

INCEST AVOIDANCE

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ABSTRACT

There are several social and genetic reasons why the avoidance of mating between close relatives may be advantageous, and an examination and evaluation of recent research in the area of primate sexual behaviour and group interaction suggests that such an avoidance exists among the non-human primates. Furthermore, certain behaviours such as the differential dispersal of males and females in the natal area, the inter-troop transfer of individuals of one sex, and reduced sexual attraction between individuals raised in close association, may function as incest avoiding mechanisms. Yet, in attempting to account for human incest prohibitions, several authors maintain that there is no "natural" human tendency to avoid incest and that the aversion to incestuous behavior arises out of the prohibition itself. This position, however, must be questioned given the fact that the non-language bearing primates also appear to avoid incestuous matings.

L'EVITEMENT DE L'INCESTE

RESUME

Il ya plusieurs raisons sociales et génétiques pour lesquelles éviter l'accouplement des parents proches peut être avantageux; par ailleurs, un examen et une évaluation des études récentes dans le domaine de comportement sexuel des primates et des interactions de groupe suggèrent qu'un tel évitement existe chez les primates non-humains. De plus, certains comportements tels que la dispersion différentielle des mâles et des femelles dans la zone natale, le transfert inter-troupe des individus d'un sexe, et l'attraction sexuelle réduite entre des individus élevés en proche association, peuvent fonctionner comme des mécanismes servant à éviter l'inceste. Mais, en tentant d'expliquer les interdictions de l'inceste humain, plusieurs auteurs soutiennent qu'il n'y a pas de tendance humaine "naturelle" à éviter l'inceste, et que l'aversion pour le comportement incestueux est née de l'interdiction elle-même. Cette position doit cependant être remise en question vu le fait que les primates dépourvus de langue parlée paraissent aussi éviter les accouplements incestueux.

INTRODUCTION

Incest is the mating between genetically related individuals, in particular, sibs, or parents and offspring. The universal prohibition of mother-son, father-daughter, and brother-sister incest among human societies has been recognized for some time. In fact, the avoidance of incest was once believed to be an unique characteristic of man. In the past twenty years, however, observations of other mammals, especially the higher primates, suggest that some tendency toward incest avoidance may also be present in animals. This paper will examine and evaluate recent research in the area of primate sexual behavior and group interaction in an attempt to determine whether such a tendency exists among the primates, and what bearing, if any, these findings have on human incest prohibitions.

ADVANTAGES OF INCEST AVOIDANCE

Before directing our attention to the specific studies, it is first necessary to address the question of why the avoidance of matings between close relatives might be advantageous. It has been suggested that the avoidance of incestuous matings serves to remove sexual competition from within the family group of an animal, particularly of those that form strong social bonds during the course of a slow maturation process (Buettner-Janusch 1973: 349). Thus, the avoidance of incest would maintain stability within the social organization of the group. Since this paper will limit its discussion of sexual behavior to the primates, it is important to note that, in comparison to other animals, primates display a relatively high degree of social organization. Therefore, this first supposition may lose some of its validity in an attempt to explain why the avoidance of incest may be beneficial to other animals.

It has also been suggested that the avoidance of mating between closely related individuals may be advantageous, in that it prevents the genetic consequences of extensive inbreeding. A certain amount of controversy, however, surrounds the nature of these consequences. Much of the discussion centers around "inbreeding depression" which can be defined as a reduction in the viability and fertility of the offspring resulting from the mating of close kin. Inbreeding depression is thought to result from an increase in homozygosity. Clearly, inbreeding leads to such an increase, for, according to Hardy-Weinberg law, the frequency of homozygotes aa will be q^2 for an allele a that has the frequency q in the general population given random mating. "However, in an inbred individual with coefficient F , it can be shown that the probability of homozygosity has the higher value $q^2 + Fpq$. Similarly, the probability of the individual being homozygous AA is $p^2 + Fpq$, where allele A is present with the frequency p in the general population. On the other hand, the probability that the inbred individual will be heterozygous Aa is smaller than the $2pq$ expected under random mating -- namely $(1-F)(pq)$ " (Bodmer & Cavalli-Sforza 1976: 372).

The dispute, however, is concerned with whether or not this increase in homozygosity is deleterious. Many geneticists maintain that an increase in homozygosity also increases the chances of a detrimental

recessive being expressed and, as a result, produces a high rate of mortality in inbred progeny. Others such as Frank Livingstone, argue that "inbreeding does not increase the death rate from homozygosity, but rather decreases the frequencies of deleterious genes" (1969: 46). In other words, inbreeding ought to be advantageous, since it would rid the gene pool of deleterious recessives by exposing them to natural selection. Yet, the magnitude of selection operating against a given phenotype must equal one, in order for the recessive condition to eventually be eliminated from the population. This, however, is not always the case.

Despite this disagreement, there is evidence to suggest that a heterozygous condition is superior, in that it provides an individual with biochemical versatility and a population with greater evolutionary plasticity (Demarest 1977: 337). Thus, it is argued that the fitness of inbred offspring is reduced since they are homozygous at a greater number of loci and are, therefore, less likely to survive a sudden change in the environment. It appears, then, that an increase in homozygosity does, in fact, lead to inbreeding depression. It would, therefore, on genetic grounds, clearly be advantageous to avoid matings between closely related individuals. But, is such an avoidance observed among the primates?

PRIMATE SEXUAL BEHAVIOR AND GROUP INTERACTION

Free-Ranging Primates

In a study conducted on a population of free-ranging olive baboons at Gombe National Park, Craig Packer observed, "no examples of incestuous mating between mother and son, presumed father and daughter, or uterine siblings, which were likely to have led to pregnancy" (1979: 8). At this point it is important to note that primate sexual behavior is very complex, and copulation may serve several functions other than reproduction. For this and other reasons which will become clearer later on, observers define an incestuous mating as one which is successful in producing offspring. Although male olive baboons transfer from their natal troop into another troop, they do not do so until after they have reached sexual maturity (Packer 1979: 3). Consequently, it was possible for Packer to examine the sexual activity of males for evidence of inbreeding avoidance. He found that natal males never consorted with their mothers or uterine siblings, although they did occasionally copulate with them (Packer 1979: 21). In addition, Packer observed only one incidence of a consortship between a female and a "familiar male" (possibly her father or brother). This particular consortship was exceptional, according to Packer (1979: 28), in the extent to which the female avoided the male by moving away from him in direct response to his advances without exchanging gestures.

This observation suggests that adult females can distinguish between familiar males and novel males. Packer (1979: 28) claims that juveniles are capable of making this distinction, and speculates that they continue to distinguish between the two after they become adults. This raises the question of whether or not kin recognition can occur in the absence of previous experience between individuals in some species. Wu, Holmes,

Medina, and Sackett (1980) designed an experiment to determine the preference of infant pigtail macaques in a free choice situation using the Sackett self-selection circus. They found that infant pigtail macaques preferred to interact with their paternal half-sibs rather than non-relatives (Hannah et al. 1980: 226). Although this preference could not have resulted from common prenatal experience since half-sibs are not prenatally related, it is possible that it is based on the subject's experience with itself in rearing, which could be considered experience with a relative (Hannah et al. 1980: 226). And, certainly, preference does not indicate discriminatory ability. Despite these obvious problems, the experiment does challenge Hamilton's kin selection hypothesis that an individual's behavior towards a conspecific will depend on the degree of relatedness between them. Packer's observations would, then, support the findings of Wu and his colleagues. Packer noticed that the differences in relationship of females with transferred males and with natal males that were the result of the behavior of the female, indicated a preference for transferred (unfamiliar) males (Packer 1979:26). Moreover, these differences were not likely to have been produced by the difference in age or dominance between transferred males and natal males, but rather by the difference in familiarity (Packer 1979:18).

Packer also observed that females in oestrus often acted in ways which may have increased the probability of the new males immigrating into their troop. Such behavior usually involved presenting to outsiders and newcomers (Packer 1979:18). He suggests that, by recruiting new males which are unlikely to be closely related to her, the female is more likely to have outbred offspring (Packer 1979: 18). It would appear, then, that female olive baboons exhibit behavior which reduces the incidence of close inbreeding. There is evidence to suggest that the males also display certain behaviors which reduce the likelihood of incestuous matings. In particular, the transfer of males from their natal troop into a new troop is associated with the avoidance of inbreeding. Packer (1979: 2) maintains that these behaviors which promote exogamy are favoured by natural selection since inbreeding is thought to result in a net loss of viability and fertility in the offspring.

Inter-troop transfer has also been observed among chimpanzees. Unlike most primate species living in multi-male troops, however, it is the females and not the males who transfer between groups. At Gombe National Park between 1965 and 1975, Anne Pusey (1980) recorded that eight new females joined the particular community which she was studying, all of whom were young and nulliparous. Of the eight, six remained permanently. In comparison, five females either disappeared or transferred temporarily from the Gombe community and two were pregnant when they returned. Several others disappeared permanently and were presumed dead (Pusey 1980:547). There was evidence that these females were not associating with males from their natal community during these absences, since the males were observed regularly during the same period (Pusey 1980:548). Pusey (1980:548) suggests that the immediate motivation for the females to transfer is a greater sexual attraction to unfamiliar males. This is supported by the fact that visits to other communities occurred while the females were in oestrus. Seven of the eight nulliparous newcomers to the community had oestrus swellings at their first visit. Similarly, three of the females that grew up in the natal community who were observed in

adjacent communities, restricted their visits to oestrus periods (Pusey 1980:548). Pusey concludes that "the fact that transfer generally occurs during oestrus periods and that females may return to their natal community between oestrus periods or when they are pregnant, strongly implicates inbreeding avoidance as the function of such movements" (1980:548).

Pusey also collected data for five female chimpanzees, all of whom displayed significant selectivity in their associations with males both before and after their first oestrus. All five associated much more with one male before the commencement of sexual cycling with the exception of Fifi who associated with two males (Pusey 1980:544). Pusey refers to these males, who were thought to be their older maternal siblings because they were observed to interact with the same older female in a manner unique to offspring and their known mother, as the females' "pre-oestrus favourites". After first oestrus, all the females were seen to copulate with most of the sexually mature males in the community. On the other hand, copulation with the pre-oestrus favourite males was very rare (Pusey 1980:546). Pusey (1980:546) suggests that this low copulation rate resulted, firstly, because the pre-oestrus favourite males showed a lack of interest in and rarely courted these females, and, secondly, because the females tended not to respond to the courtship of their pre-oestrus favourites by presenting to them as they did to other males.

It would appear, then, that female chimpanzees are capable of recognizing their maternal kin and avoid sexual activity with them. This is supported by the observation that the males at Gombe associated constantly with their mother until they reached sexual maturity. At this point association dropped rapidly (Pusey 1980:549). In addition, one nine year old male and three adult males were observed with their known or assumed mothers while they were in oestrus, but none were seen to direct courtship at, or copulate with their mothers even though other males did copulate with these females during the same period (Pusey 1980:549). On the basis of these observations, Pusey concludes that "in chimpanzees sexual activity is inhibited between maternal kin" (1980:549).

One of the most noted analyses of the inhibition of mother-son incest comes from an earlier study of a colony of rhesus macaques on Cayo Santiago Island, by Donald Sade. During the test period, only four of the three hundred and sixty-three copulations witnessed, were between mother and son. Sade considers this finding remarkable given the frequency of behaviors such as grooming, body contact, and mutual defense between mothers and sons during both the mating and non-mating seasons (Sade 1968:18-20). He proposed that part of the explanation for the rarity of mother-son mating is that some males leave their natal troop upon reaching sexual maturity and are, therefore, not available to mate with their mothers during the mating season. (Sade 1968:27). The other part of the explanation is that males who remain in their natal group are inhibited from mating with their mothers by "the reverberance of the role of infant which is incompatible with the role of mate when the same female is the object" (Sade 1968:36).

Although these studies suggest that a non-human equivalent of incest avoidance exists among the primates, and that certain behaviors such as the inter-troop transfer of members of one sex, the differential dispersal

of males and females in the natal area, and the reduced sexual attraction between closely related individuals, may be favoured by natural selection given the disadvantages of inbreeding, there are still several problems. First of all, we do not know whether incest avoidance is the cause or consequence of these behaviors. Secondly, the studies by Sade (1968), Pusey (1980), and Packer (1979) involve free-ranging primates. Therefore it is difficult to observe all the copulations that may occur during the test period, and this may lead the observer to underestimate the incidence of incestuous matings.

Another problem concerns the definition of incestuous matings. In most cases, a mating which is considered to be incestuous is one which does not result in pregnancy and, therefore, occurs when the female is not in oestrus or before one or both of the participants reaches sexual maturity. This leads us to wonder why copulation should occur at all if there is a tendency to avoid incest? The best explanation we have at this point is one proposed by Ray Bixler. Bixler (1981:531) notes that the sexual encounters between mother and son differ markedly from normal mating behavior. He suggests that such encounters have a quieting or tranquilizing function rather than a reproductive one, since females often mount their mothers when upset (Bixler 1981:534). They may also have the same ontogenetic function in young males as does the mounting of peers -- namely, preparation for mature heterosexual copulation (Bixler 1981:535).

A fourth problem with the three studies discussed thus far, involves the fact that paternity is impossible to ascertain. As a result we have no information concerning the frequency of father-daughter matings or matings between paternal half-sibs.

Captive Primates

In an attempt to determine whether or not captive groups of rhesus monkeys avoid inbreeding with respect to their patriline, David Smith (1982) designed an experiment to compare the incidence of father-daughter or paternal half-sib matings that produced offspring with that expected by chance alone. Smith's study involved three captive groups of rhesus macaques which were housed in three separate half-acre outdoor field cages. Electro-phoretically defined phenotypes for six serum proteins and five red cell enzymes, in addition to serologically defined phenotypes for eleven red cell antigen groups were used to identify the paternity of the seventeen offspring born during the test period (Smith 1982:448). Using the phenotypes of offspring, mother, and all potential fathers, the paternity of fifteen of the seventeen offspring was determined using the method of paternity exclusion. A sufficient number of exclusions were made so that the possible fathers of each of the two remaining offspring were either related or unrelated (Smith 1982: 448-9).

The null hypothesis of random mating with respect to kinship was tested by "comparing the observed number of the seventeen offspring that were fathered by a relative of their mother to the sum of the probabilities, based on random mating, of inbreeding for the mothers of all offspring" (Smith 1982: 449). These probabilities (Pr) were calculated for each offspring using the equation:

$$\frac{\text{Pr} = \text{the number of potential fathers related to that offspring's mother}}{\text{the total number of potential fathers in the cage}} \\ (\text{Smith 1982: 449})$$

Finally, the observed and expected number of inbred offspring were compared using the chi-square statistic.

Smith (1982:449) calculated that 7.35 cases of inbreeding would be expected by chance alone. Nine cases, in fact, were observed and at least two of these involved a father and daughter mating. The chi-square value, calculated at 0.65 with 1 degree of freedom, is not statistically significant. Thus, the null hypothesis of random mating with respect to kinship was accepted (Smith 1982:449). Smith then concluded that "the results of our study do not indicate avoidance of consanguineous inbreeding in captive rhesus monkeys" (1982:448). The results of his study, however, do not allow such a broad statement, for Smith has only determined the frequency of matings between paternal kin.

His study suggests that inter-troop transfer is the cause rather than the consequence of inbreeding avoidance. It would appear that the suspension of inter-troop movements leads to an increase in consanguineous inbreeding. Yet, we have to wonder, when dealing with captive animals, if a greater than normal population density does not lead to an increase in stress and consequently, abnormal sexual behavior. It is interesting that only two of the nine cases of reported inbreeding occurred between a father and daughter, given the differences in age and rank among the potential fathers. Since the higher ranking males (generally older than the females in question) have greater reproductive success than the lower ranking males (generally of the same age as the females) we would expect a greater number of father-daughter matings. If Smith had corrected the individual probabilities for rank and age, he may have found that only the frequency of paternal half-sib matings was greater than that expected by random mating. If we accept the hypothesis that inbreeding has deleterious genetic consequences and that the probability of these consequences being expressed increases with the degree of relatedness between the individuals, we could predict a greater number of matings between paternal half-sibs ($F=.125$) than between fathers and daughters ($F=.25$) when the choice of mates is limited, provided that fathers and half-brothers can be distinguished by the female. This prediction is in keeping with the results of Smith's experiment.

The results of an experiment designed by Itoigawa, Nigayama, and Kondo (1981) in order to determine whether or not incest avoiding mechanisms might be operating in the captive situation, conflict with Smith's (1982) findings. The subjects of Itoigawa's experiment consisted of a mother, her adult son, four adult males and six adult females captured from a group of free-ranging Japanese macaques at Katsuyama. The control subjects were classified as either familiar or unfamiliar. The familiar control subjects were obtained with the mother and son from the same subgroup, whereas the unfamiliar controls were unknown to the experimental subjects. (Itoigawa et al. 1981:495)

Itoigawa and his colleagues found that the son performed serial mounts that ended in ejaculation with all three unfamiliar females and

with one of the two familiar females, but never with his mother. On the other hand, the mother received serial mounts which terminated in ejaculation from all three unfamiliar males and from one familiar male, but never from her son (Itoigawa et al. 1981:501). According to the three experimenters the son and mother did not appear to be sexually aroused between themselves, although they did appear so when paired with other animals (Itoigawa et al. 1981:501). They did find, however, that the son ejaculated by performing a single mount to the mother but this occurred abruptly without displaying any behavior that would reflect sexual arousal (Itoigawa et al. 1981:501).

On the basis of these observations, Itoigawa (1981:502) concluded that "the absence of serial mounts and other behaviors reflecting sexual arousal or excitement indicates that incest avoiding mechanisms might be operating in the captive situation." It is important to note, however, that these observations apply only to the incidence of incest avoidance between mothers and sons. Moreover, the conclusion which he reaches is based on the results of a single experimental pair. Nonetheless, it reaffirms our hypothesis that a non-human equivalent of incest avoidance exists among the primates.

THE PRIMATOLOGICAL EVIDENCE AND HUMAN INCEST PROHIBITIONS

As we have seen, there are several social and genetic reasons why the avoidance of mating between close relatives may be advantageous, and it appears that such an avoidance exists among the primates. Furthermore, certain behaviors such as the differential dispersal of males and females in the natal area, reduced sexual attraction between individuals raised in close association, and the inter-troop transfer of individuals of one sex, may function as incest avoiding mechanisms. But, what bearing, if any, do these findings have on human incest prohibitions?

In attempting to answer this question, we should be aware of the fact that a certain amount of caution should be exercised in making inferences about human behavior from studies of animal behavior. Yet, in seeking to understand our own species, it is logical that we should study species which are socially and biologically similar to ourselves -- namely, the primates.

In our discussion of primate sexual behavior, we identified several incest avoiding mechanisms. But, are similar mechanisms observed among humans? Clearly, we do not see the migration of females or males at or near puberty. There is, however, evidence to suggest that sexual attraction is reduced between individuals who have closely associated with each other while one or both were very young. Spiro's and Talmon's studies of collective child-rearing practices of Israeli kibbutzim are often cited to illustrate the operation of this mechanism. In one kibbutz, Spiro observed no cases of marriage within a peer group even though the parents would actually have preferred such marriages since they would strengthen the integrity of the kibbutz (Demarest 1977:324). Similarly, Talmon found that of the 125 couples he studied in two kibbutzim, none had been reared together in the same peer group (Demarest 1977:324).

Since theorists argue that the lack of sexual attraction between kibbutzniks is merely the result of disinterest, and not the "abhorrence" which is characteristic of consanguineous matings. To support their position they refer to Kaffmann's observation that "the roles played in infancy and the familiarity of relationships within the peer groups is not conducive to the encouragement of the illusion, excitement, and mutual idealization that are such important elements of romantic love...and years of common daily routine and everyday intimacy hardly seem helpful to the development of romantic expectations and blind passion" (1977:216).

Arthur Wolf, on the other hand, has proposed that it is the inhibition of aggression that eventually leads to reduced sexual attraction. He cites Frank Beach's observation that "male mammals often fail to copulate in an environmental setting previously associated with punishment" (1951:408). Wolf then speculates that "since the socialization of aggression is a universal aspect of child-rearing, it could account for the widespread occurrence of sexual disinterest within the primary family where children are punished not only for striking their parents but for fighting with each other as well" (Demarest 1977:337). Despite the disagreement as to the nature and cause of this reduced sexual attraction between individuals who have been closely associated with each other while one or both were very young, none deny that it serves to reduce the incidence of incestuous mating.

THE INCEST TABOO

At this point in our discussion, we are forced to turn away from the findings on primate incest avoidance, in order to examine the human "incest taboo". It is important to note, however, that these findings gain particular significance precisely because the primates have no language-based prohibition to prevent inbreeding, for if a significant amount of incest avoidance can be found among the non-human primates, it must be explained, at least in part, by a "natural" rather than a verbal inhibition.

Much of the controversy which surrounds the incest avoidance question, concerns the origin and nature of the "incest taboo". Perhaps the most famous attempt to explain this taboo, is Freud's. He proposed that it arises out of what he terms the "Oedipus complex" or "Electra complex", in the case of females. According to his theory, every child directs his sexual desire toward the parent of the opposite sex. This is coupled with a hostility towards and a fear of the parent of the same sex. This conflict is finally resolved, in the case of the male, with a renunciation of mother and an identification with father. Thus, the child refrains from engaging in sexual activity within the family since he carries in his superego a constant fear of punishment (Gleitman 1981:474-6).

Freud's theory is, however, not without its problems, for the Oedipus conflict and its female equivalent are not universal, but depend on cultural variation within the structure of the family. For example, Malinowski noted that among the Trobriand Islanders of the Western Pacific, it is not the biological father but the mother's brother who acts as disciplinarian. Malinowski observed no signs of tension between

fathers and sons, although there appeared to be a fair amount of hostility directed at the maternal uncle. Thus, the Trobriand boy does not fear his mother's lover as such, for he does not hate the father who fills the role (Gleitman 1981:486).

In keeping with Freud's theory are those such as Lindzey's which endorses the "assumption that there are powerful incestuous impulses present in all humans and...the core developmental problem...is the redirection of these impulses" (1967:1056). This view, which is held by a number of psychologists and several cultural anthropologists, asserts that there is no inborn or natural tendency toward the inhibition of incest, otherwise there would have been no need for human societies to develop such strict prohibitions. They argue that there are no taboos or laws against acts that no one wants to perform anyway. To use Frazer's example, "there is no law commanding men to eat and drink or forbidding them to put their hands in the fire" (1910:97). Thus, the aversion to sexual intercourse with one's close relatives arises out of the law itself.

This argument is strengthened by the fact that in some cultures where there are religious proscriptions against the consumption of certain foods, the act or thought of eating such items may cause actual physical illness, even though these foods are perfectly acceptable dietary forms in other societies. I feel, however, that language-based prohibitions alone, although their restraining effect is unquestionable, are not sufficient to account for the fact that incest does not occur to any considerable degree in any human population. That is, incest avoidance must be explained, at least in part, by a "natural" inhibition as evidenced by the fact that the non-language bearing primates also appear to avoid incestuous matings.

CONCLUSIONS

Clearly, any explanation of human behavior may prove as complex as the behavior itself. If such an explanation is, in fact within the scope of human comprehension, it may be reached through a clearer understanding of both primate and human sexual behavior. For example, more information concerning the patterns of sexual interaction between both sexes of the primates would provide us with a clearer definition of "incestuous matings". In addition, all three dyads of consanguineous mating should be examined simultaneously both in the field and the laboratory. With respect to observations of human sexual behavior, studies should involve the general population rather than psychiatric patients whose pathology may be either the cause or consequence of incest. Moreover, it would be interesting to determine if the incidence of father-daughter incest in our own society has dropped in the last decade with the greater role that fathers are playing in child-rearing. If such a decrease could be found, it would support the hypothesis that increased familiarity in childhood decreases the incidence of incest in North American societies. In addition, attempts to determine whether or not the genetic consequences of inbreeding are as disadvantageous as believed, would prove invaluable to our understanding of why such an avoidance exists.

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