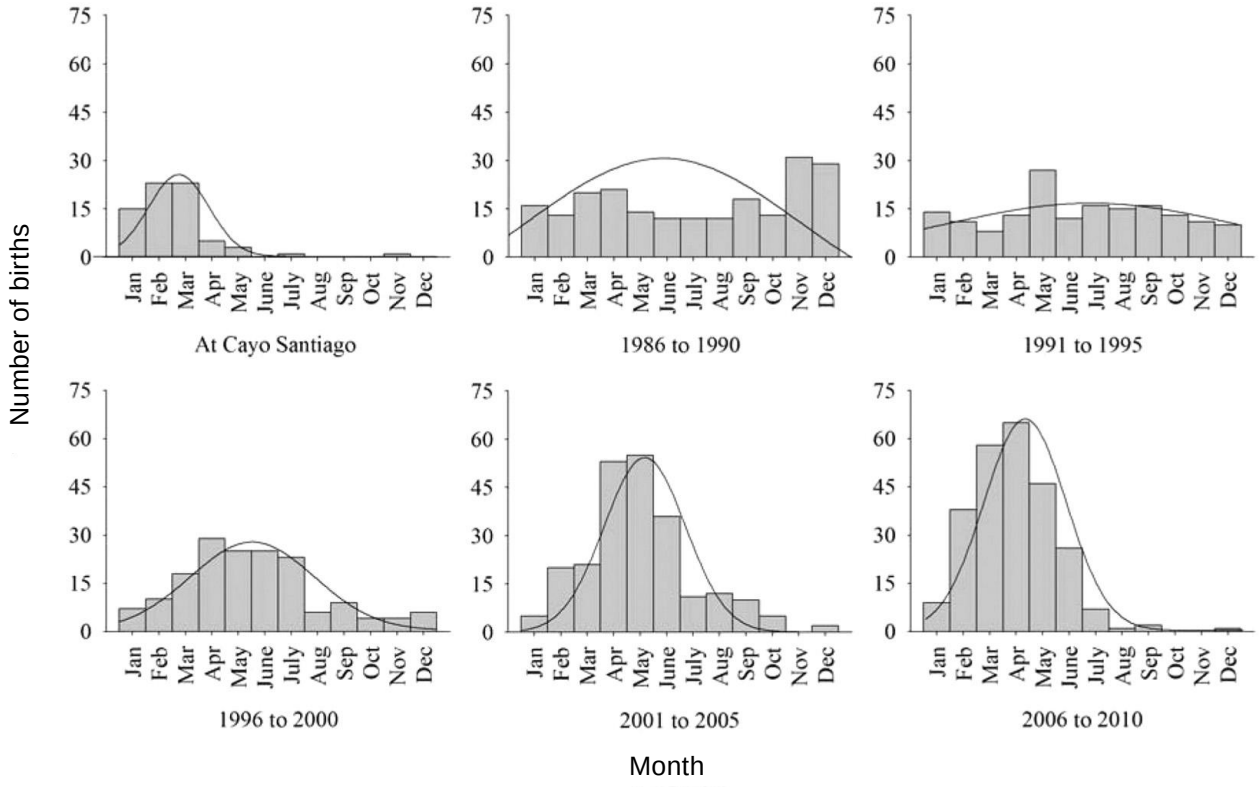

Figure 1. Number of births over different months during each five-year period.

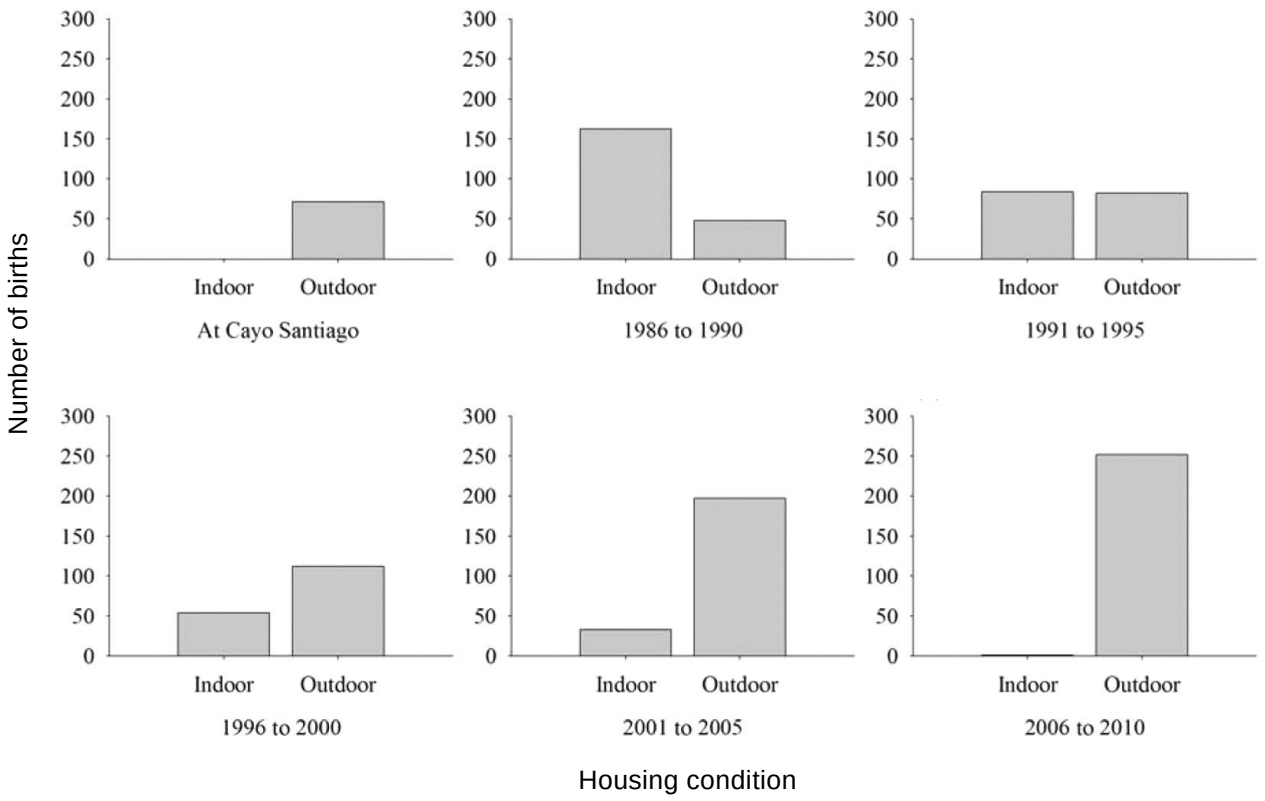

Figure 2. Number of births indoors and outdoors during each five-year period.

accordance with the results of other studies[11,16], the return of seasonality during the present study therefore can be accounted for by the exposure to variable temperature and day-length periods. Temperature and photoperiod have been found to affect reproduction not only in primates[11,16], but also in other taxa[23,24].

The rhesus macaques are highly seasonal breeders in their natural habitats in India[25] and China[26]. At Cayo Santiago, despite year-round access to food and water, analysis of birth records between 1961 and 2005, which also included Group O between 1961 and 1984, has indicated strict birth seasonality with 86% births occurring between November and March[27]. At Cayo Santiago, a population inhabiting another part of the island at La Parguera, showed a three-month difference in seasonality than at Cayo, coinciding with the onset of rainfall at La Parguera[28]. The observations in the present study where seasonality returned though during different months than at Cayo Santiago are compatible with the above observations at La Parguera.

Several studies show that primates under captivity tend to lose seasonality though the resulting patterns are varied. The spider monkeys (*Ateles* sp.) that are largely seasonal breeders in their natural habitats did not show seasonality under captivity[29]. However, captivity did not change marked reproductive seasonality in a group of Sichuan golden monkeys (*Rhinopithecus roxellana*)[30]. Likewise, groups of *Cebus paella*, despite consistent provision of food, did not change the seasonal patterns of reproduction in captivity[31]. In squirrel monkeys (*Saimiri* sp.), the groups kept in indoor enclosures reproduced throughout the year, whereas the groups maintained in outdoor enclosures showed a strict seasonal peak of birth[16]. Whereas the above studies report the loss of seasonality under captive conditions, a return of seasonality is not reported. The present study reports return of seasonality in the same population that had lost seasonality under captivity. A notable observation during the present study was that the return of seasonality in the outdoor groups was not abrupt but gradual, though quite rapid. A similar observation was reported by Herndon *et al.*[32] in which rhesus macaques, immediately after transfer from indoors to outdoors, continued high sexual activity which however declined after three months. The authors concluded that the pattern of non-seasonality continues for some period even after release to the outdoors but it is overcome within a few months with a return towards seasonality. The results point to the fact that a sudden and drastic change in environmental conditions disturbs birth patterns, but when provided with more natural day and temperature cyclicity, rhesus monkeys return to seasonal pattern of reproduction similar to their wild habitats.

The results of the present study are also of considerable significance to the managers of captive primate colonies indicating that, if required, births could be synchronized through variations in temperature and photoperiodicity.

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