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## The Biology of Menstruation in *Homo sapiens*: Total Lifetime Menses, Fecundity, and Nonsynchrony in a Natural-Fertility Population<sup>1</sup>

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Studies of female reproductive biology in humans are almost entirely limited to women who spend the majority of their reproductive years in menstrual cycling. Given that human reproductive biology evolved when pregnancy and lactation were the usual reproductive states (Short 1976), it is important to consider reproductive patterns in natural-fertility populations. In these populations, couples do not attempt to control their fertility in a parity-dependent fashion (Henry 1961). Johnson et al. (1987) conducted a longitudinal investigation of menstruation in a noncontracepting population, the Gainj of Papua New Guinea, but their sample includes only 40 menstrual cycles in 36 women. Bentley, Harrigan, and Ellison (1990) monitored 178 menstrual cycles among the Lese of Zaire, but because of endemic venereal disease many Lese women were sterile and therefore displayed the Western pattern of cycling repeatedly without becoming pregnant. Here I present the first long-term, prospective data on menstruation in a true natural-fertility population, the Dogon of Mali. The

1. © 1997 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/97/3801-0009\$1.00. I thank M. Brown, J. Warner, and D. Miller for help with the statistical analyses, S. Moulin for assistance with data collection, and R. D. Alexander, B. Gillespie, J. Warner, J. W. Wood, P. Smouse, C. Kottak, C. Vincenz, and R. Wrangham for comments on the manuscript (or an earlier draft). I am also indebted to K. Sanogo and the Dogon themselves for their generous cooperation with the study. This work was supported by the L. S. B. Leakey Foundation, the National Science Foundation (BNS-8612291), and the University of Michigan.

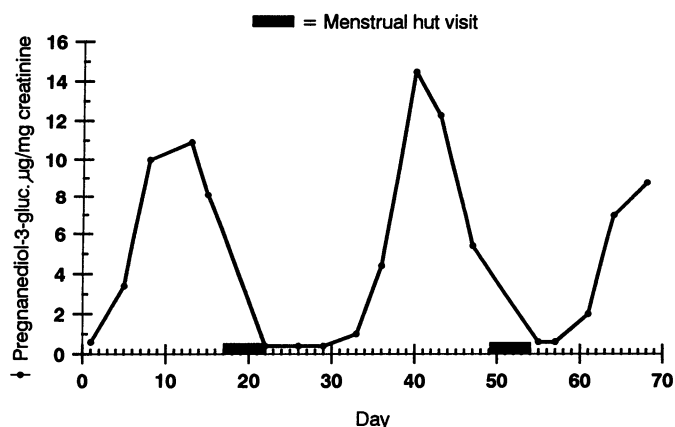


FIG. 1. A Dogon woman's visits to a menstrual hut in relation to her urinary pregnanediol-3-glucuronide (PdG) profile. As expected, she went to the menstrual hut at the end of each luteal phase as her PdG levels were reaching baseline.

sample includes 477 untruncated menstrual cycles in 58 women. I focus on three specific questions: (1) From menarche to menopause, how many menses do Dogon women experience in a lifetime? (2) How are menses patterned over the life span? and (3) Do Dogon women synchronize their menstrual cycles?

The Dogon are millet farmers of the Sahel and have a total fertility rate of  $8.6 \pm 0.3$  live births per woman (Strassmann 1992). They provide a rare opportunity for monitoring female reproductive status in a preindustrial society because strict taboos require menstruating women to be segregated at night in special huts. The function of these taboos<sup>2</sup> and of menstruation itself has been considered elsewhere (Strassmann 1992, 1996a, b). Through a nightly census ( $N = 736$  days) of the women present at the two menstrual huts in the study village (July 1986 to July 1988), it was possible to detect the onset of menstruation without interviews and thereby to avoid errors in recall or reporting.<sup>3</sup> A comparison of the timing of women's visits to the menstrual huts with the women's hormonal profiles (urinary pregnanediol-3-glucuronide and estrone-3-glucuronide) (fig. 1) indicated that women ( $N = 70$ ) went to the menstrual huts during 86% of all menses and stayed away from the huts when they were not menstruating (Strassmann 1996b). Prospective monitoring of 25 pregnancies indicated that all

25 births occurred approximately nine months after the mothers' last visits to the menstrual huts (Strassmann 1992). These results confirm that if a Dogon woman visits a menstrual hut she is in fact menstruating.<sup>4</sup>

The prolonged menstrual cycling of Western women has been invoked as a risk factor for reproductive cancers (Short 1976, Eaton et al. 1994), a leading cause of mortality. But how many menses did women typically experience prior to the advent of contraception? Because of the difficulty of collecting accurate information on menstruation from interviews, few data are available to answer this question. Eaton et al. (1994) calculated that hunter-gatherer women who lived past menopause experienced roughly 160 ovulations in a lifetime, but this estimate is not based on empirical data on either menstruation or ovulation among hunter-gatherers.

#### TOTAL LIFETIME MENSES

I used objective records of menstrual hut attendance, as corroborated by hormonal data, to determine the number of menses experienced by Dogon women over the life span, assuming survival to menopause. In my sample, the median age at menarche was 16 and the median age at menopause was 50. The mean number of hut visits per lifetime was 110 and the median was 94. These values were calculated as the sum of the mean (or median) number of hut visits by women at each age (individual women who did not visit the huts at a particular age because of pregnancy and amenorrhea contributed a value of zero to the computation). To correct for the hormonally detected menses that were not signaled by a visit to the menstrual huts, I divided the total number of menses at each age by 0.86. After this correction, the estimated mean number of lifetime menses was 128 and the median was 109.

An American physician who recorded all of her menses throughout her lifetime and who had 3 births had a total of 355 menstrual cycles (Treloar et al. 1967). Her menstrual experience spans 32 years instead of the more typical 38 years for American women, so she may have had fewer menses than the average for American women. However, Treloar et al. report that up until her first pregnancy her cycle length was at least two days shorter than the mean, which would partially cancel the effect of a short menstrual experience. Eaton et al. (1994) estimate that American women have a total of about 450 ovulations. Their estimate assumes that from menarche to menopause 96% of all menstrual cycles are ovulatory. In the postmenarcheal and perimenopausal years women have many long anovulatory cycles (Baird 1985), so Eaton et al.'s estimate of 450 ovulations per lifetime

2. In brief, the menstrual taboos of the Dogon are a male tactic for eliciting honest signals of female reproductive status. When a woman visits a menstrual hut, all members of her husband's patrilineage learn that she is neither pregnant nor in amenorrhea and that she will soon be ready to conceive. Information about the timing of conception is used in paternity assessments (Strassmann 1992, 1996b).

3. Another advantage of the menstrual-hut census is that it permitted detection of women's first postpartum menses. Such detection is critical because women of high fecundity became pregnant on one of their first postpartum ovulations. If I had monitored only those women who were cycling at the start of the study, the sample would have overrepresented women of low fecundity.

4. I monitored the hormone profiles for 70 women for ten weeks and found only one occasion on which a woman went to a menstrual hut when she was not menstruating. This woman was pregnant and appears to have been spotting. The data suggest that the primary reason women stayed home from the huts during 14% of all menses was simply to avoid an uncomfortable place (Strassmann 1996b).

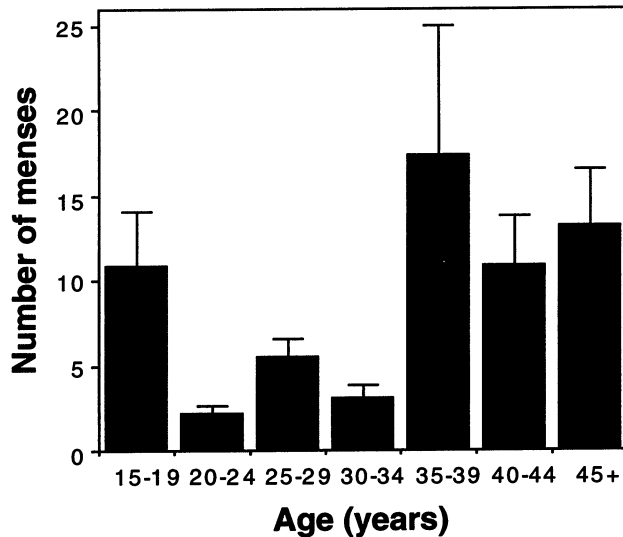


FIG. 2. Number of menses per woman per two years. Error bars, standard errors of the mean. The sample ( $N = 50$ ) includes every woman in the study village who had reached menarche (with the following exclusions: 34 postmenopausal women, 17 women who never menstruated during the study because of pregnancy or amenorrhea, 13 women not resident during the entire study, 4 infertile women, 3 women not exposed to the risk of conception because of separation or divorce, and 2 women who did not use the menstrual huts).

is probably too high. For purposes of comparison, I assume that 400 menses per lifetime is not unusual for American women. The median of 109 menses per lifetime among Dogon women is about a quarter of this value. Given that the Dogon are sedentary agriculturalists, the high frequency of menstruation found in many contemporary human populations probably originated not with agriculture but with birth control.

#### PATTERNING OF MENSES

The data also reveal striking features of the patterning of menstruation over female life histories. The frequency of menstruation among Dogon women had an approximately U-shaped relationship with age between menarche and menopause (fig. 2). To show this relationship more clearly, the graph excludes women who were continuously pregnant or in amenorrhea, and the full two years of data are presented. Women under 20 had a mean of  $10.8 \pm 3.3$  menses per two years, women aged 20–34 had  $3.8 \pm 0.6$  menses, and women 35 and older had  $12.9 \pm 2.2$  menses. This result is consistent with reports that fecundity has an inverse U-shaped relationship with age (Bendel and Hua 1978, Jain 1969, Wood and Weinstein 1988). A potentially confounding variable is coital frequency, but the numerous menses among women <20 years are probably due to adolescent subfecundity because women of these ages already had regular

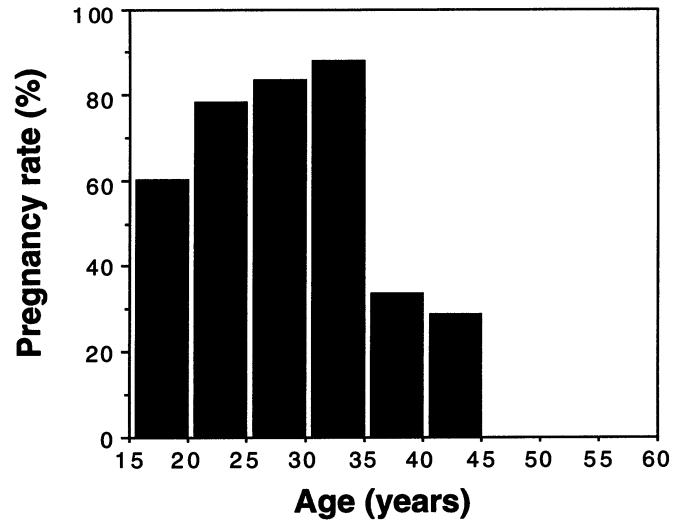


FIG. 3. The percentage of women ( $N = 50$ ), by age, who cycled during the study and who became recognizably pregnant.

TABLE I  
Variation in Reproductive Status with Age between Menarche and Menopause

Age (Years)	N	Cycling	Pregnant	Amenorrhea
15–19	5	$0.72 \pm 0.31$	$0.18 \pm 0.15$	$0.09 \pm 0.08$
20–34	46	$0.15 \pm 0.07$	$0.29 \pm 0.05$	$0.56 \pm 0.07$
35–53	15	$0.56 \pm 0.24$	$0.14 \pm 0.09$	$0.31 \pm 0.18$

NOTE: Variation is expressed as the mean proportion of time spent in each reproductive state over the two-year study period; 95% confidence limits are indicated. The sample includes all women in the study village who had reached menarche but not menopause, except for those who were not resident throughout the study or not exposed to the risk of conception because of infertility, separation, or divorce ( $N = 66$ ).

sexual partners. In fact, it is normative for Dogon girls to begin sexual relations prior to menarche. The low menstrual frequency among women aged 20–34 years reflects a high pregnancy rate (fig. 3) and lactational suppression of ovulation (table 1). Over the two-year study, cycling was the longest reproductive state for the youngest (<20 years) and oldest (>34 years) women, while lactational amenorrhea was the longest state for the women of prime reproductive age (20–34 years). After age 34, the frequency of menstruation increased dramatically and the pregnancy rate plummeted. This change can be attributed to reduced fecundity, lower coital frequencies at longer durations of marriage, and increased intrauterine mortality at the end of the reproductive years (Strassmann 1990, Wood 1989).<sup>5</sup>

5. Recent analyses indicate that husband's age is an important predictor of fecundability among the Dogon (Strassmann, unpublished data).

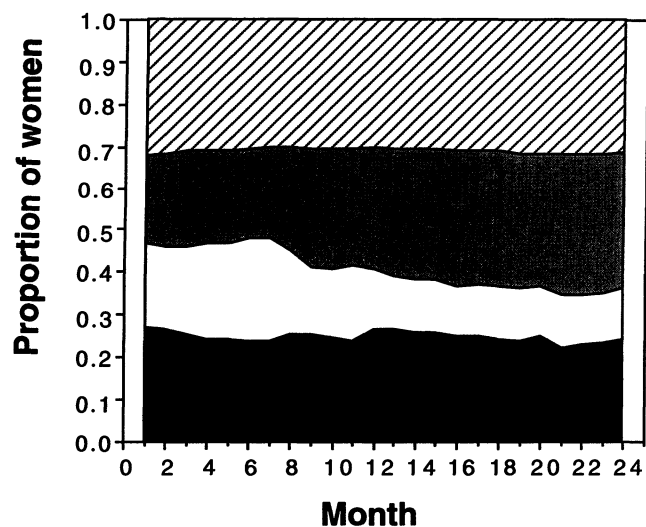


FIG. 4. Reproductive profile for the women ( $N = 122$ ) of the study village over 24 months. Black, cycling; white, pregnant; grey, in lactational amenorrhea; diagonal striped, postmenopausal.

The reproductive profile of the women ( $N = 122$ ) in the study village is shown in figure 4. Over the 736 days of the study the mean ( $\pm$  standard deviation) proportion of women who were cycling on a given day was  $0.25 \pm 0.01$ ;  $0.16 \pm 0.04$  per day were pregnant,  $0.29 \pm 0.04$  were in lactational amenorrhea, and  $0.31 \pm 0.006$  were postmenopausal. (Cycling was defined as the interval from the first day of the first postpartum menses through the first day of the last menses before a recognized pregnancy; pregnancy was defined as the interval from the second day of the last menses through the day of birth or miscarriage; lactational amenorrhea was defined as the interval from the day after birth or miscarriage through the day before the first postpartum menses.) On any given day, the subfecund women were overrepresented among the cycling women. The most fecund women conceived on one of their first postpartum ovulations and quickly dropped out of the pool of regularly menstruating women. For example, among the women aged 20–34 years, only two were sterile, and they had 23 and 29 menses each during the two-year study. The other women in their age-cohort had a mean of only  $3.8 \pm 0.6$  menses. Thus regular menses were a sign of sterility, not fecundity.

When menstrual cycle length was calculated from menstrual hut attendance, the median of the women's median cycle lengths was 30 days (lower and upper 95% confidence limits were 30.0 and 32.0 days, respectively;  $N = 58$  women, 477 cycles; age-range was 15 to 53 years, mean age  $\pm$  standard deviation was  $30.9 \pm 9.7$  years). When cycles longer than 46 days ( $N = 73$ ) or shorter than 17 days ( $N = 4$ ) were excluded for being outliers as defined by Wilkinson (1990:550), the median of the women's median cycle lengths was 28.5 days

(lower and upper 95% confidence limits were 27.5 and 29.0 days, respectively;  $N = 54$  women, 400 cycles). Estimates of cycle length in any population reflect the age-structure of the sample, but cycle length among the Dogon is biologically indistinguishable from cycle length in Western populations (Chiazze et al. 1968, Treloar et al. 1967, Vollman 1977).

#### MENSTRUAL SYNCHRONY

McClintock (1971) reported that social interaction caused the menstrual onsets for groups of dormitory friends to grow closer together by two days over a four-to-six-month period. Neither McClintock nor subsequent investigators found a tendency for menses to become concordant, but the phenomenon is nonetheless referred to by the misleading term "menstrual synchrony." In careful analyses, Wilson (1987, 1992) showed that three statistical errors undermine McClintock's evidence as well as that of subsequent investigators (Graham and McGrew 1980, Quadagno et al. 1981, Preti et al. 1986): (1) failure to correct for the convergence of menstrual onsets by chance, (2) exaggeration of the initial difference in onsets through miscalculation, leading to an erroneous impression of synchronization over time, and (3) possible sampling bias. Strassmann (1990) raised additional concerns having to do with the evolutionary novelty of the study populations (aggregations of young, cycling women) and inconsistencies in the findings across studies, suggesting the possibility of random effects. Moreover, three studies found no evidence for synchrony in Western populations (Jarett 1984, Wilson, Hildebrandt Kiefhaber, and Gravel 1991, Trevaathan, Burleson, and Gregory 1993). Despite the dearth of supporting data, many investigators continue to accept the existence of menstrual synchrony rather than confronting the methodological issues Wilson raised (Graham 1991, Weller and Weller 1993).

Prior to the present study there had been no published tests for menstrual synchrony in natural-fertility populations. Absence of synchrony in such populations would have two important implications: (1) it would seriously weaken the hypothesis (Burley 1979, Turke 1984) that menstrual synchrony is adaptive, and (2) it would refute the widespread assumption among anthropologists that menstrual synchrony occurred in preindustrial societies (Buckley 1988, Knight 1988). In natural-fertility populations, pregnancy and amenorrhea would prevent many women from cycling concurrently, but the possibility of synchrony can be tested among the remaining women. Among Dogon women of all ages who cycled during the present study, the median number of menses per two years was 6.0. McClintock (1971) reported that most of the synchronization in her study set in over only four cycles. If that is the case, then many Dogon women had enough cycles to synchronize, particularly in the age-cohorts younger than 20 years and older than 34 years.

In view of the above, I tested for menstrual synchrony among the Dogon. To avoid the methodological errors

TABLE 2  
Test for Synchronization Using Cox Regression

Variable	N Cycles	N Women	Coefficient	Standard Error	Exponentiated Coefficient	P-Value
Village	477	58	0.005	0.031	1.00	0.861
Lineage	477	58	0.057	0.050	1.058	0.258
Economic unit	477	58	-0.044	0.167	0.957	0.791
New moon <sup>a</sup>	477	58	0.029	0.094	0.308	0.758
First quarter <sup>a</sup>	477	58	-0.007	0.096	-0.068	0.946
Full moon <sup>a</sup>	477	58	-0.018	0.096	-0.189	0.850

<sup>a</sup>The first three lunar phases are shown contrasted with the omitted category, last quarter.

discussed by Wilson (1992), I introduce two new statistical approaches. Using Cox regression (Cox 1972, Dixon 1992), I asked whether, in any given cycle, a woman's risk of menstruating was influenced by the number of other women who were menstruating. The number of other women menstruating was calculated as three different independent variables: "Village" refers to all other women in the village; "lineage" refers to all other women who lived with a particular lineage of related males; and "economic unit" refers to the women who habitually worked together and ate together. These variables capture, with increasing degrees of closeness, the three main levels of social interaction among women. This analysis is modeled as follows:  $h_i(t) = a_i(t) \cdot e^{\beta x(t)}$  where  $h_i(t)$  is the  $i$ th woman's risk of menstruating at time  $t$  and  $a_i(t)$  is the baseline hazard rate for the  $i$ th woman and  $x(t)$  is a time-varying explanatory variable tested individually. The three coefficients were nonsignificant, providing no evidence for synchronization (table 2).

If menstrual synchrony is caused by the lunar cycle (Pochobradsky 1974, Law 1986, Cutler et al. 1987) or other environmental rhythms (Little et al. 1989), then it should occur village-wide. According to the null hypothesis of nonsynchrony, the menstrual onsets of different women should be independent, and thus the number of onsets per day should fit the Poisson distribution. According to the alternative hypothesis of synchrony, menstrual onsets should be clustered. Under the null hypothesis, the expected number of onsets per day,  $E(N)$ , equals the number of women at risk for menstruating on a given day (i.e., cycling and not pregnant or amenorrheic) divided by the number of days of risk. Following this logic, I calculated the expected number of onsets  $E(Nt)$  for each day ( $t$ ) as the number of women having menstrual onsets in a window centered on each day ( $t$ ) divided by the number of days in the window. Over the 736 days of the study, the observed and expected number of days with 0, 1, 2, 3, and 4 onsets did not differ significantly ( $\chi^2 = 1.50$ , d.f. = 4) (table 3). Thus the null hypothesis that the women's menstrual onsets were independent cannot be rejected.

Among the Dogon electric lighting is absent, so condi-

tions were favorable for testing specifically for lunar synchrony. I used Cox regression to ask whether a woman's risk of menstruating was influenced by lunar phase. Lunar phase was expressed as a time-varying categorical variable with a dummy variable for each of the four lunar phases. The analysis was stratified by woman ( $N = 58$ ), and each cycle ( $N = 477$ ) was an observation. None of the coefficients was significant (table 2), providing no evidence for lunar synchrony.

The lack of empirical support for menstrual synchrony among the Dogon and in Western populations does not establish the specieswide absence of the phenomenon, but it shifts the burden of proof onto those who argue that the phenomenon exists. Evidence for synchrony should also include an understanding of the mechanisms by which synchrony is achieved. At present, the pheromones or environmental influences that putatively cause synchrony in humans have not been identified. McClintock (1981) argued that menstrual synchrony is a functionless side effect of mechanisms that are adaptive in a different context. However, this context remains obscure. Synchrony does occur in other biological systems (hatching synchrony, firefly flashing, neuronal firing, to name a few), but in these cases the function of synchrony is better understood. Wallis (1985,

TABLE 3  
Test for Independence of Menstrual Onsets

Number of Menstrual Onsets per Day	Number of Days	
	Observed	Expected <sup>a</sup>
0	346.0	359.7
1	260.0	254.7
2	101.0	93.0
3	25.0	23.3
4	4.0	4.5

Pearson's  $\chi^2 = 1.50$ , d.f. = 4, n.s.

<sup>a</sup>If onsets were independent.

1992) reported synchrony of estrous swellings in chimpanzees (*Pan troglodytes*), but her methodology is unclear and appears to violate the assumptions underlying her statistical tests. For example, in the study of captive chimps, her chi-square test violated the assumption of independence of observations. Adaptive explanations for menstrual synchrony in humans assume ovulatory concordance or overlapping fertile periods (Burley 1979, Turke 1984), but if women's cycles get only two days closer together over four to six months (McClintock 1971) the impact on the timing of conceptions is probably negligible.

If menstrual synchrony exists, then during synchronization at least some of the women must shorten or lengthen their menstrual cycles so as to bring their menstrual onsets closer to those of the women with whom they are synchronizing. The plausibility of such adjustments needs to be evaluated in the light of other determinants of cycle length. In natural-fertility populations, many cycles include transient pregnancies which fail after only a few days or weeks, resulting in hormonal withdrawal, which then triggers menstruation. In these cycles, the timing of menstruation and menstrual cycle length are determined by the timing of pregnancy failure (Wilcox et al. 1988). Among noncontracepting American women, pregnancy occurred in 28% of menstrual cycles ( $N = 707$  cycles), and 31% of these pregnancies ended in loss (Wilcox et al. 1988). Thus, in 28% of cycles, menstrual synchrony would have been precluded by pregnancy.

Many other factors also impinge on cycle length and reduce the potential for menstrual synchrony. For example, long, irregular intervals between menses are associated with anovulation in the years just after menarche and prior to menopause (Baird 1985). Among women of prime reproductive age, irregular, anovulatory cycles are associated with negative energy balance (Ellison 1990), lactation (Howie and McNeilly 1982), and psychosocial stress (see Wasser and Barash 1983). In a study of 275,947 cycles in 2,702 American women, Treloar et al. (1967) concluded that the menstrual cycle is "characterized by variability rather than by regularity." At age 20, the median cycle length was 27.8 days and the difference between the 10th and 90th percentiles for person-year standard deviations was 6.3 days. Cycle length variability reached a minimum at age 36, when the median cycle length was 26.6 days and the difference between the two percentiles was 3.6 days. The inherent variability in cycle length has two components: (1) the different periodicities (cycle lengths) of different women, and (2) the substantial within-woman variability in cycle length (Treloar et al. 1967, Vollman 1977). Both are obstacles for synchrony.

Given the paucity of evidence, it is surprising that belief in menstrual synchrony is so widespread. I suggest that this belief arises, in part, from a popular misconception about how far apart one would expect the menstrual onsets of two women to be by chance alone (see fig. 5). If two women both have 30-day menstrual cycles, the maximum they can be out of phase is 15 days, and, on

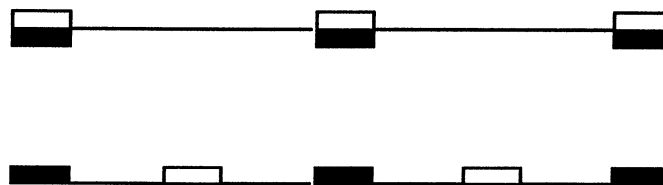


FIG. 5. Menstrual onsets for two women. Top: Onsets are maximally concordant. Bottom: Onsets are maximally out of phase (i.e., half a cycle apart). If one woman's onsets are independent of the other woman's onsets, then the difference in onsets for the two women is expected to be one-quarter the cycle length, on average.

average, their onsets are expected to be 7.5 days apart (Wallis 1985, Strassmann 1990, Wilson 1992). Fully half the time their onsets should be closer than 7.5 days. If menstrual synchrony among friends has psychological appeal, then onsets that happen to be close together may make a greater impression than onsets that happen to be disparate.

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## Population Increase and Sex-Biased Parental Investment in Humans: Evidence from 18th- and 19th-Century Germany<sup>1</sup>

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According to Fisher (1930), parents are shaped by natural selection to invest more in the sex of offspring that is expected to yield the greatest net fitness gains for them. Which of the two sexes is favoured depends on two factors: the differences in the per capita costs that parents incur when producing sons and daughters and the differ-

1. © 1997 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/97/3801-0010 \$1.00. We thank Arthur E. Imhof for generously making the data from his life-expectancy project available. Financial support came from the Deutsche Forschungsgemeinschaft and from the U.K. Biotechnology and Biological Sciences Research Council. Monique Borgerhoff Mulder provided valuable comments on the manuscript.