Sex and Gender in Evolutionary Perspective

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Many biologically oriented scientists attempt to make use of existing knowledge about the biology and behavior of nonhuman primates in an effort to understand the evolutionary background of human behavior. This information has been considered especially useful in the analysis of the evolution of human sexual behavior and sex roles, both in respect to similarities and continuities between animal and human behavior and in respect to presumed major adaptations that set humans apart from other species. The following quotations, drawn from recent summaries in the fields of psychology, psychiatry, anthropology, and biology, illustrate the kinds of interests in and uses of primate behavioral data in the current literature on the evolution of human behavior patterns:

Primatological, ethnographic, and psychiatric data suggest the hypothesis that male dominance facilitates male-female copulatory behavior while female dominance inhibits it (Abernethy, 1974, p. 813).

... the weight of available evidence favors the theory that female orgasm is a characteristic essentially restricted to our own species (Beach, 1974, p. 359).

All we need to assume is that the breeding system of the more successful populations was competitive and hierarchical. The

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relevance of the primate data lies not so much in the models of our early social organization that it provides, as in the information it gives us on the primate biogram, many aspects of which we are heir to (Fox, 1972, p. 305).

The human pattern of reproduction does not resemble reproduction of any other primate. The human system is characterized by the absence of estrous cycles in the female and of the marked seasonal variations that appear to characterize reproduction in nonhuman primates. . . . The important similarities in the social lives of higher primates, such as living in year-round bisexual groups, cannot be attributed to nonexistent similarities in mating systems (Lancaster and Lee, 1965, p. 513).

In the language of sociobiology, to dominate is to possess priority of access to the necessities of life and reproduction. This is not a circular definition; it is a statement of a strong correlation observed in nature. With rare exceptions, the aggressively superior animal displaces the subordinate from food, from mates, and from nest sites. It only remains to be established that this power actually raises the genetic fitness of the animals possessing it. On this point the evidence is completely clear (Wilson, 1975, p. 287).

The reproductive advantages conferred by dominance are preserved even in the most complex societies (Wilson, 1975, p. 288).

These summaries, written in the late 1960s and early 1970s, are largely based on data developed during the 1960s in the first round of field studies on the behavior of free-ranging primates. The remarkable aspect of all the above summaries is that they are already out of date. Primatology is a fast-moving field, and early field studies suffered major biases resulting from inadequacies in sampling technique, selection of study groups, and duration of fieldwork, which distorted observations of many categories of behavior and especially those related to the roles played by both sexes in the social organization of the group and the roles played by individuals in the mating system (J. Altmann, 1974; Bernstein, 1976; Sade, 1972; Wrangham, 1974).

This chapter summarizes recent data mostly drawn from long-term field studies and developed using careful techniques of sampling the behavior of all individuals in a social system. These
new data have important implications for the understanding of
the role of sexual behavior in integrating primate societies, the
importance of orgasm in female primate sexual behavior, the
roles played by dominance and personal preference in mate
selection in primate societies, and the question of avoidance of
incestuous matings. The final section of the chapter discusses
implications for the evolution of human sexual behavior.

Orgasm in the Female Primate

Considering that sexual orgasm in the human female was thought
by many to be either a myth or an aberration and was poorly
understood even by physiologists before the pioneer publication
of *Human Sexual Response* by Masters and Johnson (1966), it is
not surprising that little was known about the sexual responses
of nonhuman female primates. In the first publication on the
subject Zumpe and Michael (1968) reported their observations
of the clutching reaction of female rhesus monkeys, which occurs
during the ejaculatory mount of the male, most often immediately
preceding ejaculation. The clamping reaction (a spasmodic arm
reflex) is associated with other female responses including looking
backward and lipsmacking at the moment of ejaculation, reaching
back and biting, or postejaculatory pelvic flexions. Frame-by-
frame analysis of 16:mm film showed that the onset of the clut-
ching reaction occurred while the male was still thrusting and that
it seemed to trigger the male’s ejaculatory spasm.

In further experimental work the clamping reaction was de-
pressed by ovariectomy or progesterone treatment but restored
by estrogen. In females with regular access to males, the clut-
ching reaction invariably occurred during the ejaculatory mount, but
in females denied access to a male for many weeks, the clut-
ching reaction occurred early in the mounting series before the male
was ready to ejaculate. Zumpe and Michael found that of a total
of 389 ejaculations experienced by three nonpregnant females,
97 percent were associated with the clamping reaction.

A few years later Burton (1971) described sexual climax in
female rhesus monkeys brought to orgasm through stimulation
of the clitoris and vagina with a simulated penis. Burton reported
observable changes associated with the female rhesus sexual
response that appear similar to those described by Masters and
Johnson for the human female: an excitement phase, a plateau
phase, sexual climax as evidenced by behavior patterns such as the clutching reaction, low-pitched grunting, rhythmic contractions of the vagina, and a resolution phase.

More recent descriptions by Chevalier-Skolnikoff (1971) and Michael, Wilson, and Zumpe (1974) on sexual behavior of captive macaques report female orgasmic responses that are not dependent on vaginal penetration. Chevalier-Skolnikoff (1971) reported that in homosexual copulations between female stump-tailed macaques, the mounting female performed about the same number of thrusts as males generally made in heterosexual copulations and on a number of occasions displayed all the behavioral manifestations observed in males during orgasm: a pause after a series of thrusts, muscular body spasms accompanied by a rhythmic, voiced expiration, and a characteristic facial expression. Michael, Wilson, and Zumpe (1974) noted similar behavior in heterosexual copulations of rhesus in which the female played the mounting role and rhythmically thrust her pelvic region along her male partner's back. A small number of these episodes appeared to result in sexual climax for the female.

The authors were particularly impressed by the fact that these male-like patterns of mounting, thrusting, and orgasm were so complete in wild-reared females in spite of the fact that the rate of rehearsal in play behavior is probably low (less than 1 percent the rate of males as measured in caged situations). They also noted that the highest frequency of this behavior was correlated with estrus, occurred only in older, more confident females, and was often associated with failure in male performance. Hanby, Robertson, and Phoenix (1971) reported similar instances of females mounting their male sexual partners in a captive group of feral Japanese macaques. In these cases too, the females involved were mature and sexually experienced, but the authors do not report responses suggesting orgasm.

Field studies are generally sketchy on female sexual responses although in one study on mating behavior of free-ranging chacma baboons Saayman (1970) reported copulation calls (a series of staccato grunts) given by females toward the end of a copulatory series in conjunction with male ejaculation. Saayman noted that the copulation call and a bounding-away reaction, which follows as the male ceases thrusting, appear to be involuntary movements, and he suggested they may represent an orgasmic response.
in the female. Like the rhesus clutching reaction, the copulation call is hormone dependent; that is, it occurs in greatest frequency during maximal genital swelling. The copulation call was most common with mature male partners, and Saayman thought that this fact may account for the high number of presentations to adult males by swollen females. The temporal relationship noted by Zumpe and Michael (1968), in which the female’s orgasmic response usually preceded the male’s by only a few seconds, may partly account for the failure of field workers to report female orgasm in nonhuman primates.

It is interesting to note that Kline-Graber and Graber (1975) consider contraction of the pubococcygeus muscle as the most important aspect of human female orgasm. Masters and Johnson (1966) refer to it as the “penile grasping reaction,” which occurs during especially strong orgasm. Chevalier-Skolnikoff (1971) has noted that this response is found in one species of primate, *Macaca arctoides*, in which a postejaculatory “tie” is effected by an anatomical “lock and key” combination involving the enlarged pubococcygeus muscle in the female and the conelike projections on the penis of the male (Fooden, 1967; Kanagawa and Hafez, 1973).

A final consideration is the role played by swelling of sexual skin in primate copulation. Generally authors have considered sexual swelling from the perspective of the male as either an aid to mounting and penetration or as a sexual stimulus. However, laboratory studies and carefully sampled field studies indicate that the most potent sexual stimulus to the male is an estrogen-dependent pheromone-like agent secreted in the vagina, and that neither redness nor swelling of the sexual skin is stimulating to the male without the presence of the olfactory cue (Michael, Keverne, and Bonsall, 1971; Michael and Saayman, 1968; Saayman, 1973). The importance of sexual swelling to the stimulation of female appetitive behavior seems to be generally underemphasized.

In general then, the evidence for sexual orgasm in the nonhuman female primate is not particularly good, but what evidence there is suggests that further research might be fruitful. A wide range of species differences exists in the copulatory behavior of the male nonhuman primate, including the patterns of precopulatory grooming, courtship, copulatory posture, mating time,
and the number of mounts preceding ejaculation (Michael et al., 1966). Similar variability between species probably exists for females, and it is reasonable to look for differences in female arousal that correlate with variations in male behavior patterns such as the number of successive mounts preceding ejaculation. Implants to monitor brain activity or contractions of vaginal muscles would help to establish the existence of orgasmic responses in the nonhuman female primate. Further observations of the social and behavioral setting would then be warranted to establish an understanding of the role female orgasm might play in particular primate social systems.

Variations in Nonhuman Primate Sexuality

The tendency for nonhuman primates to form year-round bisexual social groups has impressed many theorists as providing a background for the evolution of human society. Zuckerman (1932) first formulated the proposition that the possibility of year-round sexual behavior in nonhuman primates provides the "social glue" for stable social groups by permanently attracting males to females and their young. Lancaster and Lee (1965) reviewed the available literature on primate mating from early field studies and found that the proposition as stated could not be correct since many primate societies have major seasonal limitations on mating so that primary sexual behavior between adults may occur during only three or four months a year. Recent reviews by Eaton (1973), Rowell (1972), and Saayman (1975) clearly indicate that, although there are seasonal limitations on primary sexual behavior, in some nonhuman primate species, females have long periods of sexual receptivity and such receptivity occurs under a variety of hormonal conditions.

Most field workers assumed originally that sexuality in nonhuman female primates was limited to a five- to seven-day period around the time of ovulation and that female primates were not receptive to males during other phases of the menstrual cycle, nor during pregnancy and lactation. If this were true, then an individual female's participation in mating activities could be limited theoretically to only a week every other year if she became pregnant during her first menstrual cycle after weaning an infant. Loy (1970, 1971) published the first careful study of female cycles in a free-ranging group of rhesus monkeys. At Cayo Santiago Loy
found that in the mating season females copulated during all parts of the menstrual cycle, but there were two points when copulations reached their highest frequency: one during midcycle around the time of ovulation and another just before the onset of menstruation. This continuing receptivity during the menstrual cycle with two peaks of higher receptivity (coinciding with dual estrogen maxima) occurs in caged rhesus and is similar to frequency of intercourse in some studies of the human female (Michael and Zumpe, 1970). Furthermore, female rhesus continue cycling during the mating season even when they have become pregnant at the beginning. Loy found that females averaged 4.2 postconception estrous periods with a range of from 3 to 7. Some of the females that did not become pregnant during the mating season continued to show estrus of varying intensity during the entire annual cycle.

Similar observations on the menstrual cycle, but with a single peak in copulatory frequency, have now been reported for the chacma baboon (Saayman, 1975), the Japanese macaque (Hanby, Robertson, and Phoenix, 1971), the pigtail macaque (Eaton and Resko, 1974), and the olive baboon (Rowell, 1972). Sexual cycling during pregnancy has been documented for a variety of monkeys and apes such as gorillas, chimpanzees, vervet monkeys, langurs, and Japanese macaques (Rowell, 1972). These data imply that in at least some species of nonhuman primates, female sexuality is not restricted to a brief period of estrus but occurs throughout the menstrual cycle and during pregnancy with increased frequencies of copulations at one or two points in the menstrual cycle: the first around ovulation and the second around menstruation. Such a description includes the sexual behavior of human and some nonhuman female primates and suggests that previous distinctions emphasizing a unique emancipation of human female sexuality from hormonal states were overdrawn.

Saayman (1975), in discussing his study of the mating behavior of free-ranging chacma baboons, stressed that an over-focus on behavior around the period of ovulation gives an inaccurate description of the full range of sexual behavior. He prefers to describe chacma mating as a rotating system in which female sexual invitations to adult and immature males and mounting of females by juvenile, subadult, and adult males occur throughout the menstrual cycle, with an elevation of frequency during the
follicular phase, particularly during the swollen cycle state. Saayman notes that previous workers have considered sex a generally disruptive agent in baboon social life. In contrast, his own field data suggest that sex may be a powerful integrating mechanism:

The mating system, comprising rotating sexual partners, may well be adapted for the periodic reinforcement of social bonds between adult females and partners selected from those age classes of males which are capable of integrated copulatory responses. It is likely that such a system functions to promote, rather than to disrupt, friendly social relationships and consequently may contribute toward the maintenance of troop cohesion (Saayman, 1975, p. 184).

Other studies from both laboratory and field suggest that sexual stimulation may be one of the most powerful expressions of an emotionally bonded relationship in a number of primate species. For example, Hanby (1974) analyzed the importance of male-male mounting in Japanese macaques to amicable play relations among both adult and juvenile males and to recementing social bonds when the social group was stressed, rather than to affirm dominance relationships. Erwin and Maple (1976) described reciprocal copulation in a closely bonded pair of male rhesus raised alone together. Chevalier-Skolnikoff (1974, 1976) published descriptions of the wide variety of sexual activities in *Macaca arctoides*, such as homosexual and heterosexual copulations and mutual masturbation, which included reversals of sex roles as well as inclusion of both adults and young. She emphasized that this wide variety of sexual behavior occurred in an amicable social context and was most likely to occur between individuals with special friendships to each other (see Figure 1).

Chevalier-Skolnikoff’s observations come from a single laboratory group. However, other investigators working with *M. arctoides* have noted similar behaviors, such as female-female copulation with orgasm (Kling and Dunne, 1976; Mass, 1972). Since there are no field studies on this species of macaque, it is not clear whether the relative openness of sexual behavior of *M. arctoides* represents a response to captive conditions or a species’ specialization in social and sexual behavior.

Sexual behavior is clearly a very important way of expressing and maintaining special affectionate relationships in nonhuman primates. Its use is seen in two very different aspects of primate
Mounting with unilateral manual genital stimulation between two males. The female-female homosexual mounting position.

Mounting with mutual oral genital stimulation between two males. A supine position observed during both heterosexual coitus and female-female homosexual interactions.

Mounting with unilateral oral genital stimulation between two males. Mutual presentations with manual genital stimulation between two males.

Fig. 1. The variety of heterosexual and homosexual interactions observed in captive Macaca arctoides (Chevalier-Skolnikoff, 1974).
behavior. First, it can be found in the relative emancipation of female sexual behavior from the restrictions of the mammalian estrous cycle in a number of, and perhaps most, Old World monkey and ape species. Second, it can be found in the widely occurring phenomenon of the use of either primary sexual behavior or of sexual behavior patterns, such as mounting, presentation, and genital investigation, in nonsexual contexts to express special affinity and affection between individuals. As Wickler argued in *The Sexual Code* (1973), sexual behavior patterns are a primary medium of primate social interaction irrespective of whether a fertile copulation is likely to occur. One final implication is clear: that the sex roles of male and female primates as manifested in copulatory positions, initiation of sexual activity, sexual responses, and variety of sexual contacts, are not strictly sex specific among nonhuman primates and that each sex may play the "opposite" role at particular points of the life cycle or in certain social contexts.

Dominance and Reproductive Success

The priority-of-access model pervaded most of the early field work on primate social behavior. The assumption was that high dominance status among males provided the individual with priority of access to all environmental incentives, ranging from food and sitting positions to choice of mates. Extending this further, researchers assumed that, if only one female were in estrus at a particular time, then the most dominant male of the group would control sexual access to her, especially during her most fertile days. Implicit in this assumption was either that females exercised little choice in who impregnated them, or that they naturally preferred males high in the dominance hierarchy for sexual partners. The first field studies on baboons (DeVore, 1965) and rhesus (Kaufmann, 1967) appeared to support the model, and subsequent generalizations as in Wilson (1975) and Fox (1972) were stated as if the case for natural selection favoring dominance through male reproductive success were a settled issue. However, a number of recent publications have discussed complex problems making the collection of adequate data extremely difficult because of a variety of built-in biases of early field work, in which data was collected on an *ad libitum* basis.
Problems Related to Sampling

One of the principal biases of ad libitum sampling is that it produces high frequencies of data on the behavior of easily observed animals, usually males, high status individuals, and females with young infants (Altmann, 1974). Often the behavior of other group members is hardly sampled at all. Drickamer (1974b) studied correlations between social rank, observability, and sexual behavior among male rhesus in a free-ranging colony at La Parguera. He found that the frequency of ad libitum behavioral observations on males was directly correlated to dominance status, with the frequency of appearance of high-ranking males being 82 percent, medium-ranking males 56 percent, and low-ranking 36 percent. When he sampled the rate of observability of females known to be in estrus, he found that on average only 37 percent were visible at any one time. Since dominant males control sexual access to estrous females mainly through visual control of the environment and harassment of subordinates' attempts to copulate, there are obviously numerous opportunities for subordinate, subadult, and juvenile males to copulate with estrous females out of sight of dominant animals.

Many field workers have noted that copulations by immature and subordinate males are usually secretive and sometimes hasty. Recent laboratory studies suggest that in some species it is only necessary for a dominant male to be visible for immature males to be sexually inhibited. Perachio, Alexander, and Marr (1973) found that the presence of a dominant rhesus male could inhibit electrically evoked mating activity by subordinate, wired males with receptive females. When the dominant male was removed from sight, both spontaneous and evoked mating behavior reappeared in the wired male. Similar observations have been made by Trollope and Blurton-Jones (1975) on captive Macaca arctoides in which subadult males demonstrated temporary inability to mount when paired with adult females in the presence of the adult male of the group. Removal of the adult male brought instantaneous recovery and normal copulatory patterns.

A number of field workers have reported on similar behavior patterns in which dominant males either inhibit or interrupt copulations between subordinate and immature males with estrous females. These interruptions do not prevent the pair from
mating but simply alter the location of the copulation to an area beyond the visual control of the dominant animal (Hanby, Robertson, and Phoenix, 1971; Hausfater, 1975a; Stephenson, 1975). It seems obvious that the only really reliable data on copulatory success will come from studies that use careful sampling techniques, the best being continuous observation of a female throughout her entire period of fertility.

Another difficulty results from short-term sampling. The question is whether individual males have long-term, stable status or occupy different dominance positions during various periods of the life cycle. In general it seems that while status hierarchies among females are highly stable over long periods of time, the opposite is the case for males. Two major factors influence fluctuations in male status: the high rate of turnover among males attached to a stable group of females and the effects of maturation on individual status. During the first 400 days of his study on dominance and reproduction in the yellow baboon, Hausfater (1975a) found that there was a demographic change (because of birth, death, and migration) in the number of adult males in the study group once every 13.3 days; among adult females the comparable figure was every 57.1 days. Agonistically induced changes in the ranking of adult males occurred, on the average, once every 21.0 study days, while none occurred among the females during the entire period. In analyzing the duration of rank occupancy he found that the number of ranks occupied per adult male during the 400 days was 3.6 and that for ranks 1 to 9 in his study group there was an average of 8.5 changes in occupancy in each rank. He concluded:

Thus, whether the rank occupancy data are ordered by rank of occupant or by identity of occupant, it is clear that adult males in the study group changed their rank frequently during the study period and, conversely, that no dominance rank was occupied exclusively by one particular male (Hausfater, 1975a, pp. 61-62).

Studies on Reproductive Success

Studies of reproductive success are likely to be useful only if they are designed to generate data on sexual behavior of all age/sex classes, with careful observation and sampling techniques. A number of studies that at least partly meet these criteria have
been published recently: Lindburg (1971) on forest rhesus in India, Drickamer (1974a, 1975) on rhesus monkeys at La Par- guera, Saayman (1970, 1975) on the chacma baboon, Hausfater (1975a, 1975b) on the yellow baboon, Enomoto (1974) and Stephenson (1975) on the free-ranging Japanese macaque, and Hanby, Robertson, and Phoenix (1971) and Eaton (1974) on a natural troop of Japanese macaques maintained at the Oregon Regional Primate Center. Although these studies hardly represent the full range of primate species, they represent the species in which dominance hierarchies seem particularly important in social life. Therefore, they constitute a good sample of societies that might provide support for the priority-of-access model.

There is only one study in this group that gives data on the reproductive advantages of high-dominance status, however, and that is Drickamer’s investigation (1974a) summarizing ten years of reproductive data for adult female rhesus monkeys in a free-ranging colony. He found that a larger percentage of high-ranking females than low-ranking females gave birth each year, that daughters of high-ranking females produced their first infants at an earlier age than daughters of low-ranking females, and that infants born to high-ranking females had a higher rate of survival than the young of low-ranking females. The other studies, all of which concentrated on male copulatory success, generally concluded either that there was no correlation between dominance and copulations or that the correlations were low and not consistent with a priority-of-access model. The summary findings of these studies follow.

**Short-term Alternative Reproductive Strategies.** Hausfater (1975a) gives the most cogent discussion of alternative male reproductive strategies in dominance-oriented social systems. He found that an individual male baboon tends to adopt the strategy most appropriate to his age and status. Mature, high-ranking males tend to concentrate their reproductive efforts on only a few

1. Rowell points out that Drickamer’s data does not correct for age effects. Since the correlation between age and rank is consistent among rhesus females, it is likely that Drickamer’s data attest to the success of the experienced mother in raising her young and in particular of older females with adult and subadult daughters as maternal helpers (personal communication).
mature females by forming consortships with them on approximately the two or three days around the time in the cycle that laboratory studies have shown to be optimal for insemination. This strategy maximizes the possibility of impregnating a female while minimizing the possible negative costs of consortship (such as loss of eating time, fights) by concentrating on only a few days of a female’s cycle. Other mature males follow a reproductive strategy of forming consortships with any female showing estrous behavior; this would include copulations with adolescent, pregnant, and young females as well as with mature females during the days of the menstrual cycle in which the likelihood of conception is reduced but still possible. A third strategy is carried out by subadult and juvenile males, who combine the strategies of the other two groups by concentrating their mating attempts on females about the time of ovulation, but without showing strong partner preferences. They avoid the negative consequences because they do not form consortships. They are able to compete only by maintaining constant vigilance and copulating with other males’ consorts during brief moments when the more dominant males are distracted. No one strategy is more effective than the others, but each strategy is more appropriate for a particular male at a particular time and place.

**Personal Mating Preferences in Males.** A number of authors were impressed by strong personal preferences in choice of mating partner found especially in fully mature, socially important males. Such preferences were so strong that dominant males often refused copulation to nonpreferred females even when they were the only females in estrus. What underlies such individual choices is not completely clear. Enomoto (1974) reported that Japanese macaque males showed strong preferences for mating with specific lineages of females and avoidance of others; Stephenson (1975) found such choices in Japanese macaques related more to what he called “social class” than to lineage; for example, high-ranking males preferred females from high-ranking lineages; Hausfater (1975a) and Saayman (1970) found what they felt was simply personal favoritism on the part of individual male baboons for individual females.

In a laboratory study on pigtail macaques Goldfoot (1971) found that a male, when given choices between joining females
of various social ranks and estrous conditions, showed that high rank in a female was more important than her ovarian condition in determining his choice of cage mate. Perachio, Alexander, and Marr (1973) also noted a male preference for dominant females, which partially overrode a preference to copulate with females in estrus. Among rhesus macaques and baboons, favorite partner relationships extend into nonmating contexts and throughout the year, strongly suggesting the development of personal attachments between particular males and females that include higher rates of sexual activity (Agar and Mitchell, 1975; Ransom and Rowell, 1972; Saayman, 1970). Most investigators have stressed that personal preferences work against the priority-of-access model because preferences tend to leave young, immature, low-status females or particular subsets of females free to mate with other males.

Correlation of High Status with Age. A number of authors have reported that the single most important correlate of high status is maturity, not fighting ability or social aggressiveness (Drickamer, 1975; Hanby, Robertson and Phoenix, 1971; Hausfater, 1975a; Stephenson, 1975). Saunders and Hausfater (in press) devised a computer simulation of differential reproduction with respect to dominance rank in males, using Hausfater's field data on the yellow baboon. They found that the highest correlations with a male's probability of consorting with a female during her most fertile day were longevity, then the initial rank of the male when he first began his reproductive career. In other words, the males that father the most offspring are those who live the longest, and since initial adult rank correlates most strongly with maternal rank in many primate societies, the second most important factor is likely to be the social status of a male's maternal lineage.

Among most species of Old World monkeys and apes as well as among humans, male social maturity is delayed several years beyond that of female age-mates. Reproductive maturity as measured by ovulation and presence of viable sperm roughly coincides in primate males and females, but most primate males take additional years to reach full adult body size. During this period female peers are raising their first young. In the most highly dimorphic species the difference between the sexes in
reaching maturity is the greatest, and in species of low dimorphism the difference is usually the least.

In some species full social maturity may take even longer to reach than does adult size. For example, Stephenson (1975) found that among free-ranging Japanese macaques, leader or central males were usually between the ages of fourteen and twenty-five. If dominance really correlates with full social maturity—or even middle age—in many primate societies, then high status may be a normal part of the male life cycle. But considering the action of natural selection on such populations, it is important to remember that most males do not live long enough to gain high rank. Large numbers of juveniles and subadults die before reaching maturity. Because population explosions result when free-ranging monkey groups are fed artificially, these premature deaths have been attributed to limited food supply.

Dittus (1975) published demographic statistics on a stable population of free-ranging toque macaques in Sri Lanka. The highest probability of survival was found in animals that had attained effective breeding age: for young adult females (4½+ years) the probable average number of years of life remaining was 16.6, and for young adult males (7+ years) it was 10.5 years. Among juveniles the death rate of both males and females was very high. Only 15 percent of the females and 10 percent of the males reached effective sexual maturity. Mortality peaked during the first months of life for both sexes. For males the risks were equally high in adolescence: approximately 72 percent of males who reached adolescence died between the ages of four and seven years. Adolescence is a high risk point for males in many primate populations because at this age males leave the protective custody of their mothers and the play group and begin to circulate among other social groups in the area. Increased risks come from predators, wounds from fighting with male strangers, and probably from accidents. Demographic data suggest that competition between males for impregnation of females is best understood in relation to differential survival to full maturity, which includes many factors beyond aggressive potential and dominance, such as efficiency in food metabolism, resistance to disease and infections, ability to form positive social attachments, and just plain good luck.
Correlation of High Status with Time Spent in Group. In an analysis of status among rhesus macaques living in free-ranging colonies Drickamer and Vessey (1973) found that, besides the high correlation of rank with age, there was an even more significant relationship between status and length of time of group membership. Norikoshi and Koyama (1975), in a study of dominance rank and group shiftings of male Japanese monkeys over an eight-year period at Arashiyama, found that a total of fifty-four males moved out of their natal groups and eight remained. The authors found no correlation between social rank and body weight among adults but did find strong positive correlations with age and also with length of time in the troop. Several factors may lie behind these correlations. First of all, among both rhesus and Japanese macaques, males born into high-ranking lineages tend to stay in their natal groups. However, it appears that remaining in the natal group is an exceedingly rare event when the total male population is considered, even though the top leadership positions of a group are sometimes occupied by males born to the top-ranking female lineage (Enomoto, 1974; Itoigawa, 1975; Norikoshi and Koyama, 1975).

A migrating male is more likely to stay long enough with a group to build up seniority and high rank when he is accepted by the resident females and permitted access to the central part of the group. Rejection of migrant males by resident females has been reported by Neville (1968). Breuggeman (1973) noted that whether a male is central or peripheral in status among rhesus at Cayo Santiago depends on female acceptance. Neville (reported in Agar and Mitchell, 1975) found that the rhesus males who remained permanently with a newly joined group were those who had formed consortships during the mating season. The readiness with which group females form coalitions against males deemed threatening to an infant has been observed for many primate species, including the vervet monkey (Lancaster, unpublished data), the North Indian langur (Hrdy, 1976; Jay, 1965), and the rhesus macaque (Lindburg, 1971). There are few indications as to the specific status of these males (central, peripheral, newcomer, and so on), but in general, females with infants prefer the presence of fully mature, well-known males. Much of the data indicates that, among species in which males enjoy central social
positions (such as baboons, macaques, and vervets), access to centrality is based on acceptance by resident females. Males not accepted have difficulty staying with the group long enough to build up seniority and high status in the male ranks.

**Female Choice.** Few field workers have seriously studied the question of female choice in mating among monkeys and apes. However, field work publications are filled with reports of females soliciting copulations and refusing copulation attempts by keeping their hindquarters lowered. As Stephenson noted in discussing Japanese macaques:

In the mounted position, the male probes for the vaginal opening with his penis. If the female has not raised her rump to the proper height, her vaginal opening will be at the wrong angle to the male's penile probes and he will not achieve intromission. This means that the female can control whether a male will succeed in his attempts at intromission; hence mounting with intromission is taken as evidence that the female is sexually receptive (Stephenson, 1975, p. 75).

Hausfater (1975a) found consistent female preference for mating with the higher-ranking male within the subset of group males with whom she mated. Saayman (1975) felt that female chacma baboons seek mature partners because these males stimulate them to orgasm. In his main study group, females showed sexual preference for the third-ranking mature male, who was the least aggressive and who frequently intervened on their behalf in agonistic situations. In a laboratory experiment on female sexual preference in pigtail macaques, Eaton (1973) found that females showed strong aversion to one highly aggressive male who frequently attacked them. Other preferences and aversions for particular males were highly idiosyncratic but important in understanding individual behavior patterns.

Tutin (1975) analyzed chimpanzee partner preferences in over one thousand copulations observed during a fifteen-month period at the Gombe Chimpanzee Reserve. The sexual behavior of nonparous and parous females differed widely. Nonparous females had a very low probability of pregnancy (chimpanzees cycle for several years before the first pregnancy), and such females most commonly copulated promiscuously with the local male population. Parous females, on the other hand, usually formed secluded
consortships during estrus. Tutin reported that the frequencies of male involvement in consort behavior did not correlate with age, dominance, or the amount of agonistic behavior directed toward females. Instead, males that spent the most time grooming females in group situations and males that were generous to females in food-sharing were the most likely to form successful consortships. Tutin concluded that social and caretaking characteristics of male chimpanzees appear more important for their reproductive success than dominance status.

Modern evolutionary theory, particularly as stated by Goss-Custard, Dunbar, and Aldrich-Blake (1972), and Trivers (1972), makes a strong case for female selectivity in primate mating patterns. In contrast to the male, the female monkey or ape has a limited number of opportunities during her lifetime to pass on genes to succeeding generations. Also, the successful rearing of offspring demands considerable parental investment for female primates compared with many other mammals. For these reasons, natural selection must favor females who are selective in whom they permit to impregnate them. The most obvious choice is the fully mature male, one who has demonstrated his ability to survive when perhaps 90 percent of his birth cohort has succumbed to genetic unfitness, disease, malnutrition, infection, accidents, and fights.

In his analysis of mate selection by rhesus macaques in India Lindburg (1975) noted the preference for alpha males shown by estrous females, especially around the time of ovulation. Lindburg concluded that the higher-than-expected, observed success of alpha males in mating was related to female preference and not to the male's ability to dominate other males and limit their access to females. The correlation of alpha-male status with age and seniority in the group fits well with this concept. The alpha male's status demonstrates his genetic fitness in the sense that he has proven his ability to survive to middle-age, and his seniority and centrality in the group demonstrate his social skills in forming stable social relations and protecting weaker group members.

In a review article on dominance, aggression, and reproduction in primate societies, Bernstein (1976) emphasized the importance of the "control role" in primate social systems. This role consists primarily of behavior involving vigilance and buffering the group against various sources of disruption and disturbance. Because
the salient features of the role relate to group protection and not to acquisition of personal incentives, the role can be observed even in species lacking evidence of a dominance hierarchy. Bernstein summarized the control role as follows:

Alpha males, however, were noted to maintain their position through social skills as members of a central core or alliance, and high rank was related primarily to seniority. Moreover, alpha males responded actively to challenges to the troop and were judged to contribute significantly to the survival of infants. It was therefore hypothesized that increased genetic fitness related to the increased survival of immature animals in the troop, most of which would already be the offspring of senior (and hence alpha) males. Selection would then be for the social skills leading to successful alliances in troop defense. Such skills might also relate to female partner preferences thus increasing the reproductive effectiveness of alpha males at any point in their careers, including years prior to and following their assumption of alpha rank (Bernstein, 1976, p. 459).

Avoidance of Incestuous Matings

The anthropological and psychological literature picked up very quickly on a report published by Sade (1968) on the inhibition of son-mother mating among free-ranging rhesus monkeys. Generalizations usually had focused on the supposed presence of a precultural incest taboo for nonhuman primates. Subsequent studies show that the reality of incest avoidance in monkeys and apes is much more complex. The data are still very inconclusive—but intriguing.

Recent data published on a wide variety of Old World monkey species show that males are generally much more mobile than females in respect to social group membership: Gartlan (Gartlan and Brain, 1968) on the vervet monkey, Lindburg (1969) on the free-ranging rhesus in North India, Drickamer and Vessey (1973) on free-ranging rhesus colonies, Dittus (1975) on the toque macaque, Itoigawa (1975) and Norikoshi and Koyama (1975) on the free-ranging Japanese macaque, Parker (1975) and Hausfater (1975b) on the yellow baboon. All of these studies indicate that females form the stable, organized core of a long-term social group, and males compose a more or less shifting population within a neighborhood. Most agree that males may transfer a number of times during their lives and that all but a small
minority leave their natal groups during adolescence and early adulthood. In groups in which mating is seasonal, much of this group shifting begins slightly before the onset of the mating season and continues until the beginning of the birth season. Higher rates of aggression and fighting also are apparent during this period. A number of authors have remarked on the importance of estrous females in attracting shifting males to join their group. For most nonhuman primates the likelihood of mother-son and brother-sister conceptions is extraordinarily low because they do not spend adult life in the same social group. The frequency of father-daughter incest is undetermined since paternity is unknowable (presumably to both the observer and the animals) in the vast majority of Old World monkeys and apes. One point that has not been carefully considered is whether males who have survived to full adult maturity avoid returning to their natal groups or simply circulate freely among all the social groups in the neighborhood. Although the data are inconclusive because of small samples and short-term observations, there are a few records of males returning to their natal groups.

The most recent field data on the closest living relatives of humans (the chimpanzee and gorilla) provide a very different pattern of group attachment than that reported for Old World monkeys. In the gorilla (Harcourt, Stewart, and Fossey, 1976) both young males and young females leave their natal group around puberty: the male to wander alone or establish a new group of his own, the female to join other groups until she finds one in which she can successfully rear young. Among chimpanzees at the Gombe Reserve Bauer (1976) found that females showed much lower intrasexual bonding than males of the same community and that young females often transferred out of their natal community, whereas males did not. The net result of these sex differences in group attachment is the same as that for Old World monkeys; high rates of inbreeding do not occur, because of differentials in mobility and group attachment between the two sexes.

Most interesting issues revolve around whether inbreeding is limited because strange females are more attractive to males than familiar ones and vice versa, or because there is some clear aversion to mating with close relatives. In his first observations on the subject of mating behavior of a group of free-ranging rhesus at Cayo Santiago, Sade (1968) formulated the hypothesis that
an adult male who remained in his mother’s group was inhibited from copulating with her by her higher dominance rank, although this inhibition did not apply to unrelated females who were dominant to him. A more recent study by Missakian (1973) on a different group at Cayo Santiago and subsequent observations by Sade (1972) on his original group indicate that son-mother copulations are not unusual during the late adolescent/early adult period of the male life cycle for those males who remain in the natal group. In fact, Missakian found the mother to be the preferred sex partner in some cases. The question of relative dominance rank is unclear since this is the time period when male rhesus become dominant over their mothers (by virtue of growth in size), but both Sade and Missakian observed copulations when the son was still subordinate to his mother.

By the time full adulthood is reached among Old World monkeys, the number of males of a birth cohort still living in their natal groups is very small. However, studies on a large number of groups of Japanese macaques (Enomoto, 1974; Itiogawa, 1975; Norikosi and Koyama, 1975) indicate that among the fully adult central males in a social group, the number of sons can be proportionally high. Enomoto found that the first three dominance positions in his study group were held by males belonging to the dominant female lineage. These males showed positive behavior toward females (mothers, sisters, aunts, cousins) of their own lineage when these females were in estrus, but the females showed strong preferences for mating with those central hierarchy males who had transferred into the group. This finding is opposed to the observations of Sade (1968) on rhesus and Goodall (1968) on chimpanzees. Both Sade and Goodall reported active sexual solicitation of sons by their estrous mothers and refusal to mount by the sons. Matings between brother and sister have been reported in the literature on rhesus: Loy (1971) found brother-sister matings at Cayo Santiago close to random frequencies, but Missakian (1973) found that, once brothers reached full adulthood, they no longer copulated with their sisters even if they stayed in their natal group.

The frequent observation that some males prefer or avoid mating with specific subgroups in baboon and macaque societies may indeed reflect preferences for mating between individuals from unrelated genealogies. Wade’s laboratory study on the response to strangers by rhesus monkey social groups may be
relevant. Wade (1976) found that, when given alternatives, males showed preference to forming social alliances with less-familiar over more-familiar females. Females, on the other hand, preferred to form alliances first with males, then with familiar females, and last with unfamiliar females. Females also showed reduced social tolerance of strange females when in the presence of a male. Such basic social preferences may underlie complex behavior patterns such as male transfers between neighborhood social groups or reduced frequencies of mating between closely related individuals.

Conclusions

Attempts to establish a primate background from which to view the evolution of human sex and gender have been based on meager scraps of data and observations without controls. Until recently, at least, we have known little about what nonhuman primate sexual behavior really is. Most generalizations have been based on presuppositions of what primate sexual behavior ought to be, backed up with the few supporting facts available. Since 1970 a number of more informative studies from both the laboratory and the field have been published. Some of these studies were performed specifically to gather data on reproductive behavior in nonhuman primates, and for the most part the data were gathered using carefully controlled sampling techniques. Some of these new data only raise more questions, but other data have important implications for developing a perspective on the evolution of human sexual behavior.

One of the most significant generalizations to come from the new data is that, like humans, Old World monkeys and apes do not engage in sexual activity only around the period of ovulation. Many different species use primary sexual activity or behavior patterns drawn from the sexual repertoire to express and cement positive social attachments. Primary sexual behavior between members of the same sex, between adults and young, and between adult males and pregnant, menstruating, or anovulatory females is not uncommon among nonhuman primates. In nonhuman primates the stimulation and rewards of sexual behavior appear to be important mechanisms of social attachment, in some species possibly comparable to behavior patterns like grooming. The evolution of human sexual behavior must be understood...
as derived from a primate background in which sexuality was already a prominent feature of social interaction. In a recent analysis of reproduction in the human female, Newton (1973) noted the importance of sexual stimulation and orgasm in all major aspects of a woman’s reproductive role, including coitus, labor, and nursing. Because sexuality is one of the most potent biological stimuli and orgasm one of the most potent rewards, it is not surprising that this system should feature prominently in the social behavior of a species whose adaptations are so highly committed to long-term, individualized, social attachments.

A second major consideration is the notable lack of evidence that female behavior and social status in nonhuman primates are largely under the control of hormonal cycles. All of the recent field studies emphasize that under normal social circumstances there is no correlation between social status and sex hormone state. On the contrary, they emphasize the general stability of female social status and dominance rank irrespective of whether a female is in estrus, anovulatory, pregnant, or lactating. Furthermore, in some species of nonhuman primates, female sexual behavior appears to be very similar to that of humans in one important respect: Females can be active in seeking copulation during all parts of their sexual cycle, even though higher frequencies of coitus occur around ovulation and just before menstruation. Such a degree of emancipation of sexuality from sex hormone cycles might be expected in species using sexuality as a major means of forming social attachments. The ability to be selective in mating partners during estrus can also be viewed as an important step in the evolution of volitional control over personal sexuality. Continuous sexual receptivity in human females is not the same thing as continuous estrus. Continuous sexual receptivity provides the female with ready and regular options for sexual activity, an evolutionary development of great importance considering the high amount of parental investment a human female must give to rearing a child successfully.

A third important generalization is the lack of evidence for major sex role differences in regard to important aspects of sexual behavior. For example, field data suggest that both males and females play active roles in selecting mating partners, in seeking consummatory responses, and in forming sexual attachments. Furthermore, accumulating evidence suggests that the
roles are not rigidly sex specific and that there is wide variation among species in the roles that males and females play during various periods of the life cycle and under different social circumstances.

Perhaps one of the most significant generalizations for the development of evolutionary theory is the relationship of dominance to reproductive success in complex social systems. Much more work needs to be done in long-term studies covering the entire life cycle of individuals, but it seems probable now that the elusive quality of "dominance" correlates most strongly with full social maturity and length of tenure in a social group and not with aggressive potential per se. As such, it is a part of the normal life cycle of those individuals who live long enough to become dominant. Competition between males for access to females is based mainly on ability to survive, and not on anything so stark as physical intimidation. Furthermore, being in a dominant role represents only one of several effective strategies for passing genes on to the next generation. Field data at present do not show that one strategy is more effective than another nor that an individual uses only one strategy during a lifetime. The probability is that these strategies are situation specific and can be used by most individuals according to their social circumstances.

The final generalization relates to the question of incest avoidance. The field studies to date strongly indicate that among Old World monkeys the male has a larger social field than the female. Typically, the male circulates among social groups in a neighborhood during various parts of his lifetime, whereas a female is most likely to spend her entire life in her natal group. This differential between the sexes in group attachment means that mother-son and brother-sister matings will be rare because they are unlikely to live in the same social group. However, a few such matings have been observed in free-ranging monkeys, particularly during the latter part of adolescence in the male. Field studies suggest that the stimulus properties of the less familiar female may have higher positive valence than those of females from the same social lineage. The attractions of the stranger may account for the lower-than-expected frequencies of incestuous matings. Similar mechanisms appear to reduce inbreeding among the African apes, but in their case it is the female who is more mobile than the male.
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