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Risky Business: Social Context and Hormonal Modulation of Primate Sexual Desire

Introduction

Sexual passion can only exist outside normal life – Benoïte Groult (1992)

Sexual intercourse is dangerous, posing social and physical challenges to the health and well-being of the partners. It is physically risky, the penetration of one body by another providing opportunities for physical injury and infection. It is energetically expensive, directing resources necessary for survival to producing other individuals. It is psychologically distracting, diverting attention from avoiding predation or finding food and shelter to seeking, courting, and consorting with a mate. Although many other behaviors, such as eating, involve similar dangers, they are essential to survival, justifying the tradeoff between risk and reward. In contrast, sexual behavior provides no immediate survival benefit, only risk and, possibly, pleasure. However, because reproductive success in internally fertilizing species requires sexual intercourse, its dangers cannot be avoided by simply not engaging in the behavior. Thus the physical and behavioral mechanisms assuring the occurrence of sexual intercourse must have been under heavy selective pressure, for any mechanism that increases the probability of reproducing directly affects reproductive success. Although many factors influence reproductive output, mechanisms limiting sexual behavior to the brief period of female fertility maximize reproductive benefit and minimize the risks of sexual behavior. It is not surprising, therefore, that most internally fertilizing species show a tight coupling between female fertility and sexual behavior.

However, evolution has produced more than one solution coordinating sexual behavior with fertility and these vary in how tightly coupled sexual behavior is to female fertility. In some species, such as insects, hormonal or pheromonal mechanisms release a stereotyped pattern of behavior when the female is fertile, leaving little to choice on the part of the mating pair (Izard, 1983). In other species, hormones regulate the physical capacity to mate, either through hormonally regulated vaginal closure, as in the guinea pig (Stockard and Papanicolaou, 1919), or through hormonally regulated female spinal reflexes required for intromission, as in rats (Diakow, 1974; Pfaff et al., 1978). In these species intercourse is physically possible only when

the female is fertile (Wallen, 1990, 1995). Other species are less strictly hormonally regulated and this chapter focuses on the system employed by primates in whom the hormones that produce fertility do not regulate the physical capacity to mate, but increase the likelihood of sexual behavior occurring by modulating sexual motivation. This loose coupling between sexual behavior and female fertility is an adaptation accommodating sexual activity in a complex social environment where sex is socially disruptive and risky. Such loose coupling allows a much wider range of expression of sexual behavior, both in form and timing during the ovarian cycle, than in species with tight fertility-behavior coupling. This variability in the timing of sexual behavior has produced debate about the role of reproductive hormones in primate sexual behavior.

The chapter begins with a description of the dangers inherent in sexual intercourse and a brief discussion of the mechanisms that have evolved to ensure that this dangerous activity occurs. This section presents the distinction between the physical capacity to engage in sex and the psychological desire to engage in sex, and introduces the idea that physical capacity for sex has been emancipated from the control of gonadal hormones. This section is followed by a historical view of human and nonhuman primate sexuality and the influence of hormones on the expression of sexuality. For example, the first study to focus on the role of hormones affecting female sexual motivation was based on the description of rhesus monkey sexual behavior in field settings. A description of the early days of primate behavioral endocrinology is followed by studies from the modern era which emphasized research from the laboratories of Richard Michael, who emphasized male control, and W.C. Young, who emphasized female control of sexual interactions. Early studies in the field led to conclusions different from those of many of the laboratory experiments. The section closes with the return of field behavioral endocrinology, which was carried out under the controlled conditions of large outdoor populations. These new studies of rhesus monkeys in a more natural context ultimately led to a reconciliation of the differences in the data that results from studies of groups vs. studies of male-female pairs.

The next section describes the evidence that social context modulates hormonal influences on female sexual motivation, followed by similar evidence from studies of women. This is followed by a discussion of risk as a modulator of sexual behavior in humans. This section suggests that pregnancy avoidance affects the type of sexual behavior displayed by women at different points in their cycle and further develops the thesis that perceived risk affects the extent to which hormonally modulated female sexual motivation affects human sexual behavior. In the next section, the principles derived from studies of females are applied to male human and nonhuman primates and found to apply equally well to both sexes. The last section presents some final considerations and addresses the relative sex drive of males and females, why female control of sexuality seems limited in American society, and discusses the role of sexuality in social cohesion. While this chapter emphasizes risk as an important factor in the evolution of hormonal modulatory systems, it also reflects the theme of this book, that knowing the context of behavior is crucial to understanding its regulation.

Early Views of Hormones and Female Primate Sexual Behavior

Full expression of sexual behavior in female primates, including humans, requires ovarian steroid hormones; however, these hormones are not necessary for the occurrence of sexual behavior (Wallen, 1995). This apparent contradiction has fueled a controversy for more than 60 years about the role of ovarian hormones in regulating female primate sexual behavior. The controversy stems primarily from a view, derived from nonprimate mammals, that hormonal effects on sexual behavior should be regulatory and not permissive. Early views of human and nonhuman primate sexual behavior often emphasized the flexibility of human sexual behavior as opposed to the fixed, and biologically determined, nature of nonhuman primate sexual behavior. For example, the anthropologist Malinowski (1927) contrasted the sexual behavior of humans with that of apes, describing the control and rigidity of nonhuman primate sexual behavior as follows: 'Among apes the courtship begins with a change in the female organism, determined by physiological factors and automatically releasing the sexual response in the male. The male then proceeds to court according to the selective type of wooing which prevails in a given species.... All the factors which define animal behavior at this stage are common to all individuals of the species. They work with such uniformity that for each animal species one set of data and only one has to be given by the zoologist... within the species the variations, whether individual or otherwise are so small and irrelevant that the zoologist ignores them and is fully justified in doing so' (p. 194).

In contrast, human sexual behavior was described thus: 'In the first place we see that in man there is no season of rut, which means that man is ready to make love at any time and woman to respond to him – a condition which, as we all know does not simplify human intercourse. There is nothing in man which acts with the same sharp determination as does the onset of ovulation in any mammalian female' (p. 195).

Malinovski, however, saw sexual behavior in both humans and animals as socially disruptive and described social and cultural controls that regulate human sexual behavior and prevent it from interfering with social order. In contrast, he saw the circumscribed and physiologically controlled period of nonhuman primate sexual behavior as serving the same function: 'Considering the great danger from outside enemies and the disruptive forces within, which are associated with courtship, the elimination of the sex interest from normal times and its concentration on a definite short period is of great importance for the survival of animal species' (p. 198).

Sexual behavior is dangerous and must be limited either culturally, as in human society, or through strict biological mechanisms, as in nonhuman primates. The view that humans have been essentially freed from strong biological determination of sexual behavior while nonhuman primates and other mammals limit their sexual behavior to brief circumscribed periods is still popular today. However, contemporaries had pointed out that nonhuman primate sexual behavior was more variable and less stereotyped than Malinowski and others believed.

Heape (1900), in his discussion of mammalian estrus, by which he meant a period of intense sexual activity, recognized that in monkeys 'estrus' was not necessarily linked to ovulation (Heape, 1900, cited in Nadler, 1994). Thirty years later Zuckerman

(1930) described the basic conundrum of primate sexuality, that sexual behavior occurred at any time but was also much more likely to occur when females were near ovulation. As he put it, 'The matings of lower mammals are confined to short periods circumscribed by the activity of the follicular hormone. The matings of the primate are diffused over the entire cycle, paralleling the continued action of the follicular hormone, but varying in frequency according to the varying degrees of activity of the hormone' (Zuckerman, 1930, cited in Miller, 1931).

Zuckerman was correct in his description of the timing of mating behavior in primates, but incorrect in attributing its occurrence throughout the cycle to the action of follicular hormone, by which he meant estrogen, across the cycle. Miller (1931), in his comparative analysis of nonhuman primate and human sexual behavior, identified the key adaptation in primates that produced this loose coupling between the female's hormonal state and sexual behavior. Miller recognized that in primates, unlike most other mammals, the physical capacity to engage in sexual intercourse was uncoupled from hormonal control. Although Miller recognized this hormonal emancipation, he still argued for humans having a unique adaptation in that '... in man alone of all mammals is the male known to be able to force his sexual will on the unconsenting or unconscious female, a peculiarity that seems to arise from human ingenuity combined with human pelvic adjustments to the upright posture...' (p. 406).

Although Miller saw the physical capacity for rape as uniquely human, which it is not, his insight that physical ability to mate had become uncoupled from fertility is essential to understanding how gonadal hormones affect primate sexual behavior. Zuckerman's description of both the highly variable nature of nonhuman primate sexual behavior, as well as its increased probability when the female was fertile, is the other piece of the puzzle, though it took almost 60 years before these two notions were linked together (Wallen, 1990). In the intervening years many investigators attempted to discover the relationship between changes in female hormones and nonhuman primate behavior. This work has almost exclusively used rhesus monkeys and thus they are the focus of this chapter. However, it is believed that the basic principles described apply to a wide range of simian primates and only the paucity of detailed information about other primate species prevents critical assessment of the commonality of these principles.

Early Studies of Primate Behavioral Endocrinology

Josephine Ball and Carl Hartman undertook the first controlled attempt to discover the relationship between female ovarian function and sexual behavior in rhesus monkeys (Ball and Hartman, 1935). They observed the behavior of single malefemale pairs separated from all other social context, a technique they developed and that dominated nonhuman primate studies of sexual behavior for the next 50 years. They reported that sexual behavior occurred at all times in the female's cycle, and in many cases, but not all, was more frequent near midcycle when the female was likely to be ovulating (Ball and Hartman, 1935). They also pointed out that the female's interest

in sex varied with her cycle, stating that female '… sexual excitability typically increases just before ovulation and falls thereafter, even though the drop is not so complete as to mean a consistent refusal to mate' (p. 117).

This study was quite remarkable in that ovulation was verified by manual palpation, a level of precision that was not to be seen again until hormonal assays were developed in the 1970s. This was the first, and for almost 40 years the only study that accurately related behavioral change to ovulation and provided the first controlled evidence that, at least in some monkeys, sexual behavior varied predictably with the menstrual cycle. However, Ball and Hartman's study also clearly demonstrated that whatever endocrine events occurred during the ovarian cycle did not strictly limit sexual behavior to a single brief period; some sexual activity occurred at all times in the female's cycle. The authors' finding of an apparent cyclicity in female excitability was the first to focus on behavioral change in the female independent of male behavior. Furthermore, the finding that sexual behavior never ceased completely during the female's ovarian cycle characterized the findings of primate behavioral endocrinology using pairs of animals for the next 50 years (Wallen 1989, 1990). In contrast studies of intact social groups of monkeys suggested a more tightly coupled relationship between hormones and behavior.

Field behavioral endocrinology was essentially nonexistent when Carpenter studied the sexual behavior of rhesus monkeys on Cayo Santiago in the 1940s. Tracking female cycles in semi-free-ranging rhesus monkeys Carpenter reported a striking periodicity midway between menstruations in both copulation with males and in female sexual solicitations (Carpenter, 1942a,b). Unlike Ball and Hartman's studies of rhesus monkey pairs, Carpenter reported that female rhesus monkeys mated and interacted with males intensely only for a few days during their menstrual cycle. Particularly striking was his evidence that females intensely followed males during this midcycle period and initiated sexual activity through a variety of sexual solicitations (Carpenter, 1942a). Twenty years later, other field researchers studying free-ranging populations of rhesus monkeys reported a similar limited period of mating (Altmann, 1962; Conaway and Koford, 1964; Southwick et al., 1965). However, whether it was because Carpenter studied nonlaboratory populations of monkeys, concerns about field estimates of menstrual cycles, the inability to validate ovulation, or because it took other field workers 20 years to corroborate his findings, Carpenter's study initially had little impact on subsequent research and was rarely cited by researchers when primate behavioral endocrinology experienced a resurgence in the 1960s.

Primate Behavioral Endocrinology: The Modern Era

Although a small number of studies of nonhuman primate behavioral endocrinology were done in the late 1940s and 1950s, it was the convergence of two trends in the 1960s that resulted in the resurgence of primate behavioral endocrinology. The first was the detailed understanding of nonprimate behavioral endocrinology that had come from studies of rodents, particularly the guinea pig in William C. Young's laboratory (Young, 1961) and the rat in Frank Beach's laboratory (Beach, 1942; 1975;

1981; Beach and Levinson, 1950). The second was an increased interest in nonhuman primates, possibly stemming from the successful use of rhesus monkeys in developing a polio vaccine in the late 1950s, which ultimately resulted in the creation of a group of regional primate research centers by the National Institutes of Health in the early 1960s. This period saw increased field studies of rhesus monkeys and very active laboratory investigations of rhesus monkey sexual behavior.

Two laboratories, W.C. Young's at the Oregon Regional Primate Research Center, later under the direction of Robert W. Goy after Young's death in 1966, and Richard P. Michael's in London, dominated primate behavioral endocrinology for almost 20 years. Both laboratories employed controlled studies of male-female pairs, but developed quite different philosophical approaches to their research. The hundreds of studies published during this period varied widely, but two principles stand out. Michael's laboratory, with his colleagues Robert Bonsall, Barry Everitt, Joe Herbert, E.B. Keverne, and Doris Zumpe, emphasized male control of mating and focused on how ovarian hormones influenced female attractiveness to males (Michael and Herbert, 1963; Michael and Welegella, 1968; Herbert and Trimble, 1967; Trimble and Herbert, 1968; Michael and Zumpe, 1970).

Specifically, these investigators emphasized hormonally induced vaginal olfactory cues they claimed released male copulatory behavior, and either minimized or were unable to detect the role of females played in behaviorally regulating sexual interactions (Michael and Keverne, 1968; Keverne, 1976; Michael et al., 1982; Michael and Bonsall, 1977 a,b). The role of vaginal olfactory cues reported by Michael and colleagues could not be replicated in a different laboratory (Goldfoot et al., 1976). In addition, it was found that anosmic male rhesus monkeys showed cyclic variation in copulatory behavior even though they could not detect odor cues (Goldfoot et al., 1978). Finally, Goldfoot (1981) produced similar behavioral changes to those reported by Michael's laboratory using nonbiological odors and a testing paradigm comparable to Michael's. Although Michael argues that the failure of other laboratories to detect reliable effects of vaginal olfactory cues stems from procedural differences (Michael and Zumpe, 1993), his latest review of rhesus monkey sexual behavior acknowledges that ovarian hormones affect female sexual motivation and no longer emphasizes vaginal pheromones as primary regulators of monkey sexual behavior (Michael and Zumpe, 1993).

Michael's laboratory presented the first controlled data since Ball and Hartmann (1935) on the occurrence of ejaculation in relation to the female's ovarian cycle and demonstrated the pattern Zuckerman described 40 years earlier of some mating throughout the cycle, with a midcycle elevation (Michael and Herbert, 1963; Michael and Welegalla, 1968; Michael and Zumpe, 1970). However, the authors found no evidence that these changes in mating across the cycle were related to changes in female behavior and argued instead that they reflected changes in female attractiveness to the male which increased and decreased his sexual initiation. Only when females were required to perform an operant to gain access to a male and it was found that females performed this more rapidly at midcycle than at other times in the cycle, did Michael's group acknowledge that female sexual motivation might also vary with the female s hormonal condition (Keverne, 1976; Bonsall et al., 1978).

In contrast, Young and his colleagues, Robert W. Goy, Charles P. Phoenix, and John Resko, focused on how the female's hormonal state affected her sexual initiation (Goy and Resko, 1972). This emphasis on the female may have resulted from the extremely pronounced effect of ovarian hormones on female guinea pig behavior which Young's laboratory had spent 25 years investigating. At that time, there was an increased interest in female sexuality in America, possibly reflecting the effects of Masters and Johnson's landmark studies of human sexual response (Masters and Johnson, 1965; 1966) which gave male and female sexual response equal attention. Alternatively, or in addition, it may have been related to the rise of the American women's movement during the 1970s, which resulted in both a greater number of women entering all fields of biology and psychology and a greater general awareness of women's sexuality.

Prior to this time, the field of behavioral endocrinology, which had seen many contributions from women, was dominated by three patriarchs, Frank Beach, Daniel Lehrman, and W. C. Young, and their mostly male academic progeny. Finally, after decades of emphasizing the role of male rodents in sexual interactions, Frank Beach published a landmark article in 1976 coining the term 'proceptivity' to describe the active solicitation of sexual activity (Beach, 1976). Though this term could ostensibly be applied equally to males and females, his description focused exclusively on females and it has subsequently been applied principally to females. It will be left to others to determine whether this focus on female sexuality was related to the rise of the women's movement or to the dramatic increase in female graduate students in behavioral endocrinology, or to both. The fact remains that interest in the sexuality of female primates increased in the 1970s along with interest in how hormones affected female sexual behavior. Studies from Young's, and later from Goy's, laboratory provided evidence of ovarian influences on female sexual initiation when male control of the sexual interaction was restricted (Czaja and Beilert, 1975; Pomerantz and Goy, 1983). However, when the occurrence of ejaculation was studied in pairs across the female's ovarian cycle, the pattern reported by Michael's laboratory, of some mating each day with a midcycle elevation, was also found by Goy's laboratory (Goy, 1979). This was not always the case. Johnson and Phoenix (1978), also from Young's laboratory, failed to find any evidence of cyclic variation in sexual behavior of rhesus monkeys pairs.

After lying fallow for almost 40 years behavioral endocrinology moved back into complex monkey social groups in the 1980s. The creation of the Primate Center Program dramatically increased opportunities to study nonhuman primate physiology and behavior. At the Yerkes, Regional Primate Research Center, Irwin Bernstein, Thomas P. Gordon, and Robert Rose had successfully investigated the behavioral endocrinology of male rhesus monkeys using techniques they developed for sampling hormones in group-living monkeys (Rose et al., 1975; Gordon et al., 1976; 1978). Gordon applied these techniques to group-living females and in 1981 published a landmark study showing that mating behavior in outdoor-housed mixed-sex groups of rhesus monkeys was limited to a few months of the year and to a few days within each female's ovarian cycle (Gordon, 1981). Unlike Carpenter's study, Gordon's animals were visible at all times and blood samples, which could now be assayed for estradiol and progesterone, were collected in addition to observing menstruation. Thus, for the first time unequivocal evidence was obtained that rhesus monkey sexual behavior was

strongly influenced by the female hormonal state, with long periods during the cycle with no sexual activity.

Subsequent work suggested that the female's behavior varied with her ovarian cycle (Cochran, 1979), a view that was verified when daily behavioral and hormonal samples were taken on group-living monkeys (Wallen et al., 1984). These studies found, in contrast to those of isolated pairs of animals, that female sexual initiation increased sharply with increases in estradiol and that sexual activity was limited to a small number of days within the female's 28-day ovarian cycle. This pattern was found whether the multiple female group had a single male (Wallen et al., 1984) or multiple males (Wilson et al., 1982). Clearly, this pattern differed markedly from that seen in the behavior of pairs of monkeys, but why?

Social Modulation of Hormonal Influences on Female Sexual Behavior

In retrospect it seems obvious that rhesus monkey sexual behavior would be less tightly coupled to female hormonal state in pair than in group tests, but this perspective developed slowly. Studies of rhesus monkey pair tests so dominated nonhuman primate behavioral endocrinology that results from other contexts, which often contradicted pair-test data, had little impact. However, surveying the last 70 years of study it is clear that the elements needed to explain these divergent findings have been present from the very beginning and were encapsulated in the early recognition that sexual behavior in primates occurs throughout the female's cycle and is more likely to occur when the female is fertile. In addition, the exact relationship between the female's cycle and the occurrence of sexual behavior is strongly influenced by social context.

This principle is illustrated in figure 10.1 which shows the occurrence of ejaculation, or the percentage of females receiving ejaculations, in relation to the female's ovarian cycle under three different social contexts. Single pairs of monkeys tested for 12 minutes in a small area show the pattern, first described by Zuckerman, of some mating every day with a midcycle elevation (Goy, 1979). In comparison, when a single male is tested with a group of females in a large area for 30 minutes, all mating occurs in the 8-day period around the midcycle estradiol peak. Even though more time is available for mating (Wallen et al., 1984). When multiple males and multiple females are observed for 3 hours in a large area, more mating is seen in the follicular phase, while mating ceases completely during the luteal phase, just as it does when only a single male is present and despite the fact that more than six times as much time was available for mating in this testing situation. Though these studies differ in many ways the conclusion that social context affects the degree of coupling between the female's cycle and sexual behavior is inescapable. Why does social context have this effect? The first part of the answer is simply 'because it can.'

Social modulation this striking would not be found if one studied female guinea pigs instead of female monkeys. Unlike female monkeys, female guinea pigs are physically capable of mating for only 2 to 3 days of their 14- to 16-day cycle because a hormonally controlled membrane closes their vagina except around the time when they are fertile (Stockard and Papanicoulaou, 1919). Similarly, female rats without any hormonal stimulation would be unable to display the lordosis posture necessary
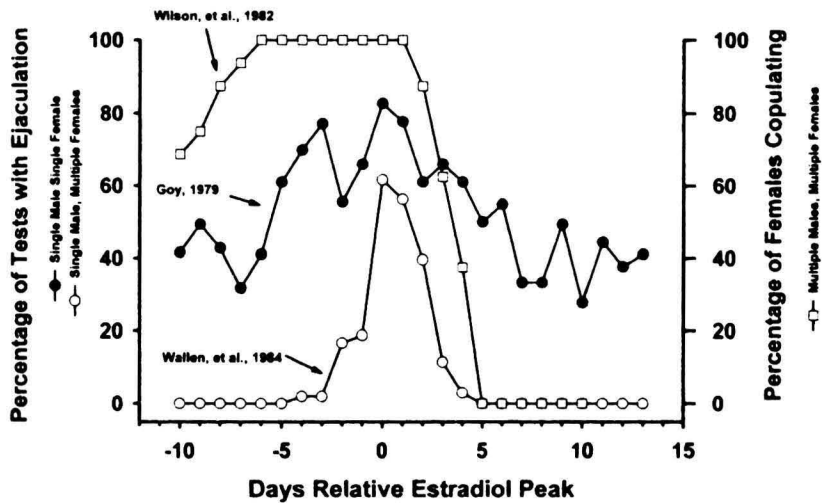
Fig. 10.1. Relationship between female ovarian cycle day, aligned relative to the midcycle estradiol peak, under three testing conditions that differ in social context, testing area, and observation time. Tests of single-male, single-female pairs display the most continuous sexual behavior across the female's cycle even though the least amount of time was available for mating to occur. (Data from Goy 1979; Wilson, et al. 1982; and Wallen et al. 1984.)

for male intromission (Diakow, 1974; Pfaff et al., 1978). Unlike these mammalian females, female primates, with the exception of some prosimian primates (Hrdy and Whitten, 1987), are always capable of engaging in sex with or without hormonal stimulation. However, this primate capacity to engage in sex at any time does not explain why sexual behavior is more tightly coupled to female hormonal state under some social conditions and less tightly coupled under others.

Explaining this aspect requires the notion that the primary psychological function of gonadal hormones is to influence sexual motivational systems in primates (Wallen, 1990, 1995). When sexual activity is physically possible at any time, sexual motivation will influence sexual behavior only when circumstances require high sexual motivation for the behavior to occur. Evidence that gonadal hormones modulate female sexual motivation comes from studies that varied the effort needed to seek a sexual partner or to engage in sex. As previously mentioned, requiring a female to perform an operant to gain access to a male partner revealed a previously hidden midcycle increase in performance with the female accessing the male more slowly at other times in the cycle (Keverne, 1976). Similarly, the sexual activity of a male-female pair was more strongly affected by the female's hormonal state, being high at midcycle and low during the luteal phase, when the pair was tested in an area 100 times larger than that typically used for pair tests (Wallen, 1982). Thus, simply increasing the physical effort necessary for sex or providing more behavioral alternatives increased the effect that the female's hormonal state had on the occurrence of sexual behavior.

Hormonally modulated female sexual motivation only becomes important under conditions where sex requires more effort or behavioral choices must be made. However, even when increased effort is required, larger physical areas must be traversed, or

an operant performed, sexual activity does not cease completely in all pairs during the nonovulatory portion of the cycle. In contrast, females in social groups of monkeys uniformly do not mate early in the follicular phase or during the luteal phase of the cycle (Carpenter, 1942b; Gordon, 1981; Wilson et al., 1982; Wallen et al., 1984). A study comparing sexual behavior in a pair test with sexual behavior with the same male and a group of familiar females found little difference during the periovulatory portion of the cycle, but sexual behavior during the luteal phase occurred only in the pair test and was completely absent when multiple females were present (Wallen and Winston, 1984). This difference could not reflect differences in physical effort between the two types of tests as both took place in the same 625 m^2 arena. However, the group tests introduced a social complexity, interactions between familiar females, not present in the pair tests. It was this added social factor that accounted for the greater influence of female hormonal state on sexual behavior in the group tests. Some description of the social context rhesus monkeys live in is necessary to develop this point.

Rhesus monkeys are a female-bonded society (Wrangham, 1980) in which relations between matriarchs and their families form the core of the social structure (Sade, 1965; Missakian, 1972; Gouzoules and Gouzoules, 1987). Males are transitory members of this social structure, leaving their natal group and emigrating to a new rhesus monkey group during the breeding season with whom they typically live for 5 years or less (Koford, 1966; Lindburg, 1969; Drickamer and Vessay, 1973). In this social environment males serve an important, but transitory social role and the crucial social interactions are
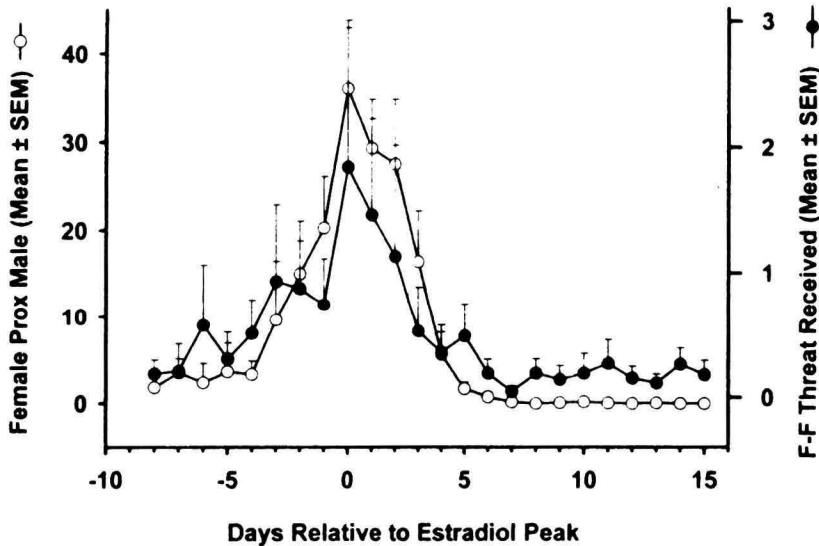

Fig. 10.2. The accurrence of female initiation of proximity (Prox) and threatening between females in relation to the female's ovarian cycle day, aligned relative to the midcycle estradiol peak in a social group of a single male and multiple females. As females interact more intensely with the group male, they are threatened more by other group females (F-F). (Adapted from Wallen and Tannenbaum 1997.)
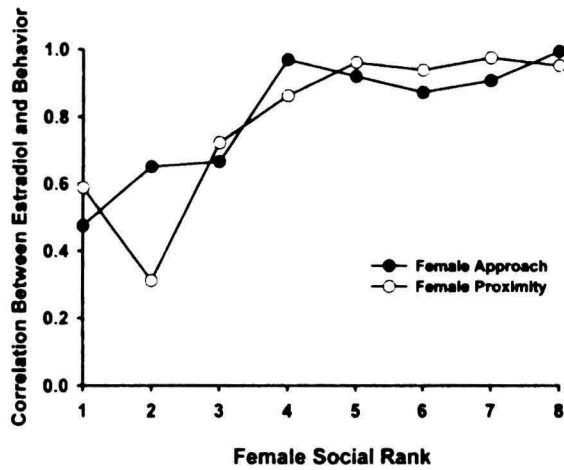
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Fig. 10.3. The relarionship between social rank and the magnitude of the correlation between serum estradiol on the 8 days prior to, and including the estradiol peak in relation of the daily occurrence of female initiation of female initiation of approach and proximity (sitting within 20 cm) to the two highest-ranking females were not statistically significant, whereas those of the five lowest ranking females were and all approached 1.0. These data support the notion that low-ranking females are more dependent upon hormonal influences than are high-ranking females.

between females and these are not all affiliative. Antagonistic relations between females vary with their ovarian cycle in group-living rhesus monkeys, with peak occurrence during the periovulatory portion of the menstrual cycle (Mallow, 1981; Walker et al., 1983; Wallen and Tannenbaum, 1997). As shown in figure 10.2, data from a single-male, multiple-female group reveal increased female threatening of other females at the same time as increased female initiation of proximity with the group male occurred. Not only does sexual activity in a social group require greater physical effort than in a pair test, but it also entails social risk, at least for lower-ranking females. This social risk makes the sexual motivational state of the female a critical regulator of sexual behavior in a social group because under such conditions females must be intensely interested in interacting with males to risk negative social interactions with other females that their attention to a male will produce. Furthermore, when many adult males are in the group, female interest in one male may elicit negative social interactions from other group males (Smuts and Smuts, 1993) creating another social impediment to expressing female sexual interest.

Further support for the idea that hormonally modulated sexual motivation is an important modulator of female sexual behavior in a group context is found in analyzing the relationship between a female's social rank and the extent to which her cyclic variation in estradiol predicts her sexual initiation behavior. For high ranking females, sex entails little social risk, whereas low-ranking females are potentially exposed to a higher social risk. Thus if gonadal hormones modulate female sexual motivation, then within a social group the hormonal state of a high-ranking female should be a poor predictor of her behavior, since she is not strongly dependent upon her sexual motivation to engage in sex. In contrast, female hormonal state should be

an excellent predictor of a low-ranking female's sexual behavior since she is much more strongly dependent upon her sexual motivation.

Figure 10.3 illustrates for eight females who mated with males in a social group the relationship between female social rank and the magnitude of the correlation between daily changes in estradiol and daily changes in behavior, approaching, and proximity initiation for the 8 days prior to the estradiol peak. For the first- and second-ranked females, the correlations for both behaviors were not significant and only significant at $P = .05$ for the third-ranking female. In contrast, for the rest of the group females, all correlations were statistically significant and greater than 8 with many approaching 1.0. Since estradiol secretion did not vary with female social rank, these data most likely reflect an increased dependence of low-ranking females on estradiol-induced increased sexual motivation. Further evidence that high-ranking females are less dependent upon hormones to mate is seen in the finding that they mated on more days of their ovarian cycle and started mating earlier in the follicular phase, when they would have been exposed to less estradiol, than did low-ranking females (Wallen, 1990). Taken together, these findings support the idea that hormonal modulation of female sexual motivation is necessary for sexual behavior to occur in a socially complex setting where both physical effort and social risks affect how easily mating occurs.

Detecting the female's degree of sexual motivation is more difficult in pair tests because the effort required in selecting a partner and the social risks of sexual activity have been markedly reduced. In addition, the economic realities of indoor nonhuman primate research resulted in using small test cages (2 m x 3 m floor areas) that accidentally duplicated the proximity cues that female rhesus monkeys use to convey their sexual interest in males (Wallen et al., 1984; Wallen, 1989). Thus in pair tests not only are physical effort and social risk low but the small physical space causes females to emit behavioral cues which, under free-ranging conditions, occur only when females are highly motivated to interact sexually with males.

It could be argued that the cyclic changes in female behavior do not reflect motivational state, but are a response to unidentified male-generated cues. The strongest evidence against this view comes from studies where female's hormonal state and sexual behavior varied with little or no response by the male. One approach has been to treat ovariectomized group-living female rhesus monkeys during the nonbreeding season when males are sexually nonresponsive. The two studies using this method found evidence that female sexual motivation increases with estradiol treatment, though the specific manner in which this was expressed varied between the two studies. Pope et al. (1987) reported that estradiol-treated ovariectomized females showed increased female-female mounting during the nonbreeding season and increased heterosexual copulation during the breeding season. Thus estradiol induced increased sexual activity that was expressed with groups females when the males were sexually quiescent. Zehr et al. (1998), studying these same females 12 years later when they were more sexually experienced, found estradiol increased female approach, contact, grooming, and presentations to group males even though the males displayed no significant change in sexual interactions with the females. Figure 10.4 summarizes these findings and supports the notion that estradiol directly affects female sexual motivation and that the female's behavior is not dependent upon the male's sexual response.
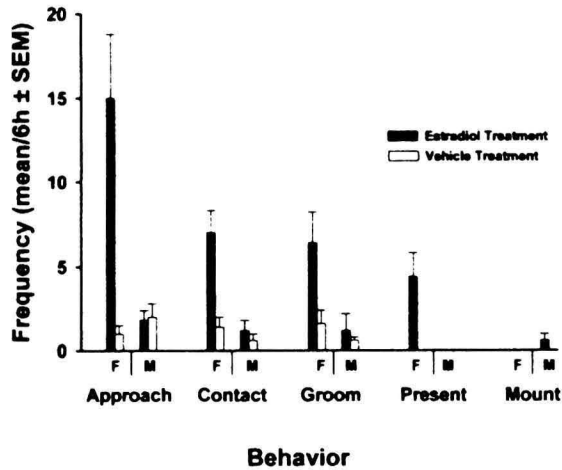
Fig. 10.4. The occurence of selected social and sexual behaviors by group-living ovariec-tomized bemales or group males during female estradiol or vehicle treatment. F on the x-axis indicates that behavior was initiated by one of the females; M indicates a male initiated the behavior. Only female-initiated behavior during estradiol treatment differed significantly from the vehicle condition. (Adapted from Zehr et al. 1998.)

Is Sexual Desire in Women Related to Ovarian Hormones?

Whether the ovarian cycle of women influences their sexual interest has been debated since the 1930s. Tinklepaugh (1933), in a review of data from more than two thousand women, concluded that two periods of increased sexual desire occurred during the menstrual cycle: one just prior to menstruation and a second immediately after menses, corresponding to the fertile period. Tinkelpaugh raised the possibility that the premenstrual period of increased female sexual desire might reflect knowledge that this time has the lowest risk of pregnancy during the cycle, suggesting that female sexual interest is affected by perception of risk of pregnancy. However, Tinkelpaugh's review had little impact on views of female sexuality. In subsequent research, if female sexual desire was considered at all, it was typically thought to be unaffected by ovarian function, a view that was bolstered by the claim that ovariectomy had no detectable impact on female sexuality (Filler and Dresner, 1944; Waxenberg et al., 1959).

Paralleling the interest in female nonhuman primate sexuality, increased investigation of women's sexuality started in the late 1960s. Reports appeared showing cyclic variation in human sexual intercourse (Udry and Morris, 1968) and female sexual initiation (Adams et al., 1978). However, the exact relationship of sexual behavior to the menstrual cycle was unclear (Udry and Morris, 1977) and the occurrence of intercourse was affected by cultural conventions such as the weekend (Palmer et al., 1982) and by psychological factors such as fear of pregnancy (Tsui et al., 1991). In addition, human studies typically investigated the occurrence of intercourse which confounded male sexual initiation with the influence of the female (Wallen and Lovejoy, 1993). However, studies accumulated showing a midcycle increase in female sexual activity in lesbian cou-

ples where male influences were eliminated (Matteo and Rissman, 1984) and in newly-weds, whose sexual activity would be expected to be heightened (Hedricks et al., 1987).

A more general view developed that the ovarian cycle influenced women's sexual activity, not just male's initiation (Wallen and Lovejoy, 1993; Hedricks, 1994). For example, when female sexual desire was explicitly investigated by asking women to report the first day they felt increased sexual desire, it peaked at midcycle (Stanislaw and Rice, 1988). The pattern of increased sexual desire reported by the more than four thousand women in Stanislaw and Rice's study strikingly paralleled the changes in sexual initiation displayed by female rhesus monkeys across the menstrual cycle, as shown in figure 10.5. Similarly, unlike Filler and Dresner's original study, which only reported the effect of ovariectomy on the occurrence of intercourse, subsequent studies that explicitly investigated female sexual desire found it almost completely eliminated by ovariectomy (Dennerstein and Burrows, 1977; Sherwin and Gelfand, 1987; Sherwin et al., 1985), just as pharmacological suppression of ovarian function eliminated female sexual initiation in female rhesus monkeys (Wallen et al., 1986). While direct comparisons between humans and nonhuman primates may seem presumptuous, it appears that sexual motivation in women is as influenced by ovarian function as is that of female rhesus monkeys.

Does Risk Affect the Expression of Sexual Desire in Women as it Does in Female Rhesus Monkeys?

While no study has specifically investigated this question, two intriguing pieces of evidence suggest that increased risk affects the way women's sexual behavior is
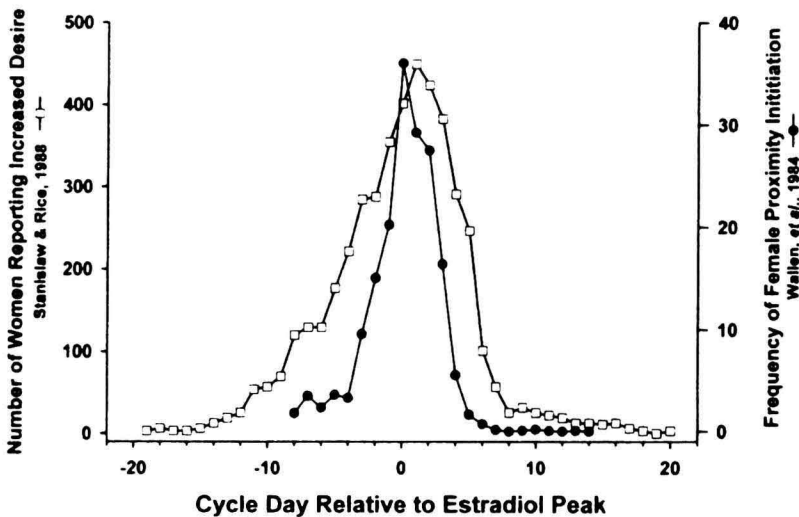

Fig. 10.5. The number of women reporting an increase in sexual desire in relation to ovarian cycle day (Stanislaw and Rice 1988). The similarity of this curve to changes in female-initiated proximity to a male by group-living female rhesus monkeys (Wallen et al. 1984) is striking. Cycles are aligned by day of peak estradiol (rhesus monkeys) or putative peak estradiol day derived from changes in basal body temperature (humans).

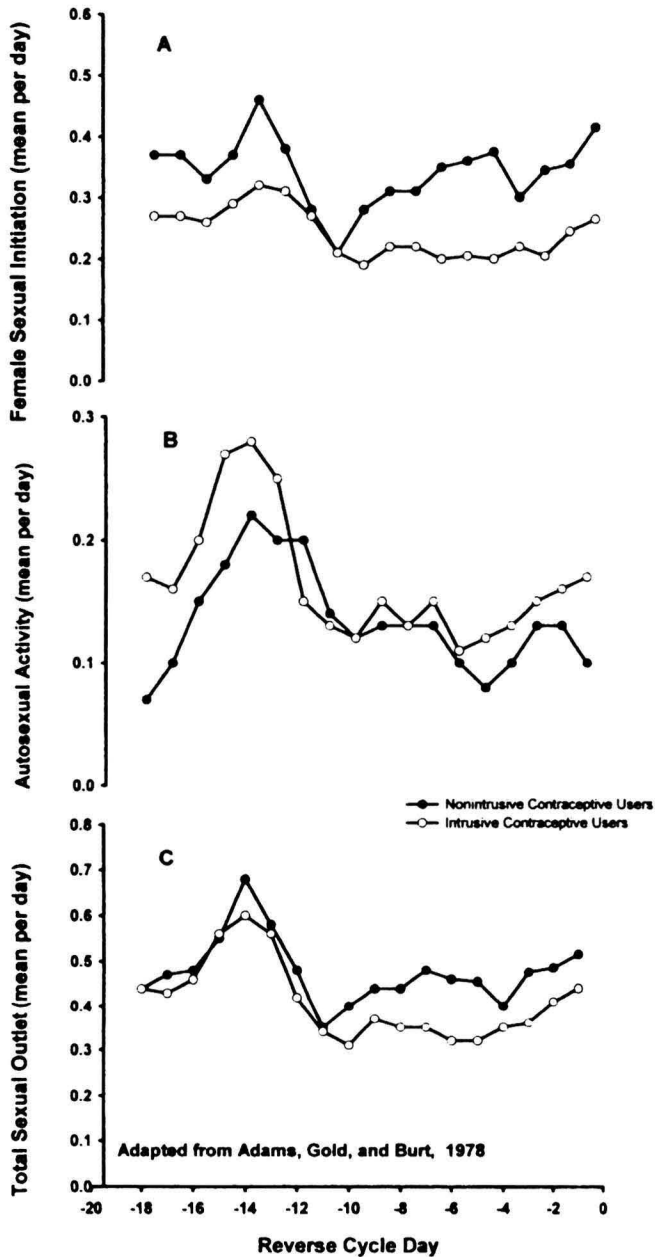Social Context and Hormonal Modulation of Primate Sexual Desire

Fig. 10.6. The occurrence of (A) female sexual initiation, (B) autosexual activity (B), and (C) total sexual outlet (the combination of sexual initiation and autosexual activity) in women using nonhormonal contraception. Nonintrusive contraceptives were permanent or semipermanent forms of contraception, such as surgical strerilization or intrauterine devices that did not intrude on the sexual interaction. Intrusive contraceptives were those that need to be utilized close to the rime of intercourse, such as condoms, vaginal foam, or diaphragms. The distribution of female sexual activity varied according to the type of contraceptive used and ovarian cycle. (Data from Adams et al. 1978.)

expressed in relation to their ovarian cycle. The first evidence comes from a study of female sexual initiation and how it is affected by hormonal birth control pills (Adams et al., 1978). In addition to investigating the effect of hormonal contraceptives on female sexual initiation, which the pill suppressed, this study compared the relationship between type of contraceptive used and cyclic variation in female sexual initiation and autosexual behavior in women with regular sexual partners. The women in the study using nonhormonal contraceptives are considered here. About half of these used highly reliable contraceptives that did not intrude on sexual interactions, such as surgical sterilization or an intrauterine device (nonintrusive contraceptive users). The rest used unreliable contraceptives that intruded on sexual interactions, such as condoms or diaphragms (intrusive contraceptive users).

The type of nonhormonal contraceptive used affected the pattern of female sexual behavior shown across the cycle. Nonintrusive contraceptive users showed an increase in sexual initiation around reverse cycle day 14, near presumed ovulation (figure 10.6A). In contrast the midcycle peak in female sexual initiation was muted in women using the unreliable intrusive contraceptives. This difference might reflect self-selection such that women who are sexually less active, or less interested in sex use less permanent forms of contraception. However, when the autosexual activity of these two groups of women are compared (figure 10.6B), both groups of women show a midcycle elevation, with the women using the unreliable intrusive contraceptives showing a higher peak than the nonintrusive contraceptive users. Combining both sexual initiation and autosexual activity to measure total daily sexual outlet (figure 10.6C) shows no apparent differences between the two groups of women, with both showing a midcycle elevation in sexual activity followed by a luteal decrease. Thus these two groups of contraceptive users differ not in their overall level of sexual activity, but in how it is distributed between heterosexual sexual initiation and masturbation.

While different interpretations of these findings are possible, it seems likely that contraceptive-using women are aware of when they can most easily become pregnant in their cycle (Small 1996) and of the effectiveness of the contraceptive method they use. Thus one interpretation is that women using unreliable contraceptives perceive sexual initiation at midcycle as risky and inhibit their heterosexual activity and substitute a higher level of autosexual activity than women using highly reliable contraceptives. In this case perception of the risk of pregnancy causes the midcycle increase in sexual desire to be expressed as masturbation rather than initiation of sexual intercourse. A second example suggests that under some conditions socially risky sexual activity is more tightly coupled to female hormonal state than is less risky sex.

Bellis en Baker (1990) used a cross-sectional method to obtain information about the sexual activities of 2708 English women who had a primary male sexual partner. Subjects were asked to report whether their last copulation was with their primary sexual partner of with an extrapair partner and to provide enough information so that the menstrual cycle length and the cycle day of the copulation could be calculated. In addition, the 162 women who claimed that their most recent copulation had been with an extrapair partner also indicated when they last had intercourse with their primary partner. Bellis and Baker were interested in obtaining evidence that women manipulated sperm competition between males, but their data are compatible with a quite different interpretation.

Bellis and Baker (1990) divided the women's cycles into three phases roughly corresponding to the follicular, periovulatory, and luteal portions of the cycle. They found that sexual intercourse with the women's primary partner varied across their cycle, being highest luteally and lowest during the follicular phase. Sexual intercourse outside of the primary relationship also varied with the cycle but had a periovulatory peak and was lower both follicularly and luteally. Extrapair sexual intercourse is a socially risky sexual activity and it more closely followed the female's cycle than did the less socially risky sexual intercourse with the woman's partner. Furthermore, the higher luteal phase sexual intercourse with the partner is consistent with pregnancy avoidance affecting the occurrence of intercourse within an established pair. The tighter coupling between sexual intercourse and the woman's cycle was even more pronounced when the distribution of sexual intercourse for the 50 women in the study who had sexual intercourse with an extrapair male and their primary partner within 5 days of each other was considered.

As shown in figure 10.7 these so-called double-matings (Bellis and Baker, 1990) were not randomly distributed across the female's cycle, but peaked on the presumed day of maximal fertility (Barrett and Marshall, 1969). While Bellis and Baker interpret these data as evidence that these women were promoting sperm competition, as sperm remain viable for at least 5 days in the female reproductive tract (Barrett and Marshall, 1969), they are also completely consistent with the notion that this risky form of sex is more likely to occur when the women's sexual motivation is highest, resulting in a tighter coupling of the behavior to her ovarian cycle. In this view extrapair intercourse occurs more at midcycle as a result of heightened female sexual interest and is therefore more opportunistic with little consideration of social consequences. Further support for this interpretation comes from the finding that for all
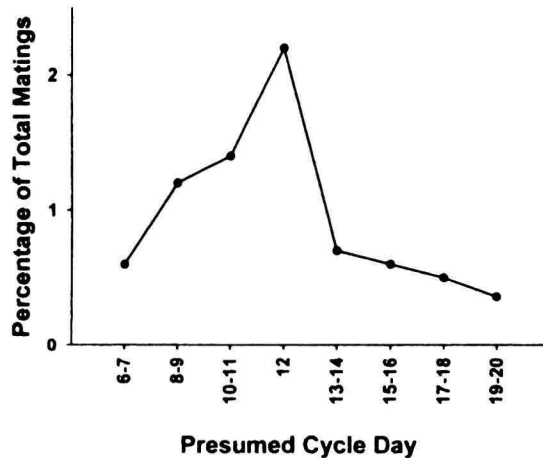

Fig. 10.7. Distribution of "double-matings," in which women had sexual intercourse with their primary partner and an extrapair partner within 5 days of each other, in relation to the female's cycle as a percentage of total copulations. Day 12 is the day of maximal fertility (Barret and Marshall 1969). (Data from Bellis and Baker 1990.)

intercourse, a greater proportion with the primary partner used contraception than was used during extrapair copulations (Bellis and Baker, 1990). Similarly, for double-matings, a significantly greater proportion of extrapair sexual intercourse during the most fertile period did not use contraception in comparison with intercourse with the primary partner (26% for extrapair intercourse vs. 14% for intercourse with the primary partner; Bellis and Baker, 1990). Thus, not only were double-matings more likely to occur when the women was maximally fertile but they were also less likely to use contraception during the extrapair mating, suggesting less consideration of the consequences of sexual intercourse.

While many caveats apply to these studies, for example, the estimates of cycle phase are less precise than those obtained in nonhuman primate studies, these results are intriguing because they do not simply suggest that sexual behavior varies with the female cycle, but that specific types of sexual behavior will be most strongly affected by ovarian influences.

Investigations of human sexuality have vocused primarily on the sexual behavior of established couples, a condition that seems unlikely to have shaped the evolution of hormonally modulated female sexual desire. Sexual intercourse within an established couple is more likely to be influenced by nonhormonal factors such as the day of the week, how hard the workday has been, whether one is on vacation, or gets a job promotion (Blumenstein and Schwartz, 1983) than it is by the blood levels of ovarian hormones. Humans, like all primates, do not require specific hormonal conditions to engage in sex, providing great latitude in the conditions under which sex occurs and allowing sex to be used for many social purposes in addition to reproduction. Instead of regulating sexual activity in established couples, it seems more likely that the system of hormonally modulated sexual desire evolved to solve the problem of seeking and engaging a sexual partner when one is not routinely available. This system provides the motivation to take the social and physical risks necessary to find a mate. In addition to motivational effects, ovarian hormones alter women's perceptions affecting their sensitivity to reproductively salient cues (Griffith and Walker, 1975; Krug et al., 1994). Although it has not been specifically investigated one suspects that social gregariousness and risk-taking would be found to be highest in women at midcycle. The view that female sexual desire is strongly coupled to fertility and increases social risk-taking has important social implications.

American society tries to manage adolescent sexuality, particularly that of young women, by prohibitions against becoming sexually active. Currently, the abstinence pledge, in which young men and women pledge to remain virgins until marriage, is popular among teenagers, particularly teenage girls, with more than 2.75 million teenagers pledging since 1993 (Bearman and Bruckner, 1998). If adhered to, abstinence pledges delay the time of transition to first intercourse (Bearman and Bruckner, 1998). However, there is little consideration of the conditions under which the pledge is likely to be broken. Young women who have pledged abstinence are unlikely to be taking hormonal contraceptives, which mute female sexual initiation (Adams et al., 1978) and thus these young women experience the full complement of hormonal changes during their ovarian cycle, probably with little discussion of how their ovarian cycle might affect their sexual feelings.

The model presented here, unfortunately, suggests that abstinence pledges are most likely to break down when teenage girls are most fertile, since at that point in their cycle their heightened sexual motivation could cause them to abandon their societally imposed abstinence and follow their sexual urges without consideration of the consequences. Since these young women are unlikely to use contraception this has potential public health implications in terms of both teenage pregnancy and disease transmission. While it is probably wishful thinking in today's anti-sex climate, a greater impact on teenage pregnancy could probably be achieved by combining a recognition that hormones influence female sexual desire with frank sexual education designed to increase awareness of, and psychological tools for, managing sexual desire. Already it has been found that abstinence pledges lose their effectiveness when more than 40% of the members of a high school participate (Bearman and Bruckner, 1998). Thus a system of simple prohibition is likely to break down for both social and biological reasons.

Do the Principles Described in Females Apply to Males?

In contrast to females, where there was debate about whether gonadal hormones played any role at all, it has always been assumed that male sexuality was under testicular control. It was common, though erroneous, knowledge that testicular function was necessary in males for penile erections. Kinsey's data on the sexual behavior of males presented striking evidence that the onset of puberty was associated in males with an almost immediate increase in many aspects of sexuality. For example, approximately 10% of males had experienced orgasm by age 12, but 100% had by 18 years of age. In contrast, while 10% of 12-year-old girls had experienced orgasm, by age 22 only 60% had and the increase was steady and gradual, with no sudden and abrupt change around puberty (Kinsey et al., 1953). Thus the notion was both popular and consistent with published information, that male sexuality was turned on by testicular activity and that males could not be sexually active without testicles. Support for this notion came from studies of rodents in which castration completely eliminated male sexual behavior (Beach, 1942; Beach and Levinson, 1950). It was assumed that the same would hold true for nonhuman primate males as it did for mice and men.

The first full-scale studies of castration in rhesus monkeys provided strikingly different results from similar studies in rodents. Studied under controlled laboratory conditions, in single male-female pairs, castration produced a gradual and steady decline, with some males continuing to achieve intromission and show ejaculatory reflexes years after castration, their capacity to actually produce seminal emissions having disappeared soon after the removal of their testicles. (Phoenix et al., 1973; Michael and Wilson, 1974; Phoenix, 1978). Similar results were reported for castration in the stumptail macaque, a species closely related to the rhesus monkey (Schenk and Slob, 1986). Thus, neither the capacity for erection nor for intercourse itself appeared to be under testicular control. However, sexual behavior did decline following castration, suggesting that testicular hormones modulated male sexual motivation.

Similar evidence for the independence of sexual activity in men came from a retrospective study of 39 men castrated in Europe for sex crimes (Heim, 1981). These men, after they were released from prison, were asked to estimate their frequency of sexual intercourse and masturbation before and after castration. Castration significantly reduced both types of sexual activity, but reduced masturbation significantly more than it did intercourse. Prior to castration 25 (64%) of the 39 subjects had sexual intercourse once per month or more often and 34 (87%) masturbated with the same frequency. Four to 7 years after castration, 14% continued to have intercourse one or more times per month and only 3% continued to masturbate at that frequency ($\chi^2 = 4.1$; P =.04)

This study demonstrates that castration does not eliminate male sexual activity but markedly reduces male sexual motivation. Sexual intercourse reflects both the sexual motivation of the male and the desires of his partner, whereas masturbation results from internal sexual desire; thus the greater reduction in masturbation than in intercourse probably reflects the decrease in male sexual motivation following castration. This study also suggests that the physical capacity to get an erection is not under testicular control, a view that was confirmed in more recent studies which found that hypogonadal men (males with endogenous castrate levels of testosterone) achieved erections in response to sexually explicit films as rapidly as males with normal testosterone levels (Kwan et al., 1983; Bancroft and Wu, 1983; Carani et al., 1992). These same males rarely showed spontaneous erections but were perfectly capable of erections in response to erotic stimuli. Thus, as in the case of female primates, the physical ability to engage in sex in males is not under gonadal hormonal control. Do males show a similar social modulation of the importance of gonadal hormones in modulating sexual behavior as that seen in females?

Social Modulation of Hormonal Effects on Male Sexual Behavior

Both studies of the effect of castration on male rhesus monkeys using pair tests reported a gradual decline in sexual behavior following castration (Phoenix et al., 1973; Michael and Wilson, 1974) which lasted for more than 6 years (Phoenix, 1978). Evidence that this slow decline reflected the relatively lower importance of male sexual motivation in pair tests came from comparing the effect of castration in pair tests with the effect of suppressing male testicular function with a gonadatropin-releasing hormone (GnRH) antagonist (Wallen et al., 1991). Figure 10.8 illustrates the more rapid decline in ejaculatory behavior that occurred in males with suppressed testicular function who were tested in a multimale, multifemale social group in comparison to the effects of castration in pair tests. This more rapid decline in sexual behavior in the group setting occurred in spite of the fact that males had 120 minutes to interact sexually, whereas only 10 minutes were available in the pair tests, a difference which biases against finding the more rapid decline in group-tests presented here.

Additional evidence of social modulation of the effect of suppressing testosterone comes from comparing an earlier study that used a GnRH agonist to suppress male testicular function (Davis-DaSilva and Wallen, 1989), but tested males in a singlemale,
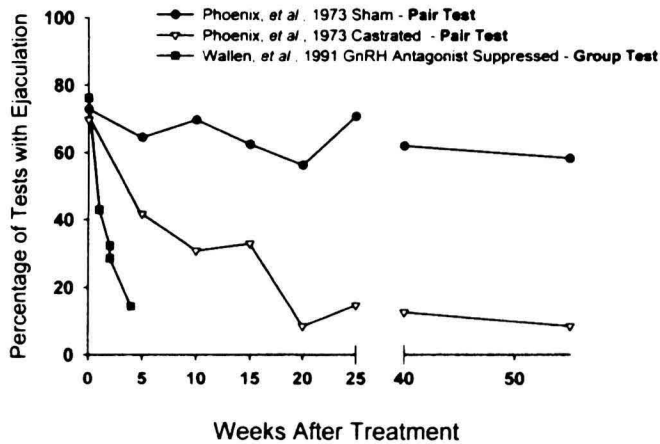
Fig. 10.8. Comparison of the effect of castration in male rhesus monkeys, tested in male-female pairs, and the effect of testicular suppression in seven group-living male rhesus monkeys on the percentage of observation periods with ejaculation. Pair tests were 10 minutes in duration and group tests were 120 minutes. The decline in ejaculation following removal of testicular function was more rapid in the group setting than in the pair test. GnRH, gonadotropin-releasing hormone. (Pair-test data from Phoenix et al. 1973); group-test data from Wallen et al. 1991.)

multifemale group rather than the multimale, multifemale groups used in the GnRH antagonist study. Testosterone suppression affected male sexual behavior in the single-male condition, but the effect was more gradual and not as complete as that seen in the GnRH antagonist study. Two males tested in both studies continued to ejaculate after 4 weeks of testosterone suppression in the single-male condition, but stopped mating after 1 week of testosterone suppression in the multimale condition. Thus, as with female rhesus monkeys, the opportunity for intrasexual competition affected the importance of hormonal state in maintaining sexual behavior. Also, as in females, there was evidence that male social rank influenced how extensively an individual male's sexual behavior was affected by testosterone suppression.

Figure 10.9 illustrates the magnitude of the overall correlation between male testosterone level and the occurrence of ejaculation prior to receiving GnRH antagonist treatment during the first 4 weeks post GnRH antagonist treatment when testosterone levels were uniformly suppressed, and during the last 4 weeks of the study when testosterone secretion was returning (Wallen et al., 1991). Two of the seven sexually active males in the group were only 4 years old and experiencing their first breeding season, whereas the other five males averaged 12 years of age and had extensive sexual experience. Both of the sexually inexperienced males, who were natal males and the offspring of high-ranking females, occupied the top two positions in the male hierarchy, yet both stopped mating within the first week of testosterone suppression. Thus, as shown in figure 10.9, there is no overall correlation between male testosterone level and the frequency of ejaculation. However, there is a significant correlation when only the five sexually experienced males are considered (see
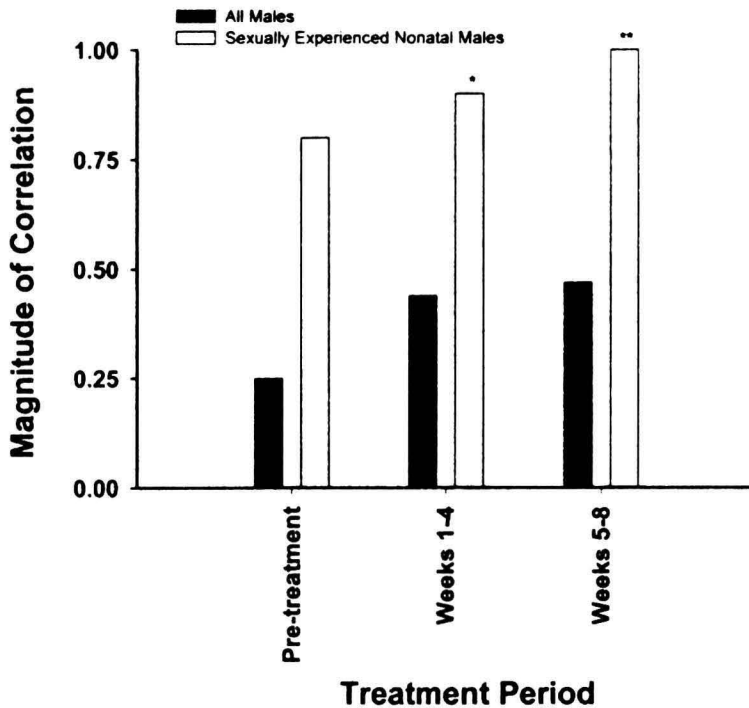
Fig. 10.9. Magnitude of the overall correlation between male testosterone level and the weekly frequency of ejaculation prior to receiving gonodotropin-releasing hormone (GnRH) antagonist treatment during the first 4 weeks post GnRH antagonist treatment when testosterone levels were uniformly suppressed, and during the last 4 weeks of the study when testosterone secretion was returning, for all males (black bars) and for the five older, sexually esperienced group males (open bars). *$P = .037$; ** $= P < .001$.

figure 10.9). Prior to GnRH antagonist treatment male testosterone level did not predict ejaculation frequency, neither in all males nor in the sexually experienced males, though the lack of significance in the latter case clearly stems from the small number of sexually experienced males. Following GnRH antagonist treatment, male testosterone level significantly predicted male ejaculation frequency, both when testosterone was suppressed and when testosterone secretion was returning (see figure 10.9).

Figure 10.10 shows the magnitude of individual correlations during all 12 weeks of the study between testosterone and weekly ejaculation frequency. Within both the sexually inexperienced and experienced males the magnitude of the correlation were higher for males with lower social rank. Thus, the third-ranking male (the highest-ranking of the sexually experienced males) showed almost no correlation between testosterone and his behavior. This was primarily because GnRH antagonist treatment profoundly suppressed his testosterone level, but this had no detectable effect on his copulatory behavior. In contrast, the lowest-ranked sexually experienced male had an almost perfect correlation ($r=.93$) between his testosterone level and his ejaculations.
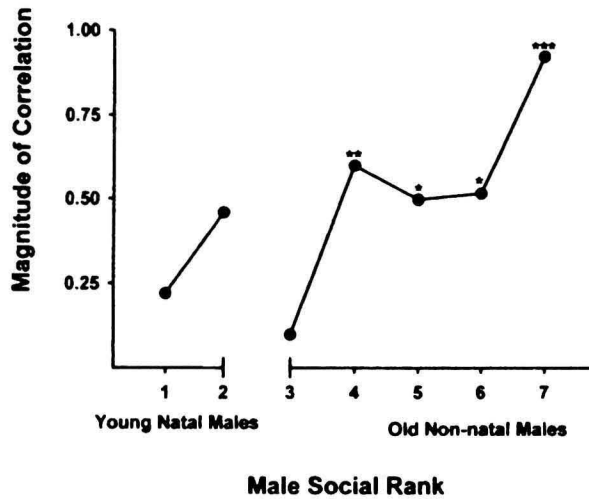
Social Context and Hormonal Modulation of Primate Sexual Desire

Fig. 10.10. Individual correlations between tesstosterone level before, during, and after gonadotropin-releasing hormone antagonist-induced testicular suppression and weekly ejaculatory frequency in relation to male social rank. The two highest-ranking males were 4 years old and sexually inexperienced, but were high-ranking as a result of being natal males born to high-ranking mothers. The five lower-ranking males, averaging more than 12 years of age and sexually esperienced, were recent immigrants into the social group. Within each subgroup of males, lower-ranking males have higher correlations between testosterone and behavior, suggesting a greater dependence upon hormonal stimulation for the occurrence of sexual activity. * $P < .10$; **$P = .04$; *** $= P < .001$.

When his testosterone level was high he mated, and when it was low he did not. As was argued for female rhesus monkeys, these findings support the notion that hormonal influences on sexual motivation are more critical in competitive social situations and either less critical or not necessary at all under noncompetitive conditions.

Although male sexual motivation does not undergo monthly cycles and is relatively constant with full testicular function, it appears that male sexual motivation serves a similar function in males as it does in females. For both sexes, sexual motivation is a critical modulator of sexual behavior only under specific social conditions, and sexual behavior can occur without any apparent hormonal input at all. The dramatic effects of social context, particularly the opportunity for intrasexual competition, in both male and female rhesus monkeys suggests that this system of hormonally modulated sexual motivation evolved as an adaptation to the problems of sexual activity in a complex social environment.

Final Considerations

In recent years the relative sex drives of males and females has been debated, in part in the discussion of gender equality (Oliver and Hyde, 1993), and partly in the discussion of evolution (Symons, 1980; Buss, 1989). The evidence presented in this chapter suggests resolving this debate by reframing the issue. It is not whether men

and woman have equal sex drives, but whether they have the same pattern of sex drive? The primary difference between males and females across mammalian species is that the male sex drive is more or less continual, whereas the female sex drive is discontinuous and, in most cases, cyclic. When females are sexually motivated they are as intensely, or perhaps even more intensely, interested in sexual activity as are males. However, this heightened interest in sex occurs less frequently for females than it does for males. Data on human sexual behavior, ranging from the frequency of masturbation (Oliver and Hyde, 1993; Leitenberg et al., 1993) to the number of sexual partners (Oliver and Hyde, 1993) support the notion that sexual interest in females is less continuous and demanding.

The intermittent nature of female sexual motivation may contribute to the higher incidence of low sexual desire reported in women (Lief, 1977; Segraves, 1988). Compared with a male standard of relatively constant sexual interest, women would appear to have lower sexual desire. Recognition that many women's sexual interest varies across their menstrual cycle and that hormonal preparations that suppress ovarian function will affect female sexual desire might result in less sexual dissatisfaction in relationships and lead to different therapeutic assessments and treatments.

In addition, comparisons of male and female sexuality are clouded by the fact that female sexual arousability, as in males (Kwan et al., 1983; Carani et al., 1992), appears to be little influenced by her hormonal state (Schreiner-Engel et al., 1981; Slob et al., 1991, 1996), but cycle phase may affect her initial response when she is observed in a laboratory (Slob et al., 1991, 1996). Women with low sexual motivation, who are less likely to initiate sexual activity, are still sexually arousable and respond sexually to the initiation of their partner. Thus the occurrence of sexual intercourse often reflects the woman's capacity to be sexually aroused and not her underlying degree of sexual motivation. Distinguishing sexual motivation from sexual arousal will lead to more sensible discussions of male and female sexuality.

Why isn't female control of sexual activity as prominent in human society as it is in rhesus monkeys? The same underlying hormonally modulated motivational system appears in both, yet human sexual activity, for the most part, appears more male-controlled than that of rhesus monkeys; a woman's pattern of sexual activity is more likely to reflect her partner's sexual motivation than her own. One likely possibility is that most human societies have minimized systems of female social control of sexual interactions, obscuring the cyclic nature of female sexual motivation with the result that sexual interactions usually occur for the benefit of males (Smuts, 1995; Hrdy, 1997). It may appear to some that marriage and the nuclear family put males and females on an equal footing, but the data suggest that these are factors that put females at a sexual disadvantage. Despite a cyclic fluctuation in desire and motivation, women show a relatively constant pattern of sexual activity.

In rhesus monkeys, a strongly female-bonded society (Wrangham, 1980) combined with a minority of males allows females to regulate sexual intercourse according to their desires. Under these circumstances mating is regulated by females and occurs over a relatively limited number of days. In this regard it is interesting that the conditions wherein rhesus monkey males seem to control mating occurs in pair tests in small areas (Michael and Zumpe, 1970; Bonsall et al., 1978; Michael and Bonsall,

1979; Michael et al., 1982). Similarly, male sexual aggression is nonexistent in multifemale, multimale groups where females outnumber males by as much as nine to one, whereas sexual aggression is common on Cayo Santiago where the numbers of adult males and females are more balanced (Carpenter, 1942a, b; Smuts and Smuts, 1993). Thus, it appears that the relative role of females in regulating sexual behavior is sensitive to social conditions and that many human societies may have minimized female control of sexual activity.

It remains to be discovered whether this is related to the relatively constant sexual interest of males, which is best served by continual female sexual availability, or is purely an economic or political phenomenon (Hrdy, 1997). The fact remains that aspects of popular culture, such as assertions of a superior sex drive in men or of an equal sex drive in men and women at all times, the institution of marriage, and the use of hormonal contraceptives by females all serve to minimize or obscure the cyclic nature of female sexual motivation, and thus may reduce female opportunity to control sexual interactions that is evident in other cyclically ovulating species. A view of gender differences in sexuality that incorporates both biological predispositions and social context (Baldwin and Baldwin, 1997) may result in greater equity in sexual relations. The fact will remain, however, that only women can become pregnant and thus sexual activity for women will always be more risky for women than for men. Whether this inherent inequity must determine the character of sexual relations remains to be seen.

Zuckerman argued that sexual behavior was the cement that bonded primate society (Zuckerman, 1932/1981). Some interpreted this as requiring the continual occurrence of sexual behavior and criticized Zuckerman's view because many primates are seasonal breeders and sex is unavailable for much of the year (Lancaster and Lee, 1965; van Horn, 1980), a fact Zuckerman was well aware of from his studies of baboons. Evidence has now accumulated, at least in rhesus monkeys, that mating affects social affiliations long after mating has ceased (Wallen and Tannenbaum, 1997; Tannenbaum, 1997; Tannenbaum and Wallen, 1997). A brief mating bout can permanently alter patterns of affiliation between a male and a female (Tannenbaum, 1997; Wallen and Tannenbaum, 1997). Thus, while sexual behavior in a social group may be socially disruptive and risky, it has long-term benefits in terms of individual reproductive success and enduring social cohesion. The hormonal mechanisms linking increased sexual motivation with female fertility ensure that the complicated mix of risks and rewards produced by sexual activity will occur in complex primate societies. As novelists and poets have long recognized, sexual passion is one of the most dangerous, yet rewarding, of human emotions. Because of its disruptive nature society limits it in such a way that it occurs outside of 'normal' times.

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