Menstrual hut visits by Dogon women: a hormonal test distinguishes deceit from honest signaling

Beverly I. Strassmann

Department of Anthropology, 1020 LSA Building, University of Michigan, Ann Arbor, MI 48109-1382, USA

In humans the interests of males and females may conflict with respect to the attribution of paternity. If a female has conceived through adultery, or changes mates while she is in early pregnancy, she may protect her reproductive investment by misassigning paternity. In Mali, West Africa, Dogon males attempt to prevent female deception by mandating honest advertisement of menstruation (Strassmann, 1992). This advertisement takes place at a menstrual hut where women are on display to all the members of their husband's lineage. Knowledge of the timing of menstruation is pivotal because no other physiological event is as useful in paternity assessments. In this article I use hormonal data and a census of menstrual hut visits to quantify female compliance with the menstrual taboos. The sample includes 93 women who provided urine samples twice weekly for 10 weeks. Analysis of urinary steroid hormone metabolites (pregnanediol-3-glucuronide and estrone-3-glucuronide) demonstrates that the women went to the menstrual huts during 86% of all menses and, with the exception of one woman who may have been spotting, they never went to the menstrual huts during pregnancy or amenorrhea. Thus the menstrual taboos of the Dogon were effective in eliciting honest signals of female reproductive status (pregnant, amenorrheic, or cycling). This study is the first to use hormonal data to test the honesty of a human behavior in a nonlaboratory setting. It also establishes the feasibility of urinary enzyme immunoassays as a tool for studying human reproduction in remote populations. Key words: animal signals, deceit, Dogon, enzyme immunoassay, honest signaling, menstrual taboo, menstruation, paternity assurance, urinary hormones. [Behav Ecol 7: 304–315 (1996)]

Studies of honesty and deceit in animal communication focus on male traits that enhance access to fecundable females. Examples include male sexual displays (Møller, 1990; Zahavi, 1975, 1977), fighting behaviors (Clutton-Brock and Albon, 1979), and the tactic of posing as a pseudofemale (Dominey, 1980; Thornhill, 1979). But what about the signals females use to convey their sexual receptivity or reproductive status—are they honest or deceitful? This question has attracted surprisingly little theoretical or empirical investigation.

In mammals, the relatively brief part of the ovarian cycle when a female is sexually receptive is termed "estrus" (Daly and Wilson, 1983). Whether estrus is an honest signal depends on how closely it coincides with the fertile period, but in most species it sharply reduces the ambiguity surrounding the timing of ovulation (Daly and Wilson, 1983). An exception is the postconception estrus of gray langurs (*Presbytis entellus*) and red colobus monkeys (*Colobus badius*) which helps prevent infanticide when a new male has taken over a troop (Hrdy, 1977; Struhsaker and Leland, 1985). Postconception estrus is one of the few known examples of deceptive signaling of reproductive status by females.

In humans, ovulation is concealed because it is unaccompanied by visual, olfactory, and behavioral changes that are sufficiently noticeable or reliable to identify the timing of the fertile period (Alexander and Noonan, 1979; Strassmann, 1981). Only in this century, and with the help of medical science, did humans first come to understand that ovulation occurs about 2 weeks after the onset of menstruation. Until the 1920s, the prevailing medical view was that ovulation and menstruation coincide (see Gruhn and Kazer, 1989:29; Hart-

man, 1932:76; Heape, 1900; Pouchet, 1842). In a classic text on reproductive biology, Marshall (1910) equated menstrual bleeding in women to proestrus bleeding in dogs. He argued that women experience greater sexual interest after menstruation and that this phenomenon is a vestige of estrus. In a sample of 186 preindustrial societies, the most common belief was that conception occurs immediately after menstruation rather than at midcycle (Strassmann BI, unpublished data; see also Paige and Paige, 1981). The widespread misidentification of the timing of the fertile period in both western and nonwestern societies supports the argument that ovulation in humans is concealed. If concealed ovulation evolved because it deprives males of accurate cues to the timing of ovulation, then it is a form of deceit in regard to female reproductive

Here, my study subjects are the Dogon, a millet-farming population who live in Mali, West Africa. I conducted field work among the Dogon for a total of 31 months (1986–1988, 1994). According to previous field-workers (Beaudoin, 1984; Calame-Griaule, 1965) and my own Dogon informants, the Dogon share the widespread belief that a woman is most fecundable immediately after menstruation. Among the Dogon, and possibly in other societies as well, this view stems from the assumption that menstruation is biologically the same phenomenon as estrus in domestic mammals.

When contraception is absent and women cycle for only a few months before becoming pregnant, the difference between estrus and menstruation is less apparent than when women cycle repeatedly. Although estrus is more closely coupled to ovulation than is menstruation, both phenomena are coupled to ovarian activity. Females do not menstruate when they are pregnant or in lactational amenorrhea, but will do so when they resume ovarian cycling. Knowledge that a female is cycling means that she is potentially fecundable. Dogon females of prime reproductive age (20–34 years) spent 15% of

Received 11 August 1993; revised 5 September 1995; second revision 28 September 1995; accepted 2 October 1995.



Figure 1
A menstrual hut in the village of Sangui. Men have placed hooked sticks above the door to pray for the birth of sons. In the foreground are the remains of two cooking fires; in the background are granaries with thatched roofs.

the time cycling, 29% of the time pregnant, and 56% in postpartum amenorrhea over a 2 year period (Strassmann, 1992). Therefore, the windows of fecundability are brief, but can be identified by the presence of menstruation. Thus, when ovulation is concealed, menstruation can be used as an indicator of female reproductive status (Strassmann, 1992).

During menses, Dogon women are segregated in a menstrual hut where they are obligated to sleep for 5 nights (Figure 1). This custom is not unusual, as menstrual huts were found in 12% of preindustrial societies (Strassmann, 1990). During menstruation Dogon women get no reprieve from agricultural labor and spend most days working in the fields. The village streets and family compounds are off limits and sexual intercourse and cooking for a husband are strictly forbidden. In a previous article (Strassmann, 1992), I argued the following: (1) the function of Dogon menstrual taboos is to force females to signal their menses, (2) menstrual signaling is imposed on senders (females) by receivers (husbands and their male relatives) through the use of social reprisals and

supernatural threats, and (3) the Dogon use knowledge of the timing of menstruation in relation to the timing of copulation to make paternity assessments. Because paternity assessments are crucial for avoiding investment in genetically unrelated offspring, I called this argument "the anti-cuckoldry hypothesis."

Previous hypotheses are incompatible with the Dogon evidence and can be excluded. For example, the hypothesis that menstrual taboos protect against bacterial "menotoxins" (Montagu, 1940; Schick, 1920) cannot account for the Dogon belief that inanimate fetishes are supremely vulnerable to menstrual pollution. The possibility that the taboos prevent menstrual odor from interfering with hunting (March, 1980), cannot explain the maintenance of these prohibitions among sedentary agriculturalists. A complex hypothesis by Paige and Paige (1981:209–254) depends on the assumption that a woman's fertility is threatening to her kin. This hypothesis is contradicted by the well-documented pronatalist attitudes of the Dogon (e.g., Calame-Griaule, 1965; Paulme, 1940). The hy-

potheses that menstrual taboos are a form of institutionalized discrimination against females (Young and Bacdayan, 1965), and that males promote the notion of menstrual pollution to dominate females (Douglas, 1975:62; Young, 1965:155), are more compatible with the Dogon data, but overlook the reproductive significance of menstruation. Through a comparison of females who use the menstrual huts against women who do not use the huts, I rejected the possibility that females promote the taboos. In particular, I found that hut use is predicted by the religion of a woman's husband. Women whose husband's were animist used the menstrual huts, but women whose husband's were nonanimist did not ($\chi^2 = 101.3$, df = 1, n = 133, p < .0001). Hut use was not predicted by a woman's own religion. These data reinforce informants' statements that the women do not like using the huts, but are obligated to do so by their husbands and fathers-in-law.

Dogon women are threatened with supernatural punishments and social reprisals if they either (1) fail to go to the menstrual hut when they are menstruating, or (2) go to the menstrual hut when they are not menstruating. Dogon informants of both sexes professed strong belief that if a woman stayed home during menstruation she would desecrate the animist fetishes (magical objects) that protect against famine and illness. When a woman believes in this supernatural threat, she cannot hope that her taboo infractions will escape detection—supernatural punishment is automatic. If a woman is caught not going to the hut during menstruation she is fined one sheep which is sacrificed by the male elders to restore the fetishes (and males alone consume the meat). If a woman goes to the hut when she is not menstruating, she commits an even more serious violation and risks becoming a social outcast. Thus, the taboos establish a rule that women must always signal menstruation, and they provide a way to *punish* women for false signaling.

The alternative to the taboos would be an informal system for detecting menstruation, in which husbands rely on casual clues. However, when menstruation is the most important physiological event used in paternity assessments, casual clues might not be dependable. If women alone control knowledge of menstruation, they can obscure the presumed timing of the onset of pregnancy. In Dogon society public recognition that a pregnancy may have resulted from adultery is potentially costly for the mother because it may result in reproductive failure through abortion or infanticide. Sons inherit millet fields through the paternal line, but if their paternity is in doubt they are barred from inheritance (Paulme, 1940:432-433; Strassmann, 1992). These are strong incentives for a pregnant woman to pretend that her husband is the father and to suppress any information to the contrary. Thus, the timing of menstruation is at the heart of a major conflict of interest between the sexes. The greater the disparity between male and female interests in regard to female sexual fidelity, the greater the potential advantages of menstrual signaling for males, and the greater the potential disadvantages for females.

Even if casual clues of menstruation were reliable, they would be difficult to monitor. One reason is that the Dogon do not use contraception, and menstruation is therefore a rare event. I censused the women present at the menstrual huts in the village of Sangui on each of 736 consecutive nights. The women who used the huts, and were between the peak reproductive ages of 20 through 34 years (N = 39), had a median of only two visits each over this 2 year period. The customary clothing for Dogon women is a long, wrap-around skirt that hides any menstrual blood on the legs; odor is controlled by absorbing the blood with rags and washing three times a day. Husbands and wives usually live in separate dwellings, and work, eat, and socialize in same-sex groups. These

customs severely limit the visual evidence with which husbands can evaluate their wives' potentially deceitful claims about the timing of menstruation and the onset of pregnancy. Husbands might discover menstruation accidentally through sexual intercourse, but, unless coital frequency was high, reliable monitoring would be difficult. In polygynous families Dogon husbands rotate between two, three, and occasionally four wives—which would decrease the chances for detection.

Dogon informants emphasized that menstrual huts signal menstruation not only to husbands, but to entire patrilineages (groups of males related through the paternal line). If a man is cuckolded, then the cost is born by his entire patrilineage because many fields are owned jointly. Land is inherited patrilineally, which means that the cost of cuckoldry is perpetuated over many generations. Members of the same patrilineage are therefore preoccupied not only with their individual but with their collective risk of cuckoldry. Because menstrual huts advertise menstruation to the entire patrilineage, rather than to the husband alone, they enable patrilineage members to participate in paternity assessments. The members of a patrilineage collectively have more information about the extramarital matings of the wives of their members than the husbands do individually, so it is potentially useful for the patrilineage as a whole to have knowledge of the timing of menstruation.

The menstrual hut used by the wives of a group of related males is usually situated next to the shade shelter (toguna) belonging to those males. For example, in Sangui, the two huts are located 23 m and 25 m from the shade shelters (toguna) belonging to the men of the corresponding patrilineages. This puts the women at the menstrual huts in direct view of the men in their husband's family. The design of menstrual huts enhances opportunities for the husband's patrilineage to monitor who is in attendance. Unlike other Dogon dwellings, menstrual huts are round, rather than rectangular, and they are out in the open, rather than inside compounds with walls that protect privacy. Menstruating women are usually gone from the huts during the day, but when they rise in the morning and return from the fields in the evening, they are highly visible. They make their cooking fires outside on the rocks, and usually sleep outside too. The interiors of the huts are cramped and windowless, which discourages the women from remaining inside.

Females could potentially cheat on the taboos in two ways. First, a female might go to the menstrual hut when she is not really menstruating so as to fake menstruation. A female might fake menstruation if she discovers that she is pregnant after having been caught in adultery (so as to pretend that she menstruated subsequent to the adultery). She might also fake menstruation if she is in early pregnancy and wants to change husbands and attribute the child to the new man. According to Dogon informants, faking menstruation is rare, although females were more convinced than males. Members of both sexes said that if a husband thought his wife was faking menstruation, he could send his sister to the menstrual hut to demand to see the menstrual blood. They also said that the women at the hut can be enlisted to check on each other, and that this is made easier by the fact that they must wash at the same places. Second, a female might cheat by failing to go to the menstrual hut when she is, in fact, menstruating. Not going to the hut would hide the presumed fertile period and possibly free women to exercise mate choice at that time. However, a simpler explanation consistent with informants statements is that not going to the huts is motivated by the desire to avoid an uncomfortable place. If females regularly engaged in either form of cheating (going to the huts when not menstruating or not going when menstruating) then the

utility of the taboos for monitoring menstruation would be undermined.

In this article, I use hormonal data on female reproductive status and a census of menstrual hut visits to quantify the actual incidence of both kinds of cheating. To my knowledge, no previous study has quantified the honesty of any human behavior that was directly observed in a nonlaboratory setting. This study is also significant in that it provides the first test of the suitability of urinary enzyme-linked immunosorbent assays (ELISA) for the longitudinal analysis of female reproductive status in remote human populations.

METHODS

This research was part of a broader field investigation of human evolutionary ecology among the Dogon of Mali, conducted from February 1986 to August 1988 and from May to June 1994.

Sample selection

The study subjects were 48 Dogon women from the village of Sangui (population 460 in 1988; $14^{\circ}29'$ N, $3^{\circ}19'$ W) and 45 Dogon women from the village of Dini (population 505 in 1988; $14^{\circ}28'$ N, $3^{\circ}18'$ W). I selected these 93 women because they were potentially cycling during a 10 week period from April to June 1987. A potentially cycling woman was defined as any woman between menarche and menopause who met at least one of the following criteria: (1) she menstruated at least one time during the 3 months prior to the start of the study (N = 63), (2) her last infant died before the start of the study (N = 2), (3) she reached menarche during the study and was added to the sample (N = 1), or (4) she last gave birth at least 7 months prior to the start of the study if the infant survived (N = 27).

The women who met criterion (4) had a strong likelihood of being in postpartum amenorrhea at the start of the study, but they were included because they had a chance of resuming menses before its conclusion. Given that the duration of postpartum amenorrhea is variable, one cannot predict when amenorrheic women will resume cycling. By including amenorrheic women in the sample, I avoided bias caused by exclusion of the first postpartum menses and overrepresentation of the less fecund women. Subfecund women experience more menses before becoming pregnant and are therefore more prevalent in any sample of menstruating women. The most fecund women become pregnant on one of their first postpartum ovulations and sometimes they do not experience a prior menstruation. In a prospective study I found that the minimum duration of postpartum amenorrhea among Dogon women is 12 months if the infant survives and continues to nurse. Therefore, by including all women in the sample if they gave birth at least 7 months prior to the start of the study (if the infant survived), I reduced the risk of bias.

Five women met the above sample selection criteria but did not volunteer to provide urine specimens. I omitted an additional four women because they provided ≤5 of the 20 urine collections scheduled and one woman because of assay error. The 93 women left in the sample comprise 90% of the potentially cycling women in the two villages during the 10 week study period. These women provided a median of 16 urine specimens each (range 7–20). Temporary absence of a woman from the village or participation in a ritual were the primary reasons for missed collections—other than menstruation itself. We did not collect urine from menstruating women because the chiefs forbade us from doing so on account of the pollution beliefs. The women who defied the taboos by staying home during menses also rarely gave us urine samples

during these lapses. Rather than admit that they were menstruating, they said they were ill. These same women were very cooperative about providing samples at other times. Women also did not provide urine samples during bleeding associated with spontaneous abortion. To remunerate the women for their participation in the study, I gave them condiments and contributed medications to a small dispensary.

Urine collections

The urine samples were overnight specimens collected on a twice weekly schedule (every 3 or 4 days alternately) for 10 weeks (70 days). I aliquoted 2 ml and added one drop of acetic acid as a preservative. Refrigeration was unavailable at my study site, so I froze the aliquots in liquid nitrogen. In 1990 I transferred them to a -80° C freezer. Each frozen aliquot was labeled only with an identification number and not with the woman's name. Because these ID numbers were intentionally different from those used in my other research involving the same women, I did not know who provided which sample while assaying them or interpreting the results 5 years later.

Hormone assays

I assayed the samples for pregnanediol-3-glucuronide (PdG) (a metabolite of progesterone) and estrone-8-glucuronide (E1G) (a metabolite of estrogen) in 1992 at the Reproductive Sciences Program at the University of Michigan. To prepare the urine samples for assay, I centrifuged the 2 ml aliquots in a CR 412 centrifuge for 5 min at 4°C and 15,000 rpm. I then diluted the urine samples 1:20 for the E1G assay (50 µl urine in 1 ml enzyme immunoassay buffer) and 1:100 for the PdG assay (200 µl of the 1:20 urine in 800 µl enzyme immunoassay buffer). I assayed the samples for PdG and E1G in duplicate using the enzyme-linked immunosorbent assay (ELISA) method of Munro et al. (1991). The standard curve for PdG had values from 1.25 ng/ml to 250.00 ng/ml and the E1G curve had values from 0.156 ng/ml to 20.000 ng/ml. I assayed all samples for a given woman on a single microtiter plate, so interassay variation was eliminated as a source of error when evaluating changes in hormone levels for individual women. For data reduction (logit-log transformation of optical densities to yield hormone concentrations), I used LigAnal, a software program for hormonal analysis developed by A. Rees Midgley of the University of Michigan.

I indexed hormone concentrations by the creatinine level to correct for variations in concentration due to changes in urine volume. I measured creatinine by the method of Taussky (1954) as adapted for use with microtiter plates. I diluted the urine for the creatinine analysis 1:50 in dd H₂O.

Human chorionic gonadotropin (hCG) was measured in singlicate using a two-site chemiluminometric (sandwich) immunoassay developed for the Ciba Corning Automated Chemiluminescence System (ACS 180). This assay provided qualitative confirmation of pregnancy when hCG levels were greater than 100 ng/ml urine.

Inferring menstruation from the hormonal data

After ovulation the ovarian follicle transforms into a corpus luteum whose primary secretory product is progesterone (Johnson and Everitt, 1988). If a menstrual cycle is ovulatory, the luteal phase will have a progesterone (and PdG) peak. In this study, I defined a cycle as ovulatory if the luteal PdG peak was greater than 3 standard deviations above the mean of the follicular phase values for that woman. In the exceptional cases when only one data point met this criterion, and the

E1G profile was flat, then I assumed that the cycle was anovulatory and that the single high value was an outlier. If a woman ovulates, she menstruates when her progesterone (and PdG) levels return to baseline, an event known as progesterone withdrawal (Johnson and Everitt, 1988). In this study, I diagnosed 82% of all menses by PdG withdrawal.

EIG is excreted in a somewhat more variable pattern than PdG, but it usually peaks at midcycle on the day of the serum luteinizing hormone surge or one day later, and has a secondary peak during the luteal phase (Munro et al., 1991). The midcycle EIG peak is usually less dramatic than the luteal PdG peak (Munro et al., 1991). Moreover, while PdG withdrawal is diagnostic for menses, EIG withdrawal is not always followed by menses and EIG levels occasionally remain elevated at the onset of bleeding (Shideler et al., 1989). For these reasons I relied primarily on the PdG data in determining the timing of menses. If, however, a cycle was anovulatory, then it was necessary to consider the EIG data. I diagnosed 8% of all menses by the withdrawal of EIG.

The first day of menstrual bleeding cannot be ascertained from hormonal data. PdG is a better predictor of menses than E1G, but there is still biological variation among women (and between cycles for a given woman) in PdG excretion at the time of onset of menses (Aldercreutz et al., 1982). Baseline follicular phase values differ among women and some individuals start to menstruate when PdG levels are still decreasing and have not quite reached baseline (Aldercreutz et al., 1982). Consequently, I could not use a single PdG or E1G value as a cutoff to predict when a woman should have started menstruating. Instead, I examined a graph of each woman's creatinine-indexed hormone concentrations, plotted against time in days, to identify the windows of time when menstruation was expected. These windows corresponded to the troughs between the PdG and E1G peaks and cannot be more precisely defined. I identified the troughs on each woman's graph before looking up the timing of her visits to the menstrual hut.

Menstrual hut visits

My research assistants and I censused the women present at the menstrual huts in Sangui on each of 736 consecutive nights including the 70 day period of the present study. In the village of Dini, the census was limited to this 70 day period

Detecting cheating

To detect cheating, I added a bar to each woman's graph to indicate the days (if any) that she spent at a menstrual hut. By visual inspection of each woman's graph, I determined whether or not progesterone withdrawal was followed by a menstrual hut visit. If any woman had an ovulatory cycle that was not followed by a visit to a hut, she was recorded as absent from the hut during menses. When a woman had an anovulatory cycle followed by E1G withdrawal and a visit to a menstrual hut, then I considered that visit to have occurred at a plausible time for menses. When E1G withdrawal in an anovulatory cycle was not followed by a visit to a hut, I assumed that menses had not occurred. I did not observe any anovulatory cycles in which a women went to a menstrual hut in the absence of E1G withdrawal, so a decision rule regarding such cases was not needed.

When a visit to a menstrual hut occurred at the start of the study, the hormone levels that preceded it were unknown. In these cases it was not possible to determine whether the visit followed PdG or E1G withdrawal, but it was possible to score the visit as appropriately timed if it occurred in a trough

(when hormone values were close to that woman's baseline) followed by a luteal peak.

Verbal reports of menses

The sample of 93 women included 19 women from Dini and 4 women from Sangui who were exempted from the taboos by nonanimist husbands. I did not regard the absence of these women from the menstrual huts as cheating because these women were not subject to the taboos. My research assistants and I asked the exempted women about their menstrual onsets twice weekly at the time of their urine collections. In the present study, I used the hormonal data for the exempted women to assess the accuracy of verbal reports of menses.

RESULTS

Seventy of the 93 women were required by their husbands to obey the menstrual taboos. Fifty-eight of these 70 women went to the menstrual huts when predicted from their hormonal profiles and stayed away from the huts at all other times. The hormonal data showed that of these 58 women, 25 were continuously pregnant or in amenorrhea and 33 cycled during the study, experiencing a total of 66 menses. Examples of typical hormonal profiles for the 33 women who cycled are shown in Figure 2.

Figure 2a is the hormonal profile of a 26-year-old woman (#25) who had two untruncated ovulatory cycles 27 days long each with two luteal peaks. Her first visit to the menstrual hut occurred on day 1 of the study, so the hormone levels that preceded it are unknown. It was scored as appropriately timed, however, because it occurred in a trough followed by a luteal peak. Her subsequent two visits to the menstrual hut followed PdG withdrawal. Thus this woman went to the menstrual hut when predicted by her PdG levels and at no other time.

Figure 2b is the hormonal profile of a 42-year-old perimenopausal woman (#18). Her PdG remained at baseline levels for 50 days, indicating that she experienced a long nonovulatory, amenorrheic interval as is typical of women who are approaching menopause. During this interval she complied with the taboos by staying home. Toward the end of the study she ovulated and had a luteal peak followed by PdG withdrawal and a visit to the menstrual hut.

Figure 2c is the hormonal profile of a 25-year-old woman (#11) who ovulated three times during the study and had three luteal peaks. She had two untruncated cycles 22 and 27 days long followed by a 23 day cycle that was truncated on day 70 by the end of the study, 2 days before she menstruated on day 72. Her first visit to the menstrual hut was scored as appropriately timed because it occurred in a trough followed by a luteal peak; her next two visits were scored as appropriately timed because they followed PdG withdrawal; her visit on day 72 also followed PdG withdrawal but was not scored because it occurred outside the study period. The reliability of this woman's visits to the menstrual hut was remarkable because she was infertile, which meant that she did not get the usual reprieve from hut visitation that occurs during pregnancy and postpartum amenorrhea. Women (N = 67) age 15-53 went to the menstrual hut a median of six times (mean ± SEM = 7.4 ± 1.0) over 24 months, but she went 29 times.

Figure 2d is the hormonal profile of an 18-year-old adolescent (#14). The follicular phase of her first cycle was truncated by the start of the study, but the luteal phase was fully included. It was scored as nonovulatory because the peak PdG value was less than 3 SD above her baseline PdG values. Her menstrual hut visit on day 12 was scored as appropriately timed because it followed E1G withdrawal. Her second cycle,

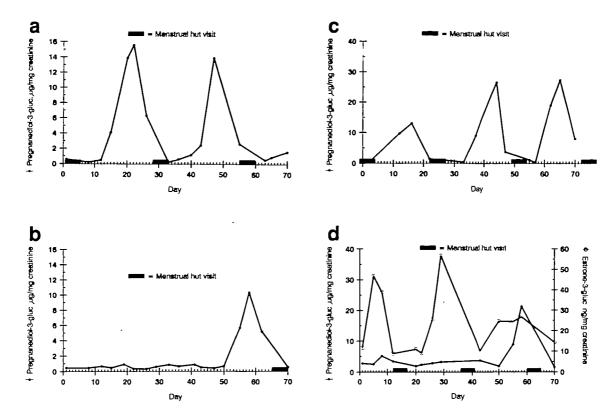


Figure 2
Urinary hormone metabolite profiles for four women who signaled menses reliably. (a-c) Pregnanediol-3-glucuronide concentrations for three women who ovulated and went to the menstrual hut after pregnanediol withdrawal. (d) Pregnanediol-3-glucuronide and estrone-3-glucuronide concentrations for a woman who had two nonovulatory cycles in which she went to the menstrual hut after estrone withdrawal. She then had an ovulatory cycle in which she went to the menstrual hut upon withdrawal of both pregnanediol and estrone.

which was 24 days long, could not be scored as ovulatory or nonovulatory due to missing data between day 29 and 43. It was nonetheless clear that her second visit to the menstrual hut was appropriately timed because it was associated with E1G withdrawal. Her third cycle was 24 days long and ovulatory with a clear luteal peak followed by an appropriately timed visit to the menstrual hut.

Figure 3 is the hormonal profile of a 22-year-old woman (#49) who had a spontaneous abortion at 2.5 months. She

experienced a dramatic fall in E1G and PdG at the time of her miscarriage on day 36 and remained at the menstrual hut for 10 days while bleeding continued. Afterwards she had a normal ovulatory cycle followed by menses and the usual 5 day visit to the menstrual hut.

In summary, Figures 2 and 3 show examples of hormonal profiles for the 33 women (21 from Sangui and 12 from Dini) who cycled during the study and who were reliable hut-goers. An additional 26 women from the two villages were required

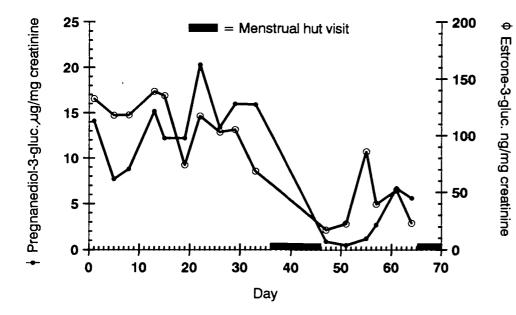


Figure 3
Pregnanediol-3-glucuronide and estrone-3-glucuronide concentrations for a woman who had a spontaneous abortion on day 36 and spent an obligatory 10 days at the menstrual hut. She then had a normal ovulatory cycle followed by menses and a 5 day visit to the hut beginning on day 65.

Figure 4
Pregnanediol-3-glucuronide concentrations for 12 women who were in postpartum amenorrhea. Each curve is offset from the curve below by 2 μg pregnanediol-3-glucuronide per milligram creatinine. The flatness of these profiles indicates that these women were not cycling and that their absence from the menstrual huts was appropriate.

to use the huts, but their hormonal profiles show that they did not menstruate during the study. With the exception of woman #90, these 26 women obeyed the taboos by not visiting the huts. Sixteen were in amenorrhea [perimenopausal (N = 3), adolescent (N = 1), postpartum (N = 12)] and 10 were pregnant. Figure 4 shows the PdG profiles for the 12 women in postpartum amenorrhea.

Figure 5 shows the hormonal profile for woman #90. Among the 70 women who were supposed to use the huts, she was the only one who did so when she was not menstruating. Her E1G rose from 11 ng/mg creatinine on day 2 of the study to 185 ng/mg creatinine on day 68; her PdG was below 2 µg/mg creatinine through day 22 and then rose to 17 µg/mg creatinine on day 44 and remained elevated at 7 µg/mg creatinine on day 68; her hCG levels exceeded 100 ng/ml urine by day 47 of the study. These results clearly indicate that woman #90 conceived during the study and was still pregnant at its close. She visited the menstrual hut on days 56–60 which was unexpected because she was already pregnant at that time. The visit of woman #90 to the menstrual hut during pregnancy has two possible interpretations,

which I will consider below: (1) she was spotting, or (2) she was faking menses.

Woman #73, who was 24 years old and from Dini, changed fiancés while pregnant (Figure 6). Her first urine sample was on day 8 of the study and at that time her E1G was 238 ng/mg creatinine, her PdG was 16 µg/mg creatinine, and her hCG was greater than 100 ng/ml urine, indicating pregnancy. On day 63 of the study she provided her last sample, at which time the levels were 665 ng/mg creatinine, 34 µg/mg creatinine, >100 ng/ml urine, respectively, indicating that she was still pregnant. Woman #73 provided 9 of the 20 urine collections. She missed collections on days 1, 5, 15, 29, 39, and 42 because she was spending the night in the village of her first fiancé. She missed collections on days 50, 54, 57, 63, and 67 because she was spending the night in the village of her second fiancé. She provided the nine other collections when she was at home in Dini in the compound of her father.

Woman #73's father was animist and she was supposed to obey the menstrual taboos while she was in Dini. During her pregnancy she did not go to the Dini menstrual hut, but she gave what appears to have been a false verbal report of men-

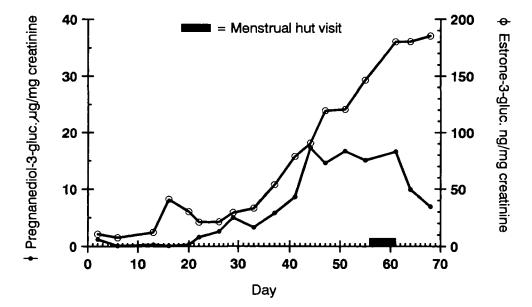


Figure 5
Pregnanediol-3-glucuronide
and estrone-3-glucuronide
concentrations for a woman
(#90) who conceived during
the study and who went to the
menstrual hut once while
pregnant.

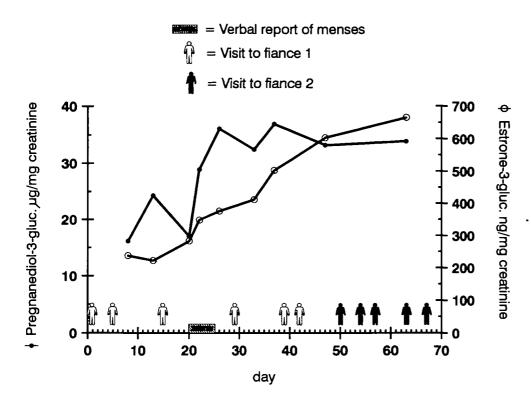


Figure 6 Pregnanediol-3-glucuronide estrone-3-glucuronide concentrations for a woman (#73) who was pregnant throughout the study but nonetheless changed fiancés between day 42 and day 50. The two men with contrasting shading indicate nights spent with her first fiancé in the village of Bongo and her second fiancé in the village of Engale. As indicated by the hatched bar, she gave a dubious verbal report that she menstruated on day 20 of the study.

ses. Specifically, she told my Dogon field assistants that she had menstruated earlier in the study (on days 20-25) and that we had neglected to record this event. This report was suspicious because (1) we did not see her at the menstrual hut even though we censused the huts on a daily basis, (2) her report was after the fact, and (3) on the days she said she had menstruated, she had provided urine collections 6 and 7 and, with rare exceptions, menstruating women did not provide urine samples. If she had a menstrual onset on day 20 and again on day 49 or so (29 days later), then she would have menstruated just prior to changing fiancés. Because she was actually 10 weeks pregnant when she made this switch, this seemed to be a possible case of deceit. I followed up this possibility during field work in 1994 at which time the son who had been conceived was 7 years old. It turned out that he was living in the village of his mother's first fiancé, who was recognized as his biological father. I will discuss the significance of this result below.

A woman can violate the taboos not only by faking menses, but also by staying away from the huts during menses. Among the cycling women who were required to use the huts, six women in Sangui and five women in Dini failed to do so following ovulation on one or two occasions each. These 11 unreliable hut-goers constitute 16% of the total sample of 70 women who were required to use the huts. If one excludes the women who were not cycling, they constitute 22% of Sangui hut-goers and 29% of Dini hut-goers. Hormonal profiles for 2 of these 11 unreliable women are shown in Figure 7. Figure 7a is the profile of a perimenopausal woman (#23), age 50, who skipped a visit to the menstrual hut following PdG withdrawal on one of three occasions; Figure 7b is the hormonal profile of a 41-year-old woman (#7) who skipped a visit on one of two occasions. Table 1 quantifies the number of menses detected by the hormonal data and compares this value to the number of hut visits and hut absences during menses. The reliable and unreliable women in the two villages had a total of 90 hormonally detected menses, and women were absent from the huts during 13 of these menses (14% of the total).

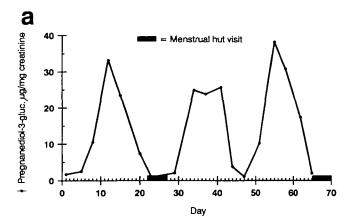
The above analysis is for the women who were supposed to obey the menstrual taboos. Among the 19 women of Dini who were exempted from the taboos, 18 had a hormonally detected menstruation during the study. Two of these 13 women (15%) did not report any of their menses (N=4) when questioned at the time of their urine collections. Eleven of these women consistently reported all (N=25) of their menses. Thus 14% of menses went unreported in Dini. The reliability of verbal reports cannot be adequately assessed in Sangui because only two of the four Sangui women who were exempted from the taboos (and were in the sample) ever menstruated during the study.

DISCUSSION

Compliance with menstrual taboos has never before been quantitatively investigated. One of the rare anecdotal reports, which is for the "Northern Indians" of the Hudson's Bay area, states that cheating is rampant (Hearne, 1795:303–304):

There are certain periods at which they never permit the women to abide in the same tent with their husbands. At such times they are obliged to make a small hovel for themselves at some distance from the other tents. . . . It is also a piece of policy with the women, upon any difference with their husbands, to make that an excuse for a temporary separation. . . . This custom is so generally prevalent among the women, that I have frequently known some of the sulky dames [to] leave their husbands and tent for four or five days at a time, and repeat the farce twice or thrice in a month, while the poor men have never suspected the deceit, or if they have, delicacy on their part has not permitted them to inquire into the matter.

By contrast with the above account, frequent violations of the menstrual taboos were not found in the present study. Among the 70 women who were required to use the huts, only woman #90 did so when she was not menstruating (Figure 5). The possibility that she was faking menses cannot be excluded, but it seems more likely that she was spotting because no



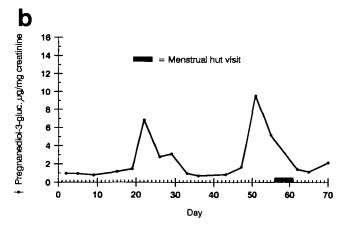


Figure 7
Pregnanediol-3-glucuronide concentrations for two women who signaled menses unreliably. (a) A woman who menstruated on day 22, approximately day 45, and day 65 of the study. As indicated by the absence of a black bar, she did not go to the menstrual hut during her second menses around day 45. (b) A woman who menstruated on approximately day 33 without going to the menstrual hut. She menstruated again on day 56 at which time she did go to the hut. This woman was in transition from postpartum amenorrhea to cycling.

motivation for deceit is apparent. I estimate that she was 38 days pregnant at the time of her visit, a plausible time for spotting to occur. Although the possibility that she was cheating cannot be excluded, I can identify no reason for suspecting that she had a motive for deceit. At the start of the urine collections she was 17 years old and her sexual relations with her fiancé had been ongoing for only two months. She did not change fiancés during the course of the study. Her father, who was animist, required her to use the huts, but not her fiancé, who was Muslim. Because she still lived at home, her father's rule held sway. I have no information on sexual partners other than her fiancé. She gave birth to a son who died soon thereafter.

According to the anti-cuckoldry hypothesis, women have the greatest motivation to go to the menstrual hut when they are not menstruating if (1) they discover that they are pregnant after having been caught in adultery (and want to pretend that they menstruated subsequent to the adultery), or (2) they are in early pregnancy and want to change fiancés or husbands. Neither of these situations is known to pertain to woman #90. If woman #90 was cheating nonetheless, then the incidence of this kind of cheating among the 70 women

Table 1
The number of hormonally detected menses compared to the number of hut visits and hut absences during menses

	Menses		Hut visits		Hut absences		Cycles not scored	
	S*	Dª	S	D	S	D	S	D
Reliable women $(N = 33)$	44	22	44	22	0	0	3	3
Unreliable women $(N = 11)$	12	12	5	6	7	6	3	0

The reliable women always went to the huts during menses; the unreliable women had one or two absences each. A total of nine cycles were not scored due to missing urine collections.

who were required to use the huts was 1.4%. If we consider only the women who were pregnant throughout this study (N = 10), or who conceived during this study (N = 4), then the potential incidence of cheating was 7% (1 out of 14).

The sample size was adequate to establish that women rarely went to the menstrual hut in the absence of menstruation. However, the sample size of pregnant women was small (N = 14), and only one of these women (#73) was known to have a possible motive for faking menstruation. Therefore, I could not measure the incidence of going to the hut during pregnancy against the provocation for this form of cheating. To obtain this information, one would need a larger sample of women in early pregnancy, when the motivation for faking menstruation should be greatest.

It is interesting, however, that the only woman (#73) who changed fiancés while pregnant, and therefore may have had a motive for faking menstruation, did not do so. She obeyed the menstrual taboos by staying away from the hut throughout her pregnancy. When she switched fiancés, she had been absent from the menstrual hut for more than 11 weeks, which made it obvious to her second fiancé that she was pregnant at the start of their relations. The child is being raised by her first fiancé, who is presumably the genetic father. Thus, in the case of woman #78, the menstrual taboos appear to have successfully served the purpose of revealing female reproductive status and preventing cuckoldry. Although woman #73 gave a dubious verbal report of menstruation, this report was unsuccessful or, more likely, was aimed only at my research assistants and myself. In conclusion, this appears to be a case in which the menstrual taboos revealed that a woman was already pregnant upon remarriage.

In previous research, I analyzed the reproductive status of 10 hut-going women who divorced and remarried in Sangui, and found that all 10 were cycling at the time of the switch. Women of their age (20–34 years) spent an average of only 15% of the time cycling, which means that the probability that all 10 were cycling by chance alone is remote: $(0.15)^{10} = 6 \times 10^{-9}$. This result supported a prior prediction that Dogon women usually remarry when cycling (Strassmann, 1992). In this regard, the behavior of human females resembles that of chimpanzees (*Pan troglodytes*). Adult female chimpanzees nearly always transfer between troops when they are sexually cycling (Pusey and Packer, 1986). The hormonal data on woman #73 extend these findings by showing that Dogon women do sometimes remarry when pregnant, and that menstrual taboos can be useful for exposing such cases.

The second type of cheating—staying home during menses—was more prevalent than I expected. Among the hut-going women of Sangui, 12.5% of all menses were not flagged

S = Sangui, D = Dini.

by a visit to the hut; in Dini the percentage was 17.6%. Among the 11 women who were unreliable in their menstrual hut visits, 9 women skipped only one visit and only 2 women skipped two visits (Table 1). Because even the unreliable women went to the menstrual hut during 54% of their menses, this type of cheating was not easy to detect.

Staying home during menses is a clear violation of the menstrual taboos and the women pay the male elders one sheep if they are caught. This type of cheating has two alternative explanations: (1) avoiding the inconvenience and discomfort of the menstrual huts or (2) hiding the presumed fertile period. The latter might prevent unwanted sexual attention (by husbands or others) or it might enable women to exercise mate choice at the time they believe they are fecundable. Although I cannot exclude the second explanation and it might apply to some instances of cheating, the first explanation is more compatible with the fact that some of the women who stayed home during menses were perimenopausal. These women were beyond the age (41 years) at which women in my study stop having live births, and their absences from the menstrual huts therefore cannot be explained as attempts to hide their fecundability. The suggestion that women dislike the menstrual huts is supported by informants statements and by a comparison of the material comforts available to a woman at home versus at the menstrual huts. When she is home, a woman always sleeps in a sheltered and private place on a mat or even a bed, but at the menstrual hut she sleeps on bare rock exposed to the wind or inside the hut on boards. For the 5 days she sleeps at the hut she must cook out of pots that she stores outside the village. She does not have access to her belongings because if she used them during menstruation they would become "polluted" and would not be allowed back in the village. Her children, meanwhile, are apt to be left in the care of a distrusted cowife. One of my young field assistants complained that his mother's cowife would not cook for him and his siblings when his mother was menstruating. Thus, a Dogon woman who stays home from the menstrual hut during menses may have ample motives other than the desire to obscure her reproductive status.

Given that a woman is married to an animist and therefore is obligated to use the huts, does her own religion influence her likelihood of cheating? Sample sizes are too small to draw any definite conclusions, but of the six cheaters from Sangui only one (17%) was animist; the other five (83%) were nonanimist. Among the reliable women who menstruated, 6 (33%) were animist, 12 (67%) were nonanimist, and the religion of 3 women is unknown. A woman who believes that menstrual blood will endanger the fetishes has more to fear from cheating than a woman who has discarded such beliefs. A woman who believes in the taboos will expect punishment from any transgression to follow automatically, but a nonbelieving woman has only to worry that her husband (or others) will catch her. Perhaps the reason why even the unreliable hutgoers visited the huts during 54% of their menses is that more frequent lapses would have been too obvious.

The women in this study stayed home from the menstrual huts during 14% of all menses (N=90) (Table 1), which raises the question: What is the effect of this sort of cheating on the capacity of husbands and patrilineages to monitor female reproductive status? If a woman has already signaled that she is cycling by going to the menstrual hut after postpartum amenorrhea, then even if she stayed home during half of her subsequent menses, it would still be clear that she was cycling. After one or more absences from the hut people might temporarily think she was pregnant, but as soon as she showed up at the hut again it would be evident that she was not. For example, although woman #23 (Figure 7a) skipped a visit to the menstrual hut around day 47, it is obvious in retrospect

that she did not have a fertile conception (defined as a conception that ultimately produces a livebirth) during the 70 day study. Given that even the unreliable women went to the menstrual hut during 54% of their menses, most absences during menstruation did not lead to significant confusion about female reproductive status. However, if a woman skipped a hut visit during her first postpartum menses, or her last menses before pregnancy, then her waiting time to conception (defined as the interval between postpartum amenorrhea and pregnancy) would appear one cycle shorter. This situation pertains only to woman #7 (Figure 7b). To find out if any of the women were pretending to be in amenorrhea for a prolonged time, when in fact they were cycling, I examined the hormonal profiles for the 16 nonpregnant women who consistently stayed away from the huts although married to animists. I found that all of these women were genuinely in amenorrhea (Figure 4). Thus, in my sample of 70 women, menstrual hut visitation was a useful tool for monitoring female reproductive status, and the confusion caused by cheating was minimal.

How good is menstrual hut visitation as a signal of menstruation if women use the huts during other types of vaginal bleeding? Only 1 (7%) of the 14 pregnant women in this study went to the menstrual hut while pregnant, and this individual (#90) did so just once during the study. If she was spotting and not cheating, then 93% of pregnant women never used the huts due to spotting so this form of bleeding was not a major confounder. In a sample of 25 pregnancies that I monitored prospectively for the full period of gestation, all 25 births occurred approximately 9 months after the mother's last visit to the menstrual hut. No birth occurred outside the normal variation around the 270 day gestation period in humans (Strassmann, 1992). Thus spotting during pregnancy is not such a common event that it seriously compromises the utility of the taboos for monitoring female reproductive status.

According to the hormonal data, all other visits to the menstrual hut were compatible with menstruation (Figure 2) or spontaneous abortion (Figure 3). From the standpoint of detecting female reproductive status, it is not important to distinguish between these two events because fetal loss often happens cryptically at the time of menstruation. According to Wilcox et al. (1988), the probability of loss per conception is 0.31 (SE = 0.03). Woman #49 (Figure 3) had an obvious miscarriage because she had been absent from the hut for longer than one cycle and remained at the hut for 10 days while bleeding continued.

The conclusion that, with the exception of woman #90, the women in this study went to the hut only during menses or spontaneous abortion is also supported by data on menstrual cycle length. These data are based on hut visitation rather than interviews. The median of the women's median cycle lengths was 30 days (lower and upper 95% confidence limits were 29.0 and 32.0 days, respectively; n = 58 women, 477 cycles). When cycles rather than women were equally weighted, the median was 29.0 days and the lower and upper 95% confidence limits were 29.0 and 30.0 days respectively (N =477 cycles) (Strassmann, 1990, 1992). The cycle lengths for women in any given study will vary with the age structure of the sample, but the values I found are similar to those of other studies (e.g., Chiazze et al., 1968; Treloar et al., 1967; Vollman, 1977). For example, Chiazze et al. (1968) (who weighted cycles rather than women equally) reported a mean cycle length of 29.1 days with a standard deviation of 7.46 days. Thus the periodicity of menstrual hut visitation among Dogon women clearly reflects the periodicity of the menstrual cycle.

In evaluating the incidence of cheating found in this study, it is important to consider any biases that might have influenced the results. For example, is it possible that women

obeyed the taboos more closely while I was monitoring them? Greater compliance during the study is unlikely because neither my Dogon field assistants or subjects were aware that I could detect menstruation by analyzing urine. They knew only that my study was about female fertility and reproductive health, which was the major focus of the urine collections although not a part of the present analysis. The sample excludes 10% of the women who met the sample selection criteria (see methods), but I cannot identify anything in their marital or reproductive profiles that suggests that they should have been more or less inclined to cheat than the others. Perhaps the nonparticipators were more concerned about the onerousness of providing urine samples or had less of a desire to please the research team by cooperation. The major reasons for missed collections were travel, participation in a ritual, or menstruation itself, none of which should have biased the results in any particular direction.

The success of this study was contingent on the cooperation of the subjects. At the outset, I requested each woman to provide only her own urine samples. The graphs in Figures 2-7, as well as others not reproduced here, are reasonably smooth, so it appears that the women complied with this request. One woman gave us water instead of urine on one occasion, but this sample was easily identified and excluded. Prior to beginning the urine collections, I had lived in one of the study villages (Sangui) for a year which meant that I had time to develop trust among the subjects and to learn the fundamentals of their language. During this time I provided basic first aid to the village (for up to 2 hours a day) and employed numerous people in connection with the research. These activities helped to build good will. At the request of the village, I also began making plans to obtain financing for a small development project—a dam and a dike to retain rainwater needed for watering onion gardens. The village completed construction of this project in 1989.

This study demonstrates the suitability of urinary ELISAs as a tool for studying human reproduction longitudinally in remote populations. Although I used this method to detect menstruation, the data also provide evidence of ovulation, luteal sufficiency, and fetal loss. Thus the hormonal results can be used to address a variety of questions about the factors that impinge on these aspects of female reproductive functioning. Urinary hormones have recently been assayed under field conditions (Campbell, 1994; Leslie et al., 1996). This is a promising new development because it obviates the need to preserve and transport samples. To date, such methods are qualitative or semi-quantitative and have been used in crosssectional but not longitudinal studies. Previous endocrinological research on field populations [e.g., |Kung of Botswana (Konner and Worthman, 1980), Gainj of highland New Guinea (Wood et al., 1985), Ituri of Zaire (Ellison, 1988; Ellison et al., 1986)] has employed radioimmunoassays, primarily of plasma, serum, and saliva. The major advantage of ELI-SAs over radioimmunoassays is that they eliminate the health risks and disposal problem of radiolabeled reagents and reduce the monetary and labor costs of analysis (Lasley et al., 1991; Munro and Lasley, 1988). Urinary assays do not require venopuncture for sample collection, which makes them less invasive than plasma or serum assays and therefore more appropriate for field studies-particularly when repeated sampling is required. In some populations salivary assays are the least invasive (Ellison, 1988), but this does not apply to the Dogon and other populations that are already accustomed to providing urine, not saliva, to health workers. A disadvantage of salivary steroids is that they occur at low concentrations so steroids introduced into the saliva through oral bleeding or food will seriously distort the assay results. Urinary assays, by contrast, are unencumbered by the problem of contaminants.

Oral health is very poor among the Dogon, as it is in many other remote populations, which means that urinary assays may often be the method of choice. Another advantage to working with urine is that hCG and many other hormones not measurable in saliva can be assayed in urine (Campbell, 1994). Other advantages and disadvantages of urine versus saliva depend on the time scale against which one is measuring hormone change. Day-to-day changes over the menstrual cycle can be more easily calculated from urine, but pulsatile release patterns and circadian rhythms can only be obtained from blood or saliva (Ellison, 1988). When subject cooperation is poor, an advantage of saliva collections over urine collections is that researchers can watch subjects spitting, but cannot watch them urinating.

In conclusion, this study employed urinary ELISAs to show that the honesty of a human behavior can be quantified through direct observation in a nonlaboratory setting. It provided a quantitative answer to the question: Do Dogon women follow the rules? Dogon women did indeed follow the rules by correctly signaling menstruation during 86% of all menses. Menstrual signaling is unusual because it is imposed on senders (females) by receivers (husbands and their male relatives). This coercion is accomplished by means of social reprisals and supernatural threats. To understand the success of this coercion, it is informative to note that the major structural features of Dogon society are designed to help males, not females, to realize their reproductive interests (Strassmann, 1992). For example, the residence rule is patrilocal (wife resides with husband's kin) which makes it easy for brothers and other related males to cooperate. To impede the formation of female kinship bonds, sisters are barred from marrying into the same patrilineage. If sisters want to cooperate, they often have to travel great distances to do so. Time allocation data show that females (age ≥30 years) spend 21% more time working than males (t = -5.10, df = 127, p < .0001), and males (age ≥30 years) spend 29% more time resting than females (t = 7.71, df = 127, p < .0001). Males expressly forbid the women from using shade shelters-places for politics and the enjoyment of leisure time. Although females spend more time working, their diet contains significantly less animal protein. Animism, the traditional religion, is a vehicle through which Dogon males have imposed a variety of taboos on females (in addition to the menstrual taboos), but is not a vehicle through which females have imposed any taboos on males. This discrepancy may explain why, in a sample of 113 women and 71 men from Sangui, men were more likely than women to have a favorable attitude toward animism (χ^2 = 10.11, df = 1, p < .001) and women were more likely to reject religion entirely ($\chi^2 = 20.61$, df = 1, p < .001) (Strassmann, 1992). An interesting task for the future is to measure the success of the animist taboos at guarding against cuckoldry. This would require a comparison of the paternity certainty of animist men (who make their wives use the huts) and nonanimist men (who do not).

I thank the women of Sangui and Dini for participating in this study and Dr. Klena Sanogo of the Institut des Sciences Humaines, Bamako, for authorizing it. Sylvie-Moulin, Sally Slocum, and Thomas Stevenson were an indispensable help in the field. Several reproductive endocrinologists provided generous assistance: James B. Brown advised me on the collection protocol; Bill Lasley, Susan Shideler, and Coralie Munro provided antibody, conjugate, and their excellent assay protocols; A. Rees Midgley offered laboratory space and equipment; and Dan McConnell and his coworkers carried out the hCG assays. Richard D. Alexander, James Wood, Peter Smouse, and Mark O'Brian helped with logistics. This research was supported in part by the LSB Leakey Foundation, the National Science Foundation (BNS-8612291), the National Institutes of Health (HD07480-02), the Evolution and Human Behavior Program and the Office of the Vice President at the

University of Michigan. Approval for this study was granted by the Human Subjects Review Committee of the College of Literature Science and the Arts, University of Michigan.

REFERENCES

- Aldercreutz H, Brown J, Collins W, Goebelsman U, Kellie A, Campbell H, Spieler J, Braissand G, 1982. The measurement of urinary steroid glucuronides as indices of the fertile period in women. J Steroid Biochem 17:695–702.
- Alexander RD, Noonan KM, 1979. Concealment of ovulation, paternal care, and human social evolution. In: Evolutionary biology and human social behavior (Chagnon NA, Irons W, eds). North Scituate, Massachusetts: Duxbury Press; 486–458.
- Beaudoin G, 1984. Les Dogons du Mali. Paris: Armand Colin.
- Calame-Griaule G, 1965. Éthnologie et Langage: la Parole Chez les Dogon. Paris: Editions Gallimard.
- Campbell KL, 1994. Blood, urine, saliva and dip sticks: experiences in Africa, New Guinea, and Boston. In: Human reproductive ecology: interactions of environment, fertility and behavior (Campbell KL, Wood JW, eds). New York: New York Academy of Sciences; 312–330.
- Chiazze L, Brayer FT, Macisco JJ, Parker MP, Duffy BJ, 1968. The length and variability of the human menstrual cycle. J Am Med Assoc 203:89–92.
- Clutton-Brock TH, Albon SD, 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145–170.
- Daly M, Wilson M, 1988. Sex, evolution, and behavior, 2nd ed. Wadsworth, California: Belmont Publishing.
- Dominey WJ, 1980. Female mimicry in male blue gill sunfish—a genetic polymorphism? Nature 284:546-548.
- Douglas M, 1975. Implicit meanings: essays in anthropology. London: Routledge and Kegan Paul.
- Ellison PT, 1988. Human salivary steroids: methodological considerations and applications in physical anthropology. Yearbook Physical Anthropol 31:115–142.
- Ellison PT, Peacock NR, Lager C, 1986. Salivary progesterone and luteal function in two low fertility populations of northeast Zaire. Human Biology 58:478–483.
- Gruhn JG, Kazer RR, 1989. Hormonal regulation of the menstrual cycle. New York: Plenum.
- Hartman CG, 1932. Studies on the reproduction of the monkey *Macacus (Pithecus) rhesus* with special reference to menstruation and pregnancy. Contrib Embryol Carnegie Inst, Washington 23:1-161.
- Heape W, 1900. The 'sexual season' of mammals and the relation of the 'proestrum' to menstruation. Q J Microscop Sci 44:1-70.
- Hearne S, 1795 (reprinted 1911). A journey from Prince of Wales's Fort, in Hudson's Bay, to the Northern Ocean. Toronto: Champlain Society (vol. 6).
- Hrdy SB, 1977. The langurs of Abu: female and male strategies of reproduction. Cambridge: Harvard University Press.
- Johnson M, Everitt B, 1988. Essential reproduction. Oxford: Blackwell Scientific.
- Konner M, Worthman C, 1980. Nursing frequency, gonadal function, and birth spacing among !Kung hunter-gatherers. Science 207:788– 791.
- Lasley BL, Shideler SE, Munro CJ, 1991. A prototype for ovulation detection: pros and cons. Am J Obstet Gynecol 165:2003–2007.
- Leslie, PW, Campbell KL, Little MA, Kigondu CS, 1996. Evaluation of reproductive function in Turkana women with enzyme immunoassays of urinary hormones in the field. Hum Biol 68:95–117.

- March KS, 1980. Deer, bears, and blood: a note on nonhuman response to menstrual odor. Am Anthropol 82:125–126.
- Marshall FHA, 1910. The physiology of reproduction. London: Longmans Green.
- Møller AP, 1990. Effects of a haematophagous mite on the barn swallow *Hurundo rustica*: a test of the Hamilton and Zuk hypothesis. Evolution 44:771–784.
- Montagu MFA, 1940. Physiology and the origins of the menstrual prohibitions. Q Rev Biol 15:211-220.
- Munro CJ, Lasley BL, 1988. Non-radiometric methods for immunoassay of steroid hormones. In: Nonradiometric assays: technology and application in polypeptide and steroid hormone detection (Hazeltine FP, Albertson BD, eds). New York: Alan R. Liss; 289–329.
- Munro CJ, Stabenfeldt GH, Cragun JR, Addiego LA, Overstreet JW, Lasley BL, 1991. Relationship of serum estradiol and progesterone concentrations to the excretion profiles of their major urinary metabolites as measured by enzyme immunoassay and radioimmunoassay. Clin Chem 37:838–844.
- Paige KE, Paige JM, 1981. The politics of reproductive ritual. Berkeley: University of California Press.
- Paulme D, 1940. Organisation Sociale des Dogon. Paris: Les Editions Domat-Montchrestien.
- Pouchet FA, 1842. Théorie Positive de la Fécondation des Mammifères. Paris: Bailière et Fils.
- Pusey AE, Packer C, 1986. Dispersal and philopatry. In: Primate societies (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker RR, eds). North Scituate, Massachusetts: Duxbury Press, 250–266
- Schick B, 1920. Das Menstruationsgift. Wiener Klinische Wochenschrift 33:895–397.
- Shideler SE, DeVane GW, Kalra PS, Benirschke K, Lasley BL, 1989. Ovarian-pituitary hormone interactions during the perimenopause. Maturitas 11:331–339.
- Strassmann BI, 1981. Sexual selection, paternal care, and concealed ovulation in humans. Ethol Sociobiol 2:3–40.
- Strassmann BI, 1990. The reproductive ecology of the Dogon of Mali (PhD dissertation). Ann Arbor: University of Michigan.
- Strassmann BI, 1992. The function of menstrual taboos among the Dogon: defense against cuckoldry? Human Nature 3:89–131.
- Struhsaker TT, Leland L, 1985. Infanticide in a patrilineal society of red colobus monkeys. Z Tierpsychol 69:89–132.
- Taussky HH, 1954. A microcolorimetric determination of creatmine in urine by the Jaffe reaction. J Biol Chem 208:853–861.
- Thornhill R, 1979. Adaptive female-mimicking behavior in a scorpionfly. Science 205:412-414.
- Treloar AE, Boynton RE, Behn BG, Brown BW, 1967. Variation of the human menstrual cycle through reproductive life. Int J Fertility 12: 77-196
- Vollman RF, 1977. The menstrual cycle. Philadelphia: Saunders.
- Wilcox AJ, Weinberg CR, O'Connor JF, Baird DD, Schlatterer JP, Canfield RE, Armstrong EG, Nisula BC, 1988. Incidence of early loss of pregnancy. New Engl J Med 319:189–194.
- Wood JW, Johnson PL, Campbell KL, 1985. Demographic and endocrinological aspects of low natural fertility in Highland New Guinea. J Biosoc Science 17:57–79.
- Young FW, 1965. Initiation ceremonies: a cross-cultural study of status dramatization. Indianapolis: Bobbs-Merrill.
- Young FW, Bacdayan A, 1965. Menstrual taboos and social rigidity. Ethnology 4:225–240.
- Zahavi A, 1975. Mate selection—a selection for a handicap. J Theor Biol 58:205–214.
- Zahavi A, 1977. The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603-605.