Primates (2006) 47: 43–50
DOI 10.1007/s10329-005-0143-y

ORIGINAL ARTICLE

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Environmental factors influencing the seasonality of estrus in chimpanzees

Received: 4 September 2004 / Accepted: 22 January 2005 /

Abstract Although the energetics of the estrous cycle in primates is not well understood, evidence suggests that energy and nutrient acquisition influence ovulation and the timing of conception. Energy for estrus has to compete with energy allocated for cellular maintenance, thermoregulation, movement for food, and predation avoidance. While some chimpanzee (*Pan troglodytes*) populations do not have a seasonal birth period, evidence suggests that there is seasonality in the number of estrous females. Similarly, the onset of postpartum cycles has been reported to be seasonal. We used 33 months of data from the Taï National Park, Côte d'Ivoire, to examine how the number of estrous females in a given month was influenced by the abundance and distribution of food, diet, rainfall and temperature. In a second analysis, we examined if there was a seasonal effect on first estrous swellings in adolescent females and postpartum adult females. Results demonstrated that the number of females in estrous in a given month was positively related to food abundance and percent foraging time spent eating insects, and negatively related to mean rainfall in the two preceding months and the mean high temperature. The timing of first estrous swellings of postpartum females and prepartum young females was positively related to the food abundance, and negatively related to mean high temperature. These results showed that environmental conditions can seasonally limit the energetically demanding estrus cycle. The presence of estrous females increases gregariousness in chimpanzee communities, and this study identified environmental factors that affect estrus directly and hence social grouping indirectly.

Keywords Chimpanzee · Environmental factors · Estrus · *Pan troglodytes* · Social grouping

Introduction

The timing of reproductive events in primates varies greatly across species; certain species exhibit very concentrated birthing seasons, while others give birth throughout the year (Lindburg 1987). The degree of seasonality in reproduction is directly related to the seasonal variation in environmental conditions (Fedigan and Rose 1995; Melnick and Pearl 1987). The timing of births in some species appears to occur so that favorable conditions in the environment coincide with the energetically demanding events of lactation or weaning (Altmann 1980; Butynski 1988; Lindburg 1987; Strier 1991). The energy budget of a mother affects lactation efficiency and time spent in maternal care (Lee and Bowman 1995). For example, energy requirements for lactation are 620 kcal/day for humans (Prentice et al. 1986) and 320 kcal/day for olive baboons (Coelho 1985). However, environmental cues that initiate breeding may not always be reliable indicators of future conditions during the time of birth, lactation or weaning (Crockett and Rudran 1987).

Although the energetics of the estrus cycle are not well understood, evidence suggests that seasonal variation in energy and nutrient acquisition influences ovulation and the timing of conception non-human primates (Bercovitch 1987; Koenig et al. 1997; Strier and Ziegler 1994; Takahashi 2002; Ziegler et al. 2000). Consequently, a birthing season may result from favorable environmental conditions for ovulation, and parturition may not necessarily coincide with favorable conditions.

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Energy for estrus has to compete with energy allocated for cellular maintenance, thermoregulation, movement for food, and predation avoidance (Bronson 1989). When sufficient energy is obtained for these latter needs, the estrous and reproductive cycle is expected to continue uninterrupted.

Chimpanzees *Pan troglodytes* do not have a seasonal birth period, but they exhibit seasonality in the number of estrous females (Boesch and Boesch-Achermann 2000; Matsumoto-Oda et al. 1998; Wallis 1995). Similarly, the onset of postpartum cycles has been reported to be at the end of the dry season at the Gombe National Park and Mahale National Park in Tanzania (Nishida 1990; Wallis 1992, 1995). Young female chimpanzees tend to exhibit their first adult size anogenital swellings during the same period of the year in which most first postpartum swellings occur (Wallis 1994).

Females are most sexually receptive when they exhibit a maximal anogenital swelling, which has a variable duration ranging from 6 to 18 days (Deschner et al. 2003; Goodall 1986; Wallis 1997). Ovulation usually occurs during the second half of the period of maximum tumescence (Deschner et al. 2003). The behavioral changes observed during estrus suggest that this period is energetically expensive. Estrous females attract other individuals, resulting in larger parties (Anderson et al. 2002; Matsumoto-Oda et al. 1998; Wallis 2002) and more social interactions and copulations (Wallis and Reynolds 1999). Larger party sizes could also result in increased patch depletion rates and reduced foraging efficiency (Chapman et al. 1995). Estrous females tend to spend more time traveling than anestrous females. However, the increase in traveling is not compensated by an increase in foraging time (Matsumoto-Oda and Oda 1998). Furthermore, males tend to direct aggression towards estrous females more than towards anestrous females (Matsumoto-Oda and Oda 1998). Consequently, if ecological conditions do not permit a female to obtain energy and nutrients above and beyond the basic maintenance level, the estrous cycle is expected to be interrupted.

Chimpanzees are ripe fruit specialists (Newton-Fisher 1999; Wrangham et al. 1998), and are subjected to monthly fluctuations in fruit availability (Chapman et al. 1992; Sun et al. 1996). They also consume seasonally a substantial quantity of arboreal and/or terrestrial herbaceous leaves, meat and insects (Boesch and Boesch-Achermann 2000; Doran 1997; Newton-Fisher 1999; Wrangham et al. 1998). Consequently, seasonal changes in the abundance, distribution, and/or quality of food may affect the energy budgets of chimpanzees, and subsequently the estrous cycle.

Consistent patterns of winter amenorrhea in captive chimpanzees in North America (Young and Yerkes 1943) suggest climatic factors influence reproductive cycles independent of food quality or quantity. Rainfall and/or temperature may have a direct effect on the estrous cycle by influencing thermoregulation, or an indirect effect by influencing the seasonal quantity and quality of food resources. Seasonal peaks and troughs in fruit and leaf production are largely affected by temporal variations rain, temperature and sunlight (Anderson et al. 2005; Chapman et al. 1999; Sun et al. 1996; Tutin and Fernandez 1993). Despite the relatively stable climate in tropical forests, extreme conditions of temperature and rainfall could raise metabolic rates significantly (Bronson 1989; Nadel 1983; Thompson 1977), which could potentially divert energy away from estrus. While it is difficult to discern if the effects of climate variables on estrus are mediated through food productivity or directly through thermoregulation, we controlled for their effects in the following analyses.

We used 33 months of data from the Taï National Park, Côte d'Ivoire, to analyze how environmental factors influenced the seasonality of estrous swellings in chimpanzees. Two questions were addressed. First, how was the number of estrous females in a given month influenced by the abundance and distribution of food, diet, rainfall, and temperature? The reproductive state of a female in a given month may be influenced by the environmental conditions of the preceding months, therefore we examined if the number of estrous females in a particular month was affected by any of the variables in the preceding 3 months. Second, was there a seasonal effect on when adolescent females first exhibit an adult size anogenital swelling and adult females had the first postpartum swelling? To address this question, we examined 10 years of data on the presence/absence of maximal anogenital swellings. The number of these events that occurred in each calendar month of the year was then related to monthly averages of the abundance and distribution of food from this 3-year study, and 9 years of rainfall and temperature data.

Methods

Study site

The study site was located on the western border of the Taï National Park in the Ivory Coast (5°52′N, 7°20′W). The Taï forest is the largest remaining tract (4,500 km^2) of undisturbed lowland rain forest in West Africa (Boesch and Boesch-Achermann 2000). The chimpanzees ranged over an area of 17.75 km^2 (Anderson et al. 2002). The climate is characterized by two rainy seasons (March–June and September–October) and two dry seasons (July–August and November–February) with approximately 1,800 mm rainfall per year (Boesch and Boesch 1983). The studied chimpanzee community has been fully habituated to observers since 1982 (Boesch and Boesch 1983). During the period of this study there was a monthly mean of 29 individuals in the community; including 4 adult males, and 11 adult females. Two adult males and 4 adult females died during the study, 4 births occurred, and 2 sub-adult females had their first estrous swellings.

Weather data

Rainfall and temperature data were collected from November 1996 to December 1999 (Noë, unpublished data). Data were collected daily at 0700 hours. Rainfall was collected and measured by a rain gauge. Daily high and low temperatures were measured by a maximum-minimum thermometer placed in a thermometer shelter.

Behavioral sampling

Data on chimpanzee behavior were collected by field assistants on standardized check-sheets during 33 months in the period between February 1997 and December 1999. No behavioral data were collected in December 1998. Data were collected on 482 days with a mean of 14.6 days of observations per month. To quantify activity budgets and percent dietary intake of fruit, leaves, insects, meat, and miscellaneous items, instantaneous focal animal samples (Altmann 1974) were collected every 15 min on single animals. We followed an individual animal for approximately 8 h each day. We changed focal animals daily (when possible) and all adult chimpanzees were followed as focal subjects. Each month we attempted to have an even distribution of observations on all individual adults. Focal animal behaviors were classified as: foraging, traveling, resting, or hunting. If the focal animal was foraging, the food item was classified as fruit, leaves, mushroom, insects, meat, or miscellaneous. To quantify the monthly percentage of foraging time on each food group we divided the number of feeding observations of each food group by the total number of foraging observations in the corresponding month.

All behavioral sampling was conducted by two trained field assistants; Kohou Grégoire and Néné Honora. Inter-observer reliability (IOR) test was conducted for data collection on activity categories. The index of concordance ($n=102$) was 0.90; indicating high reliability (Martin and Bateson 1986).

Estrous females

To quantify the number of estrous females in a month, we noted any female that was observed with a maximal anogenital swelling. In our examination of environmental factors that influence the number of estrous females, our dependent variable, "estrous score", was the number of estrous females in a given month divided by the number of females that could potentially have been in estrous during that month. Potential estrous females had to meet several criteria to be included in the analysis. First, at 5 months prior to parturition, a female was no longer considered a potential estrous female and was removed from the analysis. From 1996 to 1999, the mean time between the last estrous swelling and parturition was 5.78 months ($n=9$; range 5–7 months prior to parturition). Swellings that occurred during pregnancy were considered equal to other swellings, as we assumed them to be equally sensitive to changes in the environment. Second, a postpartum female was first considered a potential estrous female at the time of her first postpartum swelling. This is a conservative approach given that the time between parturition and the first postpartum swelling varies among females, which may be due in part to age and social position (Boesch and Boesch-Achermann 2000). Third, a young prepartum female was first considered a potential estrous female and entered into the analysis at the time of her first adult sized anogenital swelling. Lastly, if a female met the above criteria for being a potential estrous female, but was not seen on at least two different days in both the first and second halves of the month (4 days total), then she was removed from the analysis due to insufficient days of observation. However, if a female was observed on only 1 day in a month, and she had an estrous swelling on that day, then she was included in the analysis as both an estrous female and a potential estrous female. If there was a bias in this standardized approach, it would be conservative as it would tend to slightly over-estimate estrus during asocial periods (typically June, July, and August), and under-estimate it during relatively social months.

We did not keep a record of "partial swellings" (sensu Wallis 1995). All swellings in this analysis had maximal tumescence. In addition, we did not differentiate between "false start" swellings and "regular swellings" (Wallis 1992). To examine the seasonal effect on the first estrous swellings of young females and postpartum females, we used data records between January 1990 and December 1999. From these records, we noted the calendar month in which each "first swelling" occurred.

Food resource sampling

To evaluate the relationship between estrous females and food resource availability and aggregation, we conducted extensive vegetation sampling (see details in Anderson et al. 2002). We marked 840 individual trees representing 45 species for phenology monitoring and returned to each tree monthly and noted the presence or absence of ripe fruit, and new or mature leaves. Our phenology observations were conducted over a seven day period in the middle of each month. To measure the density and basal area of food trees, we distributed belt transects in the north-south direction throughout the study area. The belt transects were subdivided into contiguous quadrats of 20×30 m, and covered an area of 141.3 ha. We measured the density and basal area of all individual trees with a diameter at breast height of equal to or more than 20 cm in every quadrat along these transects. Using these data, we calculated a monthly food abundance index, which represented the abundance of ripe fruit and leaves from plant species that made up

95% of the diet for the corresponding month. We also calculated Moran's I spatial autocorrelation statistic (Sokal and Oden 1978) as an index food aggregation for each month of the study.

Analysis

To address our first question, we regressed the estrous score against food abundance index, food aggregation (Moran's I), rainfall, average minimum and maximum temperature, as well as the percentage of time foraging on fruit, leaves, meat, and insects. To determine if the estrous score in a given month was influenced by the environmental conditions or diet composition of the preceding months, we regressed the estrous score against all the independent variables from the preceding months. There were 34 months covered in this analysis, from February 1997 to December 1999. An additional 3 months of data on rainfall and temperature (November 1996 – December 1999) were used to analyze how estrous score is influenced by environmental conditions in the preceding months.

To address our second question, we regressed the number of "first estrous swellings" in each calendar month against the corresponding monthly mean of food abundance index, Moran's I, rainfall, average minimum and maximum temperature. Therefore, there were 12 data points used in this analysis; one for each month of the year. Information on the timing of first estrous swellings came from data collected between January 1990 and December 1999, whereas the data on food abundance and distribution were collected from February 1997 to December 1999, and data on the rainfall and temperature were collected from January 1991 to December 1999. By averaging food and climatic variables over several years, we assumed that inter-annual variability was less than seasonal variability, which is generally a valid assumption (Anderson et al.2005).

Results

There were typically very few, if any, females in estrous in the months of June, July and August, and more, but a variable number, from September to May (Fig. 1). There was substantial inter-annual variation in the monthly estrous scores, though a seasonal pattern emerged that is consistent with the findings of Boesch and Boesch-Achermann (2000). July 1997 and December 1998 were removed from the analysis because a lack of sufficient observations on the potential estrous females.

Chimpanzees spent 78% of their foraging time eating fruit, 18% eating leaves, 3% eating insects, and 0.1% eating meat. Regression analysis demonstrated that estrous score was significantly influenced by the food abundance index, percentage of foraging time eating insects, mean high temperature, and the mean rainfall of the two preceding months ($R^2 = 0.630$, $P < 0.001$, $n = 33$ months; Table 1). Food abundance index and

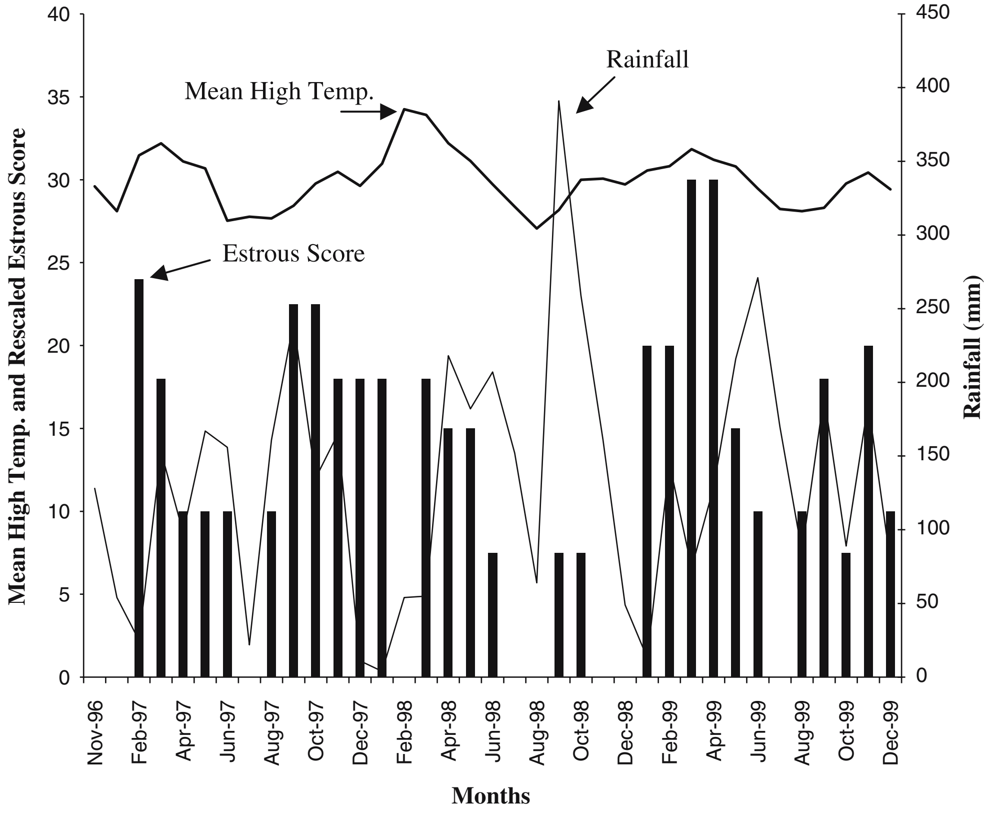


Fig. 1 Estrous scores in a chimpanzee (*Pan troglodytes*) population, rainfall, and mean high temperature are plotted for each month in the current analysis. Estrous scores were rescaled by a factor of 30 so that they would fit on the axis for the mean high temperature. Estrous scores for July 1997 and December 1998 were removed from the analysis because of a lack of sufficient observations on the potential estrous females, however rainfall and temperature are plotted in those months

Table 1 Factors influencing estrous score in a chimpanzee (*Pan troglodytes*) population. Results presented are from type III tests of fixed effects using Proc GLM, SAS 8. Non-significant variables are not shown

Source	Coefficients	*F*-Value	*P*-Value
Food abundance index	0.382	5.67	0.0246
Mean rainfall in 2 preceding months	−0.002	13.60	0.0010
Mean high temperature	2.133	0.02	0.8773
Mean high temperature squared	−0.036	15.85	0.0005
Percent foraging time eating insects	2.683	6.52	0.0166

percent foraging time eating insects both had a positive relationship with estrous score, whereas the mean rainfall in the two preceding months had a negative relationship. The mean high temperature had a hump-backed relationship with estrous score, resulting in maximal estrous scores in the middle of the temperature range. All other independent variables and potential interactions were non-significant predictors of estrous score.

While rainfall and temperature may have had a direct effect on food abundance, their effect on the timing of estrus was independent of food abundance. There were non-significant correlations between food abundance, mean high temperature and the mean rainfall of the two preceding months ($P > 0.05$). The explanatory power of the model predicting estrous score was substantially reduced when only food abundance and percent foraging time eating insects were included in the model ($R^2 = 0.354$, $P = 0.0018$, $n = 33$ months).

In the analysis of the timing of first-swelling events, we found that there were 20 first swellings between 1990 and 1999 and that they were distinctly aggregated in the months of September, October, November, and December (Fig. 2). Results of regression analysis showed that the timing of first-swelling events was significantly influenced by mean food abundance and mean high temperature ($R^2 = 0.462$, $P = 0.049$, $n = 12$ months; Table 2). Food abundance had a positive relationship with first swellings (Fig. 3), and mean high temperature in this analysis had a significant negative relationship (Fig. 4). All potential interactions between independent variables were non-significant. Lastly, all values of independent variables in the preceding three months were also non-significant.

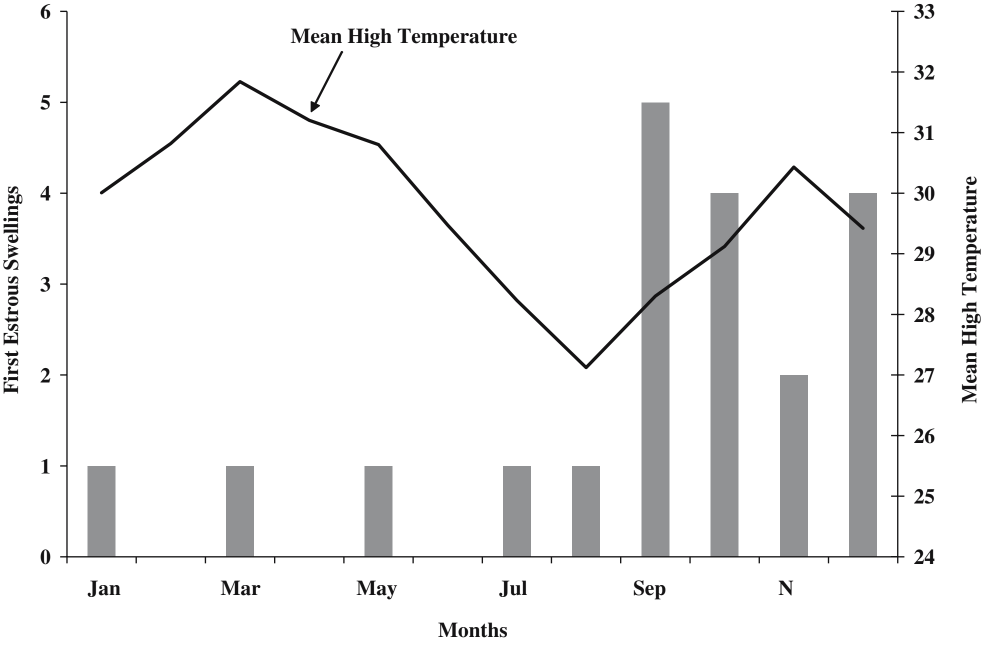
Discussion

Our results demonstrated that the seasonality of estrous swellings was influenced by food abundance, percent of foraging time spent eating insects, mean high temperature, and the mean rainfall in the two preceding months. First estrous swellings of postpartum females and prepartum young females were also found to be linked to

Table 2 Factors influencing the seasonal timing of first estrous swellings in postpartum females, and prepartum young females. Results presented are from type III tests of fixed effects using Proc GLM, SAS 8. Non-significant variables are not shown

Source	Coefficient	*F*-Value	*P*-Value
Food abundance index	6.378	5.24	0.0478
Mean high temperature	−0.847	6.07	0.0359

Fig. 2 The number of first swellings for postpartum females and prepartum young females for the calendar months from January 1990 to December 1999. Mean high temperatures for the period January 1991 to December 1999 are displayed



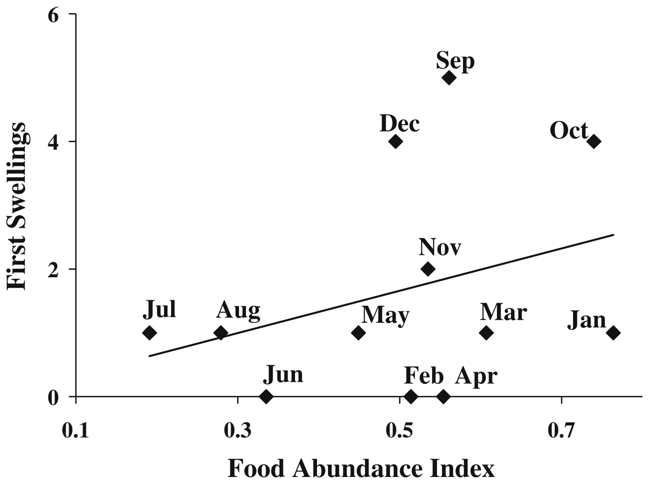


Fig. 3 Regression line for the relationship between monthly food abundance index and the number of first swellings. Months are indicated for each data point

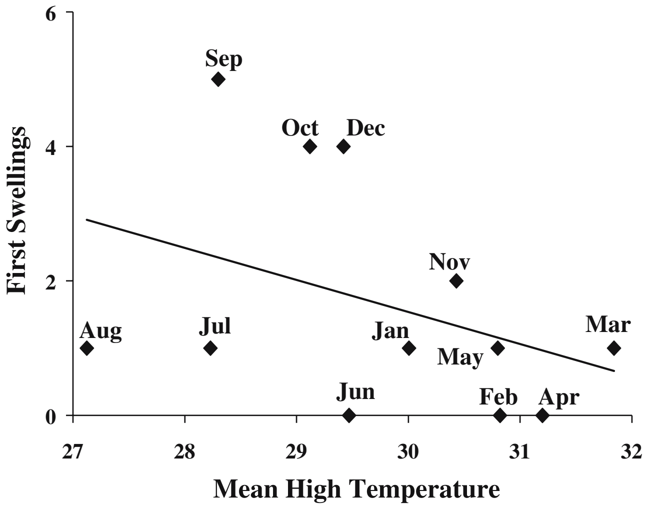


Fig. 4 Regression line for the relationship between monthly mean high temperature and the number of first swellings. Months are indicated for each data point

food abundance and the mean high temperature. Although chimpanzees are not seasonal breeders, they do exhibit seasonal patterns in the number of estrous females as was demonstrated in this and other studies (Boesch and Boesch-Achermann 2000; Wallis 1995, 2002). These results are consistent with findings in other primate species in which environmental conditions act directly on the hormonal status of females, influencing the timing of conception in *Macaca suscata fuscata* (Takahashi 2002), *Presbytis entellus* (Koenig et al. 1997; Ziegler et al. 2000), *Brachyteles arachnoides* (Strier and Ziegler 1994), and *Papio cynocephalus anubis* (Bercovitch 1987). The link to environmental conditions is not surprising in chimpanzees given that the maximal anogenital swelling phase of the estrus cycle coincides with hormonal changes (Graham 1982; Nadler et al. 1985), as well as an increase in party sizes and intra-group aggression (Matsumoto-Oda et al. 1998; Wallis 2002), which are expected to be energetically expensive.

When there was relatively more food available, the chimpanzees were better able to meet their basic energetic costs – cellular maintenance, thermoregulation, movement for food, and predation avoidance – and have a surplus that could be allocated to estrus. Chimpanzees are ripe fruit specialists (Newton-Fisher 1999; Wrangham et al. 1998) and are subjected to temporal fluctuations in availability of preferred items. Fruit and leaf production varies seasonally at Taï (Anderson et al.2005), and these results demonstrate evidence for a link between food production, nutritional condition and estrus.

Chimpanzees spent most of their foraging time eating fruit. Leaves are an important source of protein (Conklin-Brittain et al. 1998) and energy when preferred fruits are scarce, though the percent time eating leaves was not a significant predictor of estrus. The monthly percent time foraging on insects (range 0–14%) had a positive relationship with the number of estrous females. Insects are an important source of protein, and chimpanzees have been observed to repeatedly raid the nests of driver ants, *Dorylus nigricans* and *D. gerstaeckeri*, during the wet season, eating as much as 50 g of eggs and larvae in a single bout (Boesch, unpublished data). It remains unclear how the abundance of insects varies seasonally at Taï. However, evidence from other sites in the tropics suggests that the abundance and activity of insects are expected to increase in the wet season (Murah and Sukumar 1993).

The seasonal peaks in hunting and the number of estrous of females occur at the same time of year at Gombe (Stanford et al. 1994); but it is unclear if the presence of estrous females encourages more hunting, or if an increase in meat consumption facilitates the estrous cycle. Our results indicate that the consumption of meat does not have a significant relationship with estrous females. The consumption of meat is not distributed equally among individuals; males tend to consume more than three times as much as females (Boesch and Boesch-Achermann 2000). The consumption of meat by potential estrous females is probably too sporadic to have an important effect on the estrous cycle.

The biological mechanism underlying the relationship between the timing of estrus and rainfall and temperature remains difficult to interpret. Seasonal variation in rainfall and temperature has an indirect effect on estrus by influencing fruit and leaf production (Anderson et al.2005). However, the effect of the climatic variables on estrus in these analyses was significant after food abundance was already in the regression model. The Pearson's correlations among all independent variables were non-significant, discounting the potential problem of multicollinearity. Given the low variation in the mean high temperature (range 27–34°C), it is unlikely that the animals experienced seasonal periods of thermal stress.

Temporal variation in rain and temperature could influence the nutritional quality of fruits and leaves. However, this was not quantified in this study. The flushing of new leaves, which are high in nitrogen and low in mobile and immobile defenses (Coley 1988; Coley et al. 1985), occurs at the end of the dry season and continues into the wet season (Anderson et al. 2005). Peaks in the number of estrous chimpanzees in Gombe and Mahale National Parks in Tanzania (Nishida 1990; Wallis 1995), and in the number of resumed postpartum cycles in the frugivorous muriqui monkey (Strier and Ziegler 1997) also occurred at the end of the dry season. This is consistent with our findings that the number of estrous females at Taï increased as rainfall decreased in the two preceding months. An increase in leaf senescence due to dry conditions in a 2-month period should result in an increase in new-leaf production in subsequent months. Chemical defenses found in mature and well defended leaves may inhibit energy and protein uptake efficiency, act as toxins, affect metabolic processes and growth rates (Foley and McArthur 1994; Freeland and Janzen 1974; Lindroth et al. 1986), or directly inhibit estrogen processes (Patisaul and Whitten 1998; Wallis 1995, 1997; Whitten et al. 1995, 1997; Whitten and Naftolin 1991). Frugivorous primates should be sensitive to temporal changes in leaf quality (Strier et al. 2001), and this may be the link between climatic variables and the timing of estrus in chimpanzees.

In conclusion, this study demonstrated that both the estrous score and the seasonal timing of first estrous swellings were influenced by the availability of important food resources. Abundant food and a diet rich in insects helped the chimpanzees to meet energetic and nutrient requirements of estrus. In addition, rainfall in the preceding 2 months and the mean high temperature influenced the timing of estrus. The effect of the climatic variables on estrus was independent of fruit abundance, but may have had an indirect effect by influencing the quality of fruits and leaves in the diet. The estrus cycle is energetically demanding and hormone cycles are sensitive to many common plant secondary compounds. Additional research on the influence of forage quality on estrus would provide valuable insights into chimpanzee reproductive ecology. The presence of estrous females has a strong effect on social grouping patterns (Anderson et al. 2002; Matsumoto-Oda et al. 1998; Wallis 2002), therefore a better understanding the environmental factors that influence the seasonality of estrus will be essential for understanding the social dynamics of chimpanzees.

Acknowledgements D.P.A. thanks Juichi Yamagiwa for the invitation to participate in the symposium African Great Apes: Evolution, Diversity and Conservation. Funding for this research was provided by the Max Planck Society, the L.S.B. Leakey Foundation, the National Science Foundation, and U.S.A.I.D. – Program for Science and Technology (Timothy Moermond, P.I.). We are grateful to the Ministries of Eaux et Forêts and La Recherche Scientifique for granting permission to conduct this study. The Projet Autonome pour la Conservation du Parc National de Taï, the Centre Suisse pour la Recherche Scientifique en Côte d'Ivoire, and the Centre de Recherche Ecologique were valuable collaborators in this research. We thank all of the assistants of the Taï Chimpanzee Project, especially those involved with the behavioral and vegetation data collection; Néné Kpazahi Honora, Kohou Nohon Grégoire, Glebeo Pierre Polé, Bally Wabo Albert, Tahou Mompeho Jonas, and Dji Troh Camille. Ronald Noë kindly provided the climate data. Susanne Anderson assisted with data collection and management. Thomas Gordon provided computer assistance in the field. Téré Henri helped with the identification of plant species. Jakob and Marie Zinsstag provided logistic support in Abidjan. Helpful comments on the manuscript were provided by Janette Wallis Thomas J. Givnish, Monica G. Turner, Timothy C. Moermond, Karen B. Strier, and two anonymous reviewers for their comments on this manuscript.

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