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Hormones and History: The Evolution and Development of Primate Female Sexuality

Kim Wallen and
Emory University

Julia L. Zehr
Emory University and Michigan State University

Abstract

Sexual behavior is required for reproduction in internally fertilizing species but poses significant social and physical risks. Females in many nonprimate species have evolved physical and behavioral mechanisms restricting sexual behavior to when females are fertile. The same hormones producing female fertility also control these mechanisms, assuring that sex only occurs when reproduction is possible. In contrast to nonprimate mammals, hormones do not regulate the capacity to engage in sex in female anthropoid primates, uncoupling fertility and the physical capacity to mate. Instead, in primates, sexual motivation has become the primary coordinator between sexual behavior and fertility. This dependence upon psychological mechanisms to coordinate physiology with behavior is possibly unique to primates, including humans, and allows a variety of nonphysiological influences, particularly social context, to regulate sexual behavior. The independence between hormonal state and sexual behavior allows sex to be used for social purposes. This complex regulation of primate sexuality develops during adolescence, where female monkeys show both hormonally influenced sexual motivation and socially modulated sexual behavior. We present findings from rhesus monkeys illustrating how social context and hormonal state interact to modulate adolescent and adult sexuality. It is argued that this flexibility in sexual behavior, combined with a tight regulation of sexual motivational systems by reproductive hormones, allows sexual behavior to be used for nonreproductive purposes while still assuring its occurrence during periods of female fertility. The evolutionary pressures that produced such flexibility in sexual behavior remain puzzling, but may reflect the importance of sexuality to primate social attraction and cohesion.

With respect to sexuality, I have often speculated on it, and have always concluded that we are too ignorant to speculate: no physiologist can conjecture why the two elements go to form a new being, and more than that, why nature strives at uniting the two elements from two individuals. (Darwin, 1861, in Darwin, 1903)

In the preceding quote, Darwin's reference to "sexuality" was in the sense of sexual reproduction. We are, however, similarly ignorant about the behavior that accompanies sexual reproduction, the now conventional use of the term *sexuality*. What are the causes for engaging in sexual behavior? Why does sexual behavior vary across development and across species? What brings two individuals together so that their gametes can combine? We have partial answers to some of these questions, while answers for others remain elusive. However much of what is understood reflects the reality that sex is expensive, dangerous, and time consuming.

Address Correspondence to Kim Wallen, Ph.D., Emory University, Department of Psychology, 532 Kilgo Circle, Atlanta. GA 30322; e-mail: kim@emory.edu..

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The evolution of sex and the selective advantage it conveys are matters of controversy, with explanations ranging from the advantages of recombination (Charlesworth, 2002) to rapid adaptation in a changing environment (Colegrave, 2002). The only thing that can be stated with certainty is that the evolution of sex remains a puzzle, while its pervasiveness argues for a strong, as yet unidentified selective advantage to sexually reproducing species. Beyond the question of sex itself as a reproductive mechanism lies why different forms of sexual reproduction have evolved, from sequential deposition of gametes by males and females separated in time and place to internal fertilization requiring sexual intercourse and gestation. This variation suggests that sexual reproduction carries significant costs producing substantial selective pressure to create diverse solutions to the problem of sex. This paper focuses primarily on the implications and consequences of sexual reproduction for females in species relying upon internal fertilization and gestation for their reproductive output. More specifically, we discuss why sex may have evolved and attempt to answer the proximal questions of why sexual behavior occurs, what mechanisms modulate sexual behavior, and what mechanisms ensure the occurrence of sexual behavior when reproduction is possible.

The Risk of Sex

That sex is dangerous in internally fertilizing species is without doubt. By its nature, sexual intercourse requires a close and cooperative association between male and female that is not present in any other social behavior. Physical injury is always possible, especially when size and strength disparities exist between the sexes, and sexual intercourse, which requires penetration of one body by part of another, carries its own special risk of injury. Sexual intercourse provides the context for sexual aggression and sexual coercion, which has been found in a wide variety of mammals ranging from humans to water voles (Smuts & Smuts, 1993). In elephant seals, for example, researchers found that 1 in 1,000 adult female elephant seals was killed during mating (Le Boeuf & Mesnick, 1991), illustrating the cost of sexual reproduction. Sexual intercourse itself can injure the genitalia. Both penile fracture (Eke, 2002) and vaginal tearing, often requiring suturing (Anate, 1989; Dao, Diouf, Bambara, Bah, & Diadiou, 1995) have been reported. However, the injuries need not be so severe. One study found that 61% of women had vaginal microtrauma following sexual intercourse, whereas only 11% of these women had similar trauma when they had not had intercourse during at least 3 days prior to vaginal inspection (Norvell, Benrubi, & Thompson, 1984). Together such findings illustrate the increased risk of death and injury associated with sexual reproduction.

The potential physical risk of sex puts a premium on social skills and social cognition that allow sex to occur with minimal physical risk. However, even the best of social circumstances do not eliminate the risk that sex places on both partners, as successful sexual intercourse is also conducive to the transmission and growth of pathogens that can kill or maim their hosts. Risk of infection has likely been a strong selective force in the evolution of sex. More than 200 sexually transmitted pathogens have been reported in animals covering a wide phylogenetic range (Lockhart, Thrall, & Antonovics, 1996). It has been suggested that menstruation evolved to protect against sperm-borne pathogens (Profet, 1993; Sobo, 1994). While it seems more likely that menstruation evolved in association with gestation rather than as a pathogen-protection mechanism (Finn, 1998; Strassmann, 1996), sexual intercourse as an avenue for disease transmission is undeniable and likely influenced the evolution of reproductive behavior.

Gestation adds additional risks to those already associated with internal fertilization. Gestation increases maternal energetic demands thereby, threatening the mother's survival; decreases mobility, thus increasing predation risk; and requires specific adaptations for birth. While birth can be relatively easy in some species, such as fish and reptiles, in mammals the increased size of offspring markedly increases maternal mortality. In one extreme case, the spotted hyena,

birth requires splitting of the female's pseudo penis to provide a birth canal (Frank, 1997). In humans, pregnancy and childbirth presents significant risk, with the magnitude of the risk varying across cultures. Female mortality associated with child-bearing in Sweden was 7.4 deaths per 100,000 live births (Kwast, Rochat, & Kidane-Mariam, 1986) from 1980 to 1988. In contrast, maternal death in Ethiopia in 1983 was 566 deaths per 100,000 live births (Kwast et al., 1986). A direct comparison of mortality rates between pregnant and non-pregnant women in rural Malawi, found that pregnancy increased female mortality by 29 per 100,000 women (McDermott et al., 1996). Although generating accurate population comparisons is difficult, there is little doubt that pregnancy significantly increases maternal mortality. These risks, however, are possibly offset by the increased nutrition and protection directed toward the developing fetus, which in turn increases reproductive success. Again, as in the case of internal fertilization, gestation must offer a substantial selective advantage to offset the increased maternal mortality and debilitation that it produces.

In addition to physical injury and increased risk of disease, sexual intercourse and pregnancy increase opportunity for predation and use energy that could enhance survival. The occurrence of nocturnal mating, rapid sexual intercourse, and cryptic mating are all adaptations that counter this risky aspect of sexual intercourse. Given the significant risks associated with sexual reproduction, why does it occur?

Many other behaviors carry significant potential risks. Eating, for example, offers an avenue for ingesting tainted or poisonous food resulting in serious illness or death. Foraging provides the opportunity for predation. However, unlike reproduction, eating is essential for survival and the tradeoff between risk and benefit is easily understood. Sexual reproduction, because it is not required for survival, does not have a similar simple tradeoff. However, because differential reproductive success drives evolutionary change, once sexual reproduction becomes the only means to produce offspring it will be maintained within a population unless a less risky and equally effective alternative reproductive mechanism arises. Some vertebrate species reproduce both parthenogenetically and sexually, suggesting that it may be possible to evolve less risky forms of reproduction in sexual species. However, models of parthenogenic species in competition with sexual species find short-term benefits for parthenogenesis, but long-term extinction due to the more rapid evolution of sexually reproducing species (Smith, 1988). The existence of both forms of reproduction within a single species suggests that sexual reproduction produces reproductive success benefits of such magnitude that, once established, sexual reproduction is difficult to reverse (Smith, 1988). Although the exact benefits of sexual reproduction remain obscure, the mechanisms that have evolved to reduce its risk and ensure its occurrence are not.

The risks of sexual reproduction are markedly reduced and its benefits retained if fertilization occurs externally and gamete combination occurs sequentially. This method, while potentially preferable to internal fertilization, only predominates in water environments where gametes are easily dispersed. For terrestrial vertebrates internal fertilization is much more common. However, internal fertilization does not necessarily require that males directly deposit gametes within the female; in some species, such as salamanders, males leave a spermatophore that is retrieved by the receptive female (Halliday, 1990). However, sexual behavior contributes even to this asynchronous system of internal fertilization, since the male's behavior induces female receptivity and increases the likelihood that she will collect his spermatophore (Vinnedge & Verrell, 1998). Thus, the typical pattern for terrestrial vertebrate sexual reproduction entails both the physical risks associated with internal fertilization and the social risks stemming from the necessary close proximity between the sexes.

Evolution of Coordination of Sexual Behavior With Fertility

Males can increase their reproductive success by “promoting” female acceptance of their gametes in any sexual system. This is particularly effective in internally fertilizing species, where insemination lets males control a female’s reproductive output while being free to inseminate multiple females. This strategy requires that male fertility, which is relatively constant within a breeding season or throughout the year, is coordinated with the relatively shorter, cyclic periods of female fertility. Given this requirement, adaptations that coordinate the male’s sexual behavior with the female’s peak fertility will rapidly evolve in preference to behaviors that cause males to either shed gametes indiscriminately, inseminate infertile females, or mate over longer portions of the female’s cycle to encompass the fertile period. The relatively low cost of male gamete production allows males greater flexibility than females in mating strategies. However, it is still the case that males who best coordinate their sexual behavior with female fertility will be at a selective advantage to less precisely coordinated males, if only because they have more opportunity to inseminate different females.

Physical Adaptations Coordinating Sexual Behavior With Fertility

Given the risk that sexual reproduction involves, there is also strong selective pressure in females to assure that the occurrence of sexual behavior is tightly coupled with fertility. Females, particularly gestating species, are constrained from adopting a male strategy of promiscuous fertilization. Pregnancy represents a large female investment and is a significant threat to the mother’s survival. In addition, sexual intercourse itself presents substantial risks, and thus there is likely strong selection for infrequent sexual intercourse occurring in synchrony with peak fertility. For internally fertilizing species, a number of adaptations have arisen that guarantee that sexual behavior will only occur when fertilization is possible. Interestingly, these adaptations limit female sexual behavior to maximal fertility, but there are none that impede the capacity of males to engage in sexual behavior relatively constantly.

Some adaptations prevent sexual intercourse by sealing the vagina except when the female is fertile. These cyclically occurring vaginal membranes, found in guinea pigs and some species of prosimians, disappear under the stimulation of the same gonadal hormones produced by the preovulatory follicle and ensure that sexual intercourse only occurs when the female can become pregnant (reviewed in Wallen, 2001). Whether such an adaptation is the predecessor of the hymen in humans remains unknown. In females of other species, the physical adaptations are less extreme, but equally effective. In a variety of mammals, females must adopt a receptive posture for sexual intercourse to occur. In rodents, this posture, referred to as lordosis, results in rotating the pelvis and elevating the vaginal opening, allowing the male to intromit (Pfaff, Diakow, Montgomery, & Jenkins, 1978; Pfaff, Lewis, Diakow, & Keiner, 1973). The expression of the lordosis posture is under tonic inhibition by brain nuclei whose activity is suppressed by steroid hormones from the preovulatory follicles (Pfaff, 1980). Thus, the same ovarian hormones that produce ovulation suppress lordosis inhibition, allowing males to mate with the female and producing a tight coupling between fertility and mating. While male counter-strategies to rigorous female control could theoretically exist, they could not be inherited since the counter-strategy would result in males mating with non-fertile females.

In some species, behavioral mechanisms coordinate sexual behavior with fertility. In the pig, for example, compounds in the boar’s saliva induce an immobility response in the female, but only if she is fertile. This response is so stereotyped that it can be elicited by the application of the boar pheromone by a human and is used by pig breeders to find fertile sows for insemination (Melrose, Reed, & Patterson, 1971). Lordosis, in addition to making the female’s vagina accessible to the male, is accompanied by an immobilization response that is potentiated by the vagino-cervical stimulation that male intromission provides, assuring that the female will not flee the male when mounted (Naggar & Komisaruk, 1977). This is of particular

importance in species like the golden hamster, where females are larger than males, aggressive toward them, and socially dominant when not sexually receptive (Payne & Swanson, 1970). In such social circumstances, males are less concerned that a female will flee when approached than that she will attack. Ovarian hormones both reduce female aggression toward the male and increase immobility, preventing the female from displaying aggression and allowing sexual intercourse to occur (Ciaccio, Lisk, & Reuter, 1979; Payne & Swanson, 1970).

Sexual Motivation as a Regulator of Female Sexual Behavior

Several psychological adaptations crucial to sexual behavior parallel the physiological and behavioral adaptations controlled by gonadal hormones. Successful reproduction requires intimate social contact, which provides the opportunity for the evolution of male selection based on physical and behavioral characteristics. It is beyond this review to cover this vast area. Instead we focus on the psychological processes that regulate the occurrence of sexual behavior in females and coordinate mating with fertility.

The first requirement to reproduction is getting a male and female into the same place at a time when pregnancy is possible. Two underlying psychological systems ensure that this happens. The first is sexual motivation, which makes the male or female seek out a context in which sex might occur. The second is sexual attraction, which assists males and females in recognizing and associating with specific sexual partners. Some have described sexual attraction, or *attractivity* (Beach, 1976), as the principle system underlying the formation of sexual unions. However, there must also be a sexual motivation system that informs the individual about what is attractive and provides the impetus to seek a sexually attractive partner. Across a range of species, the same gonadal hormones that produce fertility modulate sexual motivation. Removal of gonadal steroids eliminates sexual motivation, and artificially replacing them restores sexual motivation. However, in the anthropoid primates, which include the monkeys and apes, eliminating sexual motivation does not eliminate the capacity for sexual arousal and mating (Wallen, 1990, 1995, 2001). This separation between hormonal modulation of interest in mating and hormonal modulation of the capacity to mate probably reflects important evolutionary adaptations that contribute to the character of primate social structure.

By separating capability from interest, sexual behavior became more sensitive to social context, and sex could easily be used for other than reproductive purposes. Once the capacity to engage in sex was released from hormonal control, hormonal modulation of sexual motivation became the primary regulator of sexual behavior. However, unlike the physical adaptations described earlier, which completely prevent the occurrence of sexual behavior, hormonal regulation of sexual motivation only modulates the frequency or likelihood of occurrence of sexual behavior. This less strict control exerted by sexual motivation has been the source of much misunderstanding about hormonal regulation of sexual behavior in primates, including humans.

Sexual Motivation as a Mechanism Coupling Mating and Fertility

Tight coupling between hormonal control of the capacity to mate and interest in mating, seen in species like laboratory rodents, produces tightly proscribed periods of sexual activity. Sexual activity is so strongly correlated with hormonal change that the onset of sexual activity can be predicted to an accuracy of minutes following appropriate hormonal treatment (Boling, Young, & Dempsey, 1938). In contrast, in species where hormones do not regulate the capacity to mate, changes in sexual motivation under appropriate hormonal exposure are generally more muted and less abrupt. Because in such species the capacity to mate does not change with hormonal fluctuations, actual mating behavior may not even vary predictably with changing hormonal conditions. This has led some to conclude that sexual behavior became emancipated from hormonal control. In one sense that is accurate, because the capacity to mate did become

emancipated from hormonal control in some species (Miller, 1931). However, from an evolutionary standpoint what was important was whether sexual behavior remained coupled to fertility.

Sex when the female is nonfertile would have little evolutionary consequence if sex also occurred during fertility. Thus, the coupling of increased sexual motivation with peak fertility through changes in the same hormones increases reproductive success and still allows the occurrence of sexual behavior in nonreproductive contexts. A reliance upon sexual motivation as the mechanism coordinating fertility with sexual behavior produces a less tight coupling between hormonal and behavioral change in primates than that seen in nonprimate species (Wallen, 1990). A loose coupling between hormonal changes and behavior would be at a selective disadvantage compared to a strict coupling if the loose coupling reduced the likelihood of mating when the female is fertile. However, if mating during peak fertility was the same, but additional mating occurred at nonfertile times, there would still be some selection against nonreproductive mating due to the risks posed by mating itself.

The maintenance of nonreproductive mating requires some selective advantage to offset its small increased cost. That such strict coupling between fertility and sexual behavior doesn't appear to exist in anthropoid primates suggests that there must be some selective advantage conferred by nonreproductive mating. What this selective advantage might be is unclear, but one possibility is that it enhances social affiliation between males and females. As Zuckerman argued 70 years ago, sexual attraction may form the basis of primate social affiliation (Zuckerman, 1932). Zuckerman knew that primate females experienced breeding seasons and that sexual attraction varied in strength, but still saw sexual attraction as crucial to primate social structure stating, "The factor underlying the permanent association of the sexes is their uninterrupted reproductive life. The sexual stimulus, even when weak, will draw male and female together" (Zuckerman, 1932, p. 55).

Without constraints on the capacity to mate, sex and sexual attraction serve as powerful social cement. This view is supported by the occurrence of sexual intercourse outside of reproductive contexts in a variety of primate species and the strong relationship between sexual activity and affiliation (Wallen & Tannenbaum, 1997). The notion that sex and sexual attraction underlie social affiliation and cohesion does not mean that sex must occur continuously. In fact, as noted by Zuckerman, sexual intercourse can occur only at certain times of the year or irregularly and still be important for social cohesion. This is likely true for humans as well. Even the most sexually active human probably spends less than 2%, and more likely less than 0.2%, of his or her daily life actively engaged in sex, yet this relatively infrequent activity motivates marriages, family rearing, and a variety of other activities. Although the specific relationship between frequency of sex and social cohesion is unknown, it is likely, as in the prairie vole, that a single act of sexual intercourse alters the social relations between a male and a female. Certainly, in one study of rhesus monkeys, social integration between males and females occurred rapidly after the onset of sexual activity and remained for over a year after sexual activity ceased (Wallen & Tannenbaum, 1997). While the exact selective forces that led to the evolution of a continual capacity to mate have yet to be adequately described, it seems likely that they reflect the social advantages of being able to use sex for multiple social functions. This capacity, when combined with coupling between peak sexual desire and peak fertility, ensures that sex effectively serves both reproductive and social ends.

Sex and Social Context: The Rhesus Monkey Model

Studies of rhesus monkey behavioral endocrinology offer two different pictures of the role that hormones play in female sexual behavior. Early studies of social groups of rhesus monkeys described discrete periods of sexual activity interspersed with longer periods of sexual

inactivity (Carpenter, 1942). In contrast, studies of male-female pairs of rhesus monkeys reported midcycle peaks in sexual behavior but some sexual activity throughout the female's cycle (Goy, 1979; Michael & Zumpe, 1970). These markedly different patterns of sexual activity reflected the hormonal emancipation of the ability to mate combined with a sensitivity of sexual behavior to social context. Subsequent studies demonstrated that the amount of space (Wallen, 1982) and the presence of multiple females (Wallen & Winston, 1984) affected the extent to which the female's hormonal condition modulated the occurrence of sexual behavior.

These and other findings suggest that ovarian hormones modulate female sexual motivation, with motivation being highest when estradiol levels are greatest (Wallen, Winston, Gaventa, Davis-Dasilva, & Collins, 1984). Furthermore, the extent to which female hormones influence female sexual behavior depends upon whether female sexual motivation is an important determinant of the occurrence of sexual behavior (Wallen, 1990, 2001). For example, when male-female pairs were studied in small cages, female hormonal condition had little influence on the occurrence of sexual behavior. Under such conditions, engaging in sex required little effort and did not entail much social risk. Instead, other factors such as partner compatibility (Goy, 1979) had a greater impact. Changing the social context of the pair such that females had to work to engage in sex, either by restricting the male's movement (Pomerantz & Goy, 1983) or by requiring the female to perform an operant task for access to the male (Keverne, 1976), revealed that sexual behavior was tied to maximal fertility. Such findings provide the basis for understanding the tight coupling between ovarian hormones and female sexual initiation seen in group contexts. Under these circumstances, sex is socially risky and disturbs the female-centered social structure of rhesus monkey groups (Wallen & Tannenbaum, 1997). Females who interact with males receive increased agonistic behavior from other group females (Walker, Wilson, & Gordon, 1983; Wallen, 1995), making a female's interest in sex necessary to overcome the social inhibition created by the females in her group. Thus, the interplay between social context and hormonally modulated female sexual motivation makes the sexual behavior of rhesus monkeys responsive to both social contingencies and ovarian hormones. This sensitivity to social context makes the rhesus monkey a valuable model for understanding human sexual behavior, where both social conditions and hormones influence the occurrence of sexual behavior (Wallen, 2001). In the following sections, we describe the development of female sexuality in rhesus monkeys and demonstrate that sensitivity to social context is part of female development and presages adult patterns of sexual behavior.

Development of Sexuality: Puberty and the Onset of Female Sexuality

Female rhesus monkeys, like human females, go through a juvenile period when their ovaries are inactive and only proto-sexual behavior is exhibited. This is followed by a pubertal transition from juvenile to adult physiology and behavior, requiring several years. Even though preadolescent females are probably physically capable of engaging in sex, they do not until puberty, when production of ovarian estradiol increases female sexual motivation (Wallen et al., 1984). Adolescent female rhesus monkeys have been little studied but are of particular interest because social context influences their reproductive development. As in adults (Wallen, 1990), it is likely that social context affects the behavioral responses of pubertal females to their estradiol. The following section describes the effects of social rank on pubertal development and presents data from individual females illustrating developmental patterns in female sexual behavior.

Pubertal Changes in Physiology and Behavior

During puberty, a female's physiology undergoes rapid change with alterations in circulating steroids, onset of menstruation, the first occurrence of ovulation, and changes in secondary sexual characteristics (reviewed in Plant, 1994; Wilson, 1992a). During the juvenile period, females have low levels of circulating steroids, and the hypothalamic-pituitary-gonadal axis is

relatively quiescent. At puberty, hypothalamic-pituitary-gonadal axis activity increases, initiating a cascade of physiological events (Plant, 1994). First, pulses of gonadotropin releasing hormone (GnRH) from the hypothalamus increase in frequency and amplitude, stimulating anterior pituitary gonadotropin secretion, ovarian follicular development, and gonadal steroid secretion (Terasawa & Fernandez, 2001). Increases in neuroendocrine activity stimulate marked perineal sexual swellings in adolescent female rhesus monkeys, swellings which are not present in adult females and which decrease with successive breeding seasons (Anderson & Bielert, 1994; Hisaw & Hisaw, 1961). Although increased steroid secretion stimulates uterine endometrial development and eventually menstruation (Salamonsen, Kovacs, & Findlay, 1999), early menstrual cycles are typically not associated with ovulation and rarely result in conception. This period prior to the pubertal onset of fertility has been termed “adolescent sterility” (Hartman, 1931) and could result from anovulatory menstrual cycles (Hartman, 1931), ovulatory menstrual cycles with inadequate luteal phases (Foster, 1977), or a failure to coordinate sexual behavior with ovulation thereby preventing insemination.

Pubertal changes occur over several years, and the rate of reproductive development varies among individuals. Onset of menstruation and sexual swellings occurs around 2.5 years (Foster, 1977; Wilson, 1992b; Wilson, Walker, & Gordon, 1984). Rhesus monkeys are seasonal breeders, with both males and females showing a suppression of hypothalamic-pituitary-gonadal axis activity in the spring and summer (Gordon, Rose, & Bernstein, 1976; Van Horn, 1980). This seasonality produces a bimodal distribution of first ovulation. Early maturing females, approximately 20% to 40% of females, ovulate for the first time around the time of menarche, about 2.5 years of age (Wilson & Gordon, 1989; Wilson, Gordon, & Collins, 1986; Wilson, Walker, & Gordon, 1983; Wilson, Walker, et al., 1984). The remaining, later maturing females ovulate in the next breeding season, around 3.5 years of age, even though they showed menarche at a similar age to early maturing females.

Although the end of puberty and the beginning of adulthood are not clearly demarcated, first conception, pregnancy, or parturition are frequently used markers. In rhesus monkeys, age at first parturition ranges between 3 and 6 years of age (Wilson et al., 1983), showing that the onset of fertility varies dramatically among individuals. However, producing offspring does not necessarily mark the completion of reproductive maturation. Lactation in young adolescent females suppresses ovulation for a longer period than it does in fully adult females (Wilson, 1992b, 1993; Wilson, Walker, Pope, & Gordon, 1988), suggesting a continued differential sensitivity of the neuroendocrine system in young females.

Pubertal changes in sexual behavior also vary among individuals and occur over a long developmental period. Sexual motivation in adult rhesus females is expressed as increased initiation of affiliation with males, such as proximity and grooming, and increased sexual soliciting behaviors, such as handslap, hindquarters presentation, headbob, and threataway (S. Altmann, 1962; Carpenter, 1942). Males typically respond to persistent female sexual initiation by mounting and copulating with the female. In adult, group-housed females, female initiation increases most dramatically around ovulation and is correlated with increases in circulating estradiol (Wallen et al., 1984). Likewise, adolescent females exhibit sexual initiation behaviors and engage in sexual behavior not markedly different from that seen in adult females. However, the length of the periods of sexual behavior within a single ovarian cycle is consistently longer in adolescents than in adults (Wilson & Gordon, 1980). This difference probably reflects the longer period of follicular estradiol secretion prior to ovulation in adolescent females (Wilson, Gordon, & Collins, 1982), although an increased sensitivity to estradiol cannot be ruled out.

Effects of Social Rank on Pubertal Development

Among primates, high social rank affects the rate of pubertal development, with high-ranking females maturing more quickly than low-ranking females. In savannah baboons, age at first menses is earlier in high ranking females (J. Altmann, Hausfater, & Altmann, 1988; Bercovitch & Strum, 1993). In rhesus monkeys, rank most clearly affects the timing of first ovulation and first parturition. The bimodal distribution of early and later first ovulation is skewed, with a higher proportion of high and middle ranked females than low ranked females among early maturing adolescents (Zehr, 2002). Similarly, high ranked females are more likely to give birth at younger ages than are middle and low ranked females (Wilson et al., 1983).

The effects of rank on reproductive maturation could be mediated through physiological and/or social mechanisms. Nutrition, body weight, and stress affect menstruation and ovulation. When females are in a state of positive energy balance—that is, they are consuming or have stored more calories than they are using—reproduction is maintained (Schneider & Wade, 2000). Evidence that this is important in rhesus monkeys comes from studies showing that adolescent rhesus monkeys fed a high fat diet, which markedly increased caloric flux, ovulated at an earlier age than did females consuming a normal fat diet (Schwartz, Wilson, Walker, & Collins, 1988). In addition, females who ovulated early with respect to their peers had higher body weights at the onset of puberty (Zehr, 2002). Thus, if high ranked females have more access to food, better nutrition, or higher body weights than do low ranked females, high ranked females could have earlier pubertal development. High levels of stress and activation of the adrenal axis also disrupt reproduction. If low ranked females experience higher levels of stress than do high ranked females, menarche or first ovulation could be delayed.

The expression of sexual behavior and resulting first parturition in adolescent females may also be affected directly by social mechanisms. High ranked females harass copulations between low ranked females and males (Wilson, 1981). In addition, female-female aggression increases around ovulation, with low ranked females receiving more aggression than high ranked females (Nieuwenhuijsen et al., 1988; Walker et al., 1983). The social rank of females is not stable before and during adolescent development, but reproductive females assume a higher matrilineal rank than their older sisters (Chikazawa, Gordon, Bean, & Bernstein, 1979). Thus, access to sexual partners may be limited or disrupted for pubertal females, who have not yet attained adult social rank (Nieuwenhuijsen et al., 1988). In addition, the tenuous social status of males within the rhesus monkey social system (Wallen & Tannenbaum, 1997) may inhibit males from responding to adolescent female sexual initiation. The combination of social inexperience, unstable social rank, and a highly variable physiology combine to make the sexual behavior of adolescent females more variable than that of adult females.

Individual Differences in Adolescent Sexuality

While in adult females the relationship between circulating hormone levels and sexual behavior varies with social context, adolescent females could show one of two patterns. Adolescent females may show a tight coupling of hormones and behavior in which adult flexibility in response to social context develops during puberty. Alternatively, adolescent females may have a loose coupling between circulating hormones and sexual behavior in which social context overrides increased sexual motivation in response to circulating hormone levels. We investigated variability among adolescent females in the relationship between sexual behavior and circulating hormone levels to address these two alternatives.

We observed the sexual behavior of adolescent females during both early adolescence, around 2.5 years of age, and late adolescence, around 3.5 years of age, as part of a larger study of the effects of prenatal androgens on pubertal development (Zehr, 2002). Female subjects lived

outdoors in large social groups at the Yerkes National Primate Research Center. Enclosures varied in size from 650 m² to 1,465 m² with an attached, temperature-controlled, indoor enclosure. Social groups consisted of 60 to 120 individuals, including 4 to 10 adult males, adult females, and their juvenile offspring. We determined social rank using a combination of historical records and opportunistic recording of agonistic interactions during the breeding season. Adult females were divided into high, middle, or low rank by thirds, and subjects were categorized as high, middle, or low ranking according to their mother's rank. We observed sexual behavior during the fall breeding season (September to February) for 1.5 hours per day, 5 to 6 days per week, using a modified focal sampling technique that captures female social and sexual interactions with breeding males (Zehr, Tannenbaum, Jones, & Wallen, 2000). Beginning in the fall breeding season when subjects were approximately 28 months of age, we collected blood samples and checked for menstruation three times per week in each subject. Estradiol and progesterone levels in blood samples were assessed using radioimmunoassay and were used to determine the timing of ovulation (Zehr, 2002). We calculated the rate of female sexual initiation for each day of observation as a sum of the frequencies of female-initiated proximity, solicitation, grooming, following, and presentation toward adult males using previously published behavioral definitions (Zehr et al., 2000). Since prenatal androgen treatments affected the expression of sexual behavior (Zehr, 2002), we describe here only the adolescent sexual behavior of seven control females.

Sexual behavior in early adolescence—Females begin to engage in sexual behavior during the breeding season around 2.5 years of age. However, since few females are likely to ovulate or conceive around 2.5 years of age (Wilson & Gordon, 1989; Wilson, Gordon, Blank, & Collins, 1984; Wilson et al., 1986; Wilson et al., 1983), studies of adolescent sexual behavior have primarily focused on females 3.5 years of age or older (Pope, Gordon, & Wilson, 1986; Wilson & Gordon, 1980; Wilson, Gordon, et al., 1984; Wilson, et al., 1982). This section describes sexual initiation behavior in both ovulating and nonovulating early adolescent females. If circulating hormones and sexual initiation are tightly coupled in early adolescence, all ovulating females would display sexual initiation behavior and only ovulating females would be sexually active. Our data suggest comparable flexibility in the sexuality of adolescent females to that seen in adult females.

Figure 1 depicts the frequency of female sexual initiation across ovulatory and anovulatory menstrual cycles in six control females. The ovulatory and anovulatory cycles shown occurred in the middle of the breeding season, well after menarche in all females. We aligned data relative to menstruation to standardize across ovulatory and anovulatory cycles. Three of seven control females ovulated in early adolescence. Among females who ovulated, the highest ranked female (Hc6, Figure 1A) showed high levels of female sexual initiation that peaked during the periovulatory phase of the cycle. One middle ranked female (Me6, Figure 1A) also showed a peak in female sexual initiation at midcycle, but showed much lower levels of sexual initiation than the higher ranked female. Finally, the third female who ovulated (Ys5, Figure 1A) was rarely observed initiating interactions with adult males during the cycle. Among females who did not ovulate, the highest ranked female (Zr5, Figure 1B) initiated interactions with adult males at a rate comparable to an ovulating middle ranked female (Me6, Figure 1A); however, the remaining, nonovulating females (Hg6 and Be6, Figure 1B) rarely initiated interactions with adult males. Interestingly, male responses to early adolescent females also differed qualitatively from responses to adult females (Zehr, 2002). When compared with their reactions to adult females of similar rank, males were more likely to display aggression toward and rarely mounted adolescent females.

Taken together, these results suggest that in early adolescence, periovulatory increases in circulating estradiol increase female sexual initiation and female sexual motivation, as they do in adult females. In addition, these results suggest that social context can suppress female sexual

behavior in early adolescent females, with one middle ranked female showing no sexual initiation at midcycle. In contrast, high social rank allows an uncoupling of circulating hormone levels and female sexual initiation behavior, since a high ranked female initiated interactions with males in the absence of periovulatory hormone levels.

Sexual behavior in late adolescence—By the fall breeding season around 3.5 years of age, all adolescent females have ovulatory menstrual cycles, and most conceive (Wilson et al., 1982; Wilson et al., 1983; Zehr, 2002). In general, late adolescent females engage in sexual behavior for longer periods than do adults, due to increased estradiol earlier in the follicular phase (Wilson et al., 1982). In adult females, social rank modulates the length of behavioral estrus, with high ranked females mating for longer periods of time prior to ovulation than low ranked females (Wallen, 1990). This section describes female sexual initiation in late adolescent females of high, medium, and low rank to determine if late adolescent females have rank-related modulation of female sexual behavior similar to that seen in adult females. In addition, this section explores age-related differences in female sexual initiation by comparing sexual behavior in early and late adolescence for those females who ovulated in early adolescence.

Figure 2 depicts the frequency of female sexual initiation in high, middle, and low ranked control females. The two high ranked females initiated sexual interactions with the highest frequency and for longer periods prior to ovulation. Both middle and low ranked females had peaks in sexual initiation behavior at midcycle, but had lower levels than high ranked females during the follicular phase. Thus, middle and low ranked late adolescent females demonstrated an adult-like pattern of a shorter period of follicular female initiation, lower levels of behavior, and a tighter coupling of behavior with the periovulatory period than that of high ranked late adolescent females.

Figure 3 compares female sexual initiation in early and late adolescence among those females who ovulated in early adolescence. All three females showed increases in sexual behavior from early to late adolescence. The observed increases occurred in females who initiated interactions with males at 2.5 years of age (Hc6, Me6) and, although not as marked, occurred in the female who did not initiate interactions with males at 2.5 years of age (Ys5). Several different mechanisms could account for age-related differences in sexual behavior among adolescent females. First, early and late adolescent females differ in their social experience. Early adolescent females have little experience interacting with males, since young females primarily associate with adult females in their social groups (Lovejoy & Wallen, 1988). In addition, the size difference between adult males and young females is much greater in early than late adolescence. Third, adult female social rank is attained during puberty, with young adolescent females ranking lower than their final adult social rank (Chikazawa et al., 1979; Datta & Beauchamp, 1991; Nieuwenhuijsen et al., 1988). Thus, a female might have a stronger rank-related suppression of sexual behavior early in adolescence than late in adolescence. Finally, the early adolescent females may be less sensitive to the effects of estradiol on sexual motivation than are late adolescent females. If this were true, follicular increases in estradiol, while sufficient to trigger ovulation, may be insufficient to increase sexual initiation. Probably, age-related differences result from some combination of experiential differences, changes in social status, or sensitivity to hormones, with no single factor accounting for the differences. Whatever the cause, this change in sexual behavior across development reinforces the notion that rhesus female sexual behavior is sensitive to both the hormonal and social environments.

Conclusions

Taken together, these examples of individual variability suggest that pubertal females represent a special social class in which social context affects the relationship between circulating hormones and the expression of sexual behavior. Rank, which strongly affects the expression

of adult sexual behavior, similarly affects sexual behavior in adolescents. However, since adolescent females are in the process of attaining their adult social rank (Chikazawa et al., 1979; Datta & Beauchamp, 1991; Nieuwenhuijsen et al., 1988), the suppression of sexual behavior which results from low social rank may more profoundly affect adolescent sexual behavior, completely suppressing the sexual behavior of some individuals. In addition, rank alters the rate of sexual maturation directly, thus affecting the development of sexual behavior by altering the timing of pubertal changes in the female's physiology. Since high ranked adolescent females mature more quickly (Wilson et al., 1983; Zehr, 2002), they are the first among their age group capable to exhibit sexual behavior. The combination of the direct effects of social context on the expression of sexual behavior and on reproductive maturation increases individual variability in the pubertal development of sexual behavior.

While social rank affects the timing of the expression of sexual behavior within an adult female's ovarian cycle, it rarely completely suppresses female sexual behavior (Wallen, 1990). Finally, adult males respond differently to sexual initiation by early adolescent and adult females (Zehr, 2002). The increased aggression and decreased mounting by males toward adolescents also limits adolescent sexual behavior and further illustrates the special social status that adolescent females have within the social group.

While age-related differences in sensitivity to circulating steroids may account for some of the differences between adult and adolescent sexual behavior, it seems unlikely that they explain a significant amount of the variance. The finding that estradiol levels do not differ between adolescent and adult females at the onset of sexual behavior during ovarian cycles suggest that both are comparably sensitive to estradiol (Wilson et al., 1982). Thus, social context and social status are perhaps the most critical modulators of adolescent female sexuality in rhesus monkeys.

Sexuality is a complex challenge to primates. It occurs in a complex social context, where long-term relationships are important to successful social living. Sexual behavior is both disruptive to these social relations as well as important in maintaining them. This seeming paradox — that sex both enhances and threatens social cohesion — suggests why sexual behavior is sensitive to social context and why adaptations have evolved allowing it to occur at any time and with few physiological restraints. This also suggests why the psychological effects of reproductive hormones are so important in primate sexuality. Without the strong interest in the opposite sex and the desire to engage in sexual intercourse produced by these hormones, sexual behavior would be less likely to occur and would be only weakly coupled to fertility. The system of hormonally modulated sexual motivation combined with a physical capacity to mate at any time has evolved in primates to balance the social and reproductive uses of sex. Under some social contexts, such as low ranking females in strictly hierarchical social structures, sex is limited almost exclusively to reproductive contexts. In contrast, sex may be less limited to reproductive contexts in less rigidly hierarchical contexts or when high social status removes hierarchical constraints. Under these conditions, sex serves social functions other than reproduction, including alliance formation and sexual affiliation. Increased sexual motivation coupled to fertility assures that sex is more likely to result in reproduction than it is likely to simply serve a nonreproductive social function.

Human female sexuality is as flexible as that seen in nonhuman primates. Ovarian hormones do not control whether sex can occur, but do increase the likelihood that sex will occur more often when women are fertile than when they are not. The lack of strict hormonal control of female sexuality results in a variety of nonhormonal factors—such as type of contraception or pregnancy avoidance, or even the day of the week (Palmer, Udry, & Morris, 1982)—influencing the occurrence of sexual behavior as much as do ovarian hormones. This flexibility allows sex to serve important social purposes, including affiliation in human couples. The

consistency of this pattern across a wide range of primate species suggests that these nonreproductive functions of sex may have been as important to primate evolution as were its reproductive functions. The nonreproductive functions of sex remain a poorly investigated area of sexuality that deserves greater consideration and may provide important insight into the evolution of human sexuality.

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Figure 1.

Female sexual initiation during ovulatory (A) and anovulatory (B) menstrual cycles in individual early adolescent females, illustrating that both social context and circulating hormones affect the expression of adolescent sexual behavior. Two of three females who ovulated around 2.5 years of age showed periovulatory female sexual initiation. The highest ranked females showed more interest in males, during both ovulatory and nonovulatory cycles, than did the middle and tower ranked females.

Figure 2.

Female sexual initiation in high, middle, and low ranked females during late adolescence, illustrating that high ranked females had higher levels of sexual initiation and a less tight coupling of behavior with the periovulatory period of their ovarian cycles than did middle and low ranked females.

Figure 3.

Female sexual initiation in early and late adolescence in three females who first ovulated during early adolescence, illustrating that the frequency of sexual initiation increased from early to late adolescence.