



Seasonal Influence on Reproduction in Chimpanzees of Gombe National Park

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Although wild chimpanzees are not seasonal breeders, there are seasonal effects on several aspects of chimpanzee reproduction. I examined the seasonal incidence of anogenital swelling in cyclic, pregnant, and acyclic female chimpanzees in Gombe National Park, May 1975–April 1992, and surveyed important reproductive events to determine whether there is a seasonal effect. I analyzed data by season (wet vs. dry) and seasonal quarter; early dry season = May–July; late dry = August–October; early wet = November–January; late wet = February–April. When data for the 17 years are combined, the percentage of females in each reproductive state remains consistent throughout the year. In a given month, 30–35% of subjects were in the cyclic category, 11–15% were pregnant, and 54–61% were acyclic. Cyclic females showed full swelling more often during the late dry season. Pregnant females exhibited anogenital swelling more often during the late dry and early wet seasons. Acyclic females also exhibited a seasonal effect with more anogenital swelling during the late dry season. There is no seasonal difference in frequency of live births (dry, 20; wet, 23). However, the timing of conception showed a seasonal effect (dry, 32; wet, 16). Consistent with earlier reports, the onset of postpartum cycles is highly seasonal; 30 occurred during dry season, 9 during wet season. The occurrence of first full swellings for young females is also concentrated in the late dry season. It appears that the dry season is a time of great change for Gombe chimpanzee reproductive physiology. Previous studies indicated that seasonal changes in food availability play a role in increasing group size during the dry season and social contact between females can enhance cyclicality. Accordingly, I suggest that seasonal changes in diet may play a role, either

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directly (food content) or indirectly (social contact), to alter reproductive physiology.

KEY WORDS: chimpanzee; reproduction; seasonality; anogenital swelling.

INTRODUCTION

Wild chimpanzees (*Pan troglodytes*) are not seasonal breeders; mating takes place throughout the year, and there is no confirmed evidence of a birth season (Goodall, 1986). There are, however, well-documented seasonal effects on other aspects of chimpanzee reproduction.

Goodall (1986) found that after weaning an infant, female chimpanzees resume cycles most often in the late dry season, which lasts from August to mid-October. Similarly, Nishida *et al.* (1990) noted that female chimpanzees in the Mahale Mountains resumed postpartum estrus significantly more often in the late dry season.

In an analysis of more recent data from Gombe, Wallis (1992) reported the occurrence of false-start swellings in lactating females. They had a normal-looking anogenital swelling phase, followed by several months to two years of anogenital quiescence. The females were not pregnant during that time. In fact, the false-start swelling occurred significantly sooner than the first swellings of the other postpartum lactating females ("false," $\bar{X} = 42.3$ months postpartum, $N = 7$; "real," $\bar{X} = 52.3$ months postpartum, $N = 10$; $t = 1.89$, $p < 0.03$). Of 17 postweaning cases, seven contained false-starts. These false-starts occurred most often in late dry season (4 in September). Using the real starts instead of these irregular false starts, I inferred a slightly earlier peak in normal postpartum cycle resumption than that reported by Goodall (1986). The data showed a seasonal pattern, with the peak in early dry season (May–July) (Wallis, 1992).

According to Nishida *et al.* (1990) the chimpanzees of Mahale have two birth peaks during the year—in the early dry season and in the early wet season. They suggested the first peak may be due to females resuming postpartum cycles in September, but offered no explanation for the early wet season birth peak.

Goodall (1983) reported a nonrandom distribution of female estrous swellings throughout the year. Citing data from 1972–1974 analyzed by Tutin (1975), and adding additional data from 1975–1977, Goodall found the mean number of swellings per month in Gombe chimpanzees showed a nonrandom annual pattern, peaking in September. It was this pattern that initially led Goodall (1965) to suggest the presence of a mating season.

Although Goodall's (1983) data involved analysis of anogenital swelling patterns in normally cycling females, anogenital swelling also occurs

when females are in other reproductive states. Anogenital swelling during the early stages of pregnancy occurs in both wild (van Lawick-Goodall, 1968; Sugiyama, 1969, Wallis and Goodall, 1993) and captive chimpanzees (Yerkes and Elder, 1936; Clark and Birch, 1948; Wallis and Lemmon, 1986). The hormonal mechanism responsible for anogenital swelling in pregnancy is not well understood, but the incidence of gestation-related genital swelling is negatively correlated with the age of the mother (Wallis and Lemmon, 1986; Wallis and Goodall, 1993).

Acyclic females also exhibit occasional anogenital swelling. As described above, females may show false-start swellings during lactation (Wallis, 1992). In addition to these relatively normal (full) swelling phases, some lactating females will occasionally exhibit partially swollen genitalia for a day or two, then return to the state of anogenital quiescence typical of lactational amenorrhea (van Lawick-Goodall 1971). There is no previous analysis of seasonal influence on anogenital swellings during chimpanzee pregnancy or lactation.

I examined the incidence of anogenital swelling in all female chimpanzees at Gombe National Park, including cycling, pregnant, and acyclic females. In addition, I surveyed important reproductive events such as birth, conception, and young females' first full swellings to determine whether there is a seasonal effect.

METHODS

The Data Set

The subjects are adult female chimpanzees (*Pan troglodytes schweinfurthii*) of reproductive age living in Gombe National Park, May 1975 to April 1992: between 11 and 19 females per month. At Gombe, the anogenital swelling level of a female is recorded on each day of observation. I analyzed records that were transferred to monthly sheets. Notations for swelling are 0 = no swelling; 1 = full swelling; $1/4$, $1/2$, and $3/4$ = estimated fractions of full swelling levels, which constitute a "partial swelling" category.

Using information from long-term birth records and a scan of the monthly swelling sheets, I determined the reproductive status of all adult females in the Kasakela community for each month of the 17 years. The three reproductive states under consideration are cyclic, pregnant, and acyclic. The acyclic category includes females that were nursing an infant (lactating) and females that had lost an infant but had not yet resumed cycling.

Occurrence of Anogenital Swelling

For each of the three reproductive states, the monthly sheets provided information on whether females in these categories showed anogenital swelling. I analyzed the incidence of swelling levels by the following categories: none, partial, full, and swollen, which combined the partial and full categories. I calculated a percentage score that measured the proportion of females in each reproductive state for each month and each category.

Each month, I categorized females according to the greatest level of swelling reported, even if the level of swelling occurred for only a day or 2; the predominant swelling condition was not considered in this analysis. For example, the partial-swelling category is restricted to subjects that achieved only partial swelling during a given month. If they reached full swelling that month, they are not in the partial-swelling category. Similarly, the full-swelling category includes females that achieved a full swelling, regardless how often that month they exhibited partial swelling or no swelling. The no-swelling category includes females that exhibited no swelling, yet were seen enough in that month to be included in the study.

The criterion for inclusion in the analysis varied, depending on a female's reproductive status and the highest level of swelling she exhibited. For example, if a female was seen only once, but with a full swelling, she is included in the full-swelling category. However, if she was seen only once, with no anogenital swelling, I was unable to determine whether full swelling was achieved that month. She is, therefore, considered "not seen enough" and omitted from the analysis for that month. Due to the relatively infrequent occurrence of swelling in pregnant or lactating females, criteria for females in these categories are less conservative than for cycling females; if a cycling female was seen with no or partial swelling during 2 weeks of the month, then was not seen for the other 2 weeks, she is considered "not seen enough" and omitted from the analysis, because she could have been swollen then. However, pregnant or lactating females are included even with such 2-week absences. I use the same criteria for each female and for each month of the 17-year period, to make all data comparable. Although I treated the reproductive categories differently, I do not compare them. Instead, I compare only data vis-à-vis quarters and seasons.

The following formula exemplifies how I calculated percentage scores for each category per month:

$$X\% = \frac{\text{No. cycling females with full swelling}}{(\text{No. females cycling}) - (\text{No. cycling, but not seen enough})} \times 100$$

I analyzed the data by month, quarter, and season. Rainfall data indicate that the wet season typically begins mid-to-late October and lasts through mid-May. However, for simplicity, and to make these results comparable to analyses of other researchers, I defined wet season as November through April, with dry season as May through October. Accordingly, the quarters are: early dry season (D1) = May–July; late dry season (D2) = August–October; early wet season (W1) = November–January; and late wet season (W2) = February–April.

I used a general linear model to determine whether there is a difference for each swelling and reproductive category according to month, quarter, or season of the year, with all 17 years combined.

Occurrence of Important Reproductive Events

I conducted an additional review of the records to determine seasonal influence on the timing of important reproductive events. These included time of conception, delivery, resumption of postpartum cycles (when the infant lived versus when it died), the occurrence of young females' first full anogenital swellings and postpartum females' false-starts.

I estimated month of conception via retrospective review of the records. A normal menstrual cycle of a chimpanzee is characterized by a gradual increase in tumescence of the anogenital area, maintenance of full swelling for several days, then a gradual decrease in tumescence (Graham, 1982). Ovulation occurs on the last day or 2 of full swelling (Graham, 1982). If the female becomes pregnant, anogenital swelling may cease completely until after she delivers, nurses, and weans the infant (4 years or more in the future). More often, however, she may show very erratic and irregular swelling off and on during gestation (Wallis and Goodall, 1993). The pattern of this irregular swelling is often used by both laboratory and field workers as the first indicator that a chimpanzee may be pregnant. Therefore, I considered the last day of full anogenital swelling occurring during the last normal swelling cycle before delivery to be the day of conception. However, if the female had not been seen for two weeks or more during the last normal cycle, I excluded that conception from the analysis.

I omitted birth data from the analysis if the first recorded observation of an infant was of one whose estimated birth month is uncertain. For analysis of first postpartum swelling cycles and postpartum false-starts, if the subject was not seen during the entire month preceding the first observed full swelling, I excluded her data.

Because of the irregular nature of early swelling patterns for adolescent females, the occurrence of a female chimpanzee's first full anogenital

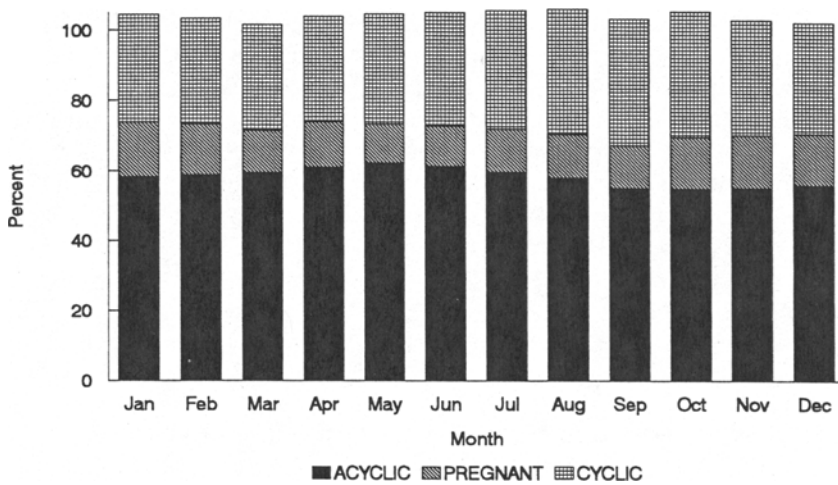


Fig. 1. The mean percentage of females in the cyclic, acyclic, or pregnant reproductive states, by month. The figure includes data from 17 years, combined into 1 calendar year. Note: numbers total more than 100%, as females were considered in each category appropriate for the month, i.e., when a female gives birth she is included in both the pregnant and the acyclic categories for that month.

Table I. Amount of Anogenital Swelling Exhibited by Female Chimpanzees in Each Reproductive State by Seasonal Quarter^a

	Late wet season (%)	Early dry season (%)	Late dry season (%)	Early wet season (%)	F*
Cyclic					
No swelling	7.6	9.8	3.1	9.3	1.56
Partial swelling	6.7	7.4	4.0	14.1	2.88 ^a
Full swelling	85.7	82.8	92.9	76.6	4.08 ^b
Pregnant					
No swelling	77.1	59.8	31.7	34.5	14.13 ^c
Partial swelling	13.7	25.5	21.7	20.4	1.00
Full swelling	9.2	14.7	46.6	45.2	13.59 ^c
Acyclic					
No swelling	97.9	95.9	91.9	94.1	3.07 ^d
Partial swelling	.7	2.2	4.3	2.9	1.98
Full swelling	1.4	1.9	3.8	2.9	1.21

^aSubjects are included in the highest level of swelling achieved in monthly observations.

*Superscript a = 0.05; b = 0.01; c = 0.0001.

swelling does not always indicate normal cycles; the first full swelling may last only 3 or 4 days (Wallis, 1994). These are the swelling data that I analyzed.

I used a chi-square test to determine whether there was a significant seasonal effect on the occurrence of these reproductive events.

RESULTS

When data for the 17 years are combined, the percentage of female chimpanzees in each reproductive state remains consistent over months, quarters, and seasons. In a given month, there were 30–35% cyclic, 11–15% pregnant, and 54–61% acyclic females (Fig. 1). Note that numbers total more than 100%, because some females fit in two categories, e.g., when a female gives birth, she is counted in both the pregnant and the acyclic categories in the birth month.

Occurrence of Anogenital Swelling

Table I lists the percentage amount of swelling exhibited for cyclic, pregnant, and acyclic chimpanzees by quarter of the year. Cyclic females show full swelling more often during the late dry season ($F = 4.08$, $p < 0.02$) and partial swelling in early wet season ($F = 2.88$, $p < 0.05$). Figure 2 combines partial and full swelling values to illustrate total presence of swelling in the three reproductive states by quarter. Pregnant females exhibit anogenital swelling more often during the late dry and early wet seasons ($F = 14.13$, $p < 0.0001$). Although the pattern is less pronounced for acyclic females, they too exhibit a seasonal effect by showing more anogenital swelling during the late dry season ($F = 3.07$, $p < 0.03$). These varying patterns for pregnant and acyclic females are further illustrated by month in Fig. 3. Analysis for monthly variation is significant for pregnant females ($F = 4.22$, $p < 0.0001$), but not for acyclic females ($F = 1.26$, n.s.)

Occurrence of Important Reproductive Events

Because of incomplete records, there are 48 conceptions and 47 births (43 live births, 4 stillbirths), but only 39 occurrences of postpartum resumption of cycles used in this analysis. The timing of conception shows a seasonal effect (dry, 32; wet, 16; $\chi^2 = 5.3$, $p < 0.02$; Fig. 4). However, although more births occurred in the late wet season, there is no seasonal

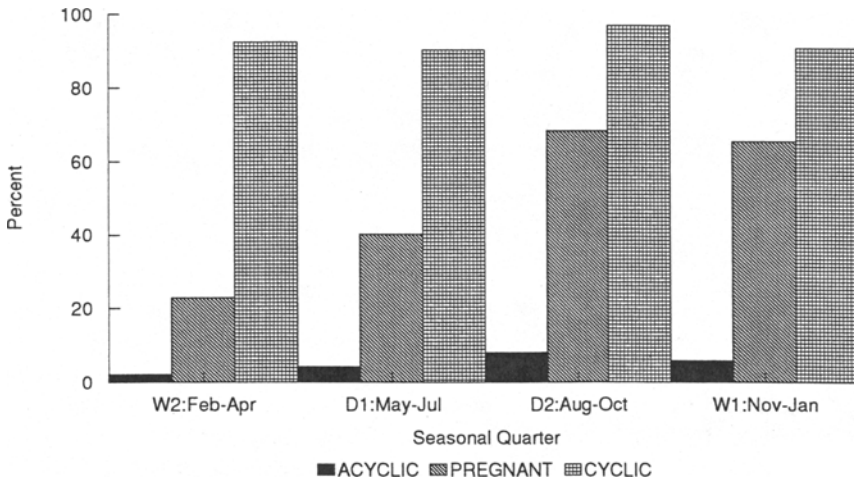


Fig. 2. Mean percentage of females exhibiting anogenital swelling during each quarter. The figure includes data from 17 years, combined into 1 calendar year and combines partial and full swelling values from Table I.

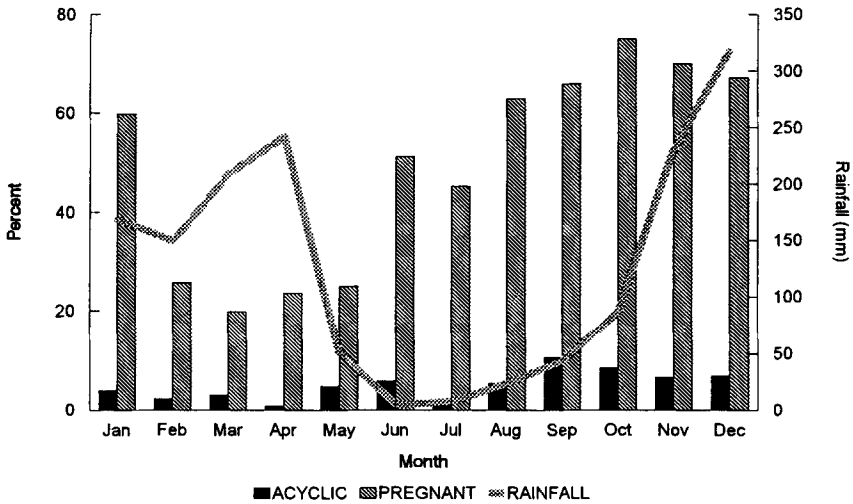


Fig. 3. Mean percentage of female chimpanzees exhibiting anogenital swelling (partial and full) in the pregnant and acyclic states by month. Rainfall data are averaged monthly totals from 1985-1989.

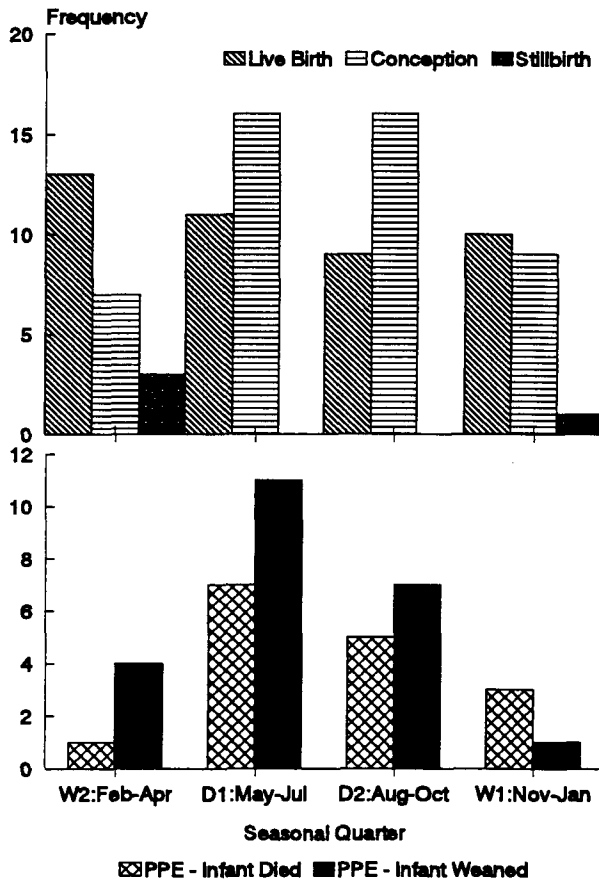


Fig. 4. The frequency of birth, conception, and resumption of postpartum cycles (after infant death and infant weaning) in Gombe chimpanzees (May 1975–April 1992).

difference in frequency of live births (dry, 20; wet, 23). All four stillbirths occurred during the wet season (Fig. 4).

Consistent with earlier reports from Gombe, the onset of postpartum cycles is highly seasonal; 30 occurred during dry season, 9 during wet season ($\chi^2 = 18.75, p < 0.0001$). Quarterly analysis indicates a significant seasonal effect on postpartum cycles resuming when the infant lived ($\chi^2 = 9.5, p < 0.02$; Fig. 4). Although there is no quarterly effect on postpartum cycles resuming after the death of an infant ($\chi^2 = 5, n.s.$), there is a seasonal difference (wet, 4; dry, 12; $\chi^2 = 4, p < 0.05$; Fig. 4).

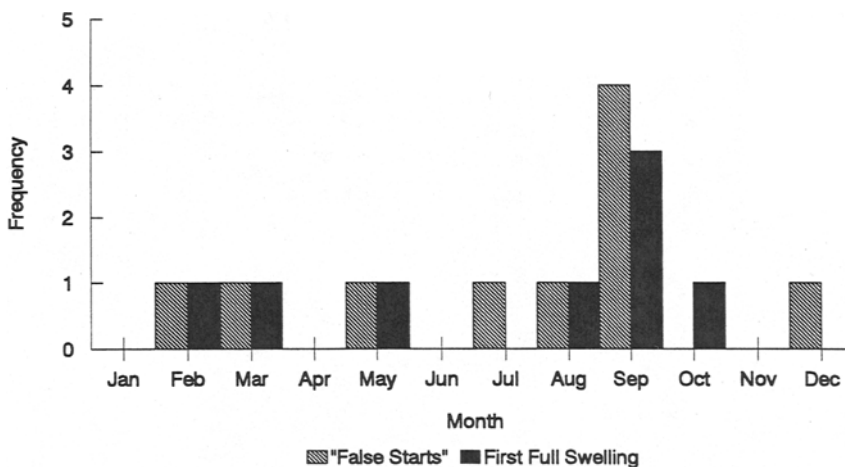


Fig. 5. The frequency of false-start cycles and young females' first full swellings in Gombe chimpanzees (May 1975–April 1992).

As reported in Wallis (1992), false-start swellings during lactation (with normal appearance and duration) are highly seasonal, occurring mostly during the late dry season. For this updated study there were 10 false-starts, 7 of which occurred during dry season. In addition, there were eight young females that exhibited their first full swellings during the 17 years under study. The first appearance of full swellings is also concentrated in the late dry season (Fig. 5) (Wallis, 1994).

DISCUSSION

These data provide strong evidence of seasonal influence on several reproductive variables in wild chimpanzees. It appears that the dry season marks a time of change for chimpanzee reproductive physiology, and perhaps behavior.

Although there is no greater number of cyclic females present during the late dry season (Fig. 1), full anogenital swelling occurs in a higher percentage of females in the late dry season significantly more often than during other quarters of the year. A "normally cycling" female should be expected to exhibit all phases of the swelling cycle in each month. The absence of full swellings in subjects during some months may be because the average length of chimpanzee menstrual cycles is 36 days, i.e., more than 1 month. However, the irregular nature of primate menstrual cyclicity

season. Because anogenital swelling occurs most often in the early stages of chimpanzee pregnancy [captive (Wallis and Lemmon, 1986), wild (Wallis and Goodall, 1993)], pregnancies that begin in early and late dry seasons should show more anogenital swelling in late dry and early wet seasons.

It should logically follow that seasonality of conceptions will result in seasonality of live births. However, the data reveal a wider distribution of births. This may be partly due to the variability of gestational duration common in chimpanzees [captive, range = 192–260 days (Wallis and Lemmon, 1986); wild, range = 203–234 days (Wallis and Goodall, 1993)]. Indeed, whereas most dry season conceptions resulted in wet season births, several very late dry season conceptions led to gestations that ended in the following year's dry season. Figure 6 illustrates the gestational durations in this study that yielded the unexpected results of apparent seasonality in conceptions but no seasonality in births. Despite the lack of significance, there is a trend for more births in late wet season (Figs. 4 and 6). Paradoxically, wet season is the more risky time of year for deliveries; all four stillbirths occurred during wet season, when other deaths and health problems often occur (Goodall, 1986).

The resumption of postpartum estrus may be tied to time of weaning. Although in most cases at Gombe, a female resumes swelling cycles while still lactating (and nursing), there has been no detailed study of nursing frequency as it relates to resumption of cycles or seasonality or both.

Despite the clear seasonal influence on reproduction, the evidence does not suggest that chimpanzees are seasonal breeders. True seasonal breeders exhibit certain times annually when they are fertile, other times when they are infertile, i.e., conception (and mating) is restricted to a specific season. The seasonal influence for chimpanzees is less strict; though trends exist, conceptions and births occur throughout the year. Neither are the seasonal effects limited to the fertile conditions. At Gombe there is seasonal influence on females in other than fertile conditions, including swelling during pregnancy, lactation, and the normally infertile stages of first postpartum estrus and first full estrous swellings of young females.

Normally species from temperate and polar latitudes display annual cycles of fertility and infertility (Lancaster and Lee, 1965). Use of a seasonal predictor allows for metabolic changes in preparation for a time when food availability and climate combine to maximize the probability of reproductive success (Tamarkin *et al.*, 1985; Bronson, 1988). Day length is a major environmental predictor for seasonal breeding (Quay, 1963; Cardinali, 1984). Although researchers have yet to determine whether tropical primates regulate their breeding by using photoperiod to track seasonal changes (Bronson, 1988), Wayne and Rissman (1991) found that some animals living close to the equator can use very small changes in day length

to alter or time reproductive function. At Gombe (4°40'S, 29°38'E), the change in photoperiod between the two solstices is only 36 min (Directorate of Meteorology, Tanzania, 1987). Such a small difference may or may not be enough to serve as a predictor of seasonal changes for the chimpanzees. Whether a predictor of seasonal change is used, however, the eventual seasonal influence is clear.

The dry season, by definition, is a time of no or very little rain at Gombe, in sharp contrast to wet season in which total monthly rainfall reaches as much as 300 mm (Fig. 3). Change in rainfall produces strong variation in food availability (Wrangham 1977; Goodall, 1986). The chimpanzees' generalist feeding strategy accommodates this change, resulting in a variable selection of food items as they become available. This shift in diet could create (directly or indirectly) the seasonal effect on resumption of postpartum cycles (Nishida *et al.*, 1990; Wallis, 1992) and may be a major factor involved in the other seasonal phenomena reported in the present study. Figure 7 presents a schematic view of the dry season's effect on reproduction in chimpanzees.

Food tends to be more abundant during the wet season at Gombe (Goodall, 1986), though the chimpanzees eat a wider variety of foods during the dry season (Wallis *et al.*, 1995). Hasegawa (1990) notes that chimpanzees travel in larger groups when preferred food items are fruiting,

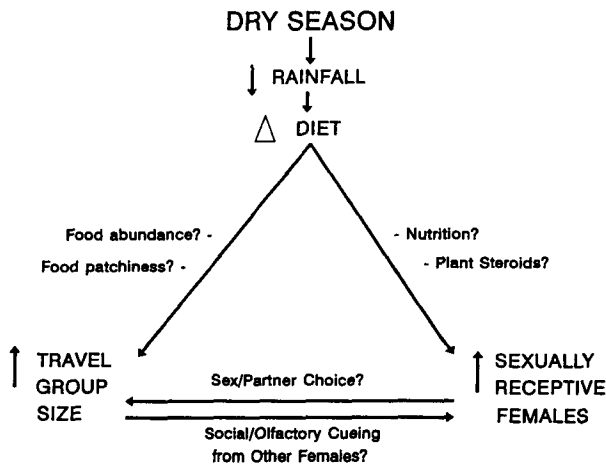


Fig. 7. Diagram depicting the proposed pathways and contributing factors that produce seasonal influence on reproduction in Gombe chimpanzees. Travel group size = number of chimpanzees traveling together.

and Wrangham (1977) suggests that when there is much food (usually wet season) many individuals tend to feed together. However, recent analysis of the long-term Gombe data indicates that significantly larger group sizes are found in the late dry season (Wallis and Matama, 1993). Moreover, the presence of estrous females is associated with large group size (Riss and Busse, 1977; Wallis and Matama, 1993), and again, it is the late dry season when both large party size and presence of estrous females are significantly increased.

Combined, these facts lead to many questions: Are large travel groups formed by estrous females seeking males or males seeking estrous females or both factors? Or does the change in food availability in the dry season bring about larger travel parties and, once formed, does the social (and olfactory) proximity in these large travel parties play a role in effecting reproductive changes in females? Social contact between females has been found to stimulate resumption of postpartum cycles in both wild (Wallis, 1992) and captive (Wallis, 1985) chimpanzees, as well as stimulating first full anogenital swelling in adolescent females (Wallis, 1994). Females traveling in large feeding parties may expose themselves to already cycling females and receive whatever olfactory or tactile chemical cues are available. Therefore, if food patchiness is responsible for forming large groups, diet may play an indirect role in seasonal variation in reproductive function.

On the other hand, diet content may directly change reproductive physiology. Most seasonally breeding mammals tend to mate during seasons when food availability is highest and weight is increased. Even the !Kung people show marked seasonal changes in body weight and a tendency toward seasonality in conceptions, most occurring toward the end of the rainy period after food becomes plentiful and after they begin to gain weight (van der Welt *et al.*, 1978). Nishida *et al.* (1990) suggest that the onset of the first postpartum estrus during late dry season is triggered by changes in food abundance. That is the season when food supply begins to increase and body weights of chimpanzees increase at Mahale (Uehara and Nishida, 1987). However, although both food availability and body weights change, there is no noticeable malnutrition or infertility-producing weight loss reported at Gombe or Mahale.

Another way in which diet can directly change reproductive physiology is through chemical content. Several researchers are investigating the potential role of phytoestrogens in promoting seasonal breeding or disrupting reproductive function. For example, plant estrogens can cause reproductive dysfunction in sheep and other domestic animals that graze on Ladino and other varieties of clover (Moule *et al.*, 1963). Similarly, Whitten (1983, 1985) provided strong evidence that seasonality of reproduction in vervet monkeys (*Cercopithecus aethiops*) is more closely correlated to the avail-

ability of acacia flowers than it is to any other environmental factor. These flowers are rich in flavonoids that have estrogenic properties (Moule *et al.*, 1963). Likewise, a phytoestrogen diet is found directly to affect estrogen-dependent tissues in the vagina and uterus of rats (Whitten and Naftolin, 1992).

Influence of phytoestrogens has even been observed in human populations. Near the end of World War II, people in Holland consumed large quantities of tulip bulbs due to severe food shortage. Tulip bulbs are high in estrogenic activities and many women who ate them showed manifestations of estrogen imbalance including uterine bleeding and abnormalities of the menstrual cycle (Bickoff, 1963). These studies confirm the possibility that diet can directly affect mammalian reproductive physiology. It is possible, therefore, that seasonal changes in diet may be responsible for seasonal changes seen in reproductive variables of the Gombe chimpanzees.

Further study of the physical, dietary, and social dimensions of the chimpanzee environment are required to examine properly the seasonal influence on chimpanzee reproduction reported in the present study. In addition to the possible implications for other species (including humans), more information regarding diet and its influence on behavior and procreation can have far-reaching consequences in our understanding of how natural selection has guided population growth and reproductive success and how changes in global climate or the local habitat or both may affect the future of wild chimpanzees.

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