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Accessibility
Diet and Reproductive Function in Wild Female Chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda

Melissa Emery Thompson* and Richard W. Wrangham

**Department of Anthropology, Harvard University, Cambridge, MA 02138**

**KEY WORDS** ovarian function; sexual swellings; estrogens; endocrinology; conception; energy balance; feeding behavior

**ABSTRACT** Human female reproductive function is highly sensitive to current energetic condition, indicating adaptation to modulate reproductive effort in accordance with changing ecological conditions that might favor or disfavor the production of offspring. Here, we test the hypothesis that reproductive capacity in female chimpanzees is likewise limited by current energetic condition. We used 12 years of data on wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Kanyawara community of Kibale National Park, Uganda, to examine the relationship of dietary quality, as assessed by fruit components of the diet, to the occurrence of sexually receptive females, concentrations of ovarian steroid hormones, and timing of conception. We found that the frequency of females having sexual swellings was positively related to the consumption of drupe fruits. Estrogen levels of both cycling and noncycling females increased during seasonal peaks in the consumption of drupe fruits. When average fruit consumption remained high across months, females conceived more quickly. These results support the hypothesis that cycling and conception in chimpanzees are contingent upon high energy balance, and they indicate that the availability of fruit is a key variable limiting reproductive performance in chimpanzees. Chimpanzees appear to share with humans a reproductive system that is primed to respond to proximate levels of energy acquisition. Am J Phys Anthropol 135:171–181, 2008. © 2007 Wiley-Liss, Inc.

The availability of energy is a key limiter to reproduction in female mammals (Gadgil and Bossert, 1970; Trivers, 1972; Schneider and Wade, 2000). However, there are many different adaptive strategies for meeting the energetic demands of reproduction (Drent and Daan, 1980; Boyd, 2000; Lewis and Kappeler, 2005). Chimpanzees pursue high-quality, unpredictable resources (Goodall, 1986; Wrangham et al., 1996), making it a particular challenge to meet the energetic demands necessary to successfully carry out a long and costly reproductive effort.

Variation in reproductive performance has been documented in wild chimpanzees among populations, among years within the same population, and among individuals (Gombe, Tanzania: Pusey et al., 1997; Wallis, 1997; Kanyawara, Uganda: Emery Thompson et al., 2007; across populations: Knott, 2001; Brewer-Marsden et al., 2006). The reasons are not well understood, but preliminary evidence suggests that relatively minor improvements in food supply might promote an increase in conception probability. Thus in Gombe, conceptions have shown seasonal peaks when feeding parties are largest (Wallis, 1997), which generally occurs when there is increased food availability (Chapman et al., 1994; Wrangham, 2000; Mitani et al., 2002). Furthermore dominant female chimpanzees had higher birth rates, increased infant survival, and faster maturing daughters, possibly due to nutritional differences (Pusey et al., 1997). In Tai, Ivory Coast, the number of females in estrus was correlated with food abundance (Anderson et al., 2006). Finally in Kanyawara, females that occupied core areas of relatively high food availability had shorter birth intervals, higher ovarian hormone levels, and higher infant survivorship than others (Emery Thompson et al., 2007). Conception data from Hanuman langurs (*Presbytis entellus*; Koenig et al., 1997), long-tailed macaques (*Macaca fascicularis*; van Noordwijk and van Schaik, 1999), and orangutans (*Pongo pygmaeus*; Knott, 1999) indicate a similar sensitivity to seasonal changes in food abundance.

These findings suggest that females might become more likely to conceive as a result of a seasonal increase in food availability. Such a pattern would conform to the reproductive system of humans, in which the probability of conception is controlled by varying ovarian hormone production in relation to energetic condition (Ellison, 1990, 2003; Ellison et al., 1993). This hypothesized sensitivity of conceptions to food abundance would contrast, however, with the system found in some smaller primates in which births, rather than conceptions, tend to occur during periods of high food availability (Lindburg, 1987).

In this article, we test the hypothesis that reproductive function is positively correlated with dietary quality. We do so by examining dietary composition in relation to

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*Correspondence to: Melissa Emery Thompson, Department of Anthropology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138. E-mail: memery@fas.harvard.edu

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the frequency of sexual swellings, the levels of urinary estrogens and progestins, the timing of conceptions and births, and the waiting time to conception. We specifically test the relationship of these reproductive variables to the predominance of ripe fruit in the diet. In addition, we evaluate whether certain subsets of fruits—those preferred in the diet of these chimpanzees—exert a particular influence on reproductive events. Our analysis uses 12 years of dietary and reproductive data from the Kanyawara community of chimpanzees in the Kibale National Park, Uganda, including 6 years of hormonal assays.

The diet of this population is dominated by ripe fruit produced by less than 20 tree species in fruiting seasons lasting at most a few weeks annually for each species (Wrangham et al., 1996, 1998; Wrangham, 1997; Conklin-Brittain et al., 1998). Fruiting seasons are unpredictable in their timing, duration, and productivity. They therefore offer extensive opportunities for testing the hypothesis that the probability of conception is correlated with the food supply.

METHODS

Study site

We studied the habituated chimpanzee community in the Kanyawara region of Kibale National Park, Uganda. The Kanyawara home range comprises approximately 35 km² (Wilson, 2001) of predominantly (60%) moist deciduous forest, with small areas of swamp, grassland, and colonizing forest (Chapman and Wrangham, 1993). Kanyawara chimpanzees have never been directly provisioned, though proximity to human villages leads to some crop-raiding (primarily banana stems).

Systematic data collection on the Kanyawara community has been continuous since 1988. This study incorporates results from over 22,500 observation hours from January 1993 to December 2004. The community consisted of 36 chimpanzees at the beginning of the study and 42 individuals (including 10 adult males and 21 subadult and adult females) at the end of the study. Observations were made daily by a team of two or more permanent Kibale Chimpanzee Project field staff (FAs), normally accompanied by one or more student researchers. FAs recorded scan samples every 15 min during nest-party follow, including the following: (a) location of chimpanzees on a trail map, (b) party composition, and (c) food species and part(s) being consumed. Sexual swelling development (none, partial, or maximal) was recorded on each independent observation of a female; in the event that swelling size fluctuated during a single day, the maximum swelling level was recorded for that day.

To control for probable individual differences in diet resulting from habitat variation we analyzed data only for feeding groups containing one or more of the 12 females who were recorded in more than 15% of scan samples and whose core areas are in the central region of the home range (Table 1, Emery Thompson and Wrangham, 2006; Emery Thompson et al., 2006). They differ from other females in their hormonal function and reproductive parameters (Emery Thompson et al., 2007). In contrast to peripheral (northern) females, these central females occupy ranges within a relatively food-rich area of the home range, and their ranges overlap considerably among one another and with the area used most intensely by males for foraging (Emery Thompson et al., 2007). These findings suggest that these females have access to the same feeding areas, and that feeding data collected on chimpanzee parties can be expected to be broadly representative of the diets of these central females (though perhaps not other females in the community).

Diet

Extensive studies of the feeding behavior of Kanyawara chimpanzees, including nutritional analyses of many foods, have previously been published (Wrangham et al., 1991, 1998; Conklin-Brittain et al., 1998, 2006). On the basis of these previous studies we defined two broad measures of dietary quality that we predicted would positively influence chimpanzee reproduction:

Ripe fruit consumption. Ripe fruit pulp constitutes the dominant food type for this species (Hladik, 1977; Wrangham, 1977; Isabirye-Basuta, 1989; Yamagiwa et al., 1996; Conklin-Brittain et al., 1998; Newton-Fisher, 1999; Furuiuchi et al., 2001) so much so that the abundance of trees producing large, fleshy fruits can be used to predict relative chimpanzee densities (Balcomb et al.,

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**TABLE 1. Kanyawara study subjects**

<table>
<thead>
<tr>
<th>ID</th>
<th>Birth year</th>
<th>Observation years</th>
<th>Mean observation hours/year</th>
<th>Parity</th>
<th>Urine samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>AR</td>
<td>1943</td>
<td>1993–2004</td>
<td>309</td>
<td>Multi</td>
<td>47</td>
</tr>
<tr>
<td>BL</td>
<td>1960</td>
<td>2000–2004</td>
<td>593</td>
<td>Multi</td>
<td>34</td>
</tr>
<tr>
<td>LP</td>
<td>1955</td>
<td>1993–2004</td>
<td>636</td>
<td>Multi</td>
<td>185</td>
</tr>
<tr>
<td>NE</td>
<td>1983</td>
<td>1997–1998</td>
<td>587</td>
<td>Nulli</td>
<td>n/a</td>
</tr>
<tr>
<td>OU</td>
<td>1979</td>
<td>1993–2004</td>
<td>774</td>
<td>Multi</td>
<td>206</td>
</tr>
</tbody>
</table>

---

*a Due to female dispersal in chimpanzees, most birth years are estimates.
*b Years of observation when sexually mature (after swelling cycles begin) and member of central female neighborhood.
*c Indicates whether females was observed while nulliparous, primiparous, or multiparous; dates are indicated if females switch categories during study.
*d Urine sampling was conducted from Dec 1997 Feb 2004, N excludes samples while pregnant.
2000). Therefore, we calculated the percentage of ripe fruit in the monthly diet as one indicator of relative dietary quality (n.b., all references in the text to fruit refer to ripe fruit pulp). The proportion of fruit in the chimpanzee diet at Kanyawara is significantly correlated with fruit availability calculated from phenological transects (Wrangham et al., 1991, 1996; Sherry, 2002).

Preferred fruit consumption. In a naturalistic setting, “preferred” foods are defined as those selected disproportionately often relative to their abundance within the population’s habitat, and these are presumed to be of relatively high value to the animal (Leighton, 1993; Marshall and Wrangham, in press). In practice, this means that the consumption of preferred foods is strongly correlated with seasonal availability. At Kanyawara, approximately half of the fruit component of the chimpanzee diet is comprised of drupe fruits which are available in short, sporadic seasons and whose consumption is significantly correlated with availability (Wrangham et al., 1996). The remaining half consists of various fig species, which are available in nearly all months of the year, yet are eaten in inverse proportion to drupe fruits (Wrangham et al., 1996; Sherry, 2002). In other words, figs are used extensively by Kanyawara chimpanzees, but primarily when key drupe fruit species are not available. Thus, we examined the proportion of ripe drupe fruits in the diet to estimate preferred fruit consumption.

We collected feeding data from parties containing at least one of the central females whose reproductive data were being studied. Diet was calculated on a monthly basis as the number of scans in which each plant species/part was consumed as a proportion of all feeding scans, and analyses were limited to months with greater than 50 h of observation time (N = 128). In other studies of wild chimpanzees, fruit consumption calculated in this manner produces estimates comparable to data taken from 15-min point scans of individual focal animals (Emery Thompson, 2005a). In monthly diets we calculated: (a) the percentage of ripe fruit; (b) the percentage of ripe drupe fruit; and (c) whether the month occurred in a fruiting “season” (i.e., when a single fruit species comprised >40 percent of the diet).

Visibility conditions limit our ability to record the feeding behavior of all individuals in a chimpanzee party, thus dietary data were analyzed as the food item being eaten by the majority of individuals in the party. Observers record any other items they see being consumed by party members, but multiplet items were consumed in less than 1 percent of feeding observations (519/57,799) at Kanyawara between 1993 and 2004. We note an exception for THV (terrestrial herbaceous vegetation) feeding, in which animals may consume a mixture of species or of THV pits and leaves; note that these observations are designated generally as THV eating. Also, many trees contain a mixture of ripe and unripe fruits, and we expect that there may be some variability in the type of fruits consumed within and between feeding sites. Unless this distinction is very clear, these feeding events are recorded as ripe-fruit eating if the tree contains mostly ripe fruits and/or individuals can be clearly observed selecting ripe fruits.

Ovarian hormone analysis

From December 1997 to February 2004, Kibale field staff collected urine samples as frequently as possible by pipetting from vegetation or from plastic sheets placed under the subjects (Knott, 1997). Samples were stored in leak-proof tubes, labeled with date, time, and identity of subject, and frozen the same day at −20°C (Kesner et al., 1995). They were later transported on ice to the Primate Reproductive Ecology Laboratory at Harvard University. We conducted enzyme immunoassay for estrone conjugates (E1C) and pregnanediol-3-glucuronide (PdG), metabolites of estrogen and progesterone, respectively, with reagents provided by the Clinical Endocrinology Laboratory at University of California, Davis (R522 anti-E1G and 13904 anti-PdG; C.J. Munro). Assay procedures and validations followed existing protocols (Czekala et al., 1986; Shideler et al., 1990; particulars on our laboratory’s E1C and PdG assays are provided elsewhere (Emery Thompson, 2005b). All urinary hormone measures were standardized to creatinine (Cr) to control for concentration (Taussky, 1954). Samples with very low creatinine levels (<0.08) were discarded.

We used reproductive records to assign each urine sample to the reproductive state of the subject. We diagnosed pregnancy by a steep, sustained increase in ovarian hormone levels (Emery Thompson, 2005b) and confirmed this with hCG test strips (Aimstick, Craig Medical, Vista, CA). Samples from pregnant females and adolescents were excluded from endocrine analysis, while the remaining samples were classified into three categories: noncycling, cycling-baseline, and cycling-peak. Noncycling samples were collected from females during the period from birth of their infant to the first post-partum maximal swelling. Cycling-baseline samples were collected from females who had initiated cycling but were currently nontumescent, excluding the 10 days following maximal swelling detumescence to exclude luteal hormone fluctuations. Finally, cycling-peak samples were collected from females during the period of maximal sexual swelling, defined by tunescence of circumcumanal and vaginal tissues and closure of the labia to form a tight slit (Dahl et al., 1991).

We calculated a monthly average E1C and PdG for each female in each reproductive state and log-transformed the data prior to statistical analysis. We next calculated a monthly grand mean for all females, considering each reproductive state separately. To examine the effect of fruiting seasons (see previous section) on hormonal levels, we used a paired t-test to compare the mean hormonal indices during each drupe fruiting season with the month that immediately preceded the season; we then compared hormonal levels in each drupe season with those in the month immediately following. Sample sizes vary because of sampling success and availability of females in each reproductive state. We present data for E1C in all three reproductive categories. Since progesterone shows little activity during sexual swelling (Graham et al., 1977; McArthur et al., 1981), PdG was only analyzed for noncycling and cycling-baseline samples.

Other reproductive variables

We investigated the relationship of diet to four reproductive events: occurrence of sexual swelling, timing of conception, timing of birth, and waiting time to conception. Frequency of sexual swelling was measured as the percentage of the observed potentially reproductive females exhibiting a maximal sexual swelling in each study month. We used Spearman’s correlations to test the prediction that sexual swellings were more frequent in months of high dietary quality. Pregnant females and
females in their first 6-months of lactation were not considered potentially reproductive. Note that three females in this community have been observed with sexual swellings between 6 and 12 months after birth with the previous offspring still surviving; cycling resumption during the first year of lactation has also been observed at Mahale (Takasaki et al., 1986) and at Tai (Boesch and Boesch-Achermann, 2000).

We identified a conception window for 19 infants born between 1993 and 2005 whose date of birth was known within 1 month (Table 2). We began by back-calculating 230 days from the estimated birth date of the infant according to observed gestation lengths for captive (range = 202–261 days, n = 56; Yerkes, 1943; Martin et al., 1978; Shimizu et al., 2003) and wild chimpanzees (range = 207–259, n = 42; Wallis, 1997; Emery Thompson, unpublished data). Eleven of these conceptions were confirmed by a urine sample taken in the first trimester of pregnancy. For 18 conceptions, we could derive a separate estimate based on the last mating day or the last day of maximal swelling prior to hormonal confirmation of pregnancy. All estimates derived from estrous dating were within 30 days of the estimates produced by back-dating 230 days from birth. We used Mann–Whitney U tests to compare dietary quality in months in which one or more conceptions occurred versus months in which no conceptions occurred. Similarly, we compared months in which one or more births occurred to those in which no births occurred.

We defined waiting time to conception as the period from the first month in which a postpartum maximal sexual swelling was observed up to, and including, the month of conception. For each conception, we calculated the mean ripe fruit and ripe drupe fruit consumption by chimpanzees over the entire waiting time to conception. We then used regression and partial correlation (correcting for female identity) to test the prediction that increased dietary quality led to shorter waiting time to conception. The mean percentage of ripe fruit in a randomly selected sample of months reaches an asymptote after approximately 20 months. Therefore, for one female who conceived after an unusually long cycling period of 40 months, we considered only the last 20 months prior to conception. Results are not qualitatively affected if this female is excluded. There were 12 conceptions for which we had data on the time of cycling start and conception. All statistical analyses were performed with SPSS 14.0 (Chicago, IL).

RESULTS

Dietary analyses

Chimpanzee diet during the years 1993–2004 conformed to earlier patterns reported for Kanyawara. Ripe fruit constituted 68.1 (range: 9.7–96.1) percent of the chimpanzees' average feeding time per month. The seven most frequently consumed fruits, according to average % of the chimpanzee diet across all months, were the same as those identified in a previous study (Table 3) and accounted for just over half (56.2%) of the chimpanzees' feeding time and 82.5% of all fruit feeding time. Two additional drupe fruits, Linociera johnstonii and Teclea nobilis comprised only 1–2% of the chimpanzee diet on average, but were used intensely during a small number of months. Three fig species (Ficus natalensis, F. sansibarica, and F. exasperata) were consumed in the majority of study months, indicating that they were broadly

| Infant | Sex | C. Birth date (C-230 d.) | E. Hormonal evidence | F. Back calculated swelling date (C-230 d.) | G. Last cycle start (C-14d.) | H. Last cycle swelling date | I. Conception month for analyses (C-230 d.) | J. Month of conception cycles began conception (C-14d.) | K. Months to conception | L. K-14d. to last cycle start (C-14d.) | M. Months to last cycle swelling date (C-14d.) | N. Months to conception (C-230 d.) | O. Months to conception (C-14d.) | P. Waiting time to conception | Q. Conception date estimate Waiting time to conception |
|--------|-----|--------------------------|----------------------|---------------------------------------------|-------------------------------|-----------------------------|---------------------------------|---------------------------------------------|------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|
| KO    | F   | Sep 25, 1993             | KB                   | n/a                                         | Mar 7, 1994                   | KB                           | n/a                             | Mar 7, 1993                   | 1993  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| LA    | F   | Jan 5, 1995              | LP                   | n/a                                         | May 20, 1994                  | May 10, 1994                 | Mar 25, 1994                   | May 10, 1994                 | 1994  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| TJ    | M   | Aug 13, 1995             | TG                   | n/a                                         | Dec 29, 1994                  | Dec 23, 1994                 | Dec 23, 1994                   | Dec 23, 1994                 | 1994  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| LS    | F   | Nov 10, 1996             | TP                   | n/a                                         | Jun 28, 1996                  | Jun 28, 1996                 | Jun 28, 1996                   | Jun 28, 1996                 | 1996  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| AK    | M   | May 15, 1997             | DT                   | n/a                                         | May 27, 1997                  | May 10, 1997                 | May 25, 1997                   | May 10, 1997                 | 1997  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| OT    | T   | May 15, 1997             | UT                   | n/a                                         | May 26, 1997                  | May 10, 1997                 | May 25, 1997                   | May 10, 1997                 | 1997  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| KG    | M   | May 16, 1998             | KB                   | n/a                                         | Sep 28, 1998                  | Oct 15, 1998                 | Oct 1, 1998                   | Oct 1, 1998                  | 1998  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| AM    | M   | Jul 23, 1998             | AR                   | n/a                                         | Dec 5, 1997                  | Dec 11, 1997                 | Dec 11, 1997                   | Dec 11, 1997                 | 1997  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| AT    | M   | Nov 2, 1999              | AL                   | n/a                                         | Mar 24, 1999                  | Mar 10, 1999                 | Mar 10, 1999                   | Mar 10, 1999                 | 1999  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| NP    | F   | Feb 21, 2000             | NL                   | n/a                                         | Jul 23, 2000                  | Jul 10, 2000                 | Jul 10, 2000                   | Jul 10, 2000                 | 2000  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| TL    | M   | Aug 13, 2000             | TL                   | n/a                                         | Oct 24, 2000                  | Oct 10, 2000                 | Oct 10, 2000                   | Oct 10, 2000                 | 2000  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| BO    | M   | Oct 22, 2003             | BL                   | n/a                                         | Apr 1, 2003                   | Mar 18, 2003                 | Mar 18, 2003                   | Mar 18, 2003                 | 2003  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| NA    | F   | Oct 14, 2003             | NL                   | n/a                                         | Jun 14, 2003                  | Jun 10, 2003                 | Jun 10, 2003                   | Jun 10, 2003                 | 2003  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| AZ    | M   | Dec 26, 2005             | AL                   | n/a                                         | Jul 14, 2006                  | Jul 10, 2006                 | Jul 10, 2006                   | Jul 10, 2006                 | 2006  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |
| TF    | M   | Dec 21, 2006             | AL                   | n/a                                         | Aug 1, 2007                   | Jul 10, 2007                 | Jul 10, 2007                   | Jul 10, 2007                 | 2007  | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             | n/a                             |

b NL began cycling abnormally early and conceived an unusually long period of cycling. We considered the 20 months prior to conception in the analyses.

Analysis of waiting time to conception excluded waiting time to females' first birth, as well as one female who was not seen with a swelling prior to conception.
available across seasons. As previously reported at Kanyawara (Wrangham et al., 1996), there was a negative correlation between drupe consumption and fig consumption ($r_s = -0.770, N = 128, P < 0.001$). Thus there was consistent evidence that Kanyawara chimpanzees use figs as intermediate fallback foods when the more-seasonal drupes are not plentiful. Low-quality fallback foods—leaves and piths, particularly of terrestrial herbaceous vegetation—comprised 29% of the diet on average.

Drupe consumption was a significant predictor of monthly fruit consumption but accounted for only 13% of the total variation in fruit consumption ($R^2 = 0.132, df = 127, P < 0.001$). Therefore, to avoid problems of colinearity, we analyzed total fruit consumption and drupe fruit consumption separately in our reproductive analyses, with the recognition that these variables were neither independent nor so tightly correlated so as to be redundant.

### Sexual swellings

Nonpregnant females with sexual swellings were observed in 101/128 (79%) of study months, with a maximum of six fully swollen females in a single month (during a fruiting season of *M. bagshawei*). We compared the percentage of potentially-reproductive females exhibiting sexual swellings during months in which a single fruit species (from Table 2) comprised >40% of the female chimpanzee diet (‘seasons’). A larger proportion of females exhibited maximal sexual swellings during seasons of the major drupe fruit than during seasons for the prominent fig species (Mann–Whitney $U$: $z = -2.669$, $N_{DR} = 36$, $N_{FIG} = 34$, $P_2 = 0.008$) or during other months when no fruit species predominated ($z = -2.973$, $N_{DR} = 36$, $N_{NONE} = 58$, $P_2 = 0.003$, Fig. 1). There was no significant difference in sexual swelling frequency between the major fig seasons and months that did not comprise a fruit season ($z = -0.318$, $N_{FIG} = 34$, $N_{NONE} = 58$, $P_2 = 0.75$). The proportion of females with sexual swellings in a given month was not significantly correlated with the percentage of all fruit in the diet ($r_s = 0.036$, $N = 128$, $P_2 = 0.68$), but was positively and significantly correlated with the consumption of drupe fruit ($r_s = 0.186$, $N = 128$, $P_2 = 0.04$). Consistent with the dietary finding of an inverse correlation between drupe and fig consumption, the strongest correlate of sexual swelling frequency was the difference in consumption rates of drupe and fig fruits in a given month ($r_s = 0.230$, $N = 128$, $P_2 = 0.009$).

### Ovarian hormones

Monthly urinary E$_1$C and PdG averages were correlated with one another in both noncycling ($r = 0.539$, $N = 68$, $P_2 < 0.001$) and cycling-baseline reproductive states ($r = 0.374$, $N = 37$, $P_2 = 0.01$). Baseline E$_1$C and

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**Table 3.** Kanyawara chimpanzee diet January 1993–December 2004, including important food items listed by average feeding intensity

<table>
<thead>
<tr>
<th>Species (family)</th>
<th>Months consumed</th>
<th>Average consumption across all months$^a$</th>
<th>Average feeding intensity$^b$</th>
<th>Maximum feeding intensity</th>
<th>Caloric content (kCal/g)$^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mimusops bagshawei</em> (Sapotaceae)</td>
<td>51</td>
<td>12.4</td>
<td>31.2</td>
<td>83.1</td>
<td>2.26–2.93</td>
</tr>
<tr>
<td><em>Uvarioptis congensis</em> (Annonaceae)</td>
<td>31</td>
<td>5.9</td>
<td>24.2</td>
<td>81.0</td>
<td>1.87–2.60</td>
</tr>
<tr>
<td><em>Linociera johnstonii</em> (Oleaceae)</td>
<td>9</td>
<td>1.6</td>
<td>23.4</td>
<td>66.6</td>
<td>2.07–2.84</td>
</tr>
<tr>
<td><em>Pseudopomias microcarpa</em> (Anacardiaceae)</td>
<td>17</td>
<td>2.9</td>
<td>21.6</td>
<td>57.1</td>
<td>1.60–2.54</td>
</tr>
<tr>
<td><em>Ficus natalensis</em> (Moraceae)</td>
<td>8</td>
<td>13.6</td>
<td>20.3</td>
<td>68.9</td>
<td>1.34–2.36</td>
</tr>
<tr>
<td><em>Teclea nobils</em> (Rutaceae)</td>
<td>8</td>
<td>4.1</td>
<td>17.2</td>
<td>48.1</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Ficus sansibarica</em> (Moraceae)</td>
<td>100</td>
<td>11.5</td>
<td>14.7</td>
<td>76.4</td>
<td>2.46–3.05</td>
</tr>
<tr>
<td><em>Ficus saussureana</em> (Moraceae)</td>
<td>42</td>
<td>3.5</td>
<td>10.6</td>
<td>51.2</td>
<td>1.73–2.60</td>
</tr>
<tr>
<td><em>Ficus exasperata</em> (Moraceae)</td>
<td>86</td>
<td>6.4</td>
<td>9.5</td>
<td>84.8</td>
<td>2.26–2.90</td>
</tr>
<tr>
<td>All Ripe Fruits</td>
<td>128</td>
<td>68.1</td>
<td>68.1</td>
<td>96.1</td>
<td></td>
</tr>
<tr>
<td>All Ripe Drupe (Non-fig Fruits)</td>
<td>120</td>
<td>30.9</td>
<td>32.9</td>
<td>84.9</td>
<td></td>
</tr>
<tr>
<td>All Ripe Figs</td>
<td>128</td>
<td>37.2</td>
<td>37.2</td>
<td>90.6</td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td>126</td>
<td>8.0</td>
<td>8.1</td>
<td>40.7</td>
<td></td>
</tr>
<tr>
<td>Piths</td>
<td>128</td>
<td>20.1</td>
<td>20.1</td>
<td>59.0</td>
<td></td>
</tr>
<tr>
<td>Other (flowers, meat, etc.)</td>
<td>111</td>
<td>3.8</td>
<td>4.4</td>
<td>58.3</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ % of chimpanzee monthly diet, months with at least 50 observation hours.

$^b$ Average % of diet for months in which the item was consumed at all.

$^c$ Metabolizable energy per gram dry weight from nutritional analyses at Kanyawara (Conklin-Brittain et al., 2006), range reflects variation in diet across all months.

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**Fig. 1.** Proportion of potentially-reproductive females with sexual swellings during different fruiting seasons (i.e., >40% of diet consisted of fruit species indicated). Mean ± SE.
time when E1C levels remained elevated. We could not
PdG levels of cycling females were significantly corre-
related with levels of non-cycling females (E1C: r = 0.275, 
N = 39, P = 0.05; PdG: r = 0.417, N = 36, P2 = 0.006).
Cycling-peak E1C levels, however, were unrelated to
baseline or non-cycling E1C levels (peak vs. baseline: r = 
0.153, N = 20, P2 = 0.26; peak vs noncycling: r = 
−0.127, N = 34, P2 = 0.24).

Sexual swelling frequencies increased during particular
drupe fruit seasons, suggesting that ovarian function might
also increase at these times. We identified 10 seasons
between Dec 1997 and Dec 2003 (our period of endocrine
sampling) during which a particular drupe fruit comprised
more than 40% of the diet for one month or more (mean 1.9
months): 5 seasons of M. bagshawei, 3 seasons of U. con-
gensis, and 1 season each of P. microcarpa and Teclea nobi-
lis. Compared with the preceding month, drupe seasons
were characterized by significantly higher E1C levels in
both noncycling (Fig. 2a: tpair = −3.633, df = 7, P2 = 0.008)
and cycling-baseline samples (Fig. 2b: tpair = −8.706, df = 
3, P2 = 0.003). Cycling-baseline PdG levels increased non-
significantly (tpair = −1.105, df = 6, P2 = 0.69), and PdG
levels of non-cycling females increased significantly follow-
ning the fruit season (tpair = −2.361, df = 8, P2 = 0.05), a
time when E1C levels remained elevated. We could not
statistically examine the effect on cycling-peak E1C levels
because estrous females were typically not adequately rep-
resented in control months. Consistent with results in
the previous section, the proportion of reproductive females
with sexual swellings increased significantly during the
drupe fruit seasons (tpair = −2.429, df = 9, P2 = 0.02), then
decreased significantly following the season (tpair = 
−2.371, df = 9, P2 = 0.02).

**Fig. 2.** Ovarian hormone levels before, during and after
drupe fruit seasons: (a) non-cycling and (b) cycling baseline.
Plots illustrate mean ± standard error, with N = number of
seasons or control months with hormonal data available.
Before1/After1 = month immediately preceding or following
fruiting season; Before2/After2 = month preceding Before1
or following After1; During = month(s) of fruiting season;
*P < 0.05, **P < 0.01.

Conception and birth

Fruit consumption was not significantly different
between conception and nonconception months (Mann–
Whitney U, z = −1.028, NC = 18, NNC = 110, P2 = 0.30). However, chimpanzees were more likely to be con-
suming drupe than fig fruits when they conceived. The
increase in drupe fruit consumption during conception
versus nonconception months approached significance
(Fig. 3a; z = −1.786, NC = 18, NNC = 110, P2 = 0.07),
while the fig composition of the diet was significantly
lower in conception months (z = −2.231, NC = 18, NNC = 
110, P2 = 0.03). Thus, the magnitude of the difference
between drupe and fruit composition of the diet was rela-
tively greater during months that produced conceptions
(z = −2.173, NC = 18, NNC = 110, P2 = 0.03). By con-
trast, birth months did not differ statistically for fruit
consumption (Fig. 3b; z = −0.389, NB = 15, NNB = 113,
P2 = 0.70), nor for drupe (z = −0.633, NB = 15, NNB = 
113, P2 = 0.53) or fig consumption (z = −0.315, NB = 
15, NNB = 113, P2 = 0.75).

We next examined whether cumulative effects of diet
could predict the speed of conception. Indeed, for 12 con-
ceptions to parous females for which we could identify
both the first month of cycling and the month of concep-
tion, waiting time to conception was significantly pre-
dicted by the mean percentage of fruit in the diet over
that period (R2 = 0.569, df = 11, P = 0.005, Fig. 4a).
Because three females contributed two data points to
Studies of reproduction in human females emphasize the importance of energy intake and expenditure for modulating ovarian hormone production and the immediate probability of conception (Bullen et al., 1985; Ellison and Lager, 1986; Ellison, et al., 1989, 1993; Panter-Brick et al., 1993; Jasienska and Ellison, 1998). Rather than portraying such response as dysfunctional, reproductive ecologists have described a model whereby reproductive function varies along a continuum with energetic condition so that reproductive effort is not wasted during conditions unfavorable to producing and raising offspring (Ellison, 1990, 2001, 2003). While animal models typically find that severe energy shortage is related to reproductive suppression (Wasser and Barash, 1993; Schneider and Wade, 2000), few data are available to evaluate the reproductive consequences of the more moderate variation in energy availability typically experienced by wild primates. Studies of primate seasonality do, however, suggest that many primates take the opposite strategy of humans: births, rather than conceptions, tend to coincide with times of highest food availability (Lindburg, 1987; Ganzhorn et al., 2003).

Our study, investigating reproductive variation in relation to natural fluctuations in feeding ecology, supports the hypothesis that chimpanzees share a similar pattern to humans. In the Kanyawara chimpanzees, female reproductive capacity was consistently linked to dietary quality as measured by the proportion of feeding time spent eating ripe fruits, particularly drupes. Specifically, peaks in fruit utilization by the chimpanzee community predicted the number of sexually receptive females, estrogen levels (in both cycling-baseline and noncycling females), conception timing, and the waiting time to conception. These data are the first to show that increased access to preferred foods leads to improved ovarian performance and/or enhanced conception probability in chimpanzees.

Unfortunately, the nature of chimpanzee social organization and weak female sociality preclude the collection of fine-grained and consistent data on individual female’s feeding behavior over long-term study periods, particularly as forest visibility conditions often inhibit our ability to simultaneously sample all individuals in a party. Therefore, one limitation of our study is that we must infer dietary quality from data collected on whole chimpanzee parties, when in fact it is likely that individual females within the community vary in their energy intake. Pusey et al. (2005), for example, demonstrated that high-ranking female chimpanzees at Gombe outweighed low-ranking females and had greater stability in body weight across seasons. Similarly, in comparison with the central group of females we examined in this article, a second cluster of females at Kanyawara (the northern neighborhood) have lower access to preferred food resources (Skorupa 1988; Emery Thompson et al., 2007), are lower-ranking (Kahlenberg et al., in review), have lower ovarian hormone levels (Emery Thompson et al., 2006, 2007), and have lower birth rates and off-spring survivorship (Emery Thompson et al., 2007). While this contrast clearly demonstrates individual variability in reproductive function, by excluding the northern females from our analysis we hope to have minimized the impact of such variation on our results.

Another limitation is that our analysis focuses on variables that estimate energy intake, while we have not been able to measure energy expenditure. In human females, high energy expenditure has a significant influence on reproductive function independent of net weight gained or lost (Bullen et al., 1985; Jasienska and Ellison, 1998). Given that chimpanzee foods have variable distribution patterns throughout the forest and that individuals vary in their tolerance for scramble competition (Wrangham, 2000), and with the added complication that increased food availability leads to energetically-costly behaviors such as hunting, copulation and associated male competition for mates (Matsumoto-Oda, 1999; Emery Thompson and Wrangham, 2006; Gilby and Wrangham, 2007), we expect that there is a complex relationship between energy intake and energy expenditure in chimpanzees.

Despite these limitations, we find several reasons to be confident that our data adequately address the hypothesis that dietary quality influences female reproductive function. First, we applied a multilayered approach to examine the influence of dietary fluctuations on repro-

Fig. 4. Waiting time from resumption of estrous cycles to conception as a factor of (a) the mean percentage of ripe fruit consumed during the waiting period, and (b) the mean percentage of drupe fruit consumed during the waiting period. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

ducing this sample, we also conducted a partial correlation to control for individual effects on the waiting time to conception. The correlation remained significant (partial $r = -0.683$, df = 9, $P = 0.02$).

Waiting time to conception was not significantly predicted by the mean percentage of drupe fruit in the diet ($R^2 = 0.232$, df = 11, $P = 0.11$, Fig. 4b). However, we noted that one female conceived over a period of the lowest average consumption, yet had conceived at the end of a season of the key drupe fruit M. bagshawetz. Excluding this one datum, there was a very strong significant relationship between average drupe fruit consumption and reduced waiting time to conception ($R^2 = 0.598$, df = 10, $P = 0.005$).
ductive function, including both proximate mechanisms (ovarian hormones) and reproductive outcomes (conception success). Second, the central group of females we examined have widely overlapping core areas, representing access to the same resource areas (Emery Thompson and Wrangham, 2007); aggression among female residents at Kanyawara is also exceedingly low (<0.005 aggressive acts/hour, Kahlenberg et al., in review), reducing the concern that direct feeding competition would lead to strong disparities in resource access. Third, given the chimpanzees’ fission-fusion strategy, an entire party is typically contained within a single food patch, meaning that all individuals are consuming the same item (though perhaps at different rates). Chimpanzees in the same party consumed different food items in less than 1% of our observations. Fourth, party-wide feeding observations have been shown to provide an accurate reflection of individual dietary composition in chimpanzees at Budongo and Gombe (Emery Thompson, 2005a). Fifth, fruiting seasons of preferred drupes were typically abrupt and brief, reflecting both qualitative and quantitative shifts in the chimpanzee diet; while individuals surely vary in rate at which they consume the best foods, the onset of a major fruiting season should positively influence the energy intake of all individuals studied.

The evidence that female chimpanzees are reproductively sensitive to fluctuation in food supply has implications for understanding chimpanzee behavioral ecology. Greater food availability can be expected to promote more sexual swellings, a shorter interbirth interval, and hence a higher frequency of sexual behavior, all of which influence behavior. For example the presence of sexual swellings is a significant predictor of female attractiveness, influencing copulation rates, association rates with males, and aggression received from males (Deschner et al., 2004; Emery Thompson, 2005b; Muller et al., 2006; Emery Thompson and Wrangham, in review). Accordingly, behavioral comparisons will benefit from comparative measures of food availability.

Second, our data provide evidence of striking similarities between chimpanzee and human reproductive ecology. In human females, reproductive function, including ovarian hormone production, timing of conception, and duration of lactational amenorrhea, is closely tied to energy balance and resource availability, and ovarian hormone production is highest at these times (Knott, 1994), which significantly impacts subsequent gamete formation, influencing copulation rates, association rates with males, and aggression received from males (Deschner et al., 2004; Emery Thompson, 2005b; Muller et al., 2006; Emery Thompson and Wrangham, in review). Accordingly, behavioral comparisons will benefit from comparative measures of food availability.

A number of primate species, including some Old World monkeys, clearly do not fit this mold, conceiving during very restricted seasons or on their first cycle, or timing conception in anticipation of a predictable future period of abundance (Landburg, 1987; Ganzhorn et al., 2003). However, a few other primate species have been found to meet conditions (1) and (2) described above. Orangutans (Pongo pygmaeus) at Gunung Palung National Park in Borneo conceive during periods of high energy balance and resource availability, and ovarian hormone production is highest at these times (Knot, 1999). Sumatran long-tailed macaques (Macaca fascicularis) cycle and conceive more frequently during the times of greatest fruit abundance (van Schaik and van Noordwijk 1985, 1999). While many other primates maintain a seasonal response to external cues (e.g., day length) in captivity, long-tailed macaques breed throughout the year in captivity, suggesting that consistent energy intake changes their reproductive function (Smith, 1984). In muriquis (Brachyteles arachnoides), the distribution of copulations and births, and a lack of interannual consistency in mating season onset, suggests that female condition may be a proximate cue for reproduction (Strier et al., 2001; Strier and Ziegler, 2004). Promising preliminary evidence indicates that females in estrogen that occur during the maximal swelling period in chimpanzees (Deschner et al., 2003, 2004; Emery and Whitten, 2003; Emery Thompson, 2005b) and the irregular nature of sampling success in the field, it is a challenge to adequately sample the maximally swollen condition well enough to examine monthly values. The influence of preswelling estrogen values, equivalent to our “baseline” category, on conception has not been expressly examined in chimpanzees, though in humans mid-follicular estrogen has been found to be more strongly correlated with conception success than late follicular estrogen levels (Lipsen and Ellison, 1996). This is perhaps because estrogen production potentiates and correlates with growth of the ovarian follicle (Wood, 1994), which significantly impacts subsequent gamete and embryo development (Mermillod et al., 1999; Nogueira et al., 2006).

Energy availability is critical to female reproductive success, particularly among primates for which reproductive costs are high (Schneider and Wade, 2000; Knott, 2001). Thus, a variety of studies of primates have demonstrated a positive effect of resource availability or maternal condition on birth rates (e.g., Papio cynocephalus: Bercovitch, 1987; Macaca fuscata, Suzuki et al., 1998; Propithecus verreauxi: Richard et al. 2000). Beyond this, however, our data suggest that humans and chimpanzees share the following set of reproductive traits: (1) responsiveness to current rather than future energetic conditions; (2) repeated cycling before conception; and (3) a continuous scale of ovarian response, as opposed to reproductive suppression that affects reproduction in an all or nothing manner. For such slow-reproducing species experiencing an uncertain food supply, selection favors an adaptable timing of conception rather than a predictable birth season. The relationship in chimpanzees between mean dietary quality and waiting time to conception suggests that there is a cumulative effect of dietary quality on reproductive capacity; this is consistent with the hypothesis that successful reproduction is dependent on the storage of suitable energy reserves to buffer a reproductive effort through successive seasons.
may experience cycle-to-cycle changes in ovarian function as conception approaches (Strier and Ziegler, 2005). In baboons (Papio cynocephalus), reproductive parameters vary among wild-foraging populations, and groups shifting to resource-rich ranges experience dramatic improvements in reproductive rates, such as a 6-month reduction in birth interval (Altmann and Alberts 2003a, 2003b). Both onset of cycling and waiting time to conception have been tied to resource availability and/or maternal body weight in baboons (Bercovitch, 1987; Bercovitch and Strum, 1993), and variability in ovarian function under laboratory conditions has been linked with conception success in this species (Wasser, 1996).

These studies provide promising evidence to suggest that, rather than being a trait linked to unique aspects of costly reproductive investment in hominoids, a reproductive sensitivity to current energetic conditions may be linked to ecological circumstances in a number of primate species. Where habitats provide similar constraints on the availability and predictability of resources, and where fluctuations in energy availability occur on a more continuous scale (as opposed to boom-and-bust), we should expect flexible reproductive adaptations with enhanced sensitivity to available energy (van Schaik and van Noordwijk, 1985). Further study of apes and these other species is needed to evaluate the extent of variation in ovarian function among females and the degree of sensitivity to varying levels of environmental distress. Study of hormonal activity in these species could help elucidate whether females experience changes in ovarian function only at a certain energy threshold or in a dose-response relationship with a range of ecological conditions. Finally, given an increased understanding of the diversity of female reproductive adaptations, variation in female conception strategy may be associated with other correlated social and physiological traits, such as dietary diversity and an enhanced ability to store energy.

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LITERATURE CITED


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Emery Thompson M, Wrangham RW. Male mating interest varies with female fecundity in chimpanzees of Kibale National Park (in review).


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