Sexuality and Sociality in Humans and Other Primates

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In the preceding chapter, Dr. Lancaster’s review of primate sexual behavior raises issues of considerable importance in efforts to understand ourselves further through comparative study. For several years, I have thought that certain unique or uniquely exaggerated attributes of the human female—such as menopause and the concealment of ovulation (the latter as compared with its advertisement in other primates)—probably represent keys to the reconstruction of the history of human sociality, if we only knew how to interpret them. More recently I have wondered if they might not even represent the principal keys for understanding the entire question of how the human evolutionary line came to diverge so dramatically from the lines of all other primates. In this discussion I will try to combine an analysis of Lancaster’s arguments with an explanation of the basis for these views and their meaning (see also Alexander and Noonan, 1978).

Comparisons of sexual and social behavior among different primate species allow us to see our own behavior in perspective with that of our closest contemporary relatives. There is also another kind of comparative study. It involves searches among even widely divergent taxonomic groups with parallel systems of, say, behavior, for correlations with other attributes which, by their independent appearance in the different groups, suggest cause-effect relationships not previously apparent. For example, Alexander and co-workers (1978) have demonstrated close correlations between harem sizes and degree of sexual dimorphism in body length in three mammalian groups with independently evolved variations in breeding systems. These findings are a quite
powerful indication that varying intensities of male-male competition are responsible for relative amounts of sexual dimorphism in all three groups.

The above comparative procedures may contribute to reconstructions of the reasons for the divergences of the human line from those lines giving rise to other primates. In turn, clarifications of the reasons for humans becoming what we apparently are may yield new insight into countless observable but incompletely understood facts of everyday human existence, and suggest new possibilities for the adjustment of human behaviors toward the alleviation of many practical and painful problems.

Dr. Lancaster examines recent data with reference to female orgasm, mate selection, incest, and the role of sex in integrating primate societies. She reviews evidence that orgasm occurs in at least some nonhuman primate females, shows that females of some nonhuman primates are sometimes sexually active outside estrus, and concludes that nonhuman primates are sexually more plastic than has been supposed. She suggests that male dominance is not as important as had been supposed in determining who mates with whom, and that female preferences are much more important than has been supposed.

I certainly agree that female sexuality in primates is considerably more complex and important than previous studies have suggested, and that female choice is a much more potent force in determining sexual and social behavior than we have usually acknowledged. I also think that the arguments for the existence in nonhuman primates of female orgasm, anestrous sexuality, and the employment of multiple strategies toward success in sexual activities are amply documented.

Proximate and Ultimate Factors
My disagreements with Lancaster—or my opinion that different interpretations will be more useful in some cases—reflect my concern with what I regard as a common deficiency in the analyses of biological and social scientists. I refer to the failure to recognize or take into account continually that proximate mechanisms exist and are maintained only because in the past (at least) they have served the ultimate function of reproduction. By proximate mechanisms I mean things like pleasure and pain—and any and all kinds of responses that could be subsumed under
learning or development, so long as the contingencies are historically relevant (and, therefore, the proximate "mechanism" is indeed a mechanism and not simply an accident or an incidental effect of some novel circumstance).

One reason why it is useful to think about the ultimate function behind a proximate mechanism is that proximate mechanisms are difficult things to understand, and we need all the help we can get. Another reason is that a proximate mechanism cannot (for long) be its own justification. Thus, the association between pleasure and, say, sex or eating does not exist because of some kind of physiological determinism: The association has evolved across our history because sex and eating have led, directly or indirectly, to reproduction. It follows that the particular manners or circumstances in which sex and eating bring the greatest pleasure ought to associate with events that in the past either most surely led to reproduction or led to the most reproduction. Bearing such thoughts in mind can assist us in analyzing the nature of physiological and ontogenetic phenomena.

There are some particularly confusing aspects of the relationship between proximate and ultimate mechanisms. For example, because we have evolved to associate pleasure with sex and eating, the connection may persist for a while even if the association with reproduction suddenly disappears. Thus, an abrupt and historically novel surfeit of food might cause us to overeat, become obese, and die young, almost certainly lowering our lifetime reproduction. Similarly, the introduction of effective, easy-to-use contraceptives allows us to indulge the pleasures of sex in ways that also almost certainly lower our lifetime reproduction. (Please note that I am not valuing success or failure in reproduction, indulgence in either sex or eating, or anyone's attitude toward any of these things—only considering their relationship to history and how that relationship might be exploited in efforts to understand humans.)

Tobacco, alcohol, drugs, innumerable products of technology, and even the results of sociological, psychological, biological, and other analyses of human sociality can also represent novelties obfuscating the relationship between proximate mechanisms and their historical functions. For the experimental scientist, whether biological or psychological, the most startling and significant realization is that essentially every experimental setup has the
potential for being so novel in terms of the organism's evolutionary history that blinding confusion is generated.

Although the introduction of novel circumstances allows exploitation of the pleasure of sex, in terms of evolution such exploitation would lead eventually to a decreased pleasure in sex, as such, because sexual pleasure would be leading to behaviors no longer enhancing reproduction. Of course, any such evolutionary effects would appear so very slowly as to be of the most trivial significance in the modern, rapidly changing world.

Sex and food cause pleasure, then, pleasure being the label we have applied to sensations that tend to cause acts to be repeated. Pleasure and reproduction have evolved to be associated because repeating acts that lead to reproduction leads to further reproduction. Conversely, pain deters us from reproductively deleterious acts. To understand the explanatory or guiding significance of these thoughts about ultimate functions, it is useful to consider paradoxical situations. For example, enormous satisfaction may result from giving one's life for a brood of offspring if it is clearly the only way to save them: We lament the situation, yet we may appreciate the opportunity to be there to save our offspring. Conversely, eating could be sheer torture if it had to occur while one's offspring or other close relatives were known to be starving.

The proposition that organisms have evolved to be reproductive systems usually seems bizarre to anyone who deals principally in human activities, yet it is quite clear that we cannot avoid dealing with it. I think that our attitude toward this proposition is itself a profoundly important topic for investigation. For reasons still unclear to me, the evolution of human abilities and tendencies to be conscious and deliberate about some activities did not carry with it abilities or tendencies to spend our waking hours totally preoccupied with conscious and deliberate plotting of how to increase our personal reproductive success—at least not in those terms. Yet, despite our tendencies to deny concern with reproduction, anyone who takes a serious look at societal laws can scarcely fail to recognize that their underlying theme—from the Ten Commandments to the legal system of modern America—is the suppression of extremes of reproductive competitiveness by the individuals making up societies. The parade example is the uniquely human phenomenon of socially imposed monogamy. The acquisition of culture resulted in cumulatively heritable
differences in resource control among individual humans leading to unparalleled degrees of difference in reproductive potential, especially among males, and even within small social groups. Yet men who are clearly capable of keeping several or many wives and successfully rearing their offspring are prevented by law from doing it, and this has apparently been true in every large, highly organized, highly unified society in history (for example, the industrialized or technological nations). Flaunting of this particular law, as Joseph Smith and his followers discovered, is one of the behaviors that may lead to death by lynching. Death penalties have historically been associated with what seem to me to be the most dramatic exploitations of others for the purpose of increased reproductive success—for example, through killing, rape, or treason (Alexander, in press).

Contrary to a widespread misimpression, the evolutionary or reproductive view of human behavior does not mean that we are forced to behave in any particular fashion in any particular circumstance; we are not subject to a genetic or ontogenetic determinism that somehow violates our own views of our potential for personal decisions or exercise of free will. Any modern human with knowledge of history and the power of self-reflection potentially can do essentially anything he wants to do with his life, including deliberate nonreproduction, or a life style that is consistently inconsistent with evolutionary history in essentially every regard (Alexander, in press). Nevertheless, the theory that all organisms have evolved to maximize the reproduction of their genes—even if they do not actually do so—is reasonable beyond doubt, consistent with every observation in biology, and overwhelmingly supported by biological facts gathered since Darwin. I can think of no valid reason for denying its applicability to the history of humans, as well as to that of every other organism (Alexander, 1975, 1977).

The question here is: How does this general idea relate to Lancaster's facts and arguments—especially when they seem to fall short of satisfactory conclusions? Is it of any use in evaluating the items she has so effectively brought to our attention?

Functions of Orgasms

We can begin with the function of orgasm. What is an orgasm good for? It gives pleasure—indeed it is often represented as a peak in human ability to experience intensity of pleasure. Why
should an orgasm give intense pleasure? I venture that there is no *a priori* physiological reason why it should have to be so. I am confident that any organism could be taught to experience enormous pain and displeasure with orgasm.

The reproductive significance of a male’s orgasm is obvious, even if male orgasms are frequently nonreproductive, and even if we do not understand all of the events associated with and leading up to every single situation in which males experience orgasms. Male orgasms release sperm, and when this happens during copulation, there is some likelihood that the sperm will find an egg and reproduction will result. Indeed, there is no other natural way for reproduction in humans to occur; and the one thing that we may safely assume about all of our ancestors is that they reproduced successfully.

Thus, we may speculate with reasonable confidence that the basis for male orgasms being pleasurable is that they have contributed to reproduction by releasing sperm in the proper places and at the proper times.

What about female orgasms? Lancaster raises this question but does not provide a very definite answer. At one point she suggests that “for some species” female orgasm may function as a preejaculatory trigger mechanism—in other words, that it may trigger or hasten ejaculation in the male. She does not take up the question of why this might be important, or why only in some species. Moreover, in another place she suggests that estrous females may choose mature males because the latter are more capable of stimulating them to orgasm.

I sympathize with Lancaster’s apparent uncertainty, and have pondered this question for a long time without developing a satisfying answer. One unsatisfactory (or incomplete) answer, for either male or female orgasm, is that the pleasure of the orgasm is its own reward. While this is a perfectly adequate description of how a proximate mechanism works to cause repetition of an act favorable to reproduction, it tells us nothing about how the act is favorable to reproduction, therefore, why it should be pleasurable in the first place. Possibly, female orgasm somehow increases the likelihood of fertilization of the egg through contributing to the movement of the sperm; and, even more speculatively, a female orgasm may also communicate to a male that this likelihood is enhanced—thus, that the female’s offspring of
the near future have a certain likelihood of being his own. In this case, as in general, males obviously would not be required to be aware that they have received such information, only to behave as if they know. Obviously, this speculation about function introduces the question of deception as well as the problem of male confidence of paternity. Both, I believe, are central issues in understanding human sexuality and sociality.

Rather than females simply preferring males able to give them orgasms (which may imply that orgasms are their own reward and does not seem to lead us toward an explanation of their existence), perhaps females are more likely to have orgasms with males they prefer, and perhaps they prefer those males for reasons not yet apparent. Obviously, if this last were the case, males who could cause even “inadvertent” orgasms in females with whom they copulated could sometimes, or briefly, be favored on this account—illustrating again the complexity of the issues involved here.

One possible suggestion is that orgasm in the human female (and perhaps other primates as well) may function as an indicator to the male of the female’s sexual satisfaction. Its apparent tendency, in humans at least, to mimic male orgasm, in the absence of a correlation with an event paralleling release of gametes, may suggest (1) that the correlation is instead with the pleasure or satisfaction of male orgasm to the male, and (2) that in humans the female orgasm is principally a communicative device that tends to reassure a male that the female is disinclined to seek sexual satisfaction with other males. If this interpretation is correct, female orgasm should (1) be characterized by obvious outward signs; (2) mimic male orgasms in regard to outward signs; (3) frequently involve deception, with females pretending to have orgasms when they do not; (4) occur most frequently (a) in deeply satisfying or long-term interactions with males committed to the female and her offspring, and (b) with dominant males or males with obviously superior ability to deliver parental benefits; and (5) occur least frequently in brief or casual encounters, and in copulation with a partner unsatisfactory in the above regards. All of these contingencies may correspond with orgasm in human females. All appear to be consistent with the information reported by Lancaster except for the suggestion that female primates achieve orgasms sooner if they have been deprived of sexual
activity. The idea that female orgasms are principally communicative devices is obviously consistent with reports that female primates vocalize during orgasm and sometimes turn toward the male and exhibit characteristic facial contortions or lip-smacking. Moreover, the value of direct communication during sexual behavior may relate to the still-unexplained human tendency to copulate face-to-face, almost nonexistent in nonhuman mammals except in the great apes, where it apparently occurs less frequently than in humans.

We are forced to leave the function of the female orgasm at an unsatisfactory stage, but maybe I have made the point that it is potentially enlightening to seek the reproductive significance of female orgasms. The speculation that female orgasm is primarily communicative is consistent with the suggestion that increases in parental investment, in particular by males, were an important aspect of the evolutionary divergence of the human line from those of other primates (Alexander and Noonan, 1978).

Female (and Male) Preferences

Lancaster speaks of "personal preference" regarding sexual partners as if it frequently involves nothing more significant than individuality. She notes, however, that males prefer mature females, that immature females are considered "uninteresting," and that mature females rear more babies. She also points to maturity as the most important correlate of high status and to the significance of maternal lineage as a factor in mate selection. Similar observations have been made in studies of human populations. Chagnon (1978) finds that in Yanomama Indians both sexes prefer mates from high-ranking families, and that members of high-ranking families—whether men or women—reproduce more than members of low-ranking families. Dickeman (1978) reaches similar conclusions regarding Asian societies with caste systems.

Lancaster notes that some primate females prefer well-known males and "fully mature" males. She supposes that the principal mating advantage to females is that such males have proved they have the genetic makeup to survive to a mature age, therefore are likely to produce sons with similar abilities, so that the sons also will be more successful in reproduction. This is a definite possibility.
Lancaster also suggests that males in Old World primates probably never know who their offspring are. This would appear to be an overgeneralization, since gorilla males, hamadryas baboon males, gibbon males, and probably many others who monopolize or sequester females would have an excellent likelihood of being able to direct their paternal solicitude toward their own offspring. I think we must introduce into Lancaster’s considerations on this topic the matter of parental investment by males. As soon as a male has something besides evidence of “good genes” to offer females, then females will profit from obtaining it. In the case of paternal care, one has to suppose that the female who is able to give her male a high confidence of paternity is considerably more likely to obtain his paternal care for her offspring than a female who is utterly promiscuous in his presence.

High confidence of paternity appears to be absent from multi-male social groups of all animals except monogamous birds, in which the male often is absolutely required to rear offspring, and in which males guard their females continuously during the period of egg-laying, the only time that fertilization can occur. Male parental care is clearly prominent in most societies of humans today and clearly not prominent in most multi-male societies of other primates. Katharine Noonan and I have argued (1978) that the increasing importance of male parental care may have been responsible for much of the divergence of the human line that caused us to become so distinctive from other primates. How did this change occur? Part of our scenario is quoted below:

The human female has commonly been described as “continually sexually receptive” because she may willingly mate at any time during the menstrual cycle (James, 1971). Most other female mammals mate only during a brief oestrus period occurring around the ovulatory period. To refer to the human female’s sexual behavior simply as “continuous receptivity,” however, seems a gross oversimplification. First, this “receptivity” is unlike the relatively uninhibited receptivity of some oestrous female mammals. By comparison, the human female’s behavior might best be described as a kind of selective or low-key receptivity, commonly tuned to a single male, or at least to one male at a time. From the point of view of males not bonded to a particular female, it might just as well be termed “continuous nonreceptivity.” It is a truly remarkable attribute of
human females that their ovulation is often essentially impossible to detect, even, in some cases, through medical technology.

In nonhuman primates the general period of ovulation always appears to be more or less dramatically signalled to males (even if only by pheromones or other means not obvious to human observers). All of the nonhuman primates in which females are known to show "pseudo-estrus" are group-living species, while the least obvious signs of ovulation seem to occur in monogamous species like gibbons, or polygynous species, like gorillas, which tend to live in single-male bands.

We believe that two coincident circumstances can explain the evolution of concealment of ovulation: First, a social situation in which females of reproductive age are not completely inaccessible to males other than their mates or consorts (e.g., multi-male groups or defensible multi-female territories) and, second, a growing importance of parental care such that the value to a female of a male's prowess in monopolizing her at ovulation time would be overshadowed by the value of male prowess and willingness as a providing or protective parent. Gradual evolution of concealment of ovulation by females behaving so as to maximize their mate's confidence of paternity, hence likelihood of behaving paternally, would with each step toward concealment improve the female's ability to secure her mate's parental care. Because no male could tell when a female was ovulating, only a male who tended her more or less continuously could be sure of the paternity of her offspring. Occasional forced or clandestine matings outside the pair bond, in the absence of information about ovulation, would have a very low likelihood of resulting in pregnancy (Alexander and Noonan, 1978).

Lancaster suggests that in some primates the function of sexual swellings may be stimulation of the female's own "appetitive behavior." She discounts its significance as a stimulus to the male because "the most potent sexual stimulus to the male is an estrogen-dependent pheromone-like agent secreted in the vagina... neither redness nor swelling of the sexual skin is stimulating to the male without the presence of the olfactory cue."

Proximate mechanisms entail physiological and genetic expense. We are justified in expecting such expenses to be minimized by natural selection. Accordingly, it would be very difficult to explain the extreme sexual swelling and coloration in some
primates solely by the effect on the bearer herself. We have no reason to believe that such evidently expensive changes are the only way an organism can cause itself to carry out effective reproductive behavior. Moreover, such an explanation leaves us with no way to account for the distribution of sexual swellings among primates.

I suggest this alternative: The sexual skin is a visual stimulus leading the male to investigate for the presence of the chemical indicating ovulation. This hypothesis suggests that the sexual skin is an aspect of female-female competition for attention of (the "best") males, hence leads to the prediction that sexual skin will be prominent only when multiple males are available. This prediction is realized since sexual swellings and bright sexual skin are absent in single-male species like gibbons and gorillas, and most prominent in multi-male troops as in chimpanzees, macaques, and baboons (Alexander and Noonan, 1978).

Male Dominance

Lancaster suggests that male "dominance" has been afforded too great a role in determining reproductive success. I agree that the whole subject needs careful review. One reason is that definitions of dominance have sometimes become essentially divorced from applicability to natural situations. Another is that many observations have occurred in clearly unusual situations, as in closely confined troops or in troops culled in ways that may have greatly altered the proportion and kinds of male-male interactions. A third reason is the significance of recognizing relationships among male dominance, female choice, and male parental care.

Nevertheless, I think Lancaster's arguments are somewhat vulnerable. For example, she notes that subordinates must copulate with estrous females out of sight of dominants and that subordinates are sometimes sexually incompetent in the presence of a dominant male. These and most of her other arguments indicate to me that dominance is indeed quite important. None of the arguments presented suggests that strategies alternative to attaining and maintaining dominance are anything but second best. The only reasonable hypothesis seems to be that in nonhuman primates living in multi-male bands all males strive toward dominance, and that they are diverted in this strategy toward alternatives because attainment of dominance is sufficiently unlikely
that relatively low-return diversions such as sneakiness are sometimes profitable, or are profitable for particular males only. Hausfater’s (1975) data, for example, tend to support what sexual differences in senescence patterns reveal on a much wider scale—namely, that males have evolved to play for higher stakes than have females, and are more likely to win big or lose completely. This is evidently true of humans, and of all polygynous species. Sex ratios as well as sex differences in parental behavior, time of maturation, and general behavior all support this interpretation (Williams, 1957, 1975; Hamilton, 1966; Alexander et al., 1978; see also Trivers, 1972).

Since “young, immature, and low status” females are in her own arguments poor bets in reproduction, and since copulation with “particular lineages of females” would lead to genetic inbreeding, I do not understand why Lancaster believes the fact that such females are neglected by mature males, hence “free to mate with any males,” is contrary to a “priority-of-access” model of male sexual behavior (thus, a model relying on dominance).

Sex as an Integrative Mechanism

In connection with Lancaster’s argument that sexuality was a prominent aspect of social interactions in our ancestors long before they had become human (with which I heartily agree), she suggests that sex is for things other than procreation and gives as an example “mechanisms of social attachment.” In this context she also argues against the view that sex is a disruptive force in a society and for the view that it is an integrative force. Indeed, she implies that the rewards of sexual pleasure represent the bonds around which primate social groups are formed and maintained.

I would suggest a change in Lancaster’s initial emphasis. Rather than sex being for things other than procreation, it appears that the ways in which sexual behavior actually leads (eventually) to procreation are more complex and indirect than had previously been supposed. One of these ways, for example, might be the promise or actuality of delivering sexual pleasure or unusual sexual pleasure; what we know of human behavior seems to support this view. Nevertheless, it is a more complex problem than we might think. Women whose beauty, intelligence, abilities to empathize, or other attributes seem to a great many men to
promise extraordinary sexual pleasure may be able to cause such responses because the attributes in question simultaneously promise other things historically of much greater importance, such as success in child-bearing and nursing, faithfulness, or a lifetime of cooperativeness in mutually beneficial and satisfying activities. In this context it should not escape us that, in historical and biological terms, lifetimes are no more nor less than reproductive acts; indeed, there is no other way to explain their finiteness (Williams, 1957; Hamilton, 1966; Alexander, 1977).

Lancaster also implies that sexuality may actually be the cement of group formation and maintenance. I agree, in the sense that male and female have to come together to reproduce. But to use sexuality to explain all primate groupings would not easily explain why some primates group more than others, or why some are enormously more sexual than others. Moreover, it would represent a return to using proximate mechanisms to explain ultimate ones, rather than the other way around. Group living entails expenses to the individuals engaging in it: increased competition for all resources and increased likelihood of contracting diseases or acquiring parasites. If the physiological rewards of sexuality were wholly responsible for group living, then, during history, those deviants who were not so sexy as to feel compelled to engage in group living would not suffer these detriments to their reproduction, and sociality would have gradually diminished as a result of the superior reproduction of less sexy, less social, more reproductive deviants.

Thus, there are solid arguments that group living is forced by extrinsic pressures—most notably, predators and the value of group hunting for large or elusive prey (see Alexander, 1974; Hoogland and Sherman, 1976). Whenever group living occurs as a result of such forces, it leads to increased sexual competition, since mates are also resources. Under these conditions, sexual activity becomes more prominent, and this is why sexuality is very prominent in multi-male groups, such as savannah baboons, and not very prominent in primarily single-male polygynous groups such as gorillas, or monogamous pairs such as gibbons.

Humans are highly sexual, and this is but one of many indications that human history involved living in multi-male groups. If we are to explain unique human attributes in terms of their history, then we may as well resign ourselves to explaining how
they could have evolved in multi-male social groups. It is also quite evident that humans have been polygynous throughout most of their history, meaning that fewer males than females have generally contributed genetically to each generation, that some males have been more successful in reproduction than any females, and that sexual competition was more severe among males than among females (Alexander et al., 1978). All of these things are almost certainly true of every extant human society.

Thus, it seems clear that sexuality is both a disruptive and an integrative factor in sociality, depending largely on the composition of the group; it may integrate a pair, integrate male and female in a harem, but disrupt female-female interactions; but it cannot be the principal integrating factor in a multi-male primate group (Alexander, 1974).

**Incest Avoidance**

I find Lancaster’s conclusions on incest difficult to grasp. This is not a very severe criticism, since so little is known of primate inbreeding and outbreeding, and so much confusion has existed in efforts to compare “incest” and marriage patterns in humans with breeding behavior in nonhuman primates.

It seems to me that ample data now indicate that nonhuman primates, like humans and the vast majority of sexual organisms, avoid sex with their closest relatives whenever they can, and especially sex likely to cause offspring. Thus, Lawick-Goodall (1968) found that adult female chimpanzees mate readily with most males in their groups, but resist their brothers violently. Adult males, moreover, do not mate with their mothers. Imanishi (1965) found no instances of mother-son matings in Japanese monkeys studied at Koshima, and Tokuda (1962) reported none in a captive group of rhesus and crab-eating macaques. Sade (1968) observed four mother-son matings in 363 copulations among rhesus monkeys on Cayo Santiago Island. Kaufmann (1965) reported only one instance of a male rhesus mounting his mother and another of a male copulating with his mother.

Missakian’s (1973) data on rhesus monkeys may at first seem contradictory. In her extensive observations 5.4 percent of all mount series and copulations involved mother-son pairs, and mating was observed in 31 percent of 36 individual pairs of mothers and sons. She also saw matings in 12 percent of 42
individual pairs of brothers and sisters. Of 59 mother-son pairs, 21 (36 percent) were separated when sons permanently left their natal groups. Of these 21 males, 19 left between three and five years of age, evidently at or near the onset of their first breeding season. The remaining two left at eleven and ten years of age when they were the alpha and beta males, respectively. Both of the old males became solitary after their departure.

Except for a single dominant male who mated with his mother, however, all of Missakian’s observations of mother-son matings involved young males from three to five years old who rarely or never mated with other females during that period. Of 30 males of that age who lacked mothers, only one mated with nonrelated females, and that when he was five years old. Similarly, all brother-sister matings involved males from three to five years old mating mostly with older sisters. Missakian’s observations suggest that the young males involved in these “incestuous” matings lacked access to other females. She stated as well that they failed to form the usual consort relations with their mothers or sisters. Under more natural conditions a higher mortality of males, or differences in troop structure owing to a different sort of “culling” by natural predators, could reduce even these figures. Yet her data still seem to support the argument that close inbreeding is rare in rhesus monkeys even when sons remain in close proximity to their mothers, and brothers to their sisters. We do not know whether or not mother-son or brother-sister matings ever produce offspring.

These primate data call for some interpretation. First, how does one define incest avoidance, and how does one identify avoidance of close inbreeding? What percentage of all matings should be expected to occur between close relatives when all tendencies or mechanisms for avoiding such matings are absent? One cannot simply measure time spent in close proximity in determining opportunities for copulation, although this measurement may be useful in some cases.

In a polygynous one-male band a female (or male) may have no mating opportunities except with a close relative. A prepubertal or young-adult male in any primate group may spend little or no time near females other than his mother and sisters; but how can one tell by counting his matings with such relatives whether or not selection has tended to reduce their frequency?
If young males tend to leave their natal troops before achieving success in reproduction, and if dominant males tend to leave the troops in which they have sired more or all offspring at about the time their daughters mature (Boelkins and Wilson, 1972; Drickamer and Vessey, 1973; Packer, 1975), how does one know whether a history of deleterious inbreeding or some other factor such as sexual competition is principally involved? If indirect effects such as sexual competition incidentally bring about outbreeding, then selection cannot improve tendencies to avoid deleterious inbreeding because it never occurs. Failures to outbreed under altered conditions, when the situation incidentally effective in reducing outbreeding has been removed, cannot be used to support an argument that the animal involved is incapable of evolving an avoidance of outbreeding or would not benefit from outbreeding.

It seems to me that rather than incest avoidance being rare in nonhuman primates, in all those (few) species that have been adequately studied, some degree of avoidance of close inbreeding has been observed. How this relates to complex incest and marriage rules and patterns in humans, and the relationships of the various causal factors in the two cases, is another matter entirely.

References


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