

Kinship, Parental Care, and Human Societies

To a Life Mate

should we be primitives you and I
 could lie together naked between bearskins
 staring at the night-time sky
 listening to the forest
 and dreaming sweet sadnesses
 about all that must have gone before us
 and all that must come after

Alexander 2011, p. vii

INTRODUCTION

Concealed Ovation in Humans: Further Evidence

Beverly I. Strassmann

Introduction to Alexander, R.D. and Noonan, K.M. 1979. Concealment of Ovation, parental care, and human social evolution. In N.A. Chagnon and W.G. Irons (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. 436-453. North Scituate, MA: Duxbury Press.

I first met Richard Alexander in 1976 when he directed my summer efforts to help my sister Joan with her research on paper wasps (*Polistes annularis*). This study entailed standing on a ladder painting dots on the wasps, sticking it out as long as possible while the wasps grew increasingly agitated. In the Texas heat, my sister wisely wore a bee veil and painter's coveralls while I wore skimpier clothing and got lots of wasp stings. At the end of the summer, I met with Alexander in his office in the Museum of Zoology and he asked me: "What is kin selection?" Alexander was unique among professors in his enthusiasm for discussing science one-on-one with undergraduates and his wonderful courses (Evolution and Human Behavior and Evolutionary Ecology) were in a league of their own. His legacy includes the many evolutionary biologists and anthropologists who got their scientific start in these courses.

I was fortunate that during my undergraduate years Alexander was writing *Darwinism and Human Affairs (D&HA)*—the book that developed his theoretical insights about evolution and culture, as well as nepotism and reciprocity. I feel that I was witness to an important time in the history of science. More than 30 years later, D&HA is still being translated into additional languages. During my first year (1986–1987) of Ph.D. fieldwork among the Dogon of Mali, I used D&HA to teach evolutionary theory to my research assistant, Sylvie Moulin. We had a small house in a remote village with a shade shelter next to an ancient baobab. Sylvie would read D&HA amid the cacophony of weaver finches and ask me questions about difficult paragraphs. In this African field setting where most human interactions take place in a web of kinship, D&HA came dramatically to life. Sylvie abandoned her competing reading material, Clifford Geertz's *Understanding Culture*, to the cobwebs in a corner of her room.

Alexander sparked fire in the minds of his undergraduate students by giving them the opportunity to figure out answers to problems in biology that hadn't already been fully solved. We were expected to come up with something original,

and he challenged us to write a publishable essay—possibly one that would identify an error he had made. I wrote my essay, “Sexual selection, paternal care, and concealed ovulation in humans,” on an idea that sprang from Alexander’s article with Katie Noonan (1979). They began their article with a discussion of distinctively human attributes—attributes not expressed in other species to the degree that they are in humans, including consciousness, foresight, tool use, language, and culture. To this list they added 25 additional traits, many of which are “sexually asymmetrical,” reflecting in particular “interactions of the sexes in connection with parental care.” The crux of their argument is that as intergroup competition became a principal guiding force in human evolution, the complexity of social competition and cooperation within groups increased, selecting for intelligence, consciousness, and foresight, as well as for increased parental care to impart social skills to offspring.

Intergroup competition had not previously been invoked to explain either the distinguishing human attributes or the unusual extent and duration of parental care in humans relative to other primates. Looking back, it is clear that the Alexander and Noonan article was a scientific watershed because it stimulated a vast literature and has stood the test of time. For example, Bowles and Gintis (2011) recently emphasized intergroup competition as the driving force for intragroup cooperation in humans and their arguments trace directly back to Richard Alexander.

Testing the hypothesis that paternal care is crucial for offspring survival and social success is currently an active area of research in human behavioral ecology. Strongly supportive evidence for the hypothesis has been found in the Ache of Paraguay where children without fathers were 3.9 times more likely to be killed in each year of childhood and children of divorced parents were 2.8 times more likely to be killed (Hill and Hurtado 1996). Many studies in other societies found no association between paternal presence and juvenile survival—perhaps because mothers, grandparents, and other individuals took up the slack when the father was absent (see Winking et al. 2011). Although fathers in many societies engage in little direct care of infants, they have an important effect on the social competitiveness of offspring—the paternal role emphasized by Alexander and Noonan. Among the Martu aborigines of Australia, for example, the presence of fathers is associated with an earlier age at initiation, which is the gateway to reproduction for sons (Scelza 2010). Comparative data on humans and other primates link the evolution of paternal care to the development of pair bonds, as suggested by Alexander and Noonan’s scenario for the evolution of concealed ovulation (Fernandez-Duque et al. 2009). Recent research on neuroendocrine mechanisms has shown that lower testosterone and higher prolactin levels are markers of fatherhood and pair-bonding (Gray et al. 2002, Gray et al. 2007, Alvergne et al. 2009). Paternal care is not merely a cultural overlay; instead it is supported by a suite of evolved proximate mechanisms.

CONCEALED OVULATION

Alexander and Noonan’s pivot investment in humans to paternal care after a brief consort period, to would compete later with her (1979, p. 443). In my paper for that stemmed from the trade-off males (Strassmann 1981). I suggest successful at getting multiple behavior, while the males succeed I suggested that the concealment it enabled females to garner the whom they had a confluence benefited from increased paternal care and Noonan had suggested that into pair bonds with females dominance rank and reproductive success has supported the view that for males (Wroblewski et al. 2009).

In his 1990 paper “How did arguments to reject the other (1979, Burley 1979, Hrdy 1979) Katherine Noonan published this volume) illustrates the test Alexander’s uncanny ability to mation. His 1990 paper explained only from their mates but also their own ovulation would be in the pair bond but would assure “intimate associate” about the their knowledge of the timing withheld paternal investment. paternal investment, would not

RECENT CLAIMS FOR “HU

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Paternal care is crucial for offspring survival and a major area of research in human behavioral evolution. The hypothesis has been found in the fact that adult fathers were 3.9 times more likely to visit their children of divorced parents were compared to mothers (Hurtado 1996). Many studies in primates link the evolution of paternal care between paternal presence and juvenile survival (see Winking et al. 2011). Although chimpanzees do not provide direct care of infants, they have an investment in the fitness of offspring—the paternal investment. Among the Martu aborigines of Australia, paternal care is associated with an earlier age at first reproduction for sons (Scelza 2010). In primates, paternal care is suggested by Alexander and Noonan’s hypothesis of concealed ovulation (Fernandez-Duque et al. 2010). Recent mechanisms has shown that lower testosterone levels are markers of fatherhood and pair-bonding (Alvergne et al. 2009). Paternal care in humans is supported by a suite of evolved

CONCEALED OVULATION

Alexander and Noonan’s pivotal contribution was to link increased paternal investment in humans to paternity certainty and the evolution of concealed ovulation. They argued that the advertisement of ovulation might cost a female her mate’s parental investment in two ways: “(1) by attracting competing males who threaten his confidence of paternity, and (2) by freeing him, after a brief consort period, to seek copulations with other fertile females who would compete later with her for his parental care” (Alexander and Noonan 1979, p. 443). In my paper for Alexander’s course, I added a further argument that stemmed from the tradeoff between mating effort and parental effort in males (Strassmann 1981). I suggested that subordinate males who are the least successful at getting multiple mates would have the most to gain by paternal behavior, while the males successful as polygynists would gain least. Further, I suggested that the concealment of ovulation was favored by selection because it enabled females to garner the paternal investment of subordinate males with whom they had a confluence of interest. Both subordinate males and females benefited from increased paternal investment (Strassmann 1981). Alexander and Noonan had suggested that the dominant males would be the first to enter into pair bonds with females concealing ovulation. In primate species, dominance rank and reproductive success are usually correlated, but the evidence has supported the view that females sometimes prefer middle or low-ranking males (Wroblewski et al. 2009).

In his 1990 paper “How did humans evolve?,” Alexander used strong logical arguments to reject the other hypotheses (Symons 1979, Benshoof and Thornhill 1979, Burley 1979, Hrdy 1979) that appeared the same year (1979) that he and Katherine Noonan published their article. His discussion of these hypotheses (ch. 7, this volume) illustrates the technique of strong inference (Platt 1964) and shows Alexander’s uncanny ability to test alternative hypotheses using qualitative information. His 1990 paper explains why females evolved to conceal ovulation not only from their mates but also from themselves. Females who were conscious of their own ovulation would be in an excellent position to obtain good genes outside the pair bond but would assume the risk associated with continually deceiving an “intimate associate” about the timing of ovulation. Moreover, if females exploited their knowledge of the timing of ovulation, then selection would favor males who withheld paternal investment. Female deceit, in conjunction with continued male paternal investment, would not be evolutionarily stable.

RECENT CLAIMS FOR “HUMAN OESTRUS” AND “OVULATORY CUES”

Alexander and Noonan’s hypothesis on concealed ovulation has been scrutinized by countless biologists, anthropologists, and evolutionary psychologists. One recent argument is that ovulation in women is not concealed after all (e.g., Haselton and Gildersleeve 2011, Gangestad and Thornhill 2008). This reaction is

due to a misperception that ovulation is concealed only if there is a *total absence* of detectable phenotypic changes during ovulation. Instead, what Alexander and Noonan (p. 442) actually sought to explain were the reasons why natural selection *reduced* the conspicuousness of ovulation in the human lineage:

In nonhuman primates the general period of ovulation always appears to be more or less dramatically signaled to males (even if only by pheromones or other means not obvious to human observers). All of the nonhuman primates in which females are known to show “pseudo-estrus” are group-living species, while the least obvious signs of ovulation seem to occur in monogamous species like gibbons, or polygynous species, like gorillas, which tend to live in single-male bands. *Human females are thus unique in that they give little or no evidence of ovulation and may be receptive during any part of the ovulatory cycle. Although some women have discovered ways to determine the time of their ovulation, it is clear that selection has reduced the obviousness of ovulation during human evolution, apparently to women themselves as well as to others (emphasis added).*

The hypothesis that human females experience estrus (Gangestad and Thornhill 2008) is at odds with the demonstrable difficulty of detecting ovulation in women. Until the 1920s, even medical experts believed that ovulation occurred during menstruation rather than at midcycle (Strassmann 1996). In a cross-cultural sample of 186 preindustrial societies, I confirmed an earlier report by Paige and Paige (1981) that the most prevalent belief was that conception occurs immediately after menstruation—a view also supported by in-depth field studies of the Dogon of Mali (Strassmann 1996) and Hadza foragers of Tanzania (Marlowe 2004). Needless to say, no man can point to the ovulating women in the room with any appreciable success.

A careful study of American women by Sievert and Dubois (2005) asked: Do women who think they know when they ovulate truly make accurate assessments? Women collected daily urine samples from day 5 of the menstrual cycle through the day they believed they ovulated. The last three samples were tested for a luteinizing hormone (LH) surge and if at least one sample tested positive for an LH surge, then that woman was scored as correct in her assessment for that cycle. To detect ovulation, the women most frequently relied upon changes in cervical mucus (“spinnbarkeit”), abdominal pain (“mittelshmerz”), and the expectation that ovulation occurs at midcycle—such information derives from modern medical research to which ancestral women would not have been privy. Using these signals, only 28% of women who believed that they knew when they ovulated actually gave accurate assessments. When the analysis included women who used basal body temperature as an assessment technique, the accuracy rate went up to 36.1%. These results suggest that even in the presence of contemporary medical information, ovulation is concealed for most women (Sievert and Dubois 2005).

The inaccuracy of self-reports of subtle changes across the menstrual cycle is a central theme in evolutionary psychology. A recent review concerning women's social behaviors, body scent, and beauty with effect sizes ranging from small to large (Gildersleeve et al. 2011, see also Alverg et al. 2011) found that women's perceptions of male attractiveness are influenced by subtle changes in body scent and appearance during the menstrual cycle. The review also found that women's perceptions of male attractiveness are influenced by subtle changes in body scent and appearance during the menstrual cycle.

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At present, there are no hormones reported ovulation cues. Testosterone (Strassmann 2010) and therefore might be a hormone (Strassmann et al. 2011), however, the difference between the midcycle and midluteal phase is not statistically significant. Estradiol is of interest, but it is androgens and not estradiol in women (Schwenkhaugen and Studer 2008). Estradiol is elevated at both midcycle and the midluteal phase. The hormone that displays a sharp midcycle peak would be a stronger candidate for an ovulation cue, only during or immediately prior to ovulation might qualify, it has not (to my knowledge) been found in humans. If a hormonal basis for ovulation is to rule out the possibility that the changes in body scent and appearance are due to mechanisms that promote adaptive camouflage, researchers have not set forth their hypotheses in the design of the observed menstrual cycle. Instead they assume that if changes in body scent and “infertile” phases of the menstrual cycle are to document psychological adaptations to ovulation.

When studies of ovulatory cues are designed to prevent subjects from intuiting the time of ovulation, as that knowledge could influence the results, the researcher can be extremely subtle.

concealed only if there is a *total absence* of ovulation. Instead, what Alexander and others were the reasons why natural selection in the human lineage:

al period of ovulation always appears to be hidden from males (even if only by pheromones from human observers). All of the nonhuman primates that show "pseudo-estrus" are group-living species of ovulation seem to occur in monogamous species, like gorillas, which tend to be. *In females are thus unique in that they give no obvious cues that they are fertile. Men have discovered ways to determine the presence of ovulation that selection has reduced the obviousness of ovulation apparently to women themselves as well as*

men experience estrus (Gangestad and others). The nontrivial difficulty of detecting ovulation cues has led medical experts to believe that ovulation is hidden from males at midcycle (Strassmann 1996). In a study of hunter-gatherer societies, I confirmed an earlier report that the dominant belief was that conception occurs during the fertile phase, also supported by in-depth field studies of Hadza foragers of Tanzania (Marlowe and others). The ovulating women in the room with

by Sievert and Dubois (2005) asked: Do women truly make accurate assessments of ovulation from day 5 of the menstrual cycle? The last three samples were tested to see if at least one sample tested positive and if the woman was scored as correct in her assessment for ovulation. Most frequently relied upon changes in cervical mucus, abdominal pain ("mittelschmerz"), and changes in the menstrual cycle—such information derives from changes that rural women would not have been privy to. Those who believed that they knew when they were ovulating. When the analysis included women using the assessment technique, the accuracy rate was high, even in the presence of concealed ovulation for most women (Sievert and

The inaccuracy of self-reports of ovulation does not preclude the possibility of subtle changes across the menstrual cycle in women's sexuality, and identifying such changes has become a particularly active area of research in evolutionary psychology. A recent review concludes that ovulation cues can be found in women's social behaviors, body scents, voices, and possibly, aspects of physical beauty with effect sizes ranging from small ($d = 0.12$) to large ($d = 1.20$) (Haselton and Gildersleeve 2011, see also Alvergne and Lummaa 2009).

Most studies in this arena are based on the hypothesis that psychological adaptations should differ when a woman is in the ovulatory phase of the menstrual cycle versus when she is not. The investigators then proceed to document differences in lap dance tips, vocal attractiveness, and other outcome variables at "fertile" versus "infertile" cycle phases. Upon finding differences, the investigators then assume that they have found support for their adaptive hypotheses about male and female sexual strategies. Although this is a burgeoning literature, few studies (Puts 2006, Welling et al. 2007, Roney and Simmons 2008) concern themselves with examining the underlying mechanisms. As Gangestad and Thornhill (2008, p. 997) noted: "The precise endocrine mechanisms that regulate these changes remain largely unknown."

At present, there are no hormones that are strong candidates for explaining the reported ovulation cues. Testosterone contributes to libido in women (Wylie et al. 2010) and therefore might be a hormone of interest. In a recent study (Rothman et al. 2011), however, the difference in serum testosterone and free testosterone between the midcycle and midluteal phases of the menstrual cycle was small and not statistically significant. Estradiol and estrone are other hormones of possible interest, but it is androgens and not estrogens that are prescribed to increase libido in women (Schwenkhagen and Studd 2009). Like the androgens, the estrogens are elevated at both midcycle and the mid-luteal phase (Rothman et al. 2011). A hormone that displays a sharp midcycle peak and is not elevated during the luteal phase would be a stronger candidate for explaining behavioral changes that occur only during or immediately prior to ovulation. Although luteinizing hormone might qualify, it has not (to my knowledge) been reported to influence behavior in humans. If a hormonal basis for ovulatory cues is found, it will be necessary to rule out the possibility that the cues are merely sideeffects rather than evolved mechanisms that promote adaptive strategies (see Haselton and Gildersleeve 2011). Researchers have not set forth their standards of evidence for detecting adaptive design in the observed menstrual cycle correlates (see Reeve and Sherman 1993). Instead they assume that if changes are detected in outcome variables at "fertile" and "infertile" phases of the menstrual cycle, that this evidence alone is sufficient to document psychological adaptations.

When studies of ovulatory cues involve surveys, exceptional diligence is needed to prevent subjects from intuiting that the researcher's focus is on the menstrual cycle, as that knowledge could influence women's responses. Such cueing from the researcher can be extremely subtle, as demonstrated in a study in which subjects

read a newspaper article about a mass murder and were asked about the precipitating causes. The respondents' answers were subconsciously influenced by the questionnaire's fictitious letterhead. When the letterhead said "Institute for Personality Research" respondents emphasized personality variables, whereas they identified social-contextual variables when it said "Institute for Social Research" (Norenzayan and Schwartz 1999). In a classic study, women who were manipulated by experimenters into believing that they were premenstrual reported experiencing a significantly higher degree of physical symptoms, such as water retention, than did women who were led to believe that they were intermenstrual (Ruble 1977). In any research involving self-reports, it is challenging to prevent the questions from shaping the answers (Schwartz 2010); researchers of ovulatory cues should address this problem up front.

Laeng and Falkenberg's (2007) study of female sexual response at three phases of the menstrual cycle is noteworthy because it employed pupillary size as an index of "interest." Changes in pupil size are not under conscious influence and do not rely on responses to questionnaires, diaries, or ratings that might reflect participants' beliefs. In this study, women's pupils got larger during the ovulatory phase of the menstrual cycle when they viewed photographs of their boyfriends but not when they viewed the boyfriends of other subjects, or if they used oral contraceptives. I wonder what results might be obtained if women were asked to view photos of dogs (own dog, random dog) to further control for recognition effects and non-sexual responses. In the sex research literature, female sexual response did not change over the menstrual cycle as measured by vaginal blood volume, vaginal pulse amplitude, labial temperature, and so forth (summarized in Laeng and Falkenberg 2007). International data from the Demographic and Health Surveys showed no evidence for a peak in coitus at midcycle for couples in stable unions (Brewis and Meyer 2005). At best, the data are conflicting.

If there are indeed "ovulatory cues" in humans, then it should be possible to document the mechanistic basis for the cues. Given the absence of evidence for the underlying mechanisms, it is premature to claim that women possess *psychological adaptations* surrounding mating that take account of whether they are ovulating or that men shift their behavior in response to subtle ovulatory cues emitted by women (Haselton and Gildersleeve 2011). Not only is the mechanistic basis for the notion of "human estrus" or "ovulation cues" insubstantial, the theoretical basis is also highly problematic. To make this argument, I turn to evidence from the Dogon of Mali.

MENSTRUAL CYCLES IN THE DOGON OF MALI

Having experienced the difficulty of testing hypotheses on the evolution of concealed ovulation, I was motivated to do my Ph.D. on questions about human reproductive behavior that could be addressed empirically. I entered a Ph.D. program in biology at Cornell University where key faculty disallowed research on

humans and where one professor is of doing fieldwork in Africa. To solve I knew that I could count on Rich aspect of Alexander's mentoring is t own projects—those who did not several months I sifted through libr choosing the Dogon after learning *the Wild* (Pern 1982). The Dogon h huts, no contraception, polygyny, 1 that had not been fully supplanted on: (1) the biology of menstruation variation in female fecundability (S

In the mid-eighties, there was menstrual cycles in a population th North American women have abc women in my data set had about 10 too young or too old to become p characteristic of subfecund and infertile of 20 and 35 years spent most of rhea—for these women, menstrea (Strassmann 1997, Strassmann & 1 ductive biology into account, evol during all phases of the interbirth and menstrual cycling). Studies th report regular menstrual cycles are

Evidence from the Dogon is al females engage in a dual mating st ulation (EPC) during ovulation wl ing faithful to their partners at oth Benshoof and Thornhill 1979, Gan to a dual mating strategy in which rate of extra pair paternity (EPP) EPP in the Dogon is 1.8% (N = 170 traditional society EPCs are rare—are a cultural feature of Dogon so females to disclose the onset of pre tational amenorrhea (Strassmann two-fold higher when the menst had been abandoned, a situation a et al. 2012). Menstrual taboos wer not unique to the Dogon (Strassi by males that helps to circumve 1992, 1996).

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DOGON OF MALI

In testing hypotheses on the evolution of consciousness I do my Ph.D. on questions about human evolution addressed empirically. I entered a Ph.D. program in a university where key faculty disallowed research on

humans and where one professor informed me that I was, in his view, incapable of doing fieldwork in Africa. To solve this problem, I returned to Michigan, where I knew that I could count on Richard Alexander's unflinching support. A great aspect of Alexander's mentoring is that he gave students free reign to develop their own projects—those who did not like this system called it "sink or swim." For several months I sifted through library books about traditional peoples, eventually choosing the Dogon after learning about them in the Time-Life series *Peoples of the Wild* (Pern 1982). The Dogon had all the features I was looking for: menstrual huts, no contraception, polygyny, nucleated villages, and an indigenous religion that had not been fully supplanted by a world religion. My dissertation focused on: (1) the biology of menstruation, (2) the function of menstrual taboos, and (3) variation in female fecundability (Strassmann 1990).

In the mid-eighties, there was no previous, long-term, prospective study of menstrual cycles in a population that was experiencing natural fertility. Whereas North American women have about 400 menses during their lifetimes, Dogon women in my data set had about 100 menses, most of which occurred in women too young or too old to become pregnant. Repeated menstrual cycles were characteristic of subfecund and infertile women. By contrast, women between the ages of 20 and 35 years spent most of their time pregnant or in lactational amenorrhea—for these women, menstruation and ovulation were extremely rare events (Strassmann 1997, Strassmann & Warner 1998). To take women's evolved reproductive biology into account, evolutionary psychologists should sample women during all phases of the interbirth interval (pregnancy, lactational amenorrhea, and menstrual cycling). Studies that are restricted to undergraduate women who report regular menstrual cycles are not well suited for testing adaptive hypotheses.

Evidence from the Dogon is also pertinent to the theoretical expectation that females engage in a dual mating strategy, seeking good genes from extra pair copulation (EPC) during ovulation while limiting threats to paternal care by remaining faithful to their partners at other stages of the menstrual cycle (Symons 1979, Bensch 1999, Gangestad et al. 2002). If Dogon females were prone to a dual mating strategy in which they sought EPCs during ovulation, then their rate of extra pair paternity (EPP) should be much higher than it is. The rate of EPP in the Dogon is 1.8% (N = 1704 father-offspring pairs), suggesting that in this traditional society EPCs are rare—at least during the fertile period. Menstrual huts are a cultural feature of Dogon society that helps to prevent cuckoldry by forcing females to disclose the onset of pregnancy and the resumption of fertility after lactational amenorrhea (Strassmann 1992, 1996). Extra pair paternity was more than two-fold higher when the menstrual taboos were not enforced versus when they had been abandoned, a situation associated with religious conversion (Strassmann et al. 2012). Menstrual taboos were found in most pre-industrial societies and are not unique to the Dogon (Strassmann 1992). They are a cultural tactic enforced by males that helps to circumvent the concealment of ovulation (Strassmann 1992, 1996).

With the possible exception of the Jewish Halakha laws (Boster et al. 1998), males do not use menstrual huts or other menstrual taboos to count to day 14 or to identify the precise timing of the fertile period of the menstrual cycle. When lactational amenorrhea lasts about 20 months—as in the Dogon—knowing that a woman has resumed menstrual cycling provides strong evidence that she will soon be fertilizable and must be mate-guarded (Strassmann 1996). Hormonal data show that the postpartum resumption of the menses is closely tied to the resumption of ovulation (Howie et al. 1982). Sometimes ovulation occurs first, other times menstruation is first—either way the two events are usually only about two weeks apart, which is minimal compared with the previous two-and-a-half years when the woman was not fertilizable. The evidence for widespread menstrual taboos in conjunction with the pervasive misimpression that the fertile period occurs immediately after menstruation, suggests that: (1) human males are greatly concerned about their risk for cuckoldry, and (2) their strategies usually do not precisely pinpoint the fertile period within the menstrual cycle.

Notwithstanding some fanciful accounts, it was males who imposed the taboos on females in every society in which menstrual taboos were directly observed by the ethnographer (Strassmann 1992). When females can successfully hide their menses, then they can avoid more intensive mate guarding when they are cycling, which may free them to copulate with extra-pair partners. They can also keep greater control over knowledge of the genetic father's possible identity. In societies as diverse as the Inuit of the Arctic (Balikci 1970) and the Dogon of Mali (Strassmann 1992, 1996), fear that females might hide their menses was a major male concern. When a woman is forced to obey menstrual taboos, then her reproductive strategies are constrained—the husband and his family have the same knowledge that she has about the timing of the menses and in the absence of genetic data, this knowledge is important for paternity assessments (Strassmann 1992, 1996). Hormonal data show that menstrual hut visitation is an honest signal of menstruation in Dogon women of reproductive age (Strassmann 1996). If women want paternal care for their offspring, and to bear sons who stand a chance of being accepted into their social father's patrilineage, then they must signal menstruation honestly. In the Dogon, there is usually one menstrual hut and one shade shelter for each patrilineage—the two structures are placed in close proximity to each other so that the women at the menstrual hut can be monitored. Menstrual taboos are embedded in religion because in all societies religions play a major role in enforcing sexual morality (Strassmann et al. 2012). The addition of supernatural threats to social norms is aimed at increasing compliance with the taboos (Strassmann 1992, 1996).

In sum, females may benefit from EPCs, but they cannot engage in them without risking the loss of paternal investment. When Dogon women divorce, they do so immediately after leaving the menstrual hut because at that time they are demonstrably nonpregnant (Strassmann 1992, 1996). In contrast with the report that American undergraduate men are more proprietary toward partners who

are near ovulation (Gangestad et al. 2002), males may be more intensive immediately after ovulation to believe that females are most fertile (Strassmann 1992, 1996). I would expect males to usually seek to package “good gene” males at a time—as best they can. When then women can use EPCs as a strategy with a different (hopefully better) alternative to the “dual mating hypothesis” occur during ovulation. The “combination” predicts relatively high paternity competition.

Aside from the Dogon, the only additional, small-scale society come from Venezuela. In this study, the EPP rate and Weiss 1975). A survey of 67 genes rate was 1.7% (range 0.4–11.8) for mating laboratories (Anderson 2006). A EPP rates are around 2% in Europe. Together with the Dogon result, there is paternity in many human populations.

The diverse morphology of sperm in low quality of human semen samples in which postcopulatory sexual selection with a high degree of postcopulatory sperm morphology (Calhim et al. 2007) age of motile sperm per ejaculate (Anderson et al. 2007, Simmons et al. 2007) numbers, a reduced duration of ejaculation high sperm counts in successive ejaculations (2007). Chimpanzee spermatozoa have a potential which may improve sperm (Anderson et al. 2007).

For humans, the ratio of testes to body mass is 0.02 that of orangutans (*Pongo pygmaeus*) (0.02), and 22% that of chimpanzees. Gorillas usually (but not always) live in solitary active male (Harrison and Chimpanzee male groups and have a promiscuous mating system. Orangutans have a dispersed harem system with two adult male morphs (flanged and

ish Halakha laws (Boster et al. 1998), menstrual taboos to count to day 14 or period of the menstrual cycle. When this—as in the Dogon—knowing that provides strong evidence that she will be pregnant (Strassmann 1996). Hormonal data show that ovulation is closely tied to the resumption of ovulation occurs first, other times when menses are usually only about two weeks after the previous two-and-a-half years when menses occur for widespread menstrual taboos. The evidence that the fertile period occurs during the period of: (1) human males are greatly concerned about (2) their strategies usually do not change during the menstrual cycle.

It was males who imposed the taboos on menstrual taboos were directly observed by males and females can successfully hide their menses from mate guarding when they are cycling, and from pair partners. They can also keep track of their partner's possible identity. In societies such as the Dogon of Mali (LeVine 1970) and the Dogon of Mali, where women might hide their menses was a major reason for menstrual taboos, then her reproductive partner and his family have the same knowledge of the menses and in the absence of formal paternity assessments (Strassmann 1996). Menstrual hut visitation is an honest signal of a woman's reproductive age (Strassmann 1996). If a woman is to bear sons who stand a chance of inheriting the lineage, then they must signal men that they are menstruating. Menstrual huts are usually placed in close proximity to the menstrual hut and can be monitored. Menstrual taboos in all societies religions play a major role (Strassmann et al. 2012). The addition of superstitious beliefs increasing compliance with the taboos

if they cannot engage in them with their partner. When Dogon women divorce, they leave the menstrual hut because at that time they are menstruating (Strassmann 1996). In contrast with the report that women are proprietary toward partners who

are near ovulation (Gangestad et al. 2002), mate guarding in the Dogon is said to be more intensive immediately after the menses—the time when the Dogon believe that females are most fertile and are most prone to deserting their mates (Strassmann 1992, 1996). I would expect that due to the riskiness of EPCs, women usually seek to package “good genes” and paternal investment together in one man at a time—as best they can. When the man proves deficient in either regard, then women can use EPCs as a strategy for securing another combination package with a different (hopefully better) man. I present this “combo hypothesis” as an alternative to the “dual mating hypothesis” which holds that EPCs are timed to occur during ovulation. The “combo hypothesis” unlike the “dual mating hypothesis” predicts relatively high paternity certainty in humans and low levels of sperm competition.

Aside from the Dogon, the only genetic data on paternity certainty in a traditional, small-scale society come from a study of the Yanomamo of Brazil and Venezuela. In this study, the EPP rate was 9.1% in a sample of 132 offspring (Neel and Weiss 1975). A survey of 67 genetic studies reported that the median EPP rate was 1.7% (range 0.4–11.8) for men who were not sampled at paternity testing laboratories (Anderson 2006). Another review of the literature concluded that EPP rates are around 2% in Europe and North America (Simmons et al. 2004). Together with the Dogon result, there is emerging evidence for high paternity certainty in many human populations.

The diverse morphology of spermatozoa in human semen samples and the low quality of human semen samples (Cooper et al. 2010) are indicative of a species in which postcopulatory sexual selection was minor or even trivial. Species with a high degree of postcopulatory sexual selection have reduced variation in sperm morphology (Calhim et al. 2007, Kleven et al. 2008) and a high percentage of motile sperm per ejaculate (Møller 1988, Pizzari and Parker 2009). Human semen samples do have some features in common with those of chimpanzees (*Pan troglodytes*), but the evidence points to far less sperm competition in humans (Anderson et al. 2007, Simmons et al. 2004). Chimpanzees have higher sperm numbers, a reduced duration of epididymal transit, and the ability to maintain high sperm counts in successive ejaculates (Marson et al. 1991, Anderson et al. 2007). Chimpanzee spermatozoa also have a higher mitochondrial membrane potential which may improve sperm swimming speed or longevity (Anderson et al. 2007).

For humans, the ratio of testes mass to body mass (0.06) is similar to that of orangutans (*Pongo pygmaeus*) (0.05), three times that of gorillas (*Gorilla gorilla*) (0.02), and 22% that of chimpanzees (*Pan troglodytes*) (0.27) (Harcourt et al. 1981). Gorillas usually (but not always) live in single-male groups with only one sexually active male (Harrison and Chivers 2007) whereas chimpanzees live in multi-male groups and have a promiscuous breeding system (Wroblewski et al. 2009). Orangutans have a dispersed harem polygynous social system in which there are two adult male morphs (flanged and unflanged); females prefer to mate with the

flanged males during the periovulatory period and flanged males sire most (but not all) of the offspring (Harrison and Chivers 2007, Stumpf et al. 2008). Although the ejaculates of chimps and orangutans are similar in volume, orangutans have only one-tenth the sperm concentration (Graham 1988). The ratio of seminiferous tubules to connective tissue in human testes is 1.3—similar to that of monogamous gibbons (1.1), but far smaller than that of the primates with multi-male breeding systems: chimpanzees (2.4), baboons (*Papio*) (2.8), and macaques (*Macaca*) (2.2) (Schultz 1938, Harcourt et al. 1981). Thus, several lines of evidence suggest that postcopulatory sexual selection has been relatively weak in humans, casting doubt on the hypothesis that women have an evolved tendency to seek EPCs during ovulation.

Alexander and Noonan's hypothesis on concealed ovulation has been challenged by studies that report that the sexual strategies of men and women are contingent on phase of the menstrual cycle—fertile or infertile (Haselton and Gildersleeve 2011, Gangestad and Thornhill 2008). I have outlined several reasons for being skeptical of these reports: (1) the high level of paternal investment that characterizes most human populations is incompatible with high levels of cuckoldry, (2) genetic studies show relatively high paternity certainty compared with the levels predicted by the “dual mating strategy” hypothesis, (3) morphological and physiological comparisons of humans with other primates do not provide evidence for postcopulatory sexual selection, (4) ethnographic and demographic studies show that ovulation is indeed concealed, and (5) the mechanistic basis for ovulation cues has not been identified. It is an honor to introduce Alexander and Noonan's chapter on concealed ovulation, as it sparked in me a lifelong interest in the divergent strategies of males and females, and in the reproductive events of menstruation, ovulation, fertility, and cuckoldry. It is a classic article, and with each reading I notice something new.

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