

RAISING DARWIN'S CONSCIOUSNESS

Female Sexuality and the Prehominid Origins of Patriarchy

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Sociobiologists and feminists agree that men in patriarchal social systems seek to control females, but sociobiologists go further, using Darwin's theory of sexual selection and Trivers's ideas on parental investment to explain why males should attempt to control female sexuality. From this perspective, the stage for the development under some conditions of patriarchal social systems was set over the course of primate evolution.

Sexual selection encompasses both competition between males and female choice. But in applying this theory to our "lower origins" (prehominid ancestors), Darwin assumed that choices were made by essentially "coy" females. I argue here that female solicitation of multiple males (either simultaneously or sequentially, depending on the breeding system) characterized prehominid females; this prehominid legacy of cyclical sexual assertiveness, itself possibly a female counter-strategy to male efforts to control the timing of female reproduction, generated further male counter-strategies. This dialectic had important implications for emerging hominid mating systems, human evolution, and the development of patriarchal arrangements in some human societies. For hominid males who will invest in offspring, there would be powerful selection for emotions, behaviors, and customs that ensure them certainty of paternity. The sexual modesty that so struck Darwin can be explained as a recent evolved or learned (perhaps both) adaptation in women to avoid penalties imposed by patrilines on daughters and mates who failed to conform to the patriline's prevailing norms for their sex. Other supposedly

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innate universals, such as female preferences for wealthy husbands, are also likely to be facultative accommodations by women to constraints set up when patriline monopolized resources needed by females to survive and reproduce, and passed on intergenerational control of these resources preferentially to sons.

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WHY WOULD A PRIMATE REQUIRE YOUTH AND BEAUTY IN HIS MATE?

"Was she beautiful or not beautiful?"

Daniel Deronda, George Eliot (1876)

According to nineteenth-century social Darwinists like Herbert Spencer, it was the natural function of woman to be beautiful. "Nature's . . . supreme end, is the welfare of posterity . . . as far as posterity is concerned, a cultivated intelligence based upon a bad physique is of little worth, seeing that its descendants will die out in a generation or two" (Spencer 1859:395). Privately practicing what he publicly preached, Spencer rejected a liason with a woman he much admired—Mary Ann Evans—on the grounds that she was more intelligent than she was beautiful. "Physical beauty is a *sine qua non* with me" Spencer wrote, perhaps in reference to his own choice (1904:445).¹

Like Spencer, some contemporary evolutionary psychologists are convinced that they have discovered a "species-typical" universal male preference, insisting that "Beautiful young women are sexually attractive to men because beauty and youth are closely linked with fertility and reproductive value. In evolutionary history, males who were able to identify and mate with fertile females had the greatest reproductive success" (Buss 1994b:244, caption for figure showing young girls in a pickup bar). Somehow, in both the scholarly and popular literature on this topic, fertility is equated with youth, so for example Buss predicts that "men would prefer younger women as short-term and long-term mates" (1994b:244).

There is no disputing that, as Buss points out: "A fourteen-year-old woman has a higher reproductive value than a 24-year-old woman, because her *future* contribution to the gene pool is higher on average" (Buss 1994b). Along with symmetry and other indices of past and current developmental health, researchers have documented human male preferences for neotenous or "baby-faced" features. These include large

eyes, small nose and ears, large brow relative to chin ("high ratio of neurocranial to lower-facial features": Jones 1995:Fig. 1), and more reduced vertical dimensions than the average face of an adult female (Jones and Hill 1993; McArthur and Berry 1983; Riedl 1990; see the recent overview by Jones 1995).² To a primatologist, however, reported preferences for young females and for neotenuous traits are puzzling. There is not a shred of evidence for any other primate that youth or neoteny affect male willingness to mate. Instead, for every monkey or ape species for which information on male preferences is available, priority is given to fully adult females who have had one or more offspring and who are signaling probable ovulation (Anderson 1986). Even in those monkey and ape species where adolescent females exhibit unusually large or "exaggerated" sexual swellings, high-ranking full adult males rarely choose to copulate with them, and the adolescent females mate instead with subadult, subordinate males (Anderson and Bielert 1994:288; see also Wolfe and Schulman 1984).

Consider the case of Jane Goodall's famous "Old Flo." Tattered and misshapen by life's insults, when fully swollen at midcycle, Flo was peerless in her attractiveness to locally dominant males (Goodall 1971). Based on records for 166 wild chimpanzees at Gombe, primatologist Caroline Tutin was able to study male criteria for mate selection whenever two females happened to be maximally tumescent on the same day. "On 30 of 38 occasions, the older female was selected" (Tutin 1975:165 and 256). Excluding eight cases involving young adult males, full adult males chose the older female 90% of the time. Tutin attributes chimp preferences to the greater fecundability and maternal experience of parous females.

In Flo's case, even more would have been at stake. This redoubtable old female's range was nestled deep within territorial boundaries patrolled by Flo's older sons (several of whom became high-ranking males at Gombe) and their fathers, and this familiar and productive larder eventually passed to Flo's daughter Fifi, a female who—instead of migrating at puberty as do most other female chimps—managed to stay on near Flo, eventually inheriting her mother's range and producing there six healthy offspring, the Gombe record for female reproductive success (Wallis and Almasi 1995). Reproductively speaking, such male preferences were well placed: matings with Flo were fertile, and daughters and sons born to her survived to maturity and became successful breeders in their own right.

Across primates (including humans), young females are characterized by adolescent subfertility or, if conception does occur, are more prone to pregnancy failure (Lancaster 1986; Anderson and Bielert 1994), and more important, across virtually all primate species, infants born to first-time

mothers suffer higher rates of infant mortality than do offspring born to experienced, parous females (Drickamer 1974; Glander 1980; Silk et al. 1981). Clearly it makes evolutionary sense for males to select females not only on the basis of fecundity but also on the probability of producing offspring that survive. When intergenerational effects are likely to be important, males should also take into account female status, kin ties, or home range quality.

Given these realities, why would male *Homo sapiens*, unique among primates, be so attracted to neotenuous traits? Surely such preferences do not derive from the greater fecundability of young females, where fecundability is defined as the probability that a female will become pregnant over the course of a year of unprotected intercourse. For, fourteen-year-old girls are higher in future potential reproductive value, but *not* more likely to become pregnant than twenty-four-year-olds (Lancaster 1986; Wood 1994: esp. Fig. 2.9). Rather, such preferences derive from uniquely human institutions whereby men in many societies don't merely *mate* with virginal and compliant young females, but *acquire* them as wives, concubines, or slaves, whom they essentially "own" and, as a consequence, in many societies are also obliged to provide for long-term.³ In every other primate species, males and females provide for themselves, whereas in our own species, male desire to "own" females is apparently great enough for men to undertake to provide for them long-term. From the Code of Hammurabi (probably the first full-fledged codification for a patriarchal system) onwards, patriarchal marriages guaranteed maintenance for discarded or superseded wives, as well as widows (Lerner 1986:106–108, 265 n. 20). But when marriage or "ownership" of women is not an option, as for example when men are not in a position to provide resources for offspring, men should make reproductive decisions by selecting healthy mates on the bases of fertility indices (e.g., signs of maturity and adequate fat deposits to sustain pregnancy and lactation) and/or the stability of the woman's resource base, rather than on how young or neotenuous the woman appears.⁴

PATRIARCHY VIEWED AS A CONSTRUCT TO CONTROL FEMALE SEXUALITY

"We don't ask what a woman does—we ask whom she belongs to. . . ."

Mill on the Floss, George Eliot (1860)

Most scientists view a term like *patriarchy* as too broad to be useful. As biologist Patricia Gowaty puts it, the term "reifies more about female-male interactions than is useful" (personal communication, 1996). She is

right of course. But at present we lack finer-grained classifications as we grapple to construct the theory that might help devise them.

In the interim, I subscribe to pioneer feminist historian Gerda Lerner's working definition. *Patriarchy* refers to "the manifestation and institutionalization of male dominance over women and children in the family and the extension of male dominance over women in society in general. It implies that men hold power in all the important institutions of society and that women are deprived of access to such power. It does *not* imply that women are either totally powerless or totally deprived of rights, influence and resources" (1986:29). Obviously, only some societies are patriarchal, and even within patriarchal societies, institutions are male-controlled to varying degrees depending upon a range of ecological, economic, and especially historical factors.

Marxists, Feminists, and Sociobiologists All Agree

I concur with Lerner that patriarchy predates classical antiquity. But whereas Lerner dates its origins in historical time, around the third millennium B.C., I have insisted that the origins of patriarchy must be far older (Hrdy 1981:9; see also Smuts 1995). I am convinced that male control over productive resources needed by women to reproduce lies at the heart of the transformation from male-dominated male-philopatric primate societies to full-fledged patriarchy (Hrdy and Judge 1993).

Following the Marxist theorist Friedrich Engels, feminist historians have traced the origins of human patriarchal marriage as male-dominated family structures expanded to include male authority and customary male control over both property and labor. Rarely however are we permitted more than sketchy glimpses of this early patriarchal history where men not only dominate, but own, women.

The capture of women was a primary objective of early warfare (Lerner 1986; Spencer 1885), and it was under such circumstances during the Trojan War that the Greek warrior Achilles obtained his beautiful concubine Briseis. A Greek vase painting by Makron in 480 B.C. depicts Agamemnon, commander-in-chief of the Greek army, commandeering Achilles' prize (Figure 1). Originally awarded to Achilles, Briseis was subsequently taken back by Agamemnon—generating Achilles' wrath at the outset of the *Iliad*. The painting depicts Agamemnon holding Briseis by her wrist, in the time-honored gesture of the bridegroom, or in this instance, signaling ownership of a trophy of war—the origin of the current term, not then a joke, "trophy wife."

Serendipitously, three independent interpretations of this scene from the opening of the *Iliad* depicting life in Homer's Greece are laid out for



Figure 1. Agamemnon holds Briseis by the wrist in the time-honored gesture of the bridegroom leading his bride, denoting both “taking possession of” and the marriage union. From an Attic red-figured skyphos attributed to Makron, and signed by Hieron on one handle (courtesy of the Louvre).

us, first by Engels (1973:126) in the 1880s and then, a century later, by sociobiological science writer Matt Ridley (1993:205) and by feminist historian Gerda Lerner (1986:84). Each examines the question of why men captured women by focusing on the quarrel over Briseis. At issue (in Ridley’s words) is “Agamemnon’s insistence on confiscating a concubine, Briseis, from Achilles in compensation for (Agamemnon) having to give back his concubine, Chryseis, to her priest-father” (Ridley 1993: 205). Ridley and Engels had no doubts that “In Homer young women are booty and are handed over to the pleasure of the conquerors, the handsomest being picked by the commanders in order of rank . . . (and) these girls were also taken back to Greece and brought under the same roof as the wife,” sons begotten from them becoming freemen and receiving a small share of the paternal inheritance (Engels 1973:126). On this point both follow Darwin: “women are the constant cause of war both between members of the same tribe and between distinct tribes” and “The strongest party always carries off the prize” (Darwin 1974: 556–557).

Feminist Lerner concurs, save on one point: "After Agamemnon carries out his threat and acquires Briseis by force, which causes Achilles to sulk in his tent and withdraw from the battle, the king does not touch her. He in fact *does not actually want her* but wanted to win a point of honor against Achilles—a fine example of the reification of women" (emphasis added). For Lerner, "the meaning of the enslavement of women (is) to win status and honor among men" (Lerner 1986:84).⁵

Normally viewed as antagonists, a Marxist, a feminist, and a sociobiologist⁶ concur that men seek to control women, and to a lesser extent, they concur on why patriarchal systems (under certain conditions)⁷ emerge: a perceived need by males to control female sexuality, and in Engels' words to "produce children of undisputed paternity." An obscure feminist pamphlet—the kind passed out on American sidewalks in the early 1970s—summarizes important areas of agreement:

In patriarchal cultures like the one we were all brought up in, sexuality is a crucial issue. Beyond all the symbolic aspects of the sexual act (symbolizing the male's dominance, manipulation and control over the female), it assumes an overwhelming practical importance. . . . Under normal circumstances it is agreed that a man is needed to provide sperm to the conception of the baby, but it is practically impossible to determine *which* man. The only way a man can be absolutely sure that he is the one to have contributed that sperm is to control the sexuality of the woman. . . . He may keep her separate from any other man as in a harem, he may threaten her with violence if she strays, he may devise a mechanical method of preventing intercourse like a chastity belt, he may remove her clitoris to decrease her erotic impulses, or he may convince her that sex is the same thing as love and if she has sexual relations with anyone else, she is violating the sacred ethics of love (Marval 1971).⁸

Where a Sociobiologist and a Feminist Disagree

The main difference between arguments made by feminists like Lerner and those made by sociobiologists is that such feminists tend to view male dominance as a historical construction, as illustrated in the dispute between Agamemnon and Achilles. Male dominance is a socially constructed end in its own right. As Gerda Lerner puts it: "Patriarchy is a historic creation formed by men and women in a process which took nearly 2500 years to its completion. . . . The basic unit of its organization was the patriarchal family which both expressed and constantly generated its rules and values" (Lerner 1986:212). By contrast, sociobiologists (and to some extent feminists like Marval, as well, for there is no strict dichotomy here) assume that the ultimate goal of male domination is reproductive success, and they identify sexual selection—rather than male desire for power—as the engine driving the system (Dickemann

1979, 1981; Hrdy 1981; Smuts 1995). As discussed by Gowaty (1992) it is a case of feminists focusing on proximate causes while Darwinians seek to elucidate ultimate causes; they are dealing with "complementary hypotheses at different levels of analysis" (P. Gowaty, personal communication 1996). Instead of looking in places like third millennium B.C. Mesopotamia, however, an evolutionary perspective pushes the search for patriarchy's origins back in time by millions of years by asking an additional question: *why* should males seek to control females?

WHY SHOULD MALES ATTEMPT TO CONTROL FEMALES?

"Our reputation, Lord! Why should you not think that we women make use of our Reputation, as you men of yours. . . ."

Admonition of the flirtatious Lady Fidget,
in *The Country Wife* by William Wycherley, 1675

Darwin's Innately "Coy" Females

As conceived by Darwin, sexual selection involves two processes: "competition between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive" and *female choice*, being competition "between individuals of the same sex in order to excite or charm those of the opposite sex, generally the females," who are no longer passive. (Darwin 1974:239, 256–258; for valuable overviews of Darwin's ideas on female choice see Small 1989; Cronin 1991). Guided by a theory that was not only very powerful but largely correct, Darwin had an uncanny knack for separating the anecdotal chaff from the true kernels of natural history reaching him from all corners of the globe, but when it came to females, and especially female choice, his vision was impaired by the blinkers of Victorian prejudice (Hrdy 1986).

Accustomed to the country gentry among whom he lived, familiar with medical opinions of the day to the effect that "the majority of women (happily for them) are not much troubled with sexual feelings of any kind" (Acton 1865:112–113), Darwin concurred with contemporary nineteenth-century wisdom about women. According to Darwin, "The female . . . with the rarest exception, is less eager (to copulate) than the male . . . she generally 'requires to be courted'; she is coy, and may often be seen endeavoring for a long time to escape from the male" (Darwin 1974:273). "Coyness," he believed, was part of a universal female strate-

gy to ensure that she only mate with the best locally available male. Clearly, if this assumption were correct, no male would need to curtail the sexuality of a mate who had specifically selected just him.

Darwin's working assumptions might have been different had he been working out sexual selection theory three centuries earlier! By 1594 in what can be regarded as the first adventure novel to be written in the English language, Thomas Nashe's *The Unfortunate Traveller*, the ape had become a symbol for a wife's "unconstant wantonness" (Janson 1952: chap. IX and especially p. 280 n. 41). Although Darwin was clearly familiar with sexual swellings, he apparently never had the opportunity to observe the twelve-day period around a female chimpanzee's maximal tumescence, when she typically mates about one to four times an hour with thirteen or more partners. Over her lifetime a female chimpanzee will copulate around six thousand times (Wrangham 1993), resulting in, at most, six living offspring (Fifi's record).

Surely it was Darwin's presumption that females hold themselves in reserve for the best available male that left him so puzzled by sexual swellings. Animals like pronghorn antelopes (Byers et al. 1994) do exactly this, but primates don't. Somehow, the obvious function of sexual swellings to advertise female readiness to mate eluded him. "No case," he confessed, "interested and perplexed me so much as the brightly colored hinder ends and adjoining parts of certain monkeys" (Darwin 1876:18–19).⁹

Although appropriate for many animals, the appellation "coy"—which was to remain unchallenged dogma for the succeeding hundred years—did not then, and does not today, apply to the observed behavior of monkey and ape females at midcycle (Hrdy 1986). Instead, I would argue that sexual "coyness," extreme discretion, and a concern for "reputation" found in so many women today derives not from prehuman "lower origins," as Darwin supposed, but rather from the tens of thousands of years hominid females have been socialized, exchanged between social groups, and have reproduced and died (some sooner than others) in various permutations of the patrilocal (or, in ethological parlance, "male philopatric") patrilineal breeding systems that eventually gave rise in places like the ancient Near East to full-fledged patriarchy.¹⁰

Should the hypothesis be true that one of the requisite cornerstones upon which all modern civilizations were founded was *coercive* suppression of women's inordinate sexuality, one looks back over the long history of women and their relationships to men, children, and society since the Neolithic revolution with a deeper, almost awesome sense of ironic tragedy (Sherfey 1972:140).

The Evolution of Woman's Libido

Given that it was the first of its kind, it seems odd that Sherfey's 1966 work, expanded into her 1972 book on *The Nature and Evolution of Female Sexuality*, is rarely cited in the current crop of books about the *evolution* of human sexuality. In the words of evolutionary psychologist Donald Symons, her work is simply "not taken seriously" (Symons 1979:91). When Symons—who is about the only evolutionary psychologist to cite her—does so, it is to debunk her notion of females whose capacity for multiple orgasms suggests to Sherfey that "women's inordinate orgasmic capacity did not evolve for monogamous, sedentary cultures" (Sherfey 1972:37). Symons, wittier than he is generous, writes: Sherfey's "sexually insatiable woman is to be found primarily, if not exclusively, in the ideology of feminism, the hopes of boys, and the fears of men." Even a sympathetic mention of Sherfey (as in Hrdy 1981) is to invite derision (his charge of "parapsychology" [Symons 1982:299] still stings). Sherfey herself, a problematic combination of both woman and scientist, displayed a poignant insight into her own predicament: she ended her book with the ancient Greek tale of Tiresias, the only mortal ever to have experienced life as both male and female. Outraged because Tiresias had revealed the depths of female sexual sensations, the goddess Hera struck him blind as punishment.

Still, it is difficult to know how to deal with this pioneering, idiosyncratic, brilliant and tragically flawed heroine of feminist sexology. Understand, Sherfey was writing years before primatologists knew much about sexual behavior in wild primates, certainly before we guessed at the existence of orgasmic capacity in nonhuman females; yet Sherfey's wild hunches anticipated future discoveries. Admittedly, her work contains errors in scholarly judgement (e.g., Sherfey gives too much weight to skimpy evidence supposedly documenting sexually libertarian matriarchies), and other problems. It is not the sort of book one could vouch for or assign to students. Yet, returning to her work after a hiatus of fifteen years, I remain convinced that Sherfey's central premise provided feminists—if not biologists—with important insights: key features of patriarchal social organization *were* partially consequences or by-products of male counter-strategies for controlling an assertive, cyclical, female sexuality of *prehominid* origin. Such a sexual nature comes as part of our physiological legacy as primates, and although not invariant, such a legacy can only change gradually and within limits. What was revolutionary and prescient was Sherfey's insistence that feminist analyses need to take into account the primate roots of female sexuality. I only wish Sherfey—whose work was initially so very controversial, and then largely forgotten—could have lived to see some of her most ma-

ligned guesses validated in general outline by primate sexologists like Kim Wallen (1990, 1995) and Koos Slob (Slob et al. 1986; Slob and van der Werff ten Bosch 1991), as well as myself (Hrdy 1981). In retrospect, her early (admittedly outrageous) proposal—that “the satiation-in-insatiation state may have been an important factor in the adaptive radiation of the primates leading to man—and a major barrier to the evolution of modern man” (Sherfey 1972:144) was at once overstated, and visionary.

Any attempt to understand either the evolution of the primate sexual swellings that so perplexed Darwin, or the evolutionary *and historical* pressures that would lead to patriarchy, requires us to set aside the old assumption that female primates evolved to select and mate with a single best male. Rather, anthropoid females were selected to ensure—in one way or another—that they mate with a range of male partners. Female sexuality among anthropoid primates (as Sherfey suspected) is qualitatively and quantitatively different than it is in many of the mammals with which Darwin would have been most familiar (Hrdy and Whitten 1987; Keverne 1981).

Among some mammals, mating is strictly confined to the period of “heat” at ovulation. Moreover, estrous females may sample available males, select the most vigorous, and—in line with the Darwinian ideal—mate only once with that chosen partner (see Byers et al. 1994 for pronghorn antelopes). Mating simply does not occur at other times. Similarly, among prosimian primates like galagos, an epithelial membrane seals the vagina except for a 48-hour window at ovulation, rendering mating at other times impossible (Doyle 1974; Lipschitz 1992).

Such strict curtailments of receptivity do not pertain to many (if any) anthropoid primates. Receptivity is less circumscribed. Imagine then a continuum ranging from the strictly circumscribed receptivity of galagos to females—like humans—who are more facultatively receptive, capable (if not desirous) of engaging in sex on any day of the menstrual cycle. Monkeys and apes fall along the continuum. In those monkey and ape species that advertise the period around ovulation with edematous pink swellings in the perineal region, as savanna baboons and chimpanzees do, females usually do confine matings to a period of a week or so around the middle of the menstrual cycle, near ovulation. But differences between individuals, and between species, yield many exceptions.

Chimpanzees, for example, restrict matings to midcycle but exhibit a rarely expressed *capacity* to mate outside of this internally defined endocrinological window as well. Under some conditions, the sexual skin may swell or deflate in response to social conditions. The overwhelming majority (96%) of 1,475 matings at Gombe recorded over a five-year period involved maximally or nearly maximally swollen females. The fractional remainder involved partially swollen females, except for an

idiosyncratic 20 copulations where females lacked detectable swellings (Goodall 1986:445).

This rarely expressed potential (expressed slightly more often in captive than in wild *Pan troglodytes*) is strongly expressed in *Pan paniscus*. Bonobos may exhibit sexual swellings for more than 50% of cycle days in the wild (swellings last anywhere from 3 to 22 days out of a 38-day cycle), or as much as 75% of the cycle in captivity, with copulations occurring at a low level throughout the period of swellings, possibly peaking in frequency when swellings are maximally firm. According to the Japanese primatologist Furuichi, duration of such swellings among wild bonobos in Zaire is influenced by social factors. Prolonged swellings are frequently observed in newly immigrant females, or when the group is in a "state of high social tension" (Dahl et al. 1991; Furuichi 1992).

In primates without sexual swellings, some females lapse from any clear-cut cyclical pattern, exhibiting spurts of sexual proceptivity lasting several weeks or more, as in Japanese macaques or African vervet monkeys. Even in species that are normally cyclical, like howler monkeys, or normally monogamous gibbons, who exhibit only infrequent periods of sexual activity, specific circumstances such as encounters with unfamiliar males from outside the group may precipitate lapses (Andelman 1987; Palombit 1992, 1994; Takahata 1980; van Noordwijk 1985; see also Hrdy and Whitten 1987).

Regardless of how frequent situation-dependent rather than strictly cyclical receptivity is, there is a tendency for female-initiated sexual behavior to increase at midcycle. Among rhesus macaques, where breeding in the wild is typically confined to discrete intervals during specific months of the breeding season, the perineum reddens but there is no clear-cut visual signal at ovulation. Nevertheless, female attractiveness to males, as well as proceptivity, can be observed all through the follicular phase (especially in captive situations), peaking at midcycle and then subsiding in the luteal phase (Wilson et al. 1982, reviewed in Wallen 1990).

A range of studies involving heterosexual and homosexual women living in both western and tribal settings, both in and out of stable relationships, also documents peaks in libido around midcycle, providing researchers focus on *female-initiated* sexual interactions and female self-reports of mood changes. Erotic fantasies, feelings of restlessness (measured in terms of how far women walked), likelihood of self-stimulation through masturbation, and probability that sexual behavior will culminate in orgasm—all of these rise around midcycle (Table 1). Prospective data covering 4,433 cycles taken from 590 women who were monitoring both changes in body temperature and mood show that

Table 1. Studies Showing Increase in Female Libido at Midcycle

Midcycle Characteristic	References
Female-initiated sex	Adams et al. 1978; Matteo and Rissman 1984; Worthman 1978
Female-reported desire or erotic fantasies†	Stanislaw and Rice 1988 Adams et al. 1978; Grammer 1996
Masturbation	Adams et al. 1978
Probability of orgasm	Matteo and Rissman 1984; Worthman 1978

† Both Matteo and Rissman's (1984) study of erotic fantasies by women in lesbian relationships, as well as experiments studying female responsiveness to erotic stimuli (such as films; Slob et al. 1991), found peaks across the follicular phase of the cycle rather than specifically at midcycle (also see Sanders and Bancroft 1982). Such findings are consistent with nonhuman primate data for macaques (e.g., see Wilson et al. 1982 for *Macaca mulatta*).

sexual desire rises a few days prior to the basal body temperature shift that follows ovulation (Stanislaw and Rice 1988). Not only do women at midcycle move about more, as documented in Morris and Udry (1970), but women at midcycle exhibit enhanced motor capability (but *not* visual perceptual ability) at midcycle (Hampson and Kimura 1988). A more in-depth study of a small sample of eight hunter-gatherer women living in the Kalahari, undertaken by anthropologists Carol Worthman, Marj Shostak, and Mel Konner, combined personal interviews with endocrine measures. This study reported statistically significant increases in females reporting "sexual desire" at midcycle. It also documented increased extroversion and statistically significant increases in likelihood of intercourse with husband during the follicular phase of the cycle, and it documented a (nonsignificant) increase in likelihood of sexual relations with lovers and a (nonsignificant) increase in probability of female orgasm at midcycle (Worthman 1978, 1988, personal communication 1995).

Given these new findings, Sherfey's radical assessment (1972:52) that "sexual responses of women and (other) primates are so nearly identical that the significant differences must have evolved only recently" seems stunningly prescient, since Sherfey (who died in 1983) could scarcely have known what primatologists and sexologists have since learned. The patterning of female sexual desire is far more cyclical than the designation "continuously receptive" would lead unsuspecting members of our species to believe. At the same time, the cyclical "estrous" patterning of sexual behavior thought to set other primates apart from humans reveals more lapses than old dichotomies would lead us to expect. Why?

From Darwin onward, it was assumed that the function of mating was conception, and that sexuality in males and females evolved to insure

insemination—in the female’s case, insemination by the best locally available male. In an influential 1976 essay Clutton-Brock and Harvey proposed that “by attracting several males,” females increase their chances “of being mated by a relatively high-ranking male,” which it almost certainly does (Moore 1995). Pursuing this line of argument, Pagel (1994) speculates that sexual swellings are a product of female-female competition to attract the best male or to ensure fertilization.¹¹ But what if mating has additional functions, ones not necessarily linked to fertilization? What if males and females benefit from mating in different ways, so that among females mating has multiple, conceptive and *nonconceptive* functions? Female primates—especially those with swellings—act as if they are trying to solicit multiple partners. What if, in fact, this is precisely what females have been selected to do? Assume for a moment that the “goal” of female sexuality is to motivate females to mate with a range of male partners; how to manage this becomes the “problem” they must “solve” (Hrdy 1988).

How Old World monkey (Cercopithecoid) and ape (Anthropoid) females solve this problem depends on phylogenetic constraints, current mating system, and local histories.¹² In multimale breeding systems such as those of baboons and chimpanzees where a range of males are permanently in residence, the most efficient solution is for females to compress mating into a brief period around ovulation which is signaled by sexual swellings so that males have to follow the female around and compete among themselves for the opportunity to mate, and when it’s over, females go back to business as usual—foraging.¹³

Sexual swellings have probably evolved independently under multimale breeding conditions at least three times among catarrhine Old World monkeys (Dixson 1983). In unimale systems where the female mates primarily with a single partner, but may mate with extra-unit males on an opportunistic basis, there is no external sign at ovulation (Table 2).

Table 2. In the “Females Benefit from Mating with a Range of Partners” Model, Solutions to the “Problem” Vary According to Type of Phylogenetic Constraints, and Type of Breeding System

<i>Multimale Breeding System</i>	<i>Primarily Unimale System with Occasional Opportunistic Encounters with Extra-Unit Males</i>
1. discrete estrous intervals	1. midcycle peak in libido with potential for situation-dependent receptivity
2. conspicuously advertised	2. nonadvertised ovulation

Human females constitute an extreme manifestation of this ancient primate potential. Women exhibit a midcycle peak in libido, combined with a potential for situation-dependent receptivity both at ovulation and at other times as well (under some circumstances, even during pregnancy) when they happen to encounter outside males.

But when females solve "their problem" by mating promiscuously, this in turn creates a special problem for males attempting to inseminate females who are simultaneously mating with several partners. The evolutionary outcome is the now well-documented correlation across all primates between testes size and magnitude of polyandrous mating (Harcourt et al. 1981), a correlation which has only been strengthened with each challenge from apparent exceptions (Harcourt 1996).

At first glance, the extremely large testes of supposedly monogamous tamarins fail to conform to the model. However, subsequent field studies have revealed that tamarins in fact often breed in polyandrous arrangements. Similarly, gibbons have long been held up as paragons of primate monogamy, yet their testicles are slightly larger than would be expected in monogamous primates, and some gibbon females occasionally exhibit modest (possibly even facultatively expressed?) sexual swellings. The occurrence of such traits in monogamous primates was considered a challenge to sexual selection theories (Dahl and Nadler 1992)—that is, until Palombit (1994) and Reichard (1995) reported avian-style extrapair copulations among socially, but not necessarily reproductively, monogamous lesser apes and clarified the situation. Such findings transformed larger-than-anticipated testes in tamarins and gibbons into a validated *prediction of*, rather than challenge to, the model.

Why Solicit Multiple Males?

A variety of benefits has been postulated for females soliciting multiple males, some genetic in nature, others having to do with nongenetic processes. These rationales are discussed at greater length elsewhere (Baker and Bellis 1995; Hrdy 1981, 1986; Petrie et al. 1994; Smith 1984; Keller and Reeve 1995; also see Table 3).

Evidence is accumulating for various organisms that female mate selection not only theoretically *can* but in fact *does* affect the long-term viability of their offspring. As among many birds, female great reed warblers (*Acrocephalus arundinaceus*) choose their mates on the basis of territory quality and the size of the male's song repertoire, which are both correlated with number of offspring produced. However, recent studies using DNA fingerprinting to determine paternity of fledglings reveal that these females are also engaging in extrapair copulations with near neighbors. Moreover, the size of the song repertoire of the males

Table 3. Hypothetical Benefits to Females from Mating with Multiple Partners (adapted from Hrdy 1986)

Genetic Rationales

1. "best" male (or alternative to inferior one)
2. fertility insurance
3. diverse offspring
4. generate sperm competition

Nongenetic Processes

5. female libido an endocrinological by-product
 6. therapeutic benefits
 7. elicit investment or tolerance from "possible" progenitors
 8. exchange sex for current benefits
-

involved in these extrapair copulations predicts *post-fledgling* survival long after parental care has ceased and some birds have migrated away (Hasselquist et al. 1996). Hasselquist and colleagues conclude that this enhanced survivorship of offspring is "affected by indirect (genetic) benefits obtained from males with large song repertoires" (1996:232; see Madsen et al. 1992 for how female choice affects fitness among adders, and Keller and Reeve 1995 for an overview). To date, however, there is no evidence from nonhuman primates to indicate that this sort of "female choice for genes" is going on (Bercovitch 1995; Manson 1995; Small 1993). Thus, even those who (like myself) normally emphasize female agency are for the time being compelled by scientific prudence to remain agnostic concerning whether or not prosimian, monkey, and ape females choose mates on the basis of genes.

So far, based on those few primate species for which reliable paternity data are available, it would appear that as was argued by primatologists for many years before we understood as much as we do now about the importance of female choice (Cronin 1991), male-male competition for rank *is* more important than female choice in determining male reproductive access. As data from molecular genetics come in, paternity assignments in multimale breeding systems provide support for the longstanding but oft-challenged notion that high rank in the male hierarchy predicts greater access to ovulating females (Altmann et al. 1996; de Ruiter et al. 1992; Moore 1995). In macaques and baboons, breeding with fertile females appears to be largely (not completely) monopolized by those males who competed successfully to spend time at the top of the male hierarchy.

It is possible of course that males who survive to adulthood and succeed in attaining high rank might in fact be displaying "good enough genes" by doing so, so that the interests of dominant males and females coincide. If so there might not exist much incentive for females to strive

to escape an advantageous status quo, except in special circumstances. For example, if a dominant male remains in residence for such a long time that his own daughters were maturing in his group, then females should avoid him.¹⁴

Reduced importance of female choice for genes is also suggested by the nature of primate sexual dimorphism. Accouterments of male-male competition like larger body size and canine teeth are more salient than ornamental traits like the peacock's tail, though there are obvious exceptions: facial coloration of male mandrills, gibbon songs, the same male anogenital colorations Darwin noted in 1876, and perhaps significantly, various human traits, including beards, musical talent, or rhetorical gifts.

The finding that intervals between births were longer in groups with many females, where a number of estrous females solicit the same males (reported for *Macaca fascicularis* and *Presbytis entellus*), led some authors to propose that sperm may be a limiting resource, even suggesting that females solicit multiple males *in order to deplete* sperm available to other females (Small 1988; Sommer 1989). It seems circular, however, to argue that females solicit multiple partners *in order to overcome* sperm depletion caused by multiple matings. Even less convincing (as an ultimate explanation) is the argument that assertive female sexuality evolved *in order to generate competition at the level of the sperm*.

Unquestionably there has been selection on male primates to compete at the level of sperm, resulting in large testes and voluminous ejaculate, and possibly even specialized sperm (Harcourt et al. 1981), and females have had to make the best of this.¹⁵ But from a female's perspective, sperm competition is more probably an unfortunate consequence of polyandrous matings than something females were selected to promote. Competition inside her reproductive tract is scarcely the optimal arena for male-male competition, though once such competition gets going in males, females may have no choice but to make the best of it.¹⁶ A female primate's highest initial priorities should favor survival of the daughters and sons she produces. Rewards to be gained from conceiving a son who himself produces competitive sperm can only be reaped if that "sexy son" survives to maturity and also happens to compete successfully for opportunities to mate; companion benefits will be completely lost on daughters unless they survive to produce successful sons. To the extent that genes affect offspring quality, females should fare better under a "priority of access" system (distinguishing between individual males) than under a system emphasizing priority of fertilization (distinguishing between sperm).

Some of the hypothesized benefits of females mating with multiple partners do not depend on "genetic rationales." Progress in testing such

hypotheses has been variable. One old idea, the "prostitution hypothesis"; Symons 1979; Zuckerman 1932), that females trade sex for favors such as access to male-controlled resources like meat, has received some support from studies of the few primates among whom the adults share food (Parish 1994). However, Sherfey's idea that copulations leading to orgasm have therapeutic benefits for females—a notion dating back to Greek Hippocratic authors and also assumed by such tribal peoples such as the !Kung (Shostak 1981:287)—has received no support. A third hypothesis, that females might influence the survival of their offspring by manipulating information available to males about paternity (suggested by Hrdy for langurs in 1974, and extended to other primates in Hrdy 1979) has been tested, but alas the predictions that it generates have been substantiated only among birds (Burke et al. 1989; Davies 1992), not among the primates for whom the hypothesis was first proposed.

Female dunnocks (*Prunella modularis*) solicit multiple males, who in turn help to feed and care for chicks more or less in proportion to their sexual access to the mother when she was fertile (Davies 1992). That is, both the alpha *and* the beta male were significantly more likely to feed the young if they had fathered, or even if they could have fathered, them. Consistent with the paternity confusion hypothesis, DNA fingerprinting to determine paternity revealed that males were often, *but not always*, accurate in their paternity assessments. Furthermore, beta males who failed to mate were most likely to harass incubating females, and may even be responsible for destroying eggs. Most interesting in regards to Davies' dunnock findings is the case of the related species, *Prunella collaris*, the Japanese accentor, which live in multimale, multi-female groups rather like baboons and chimpanzees. Among the Japanese accentors, Masahiko Nakamura (1990) notes that "the female's cloacal region protrudes and turns scarlet" during periods of fertility, in the only case known to date of sexual swellings outside the Primate order. Nakamura hypothesizes that the swellings evolved to promote sperm competition, but I continue to worry over the fact that it is females who evolve the signals, yet I do not see how females benefit that much from competition at the level of the sperm. Thus I suggest that the evolutionary sequence was as follows: female accentors mate with multiple males, and to promote this, some accentors evolved "sexual swellings." But sperm competition was already incorporated in the breeding system prior to the evolution of swellings.

The hypothesis that a female might inhibit males from subsequently attacking her infant, or else elicit extra protection or support for her offspring by casting wide the net of possible paternity, predicts that past consortships do indeed affect male behavior towards the offspring of

former consorts (Hrdy 1974, 1979). Observations in support of this hypothesis remain roughly the same as those that inspired it to begin with: (a) in species like savanna baboons, barbary macaques, and humans, *possible progenitors and former consorts of the mother appear to look out for the well-being of infants* (Altmann 1980; Taub 1980), and (b) in a wide array of animals, including some sixteen species of Old and New World monkeys and great apes, *infanticide by adult males—which can be a major source of infant mortality—is most likely to occur when males enter a group from outside it, or else when a male rises from a subordinate nonbreeding to a breeding position within the group* (Daly and Wilson 1988; Hausfater and Hrdy 1984; Parmigiani and vom Saal 1994; but see Sussman et al. 1995 for dissenting opinions, and reply by Hrdy et al. 1995). Infanticide by adult males has been reported for more than a dozen species of anthropoid primates (Hiraiwa-Hasegawa and Hasegawa 1994; Leland et al. 1984; Sommer 1996); additional information is also emerging on infanticide among prosimians (Pereira and Weiss 1991; Wright 1995).

Based on data from the longest running relevant field study spanning sixteen years of observation of a population of Hanuman langurs at Jodhpur, Rajasthan, India, by more than a dozen researchers, Volker Sommer calculates that of 112 infants present in troops when new males forcibly ousted the former resident male, 82% were attacked by the new males, though not all were killed (1994:159ff., 1996). At Jodhpur, a minimum of 33% of all infants born were lost due to infanticide. Typically (90% of the time) the infanticidal male subsequently gained sexual access to the mother, although in at least 40% of those cases, he had to share that access with other males (Sommer 1994:166). Apparently, gaining exclusive access to females was beyond the capacity even of males who succeeded in usurping rival males as resident breeding male in a troop.

Infanticide is a protean phenomenon across animals, especially so in humans. Cases superficially similar to the langur case are reported anecdotally in societies with long traditions of raiding for women (e.g., in biblical accounts, and among the Yanamamo where suckling infants of kidnapped women may be killed outright, or left behind, with the same physiological outcomes: death for the infant, earlier resumption of ovulatory cycles for the mother). However, most documented cases of infanticide among humans involve one or more parents, or else substitute parents residing in the same household. Currently, researchers like Martin Daly and Margo Wilson tend to attribute the elevated risk of infants living with unrelated males associated with their mothers, now well documented in western societies, to “discriminative parental solicitude” (Daly and Wilson 1988). Adults caring for infants may have a higher threshold for responding with solicitude towards offspring that are un-

related, poorly timed, poor bets for transforming parental investment into successful breeding adults, and so forth (Daly and Wilson 1988; Hrdy 1992).

Whatever the rationales and/or motivations for the killing of human infants by unrelated males, whether they involve reproductive access to the mother or the elimination of competitors for family resources, or various combinations of reasons, providing potentially infanticidal males with some probability of paternity may not be as absurd as some critics have made it sound. (For example, in an influential opposing argument, Symons has argued that casting wide the net of possible paternity can only backfire, since men less than certain of paternity will never invest; Symons 1982:182.)

Social theorists and literary figures concerned with human nature—and encompassing a wide range of male-oriented perspectives—such as Samuel Johnson, Jean-Jacques Rousseau, Friedrich Engels, and August Strindberg, have remarked on their sex's sensitivity concerning uncertain paternity and its implications for paternal investment. However, this topic has rarely been the focus of empirical study. In one of the few empirical case studies among tribal peoples, behavioral ecologists Kim Hill and Hillard Kaplan reported that women among Ache foragers in eastern Paraguay routinely rely upon former consorts to increase protection as well as resources available to their offspring. Interviews with seventeen women reveal that each of 66 offspring was attributed to a mean number of 2.1 possible progenitors. In terms of child survival, this was around the optimal number; beyond two or three "godfathers," survivorship went down.

This maternal casting of the net is sufficiently pervasive that the Ache recognize different categories of fatherhood. "One type refers to the man who is married to a woman when her child is born. Another type refers to the man or men with whom she has had extramarital relations just prior to or during her pregnancy. The third type refers to the man who *she* believes actually inseminated her" (Hill and Kaplan 1988:289). The presence of such "godfathers" means more game brought in (meat constitutes 60% of the Ache diet). Marjorie Shostak (1981:281) provides similar examples of lovers who provide their paramours with supplementary food among San foraging people in the Kalahari Desert.

Possible fathers also provide critical protection for immatures against other men. Infanticide/pedicide rates among South American foraging people like the Ache can be relatively high (Hrdy 1992). In the Ache case, 12% of liveborn children between the ages of birth and five years die at the hands of adults. Data on 26 cases of child homicide are reported by Hill and Hurtado (1996). Loss of male protectors renders children particularly vulnerable, and they may be killed either by other band

members who no longer wish to provide for them or by the mother's subsequent husband. Hill and Kaplan report that children whose reported biological father dies before the child reaches age fifteen are significantly more likely to die. Of children whose fathers died, 43% of a sample of 67 died prior to age fifteen, compared with 19.3% of 171 children whose fathers remained alive until after the child reached age fifteen (Hill and Kaplan 1988:298; and see Hill and Hurtado 1995 for in-depth discussion of Ache life histories).

A variety of additional hypotheses about female sexuality flow from the proposition that female primates have been selected to mate with a range of male partners. For example, orgasmic "reward" systems dependent on prolonged stimulation—now documented among rhesus and stump-tailed macaques (Burton 1970; Goldfoot et al. 1980; Slob et al. 1986; Slob et al. 1991)—can be viewed as having evolved in nonhuman primate females to condition them to continue soliciting male partners. Although Symons (1979) and Gould (1995) have argued that female orgasms and the clitoris (an organ whose only known function is to translate physical stimulation into psychophysiological sensations sometimes associated with orgasm) are incidental, present in females because they are selected for in males, this proposition ignores comparative evidence for different primate species.¹⁷

The clitoris varies in size, shape, and placement between species in ways that are not parallel (or "homologous") with, and indeed are often divergent from, differences between species in size and shape of the penis. For example, the clitoris is relatively and absolutely larger in both species of chimpanzee than it is in humans, while the penis is relatively and absolutely larger in humans than in either species of chimpanzee (Baker and Bellis 1995:167–171; McFarland 1976). Even in the relatively brief evolutionary time span since *Pan paniscus* diverged from other chimpanzees, there has been sufficient selection pressure for substantial changes in the bonobo clitoris to evolve (presumably due to the significance in bonobo mating systems of frontal rubbing of the genitals during sexual behavior). In addition to emphasizing heterosexual couplings, Amy Parish has recently argued that sexual behavior between two females plays a role in forging social alliances between unrelated females, counteracting negative effects for females constrained to live in patrilineal communities, without female kin (Parish and de Waal 1992; Parish 1994, 1996). Whatever the explanations for observed hypersexuality in this species turn out to be, the bonobo clitoris is distinctively shaped and frontally placed (Dahl 1985); I am not aware of any corresponding (or "homologous") differences in the bonobo penis (Short 1979; Amy Parish, personal communication 1996). Unless one wishes to argue that the female bonobo's remarkable morphology (already apparent in young

females) has resulted ontogenetically from bonobo sexual practices (frontal genital-genital rubbing during infancy), it seems likely that selection has operated on bonobos to favor the different shape and placement of the clitoris in *paniscus* compared to *trogodytes*. Facultative expression of different patterns of sexual activity in *paniscus* and *trogodytes* may in fact have provided precursors or "preadaptations" for eventual speciation in these great apes (e.g., see discussions of flexible phenotypes in West-Eberhard 1991, 1992). As West-Eberhard suggests: "Perhaps the best way to begin to shake off the inhibitions that come from an obsession with stability, equilibrium and stasis, and constraints is to think about . . . sexual behavior" (West-Eberhard 1992:60).

FLEXIBLE PHENOTYPES IN COERCIVE SOCIAL SYSTEMS

Coercive Male Strategies, Female Counter-Strategies, More Coercion

"Concealed ovulation" (or, more nearly, "absence of advertised estrus"), "continuous (situation-dependent) receptivity," face-to-face copulations, and a female capacity for orgasm, which have long been considered uniquely human attributes that evolved to cement pair bonds (Lovejoy 1981; Morris 1967), are viewed here as part of a much older prehomimid heritage that does not assume monogamous mating systems (Hrdy 1981; Sillen-Tullberg and Moller 1993). This would have been the "raw material" available to our ancestors in forging variably monogamous to polygynous, unimale mating arrangements and developing diverse systems of marriage and inheritance that define modern *Homo sapiens* (Hrdy 1988).

Understanding exactly how the sexual discretion that struck Darwin as so curious came to characterize so many women (compared with, say, bonobos) will require a combination of evolutionary, historical, and developmental approaches. No doubt, many social scientists find it circuitous to pay so much attention to female libido in nonhuman primates (e.g., Rossi 1995), but I am convinced that a comparative perspective leads to an illuminating question: why do women differ from other female primates in respect to sexual discretion or (in Darwinian terminology) "coyness"?

Clearly female primates are more sexually assertive than Darwin and his successors realized, and by extension, so were our remote ancestresses. Largely in consequence of this first oversight, there was a second underestimation. Biologists underestimated the full extent and

importance of repressive strategies by males—some evolved, some possibly learned (Kummer et al. 1974)—in order to counter this sexuality, subverting female mate choices by harassing, sequestering, punishing, or intimidating them, and by monopolizing access to the resources that females need to breed (Clutton-Brock and Parker 1995a, 1995b; Smuts and Smuts 1993). Although feminists and animal behaviorists have in fact long understood that coercion of females played some role, subversion of female choice has not been a focus for study until recently.

When a male langur enters a breeding system from outside and kills infants sired by his predecessor (Hrdy 1974; Leland et al. 1984; Sommer 1994) he nullifies any female “choice” in the sense that he eliminates the genes of the last male she mated with. But in addition, and perhaps even more important, the infanticidal male has subverted the mother’s control over the timing of her own reproduction. Rather than bear the evolutionary costs of a barren interlude, infanticide puts the female (now freed from lactational amenorrhea) under pressure to conceive again after a shorter interbirth interval than might otherwise be optimal for her (Hrdy 1979).

Viewed from a female perspective, male coercion takes on a more pernicious meaning from the one animal behaviorists have traditionally ascribed to “male dominance.” Viewed from an evolutionary perspective, coercion with reproductive implications has tremendous potential significance. Many scholars are increasingly sensitized to recent and past efforts by husbands, parents, religious groups, and state officials to monitor or police a woman’s control of her own fertility, to alter her anatomy (e.g., through clitoridectomy), or cloister her behind guarded walls (Dickemann 1979)—often with devastating psychological, physiological, and even fitness consequences for the mothers involved (Hrdy 1992; Kertzer 1993). But the full potential genetic implications of suspending female choice are only beginning to be understood (Rice 1996, discussed below).

In recognition of the fitness costs imposed on females by male coercion, some evolutionary theorists have proposed giving “sexual coercion” pride of place—or at least third place—in Darwinian sexual selection theory (Smuts 1992; Smuts and Smuts 1993; see also Clutton-Brock and Parker 1995b:1347). “Sexual selection” is thereby transformed into a tripartite process, with equal billing given to *male-male competition*, *female choice*, and *female coercion by males*.

Episodes of male coercion of females can be located in the animal behavior literature from Darwin onwards. Since Trivers (1972), sociobiologists have tended to view conflicting interests of males and females as a routine by-product of sexual selection. The circumstances in which male coercion was likely to be important (e.g., in nonterritorial, polygynous

species like hamadryas baboons) were set forth by Searcy and Yasukawa just over a decade later (1989). Subsequently, data on reproductive costs imposed upon females by mates who married more than one wife were analyzed in terms of a "male coercion model" by Chisholm and Burbank (1991) for Australian aborigines, making theirs the first human application of such models (see also brief discussions in Alexander 1979; Irons 1983). More important, Chisholm and Burbank (following the lead of William Irons) called attention to the possibility of men and women negotiating "compromises" of their conflicting interests specifically through sororal polygyny (i.e., marrying several sisters) so that shared interests of related co-wives make them less antagonistic towards one another. However, the theoretical significance of male coercion of females (see especially Smuts and Smuts 1993) has only recently been incorporated into theories about mating systems, along with the idea of "punishment" of females for straying as a means of solidifying male reproductive control over females (Clutton-Brock and Parker 1995a, 1995b).

A key point to emerge from this consciousness raising is that once females are viewed as active agents, we are forced to acknowledge male subversion of female choice and its importance (Gowaty 1992). It also focuses attention on female strategies to counter and ameliorate such male counter-strategies, challenging us to identify and measure processes in what Gowaty (1996) terms the endless and ongoing "dialectics of sex."¹⁸ If some male domination of females in the course of herding or sequestering them from other males seems unnecessarily violent or "gratuitous"—occasionally a female is injured or killed—such force is nonetheless on average an effective way of guaranteeing female compliance (Smuts 1992; Clutton-Brock and Parker 1995b). In contrast to those feminists who see such domination as an end in itself, for evolutionists, it does not suffice that males are subverting female choices simply for the satisfaction of doing so. Rather, evolutionists assume that males do so because on average such tactics make them reproductively more competitive with other males.

Male coercion is an important concept. But does recognition of its significance mean we need to revamp Darwin's sexual selection theory? Clearly, both components (male-male competition and female choice) are more complicated than Darwin—with his focus on competing males and coy females—originally contemplated (e.g., Gowaty 1996). Nevertheless, Darwin's focus on intrasexual competition remains a brilliantly serviceable framework. Rather than tinker with the armature, to me it makes more sense to retain Darwin's overarching assumption that when males compete, *the ultimate goal is to outreproduce other members of the same sex*, and then go on to inquire further about specific ecological,

developmental, and historical processes that shaped motivations and behaviors that nevertheless originally evolved in the service of male-male competition. Without intrasexual selection (usually male-male competition) there would be no point to female choice and hence no point to male attempts to "bypass female choice and 'coyness' by force" (West-Eberhard 1991).

There are many permutations of sexual selection. Fallout from male-male competition and female counter-strategies to male coercion can take many forms (e.g., males can compete by trying to exclude rival males from contact with fertile females, or they can tolerate contact but compete at the level of sperm). In the human case, were it not for our extraordinary mobility and the ease of interbreeding in our species, I think it possible that our facultative sexual natures combined with variable behavioral ecologies, mores, and institutional histories would have long ago led to subspecies as different in sexual habits and attributes as *Pan troglodytes* and *Pan paniscus*!

Male-male reproductive competition among anthropoid primates takes place in the face of female sexual assertiveness. Whether sexual swellings and situation-dependent receptivity evolved as female counter-strategies to forestall infanticide, and to secure male protection and assistance, or for other reasons, the fact remains that *none of this occurs in an evolutionary vacuum*. Selection on males to counter female strategies would in turn have operated to select (in the multimale breeders) for larger testes and more competitive sperm, thereby moving competition over "promiscuous" females to another zone. Alternatively, males in unimale systems like hamadryas baboons or gorillas would be forced to devote energy to excluding other males and/or sequestering females rather than producing more, and more competitive, sperm (Harcourt 1996). More innovative apes, like *Homo sapiens* (among whom male investment in offspring also takes on new and special significance), invented whole new modes of policing females. These involved claustration, indoctrination, surveillance, gossip, inheritance rules, and laws (Boone 1986; Dickemann 1979, 1981; Hrdy 1981; Hrdy and Judge 1993).

Furthermore, with the emergence of family-controlled wealth and formalized inheritance, such internalized values can be intensified by intrasexual competition among women and their families to place "chaste" daughters in high status patriline through marriage (Boone 1986, 1988; Dickemann 1979). Intergenerational transmission of status and property in patrilineal systems can in this way create "runaway" selection for the appearance of chastity in women. Within such a system, coyness can be viewed as a female signal advertising her willingness to trade paternity confidence for parental investment (James Boone, personal communication 1996).

However elaborate, such subversion of female counter-strategies is ultimately just another form of male-male competition in Darwin's classical sense. The goal remains outreproducing rival males, even though it is accomplished by prevailing over females. The fact that selection acts on males to compete with other males does not make consequences for females any less detrimental.

Curtailing female freedom of movement interferes with foraging or productive labor (Dickemann 1979, 1981). Sequestering may increase female-female competition or subject them to unhealthy living conditions (more crowded, exposed to pathogens, etc.). Under some circumstances (and this would assume that female choice for genes had been at work previously) curtailment of female choice could drastically affect the ability of females to respond to selection upon males and to hold their own in any coevolutionary dialectic (Rice 1996). Extensive curtailment of female control over their own mating has potentially profound evolutionary consequences.

Experiments on intersexual coevolution in *Drosophila* undertaken by William Rice (1996) illustrates such evolutionary processes. Rice permitted *Drosophila* males to adapt to female breeding stock while experimentally arresting corresponding evolution and adaptation to male strategies among his female study population. Rice employed draconian methods of *Drosophila* husbandry (pun intended) to constrain one sex's ability to adapt evolutionarily to the other. Whereas breeding females were obtained from a "control" population derived from the initial breeding stock, males were permitted to breed freely. As Rice put it: "When female *D. melanogaster* are experimentally prevented from coevolving with males, males rapidly adapt to the static female phenotype" (1996:232). Over 41 generations, females were rendered incapable of "countering" evolving sexual strategies in males. By contrast, "experimental males evolved increased net fitness in response to the fixed phenotypes of target females. Adaptation by experimental males resulted in a marked decrease in the survival of their mates with no compensating increase in female fecundity" (1996:234).

Rice's experiments are on *Drosophila*—one of the few species where mate choice is already known to affect offspring fitness in ways that have been suspected but never documented in primates. Nevertheless, imagine a breeding system in which females are paired with males in sexually exclusive arranged marriages, and thereafter completely cloistered with no opportunity to exercise any mate choice whatsoever, and that this regime is maintained over many generations. Would selection pressure be relaxed for those features of female sexuality that contributed to mate choice (possible examples would be behavioral correlates of fluctuating libido, or physiological capacities

to filter sperm, assuming such features existed)? The answer to this question has to be "yes."

If women like Briseis are "assigned" as wives or concubines at an early age and thereafter completely cloistered, with no possibility of choosing between males, selective pressures for capacities which permit females to choose between progenitors become irrelevant. By contrast, men who continue to mate within and outside the seraglio, with varying degrees of choice, continue to be subject to selection pressures in this regard.

I have long assumed that partner identity was less important to the occurrence or nonoccurrence of female orgasm than other variables (such as cycle state, level of clitoral stimulation, or level of inhibitions, which may of course be partner related) but for the sake of this hypothetical example, imagine further that the occurrence of orgasm is geared to partner identity and plays an active role in sperm retention and female choice, as proposed recently by evolutionary biologists and psychologists (Baker and Bellis 1995; Thornhill, Gangestad, and Comer 1995). Baker and Bellis (1995) for example propose that a female increases her probability of conception by experiencing orgasm when coupled with a progenitor likely to produce superior progeny. If any of these arguments were correct, consider what would happen to the selection pressures maintaining them under patriarchal breeding protocols: male breeding advantage would breed male advantage.

Sperm competition represents another consequence of male-male competition potentially detrimental to female reproductive interests over the long run. Even though it is assumed that "sexy sons" inherit their father's gifts in this respect, pay-offs from producing competitive sperm would not arise until after a son had survived to maturity and become competitive for mates. Given that competitive sperm does not necessarily correlate with the most robust phenotypes and that fathers producing competitive sperm need not create advantageous conditions for infant survival, in species like primates where individuals are only long-lived *if* they survive the very vulnerable infant and juvenile years, I would expect competitive sperm to fall rather far down the "list" of a mother's criteria for an ideal mate. Certainly ejaculate quality does not necessarily correlate with other measures of survivorship or phenotypic success (Birkhead et al. 1995).

Among humans, the most important male strategies involve not just physical coercion, intimidation, and indoctrination of females, but monopolization by patrilineal resources needed to survive and rear offspring successfully, forcing females (and their families) to favor wealthy mates, and further encouraging the parents of sons to channel resources in ways that make their children competitive. These circumstances encourage the development of complex marriage and intergenerational

systems that concentrate resources in male hands (Boone 1986, 1988; Borgerhoff Mulder 1988; Hartung 1976; Hrdy and Judge 1993; Sieff 1990; Voland 1984). Although cultural anthropologists and historians will no doubt find such interpretations reductionist (which they are), and even fellow sociobiologists will caution about not overlooking the increasing importance of parental investment over the course of human history and in the emergence of patriarchal systems (Boone 1986), I nevertheless remain convinced that the focus on male-male competition in Darwin's original theory of sexual selection clarifies the motivations underlying manifold and very diverse processes contributing to male domination, and clarifies our thinking about the *prehominid* origins of these trends.

To sum up then, feminists have argued that patriarchy is a cultural and historical creation by men and women in a process that took some 2,500 years. By contrast, a Darwinian perspective—without necessarily discounting historical processes involved—would lead us to push the search for patriarchy's origins millions of years earlier by asking the additional question of why so many hominid males and their patrilineal lines experienced such an urgent need to control females. Far from preserving an oppressive status quo, sociobiological analyses provide important insights for those who seek social change (Hrdy 1990). More important, evolutionary analyses illustrate why it is simply good science, not just "political correctness," to take into account the perspective of both sexes.

Male Control of Resources Constrains Female Choices

Men argued with the giants that precede them; women argued against the oppressive weight of millennia of patriarchal thought . . . (Lerner 1993: 166).

Technically, patriarchy refers to male domination of women and children in their own families. But when male dominance comes bolstered by patrilocal living arrangements (males being not only physically stronger but advantaged by the availability of relatives, e.g., Quinn 1977) sons will have greater resource holding potential than daughters, encouraging parents to bias intergenerational transfers of resources further in favor of sons who can keep hold of cattle or land, versus daughters who are particularly vulnerable from having it taken away or diverted to their husband's lineage (Hrdy and Judge 1993; Hrdy n.d.).

Across all well-studied species of primates, so far, humans provide the only well-documented cases of female choice for male attributes. Female preferences for wealthy and/or powerful mates have been documented for both contemporary, western populations (Buss 1994b) and

for some tribal societies (Borgerhoff Mulder 1990). Although these convergent findings are sometimes taken to mean that women innately prefer powerful, resource-controlling males, such preferences emerge in the context of specific ecological, marriage, and inheritance systems, as Borgerhoff Mulder takes pains to emphasize. It does not necessarily follow that women evolved to prefer powerful, resource-controlling males (Buss 1994a:25). Practically speaking, a woman's preference for a wealthy man can be explained by the simple reality that in such societies males monopolize ownership of productive resources (cattle, land, high-paying jobs); a woman gains access to the resources that she needs to survive and reproduce through her mate.

In spite of such caveats, the fact that females under such diverse circumstances prefer powerful men continues to be construed as proving that female preferences are innate (Buss 1994a) and that patriarchy is inevitable (Goldberg 1993). Yet many predispositions are both biologically based *and* situation-dependent, and hence malleable (Gowaty 1995; Hrdy 1990). Consider a single example drawn from research on property transmission.

Since the dawn of civilization (Lerner 1986) and probably far longer (Ghiglieri 1987; Hrdy and Judge 1993; Murdock 1976; Rodseth et al. 1991), intergenerational transfer from parents to offspring of territories and of resources has favored males (Boone 1986; Hartung 1976). Colonial America was no exception (Judge 1995). Most fathers bequeathed most of their resources to one or more sons, more or less excluding daughters who, with no legal right to own property and no powerful allies, had no way to defend property ownership. (Mothers don't even show up in these probate records until the eighteenth century; married women did not have the legal right to own real property, and hence had little to bequeath.) Yet, as demographic, ecological, and legal conditions changed over the course of the eighteenth and nineteenth centuries, so did parental treatment of heirs. As Debra Judge (1996) has demonstrated, smaller families meant that more parents only had daughters as potential heirs. Married Women's Property Acts during the mid-nineteenth century meant that daughters, even those with no kin on hand, had a powerful new ally—the state, a figurative “Big Brother” who intervenes to protect women against forcible confiscation of their property by more powerful males. New legal rights meant that parents with smaller families, including families without male heirs, now had another option. Inheritance by daughters increased dramatically (Judge and Hrdy 1992, n.d.). These new property rights were critical to the experiment in equal rights and increasingly equal opportunities that women in western societies are tinkering with today. An age-old pattern of preferential treatment of sons changed in a matter of decades. Preferential treatment of

sons is a very ancient and a very widespread hominid pattern, and many factors reinforce its persistence, yet son preferences are *not* inevitable given social or ecological changes that alter cost-benefit ratios to parents (Hrdy 1990; Smuts 1992).

Ironically, evolutionary psychologists and their popularizers propose—under the guise of feminist sensibility and progressive thinking—that women would benefit from polygynous marriages because while harming subelite men (forced to go wifeless), polygyny *benefits* women because more of them get to marry wealthy providers. Multiple wives/concubines would be permitted to share access to wealthy men instead of being forced to settle for some economically inadequate also-ran or, worse, a nonprovider (Wright 1994:98–101). But note that this supposedly feminist polygynous utopia remains essentially patriarchal: male patrilines still control access to productive resources (and/or higher-paying jobs). Patriarchal property arrangements are *taken for granted*.

Women (and their offspring) not only depend on husbands to provide for them, but as is typical in patriarchal societies, a woman's status is defined by whether or not, and whom, she marries. Only as this situation changes would criteria for mate choice gradually be expected to change as well. But such an experiment in unconstrained choice, what Gowaty terms "free female choice" (personal communication, 1996) has not yet been tried on any large scale or over any period of time. Furthermore, it is questionable whether "free" choice for any human committed to reproduction, and certainly any woman committed to long-term fitness, could exist (Hrdy n.d.). Without the relevant experiments or comparative studies, we cannot claim to know what the innate or "universal" nature of female criteria in mate choice actually is.

Understanding the development of criteria for mate choice, and particularly, understanding the unique role that sexual "coyness" (modesty, prudence, or attention to "reputation" might be better terms) still plays in our own species, will demand economic, cultural, developmental, and historical, as well as evolutionary, perspectives. What has happened in the course of hominid evolution *and history* to alter selection for assertive female sexuality?

Relative sexual freedom is permitted women under some circumstances, but the vast majority of human cultures practice a double standard of sexual morality (Broude 1980; Broude and Greene 1976) which, combined with the human capacity for language and propensity for gossip, subjects any woman who cannot account for her whereabouts to damaging, even lethal, penalties, as well as to internally produced feelings of mortification and shame. Given the long time frame for the development of such traits as male sexual jealousy and female "coyness," modesty, or discretion, it is worthwhile taking seriously the prop-

osition that such emotions may be more than cultural constructions, as in the case of blushing (Darwin 1965). But the fact is, of course, we do not know. Therefore, we need to be careful not to mistake for supposed "species-typical" universals (male preferences for neotenous females, female preferences for rich men) traits that may in fact be ontogenetic coping strategies in a socially constraining world.

Some evolutionary psychologists have argued that female preferences selected for male acquisitiveness and a high motivation to compete for resources. In the words of one prominent evolutionary psychologist, "Women's preferences . . . established an important set of ground rules for men in their competition with one another. Based on sexual selection theory, the desires of one sex establish the critical dimensions along which members of the opposite sex compete. Since ancestral men tended to place a premium on women's physical appearance . . . this established attractiveness as a major dimension along which women compete with one another. . . . Analogously, women's desires for men with resources established the acquisition of resources as a major dimension of men's competition with each other" (Buss 1996:307–308). That is, Buss assumes that greater risk-taking by males (see Daly and Wilson 1988 for documentation of the phenomenon) is a result of competition between males for resources, rather than attempts to impress women (through bravery, etc.) or to acquire or defend them through combat (as others have argued; Daly and Wilson 1988).

In contrast to Buss, behavioral ecologists and sociobiologists who take into account comparative evidence across taxa (Emlen 1995; Hrdy 1981; Hrdy and Judge 1993) view male control of territories and resources as a corollary of differential male and female migration patterns, male philopatry, and selection for greater male strength through male-male competition for access to mates. Among primates, male control of resources *preceded* female choice for males with resources. For example, Hrdy and Judge (1993) point to male philopatry, availability to sons of patrilineal allies, preferential treatment of sons by parents, and male-biased transmission of territorial control and of resources as prior to, and setting the stage for, preferences for resource-controlling mates by both daughters (who migrate from outside to join mates) and their parents. Furthermore, male philopatry predisposing males to form coalitions with patrilineal male relatives further reinforces male dominance over females (Hrdy 1981; Smuts 1995). In such systems, behavioral ecologists would expect that females will choose mates on the basis of the resources they control, and this prediction is supported by a growing body of empirical evidence (Borgerhoff Mulder 1987, 1990; Buss 1991). But empirical support for this prediction does not mean that female choice for males with resources *was responsible* for males being competitive or for males con-

trolling resources in the first place. Both male-male competition for females and male control of productive resources were already present in the hominid line, and almost certainly preceded the development of female preferences for resource-holding males in the human case. This "patriarchal constraints" hypothesis is silent as to whether female criteria awarding priority to resource-rich males are innate or primarily learned in the course of socialization.

Whether learned, evolved, or both, however, the "patriarchal constraints hypothesis" predicts that when female status and access to resources do not depend on her mate's status, women will be likely to use a range of criteria, not primarily or even necessarily prestige and wealth, for mate selection. Indeed, as I write this, an odd story has just been published in the *New York Times*, describing what is in some ways a mirror-image of Bill Rice's draconian experimental protocol in which females were constrained from choosing mates. In her piece entitled "Bride Wore White, Groom Hopes for Parole," journalist Donatella Lorch (1996) describes women from a wide range of professions—bankers, journalists, judges, teachers, for whom resources are obviously not the issue—who marry men whose freedom of mate choice is severely circumscribed by the fact that they are in prison. Assuming these inmates don't have loot stashed away somewhere, their allure obviously does not reside in either their earning power or their labor potential, or even their ability to protect the female. Indeed, the guarantee of fidelity loomed large since inmates with the longest terms to serve were apparently most attractive (Isenberg 1991, cited in Lorch 1996). Peculiar as it is, this vignette of sex-reversed clausturation makes a serious point about just how little we know about female choice in breeding systems where male interests are not paramount and patrilineal rules are not making the rules.

The situation with male mate choices is little better. When, for example, resources are important for reproduction, and when females possess (or are able to obtain) resources, males will be likely to value resource-potential along with or over beauty. Given the same playing field, and controlling for body strength (which indeed is rendered feasible by modern technologies and current legal protections), men and women are predicted to be about equally motivated when competing for those resources that pertain to their long-term reproductive success even though the form that competition takes may differ (Hrdy 1981:129–130; see especially Paul et al. 1996 for the sort of surprises we can expect as we begin to approach the question of innate sex differences in a less dogmatic way). Raising the consciousness of Darwinians has important implications for contemporary debates. Critics of affirmative action have pointed out that men are by nature more aggressive, assertive, competi-

tive, and achievement-motivated than women are (reviewed in Browne 1995). Hence, they argue, the "glass ceiling" on remuneration for women versus men can be attributed to innately less competitive temperaments in women (Browne 1995) rather than to male-biased institutions and the quite different fitness trade-offs in the case of men versus women. For women, single-minded pursuit of high-status jobs has typically meant choosing between investing in a career and investing in offspring; men have had more leeway in finding women to rear offspring for them. More important, in all other species of primates save our own, females compete directly for the resources they need to survive, to reproduce, and to rear surviving offspring (Hrdy 1981). To the extent that humans are exceptional in this respect, to the extent that women differ from other primates by competing for resources indirectly, competing for resources by competing for mates who provide them, we really must first start by asking: why?

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NOTES

1. The woman Spencer rejected on these grounds was none other than the novelist George Eliot. This failed romance, and the ensuing decades-long intellectual dialogue between them, is dealt with elsewhere (Hrdy n.d.).

2. To those who fear that feminist perspectives constitute some spin-controlled monolith of politically correct opinion, it may be reassuring to note that I am in far closer agreement on this point with evolutionary psychologist

David Buss than I am with my fellow feminist, evolutionary biologist Patricia Gowaty, who has argued that male preferences for neotenous traits might be due to juveniles being easier to dominate (1992:240). Evidently we are scholars first, evaluating the evidence as we read it, and feminists second. There is no monolith of "correct" interpretation.

3. As Doug Jones (1995) points out, menopause may make it especially important for human males to avoid acquiring females approaching the end of their reproductive careers. But even assuming women live long enough to reach menopause, one does not need a preference for neotenous traits in order to accomplish this. Attention to hair color, skin tone, or breast shape make excellent indices. Prior to cosmetics, dyes, and plastic surgery, women who survived long enough to reach menopause would be qualitatively different (in appearance) from fertile women. As for older women whose fecundity is beginning to decline but are still capable of conceiving, their condition would be of little relevance to male mating decisions unless the man sought to acquire her as his property to hold long-term—which is my point. Nevertheless, readers should be aware that the points I make here barely scratch the surface of the dynamic complexities surrounding sexual selection for physical attractiveness; see especially Buss 1994a; Gangestad 1993; and Thornhill and Gangestad 1993.

4. Note that this prediction is not the same as the prediction made by those who study criteria of mate choice for short-term versus long-term (marriage) pairings (Buss 1994a:78). Buss and his co-workers have documented an across-the-board relaxation of standards (concerning age, education, wealth, charm, etc.) for short-term relationships: as sexual *availability* looms larger, standards of attractiveness shrink. I am not talking here about relaxed standards, but different criteria likely to be correlated with immediate versus long-term fertility. This difference reflects larger differences in perspective between those who focus on probable reproductive outcomes (Chisholm 1991) and evolutionary psychologists who argue that "correlating attributes with any measures of fitness is a poor and potentially misleading source of information about adaptation" (Buss 1991:521). It is likely that our philosophical differences reflect larger differences in perspective. For a sociobiologist steeped in the comparative perspective, valuing neotenous features rather than outright signals of fertility is bound to raise questions about what on earth is going on, whereas for an evolutionary psychologist focused on specifically human mental adaptations acquired in some imaginary point in the Pleistocene (that fabled Environment of Evolutionary Adaptedness) it might not seem so curious.

5. This same discrepancy surfaces in the debate between feminist and sociobiological interpretations for rape. For some feminists, rape is a "process of intimidation," essentially an act of domination with primarily symbolic intent, while for sociobiologists it represents an act of domination with a primarily *reproductive* intent. Compare for example Susan Brownmiller (1975) on rape with the sociobiological analysis by Thornhill and Thornhill (1983).

6. For the non-Engelian, purportedly Marxist view that "we are the being whose essence lies in having no essence," see Stephen Jay Gould (1976) on "Biological Potential vs. Biological Determinism." For the view that "The sexism in sociobiology is an outgrowth of the theory itself," see Alper et al. 1978. For more on feminist critiques of sociobiology, see Hubbard et al. 1979. Masters (1982) provides an interesting explanation for sociobiology becoming erroneously equated with "conservative" points of view: "the Marxist theory of human history is, par excellence, a systemic or 'sociological' one. In contrast to the social contract approach of Anglo-Saxon liberalism . . . Marxism denies the possibility

of deriving social attitudes from the interests or 'rights' of isolated individuals" (1982:288). For replies to feminist critics of sociobiology, see Liesen 1995.

7. There has been a tendency among scholars from Bachofen to Gimbutas to confuse a widespread fascination with female sexuality manifested in figurines termed "fertility goddesses" unearthed across large areas of the ancient Near East and Europe with evidence of female political power. Even Engels, as well as modern historians like Gerda Lerner, assumed that at one time humans passed through matriarchal or at least matrilineal and matrilocal phases with considerable equality between the sexes, before becoming patrilineal, patrilocal, and more or less male-dominated. This may have been the case in some instances. However, there is no necessary social progression from matriarchy to patriarchy to, finally, egalitarian societies. The task that lies before social scientists is to identify those ecological, demographic, and historical conditions that contribute to the development of particular family systems. However, specifying the ecological conditions under which patrilineal and patrilocal social systems develop in hunter-gathering, herding, and horticultural economies, and specifying the inheritance and other customs that cause paternity certainty to become a paramount concern for patrilineal systems, are beyond the scope of this article. These complex topics are discussed preliminarily in Hrdy and D. Judge (1993) and will be dealt with in greater depth elsewhere (Hrdy n.d.).

8. Although this work is cited by Hite (1976:151) and Hrdy (1981:178), I have been unable to learn more about the author or to trace the development of her views. I have a hunch that Marval's views were influenced by the remarkably bold—indeed some would say foolhardy—scholarship of psychiatrist Mary Jane Sherfey, whose ideas were published in book form in *The Nature and Evolution of Female Sexuality* (1966). Hopefully, feminist historians of science will pick up from here and pursue some of these leads.

9. In this brief 1876 note Darwin actually starts with a question about anogenital coloration generally, but then is diverted from the larger question of why sexual swellings and coloration exist to explain why they exist in males, mimicking female swellings and colorations at midcycle and during the breeding season. That is, in his only publication specifically devoted to sexual coloration in monkeys, Darwin focuses on males and the possibility that sexual swellings in *males* might (like the peacock's tail) have evolved in order to attract females.

10. Hrdy (1986) traces through time the view that "there is nearly always a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females" (Bateman 1948:365), as this stereotype is picked up from Bateman and passed on via Trivers (1972) and Daly and Wilson (1983)—some of the best evolutionary biologists of our time—into contemporary evolutionary dogma. So compelling is this stereotype of "urgent males and coy females" that it persists, even in a recent book seeking to document that human females create an arena for sperm competition by engaging in extrapair copulations (Baker and Bellis 1995:8ff. and especially section w.3.2). Under "coyness" in the book index the entry reads: "See: females."

Interestingly, the word *coy* appears to derive from an old French word for "quiet"—hence reserved—or from the word used to describe a cage or a hollow trap for ducks (hence, decoys?). Hence current usage, which refers to a creature who holds herself in reserve while possibly flirting or enticing, may reflect some conflation of these old meanings. Nevertheless, like my colleague Helena Cronin, "I can't resist wondering if males were choosy about mates, would they be described as 'coy'—or discriminating, judicious, responsible, prudent, discerning?" (1991:248).

11. If sperm were in short supply, and fertilization a problem for females, one would expect pressure to be greatest when many females were competing for sperm from just one male. One problem with this hypothesis then is that the majority of species with sexual swellings are found in multi- rather than unimale breeding systems—the opposite of what the scarcity of sperm hypothesis would predict (Hrdy 1988:Tab. 2).

12. For the time being, I have omitted Ceboid (New World) primates because I do not feel that I have sufficiently mastered the emerging literature on the patterning of female sexuality in this less well known group of monkeys, probably currently the most rapidly expanding branch of primatology. In defense of this accommodation of my own ignorance, note that in terms of human ancestry, Old World monkeys and apes are more directly relevant. However, this is a problem I need to pursue.

13. Some 25 species of Old World monkeys and apes exhibit conspicuous sexual swellings at midcycle, and as Clutton-Brock and Harvey (1976) pointed out years ago, most of them breed in multimale systems. Exceptions to this generalization include *Papio hamadryas*, which although living today in unimale breeding systems recently diverged from multimale ancestors; the West African drill; and three species whose breeding systems are not yet known. For list see Hrdy 1988:Tab. 2.

14. Among the langur monkeys I studied at Mount Abu the average duration of male residence in a troop of breeding females was 27 months. Females exhibited the highest rate of “adulterous” solicitations of males outside the troop in the case of a troop where the dominant male had been there over five years, long enough for him to mate with his four-year-old daughters from his first year in residence (Hrdy 1977:137–141, especially Tab. 5.6).

15. Traditionally, anthropologists and primate anatomists have not regarded humans as a species in which sperm competition could be important because it was assumed that women rarely mate with more than one male around the time of ovulation. In a series of provocative papers in *Animal Behavior*, culminating in their book, Baker and Bellis (1995) essentially take as given that female solicited extrapair copulations around ovulation are sufficiently common to maintain selection at the level of sperm in modern humans, and they proceed from there to study the natural history of resulting sperm competition. Although Baker and Bellis for various reasons (including the use of self-selected samples for their survey) may overemphasize the role of female infidelity (sometimes at the expense of matings coerced by powerful males), there clearly do exist subpopulations in which the conditions for their models of sperm competition will be met. Furthermore, primatologists are going to need to do some rethinking in genera such as *Hyllobates*, previously presumed to be unimale and clearly falling beneath Harcourt’s regression line plotting testes weight for body size in relation to breeding system (Harcourt 1996: Fig. 2), for we now recognize that they are not strictly monogamous (Palombit 1992). Data points that fall near Harcourt’s regression line (as the human datum point does) will almost certainly include species where philandering is an important component of breeding systems, compared with genera that are both socially and reproductively monogamous (like *Aotus*). Even if there is not currently enough sperm competition in humans to jump-start evolution of the different morphs of sperm or modes of selective sperm rejection and selection that Baker and Bellis hypothesize, I would put my money on Smith (1984), as well as Baker and Bellis, being proven right in the end at least to the extent that sperm competition has played some role in human

evolution, and that under particular breeding systems involving low levels of paternal investment, sperm competition continues to be important.

16. Competition at the level of sperm is scarcely ideal for a male either. In cases such as chimpanzees it would appear that competition at the level of the sperm is primarily relevant in intracommunity competition among related males. Unrelated males (in different communities) compete by trying to eliminate or exclude their rivals.

17. For further discussion and references see Hrdy 1988 (especially pp. 122–125 and 131 n. 42). Gould (1995), in a reprint of his famous 1987 *Natural History* column called “Freudian Slip,” now retitled, “Male Nipples and Clitoral Ripples,” critiques the “adaptationist assumption that orgasm must have evolved for Darwinian utility in promoting reproductive success.” In doing so, he cites me selectively and out of context, providing no reference which would permit readers to put my views in context. In fact, the comments Gould cites appeared in *The Woman That Never Evolved* (1981:165–172) and followed a long discussion of the undue readiness scientists have of assuming that selection weighs primarily on males. I never suggested that orgasms were current adaptations (they may or may not be; see especially Baker and Bellis 1995, who argue that they are). Rather, I proposed that selection for orgasmic rewards systems occurred in prehuman contexts and that they are a contemporary vestige of past selection pressures. This hypothesis explaining original selection pressures for orgasmic responses in females is silent concerning current function; it neither presupposes nor rules out the possibility that orgasms which evolved in a different context have subsequently become enlisted in maintaining contemporary pair bonds, or even, as Baker and Bellis would have it, in discriminating preferred from nonpreferred sperm. Whatever turns out, no one should be surprised by the imperfections of such a system, the product of a long, opportunistic, and makeshift evolutionary history.

18. Lest I misrepresent her, I must acknowledge that I apply Gowaty's term “sexual dialectics” any time female counter-strategies to male strategies generated male counter-strategies, and so on, ad infinitum, perhaps all the way to extinction. Gowaty, however, prefers to confine use of the term *sexual dialectics* to a specific situation involving “evolutionary interactions of male manipulation-control and female resistance” (1996). She has tried in vain to make me understand the importance of the distinction (Gowaty, personal communication 1996).

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