

Nonhuman Primates Homosexual Behavior: *A Critical Review of Literature**

Abstract This paper provides a critical review of the literature on nonhuman primates sexual behavior. Reproduction and sexual behavior are of crucial importance in the biological and social sciences. Therefore, homosexual behavior presents a major challenge for those who hold that Darwinism is the great general theory to be applied with equal success in biology as well in social sciences. The same-sex activity can be found among animals of all kinds. However, based on the available literature and data, it is more likely that what looks like homosexual behavior may be more correctly classified as infantile play, poor discrimination or dominance-submission behavior.

Key words: animal homosexuality, Darwinism, primates.

Introduction

The cause of homosexual activity is a controversial topic within the legal, political and psychiatric professions. Etiologic theories and terms are intertwined with speculative opinions about the possibly pathological and irresistible nature of homosexuality. Many writers with a tolerant or positive view of homosexuality often begin their discussions by emphasizing the frequency with which nonhuman animals engage in homosexual activities, implying that homosexuality is natural (natural as opposed to "unnatural", defined as "not occurring in nature") and hence should be acceptable. Kirkpatrick (2000: 385), for example, argues that "Nonhuman primates, including apes, use homosexual behavior in same-sex alliances, and such alliances appear to have been key in the expanded distribution of human ancestors during the Pleistocene."

It is well documented that certain forms of homosexual behavior go on in more than 450 different animal species worldwide, and same-sex activities are found in every major geographical region and every major animal group (Bagemihl 1995). However, the existence of homosexual behavior in human and non-human animals likewise is a Darwinian puzzle because it seems to contradict the fundamental Darwinian logic of individual reproductive success. Based on Darwinian

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selection, inheritable traits become widespread only when they help individuals leave descendants. Homosexual behavior should reduce the chances of leaving descendants. For example, an imaginary species consisting only of individuals with an exclusive and life-long homosexual behavior will be extinct in one generation. On the other hand, parthenogenetic species do exist in nature, they consist of 100% females, but a 100% homosexual species has never been found (Daly and Wilson 1983). What does exist in nature are species with up to several percent of individual who sometimes exhibit homosexual behavior. The percentages vary from study to study, but the best estimate is that, among humans for example, there are around 1-3 % who declare themselves exclusively homosexual (Gonsiorek and Weinrich 1991). But even this is a puzzle. If those individuals do not reproduce, evolution theory predicts that the percentage in the population must decrease continuously down to a level that is produced by new mutations. How should the excess be explained? One possibility is bisexuality, the combination of homosexual and heterosexual behavior in the same individual. Empirical data offer a number of challenges to the notion that homosexuality is a condition for which some homosexuals are unable to substitute normal sexual behavior. Most surveys have reported that the great majority (80-90%) of those with homosexual experience, both men and women, have also had full sexual relations with the opposite sex, and most of those who call themselves "gay" or "lesbian" have also had full sexual relations with the opposite sex. Not that infrequently, these heterosexual contacts occur in so-called gay ghettos, with other gays and lesbians (Cameron 2000, Lemp et al. 1995). It appears that most adult homosexuals also engage in heterosexual relations over their lifetime. Many homosexuals go through a phase lasting a year or two or more of exclusive or near exclusive homosexuality, followed and/or preceded by periods of generally heterosexual or bisexual behavior. Other evidence of the sexual flexibility exists. Ethologists have even claimed that they can induce adult homosexuality in certain birds by exposing young males to certain treatments (Evans 1974). From an evolutionary point, homosexuality has no function: to say that a given effect of a trait is the function of that trait, is to say that the character was molded by natural selection to produce that effect (Williams 1966). In other words, a trait that has no function, like homosexuality, is referred to as a by-product or artifact (Berman 2003). It developed as a variant of biologically functional sexuality, a by-product of human animal and non-human animal evolution. This points to a general principle: once natural selection has created a form of gratification, that form can come to serve other functions as well.

Nonhuman Primates Homosexual Behavior

Scientific interest in homosexual behavior among nonhuman primates dates to the beginning of this century (Hamilton 1914, Kempf 1917, see review in

Nadler 1990). Much of this research has focused on captive animals; homosexual behavior was characterized as an abnormal product of captivity, not likely to be found in nature. It is said that a great deal of mounting among non-human animals is not sexually motivated, and such "homosexual" behavior is more frequent among captive than among free-ranging animals (Parish 1993, Symons 1979). Also, there are no real animal analogues of human homosexuality: such homosexual acts that do occur are either pathological (Calhoun 1962), or serve purposes clearly unrelated to human behavior (Ridley 1994). It is also stated that despite decades of scientific investigation, primate homosexual behavior remains poorly documented and poorly understood (Vassey 1995). It is estimated today by primatologists that of the 33 primate species that exhibit homosexual behavior, 13 do so under both free and captive conditions, 7 have been observed only under free-ranging conditions, while 13 have been observed to do so only in captivity (ibid.: 177). Of the 31 species in which males engage in some homosexual contact, 13 do so rarely, 9 occasionally and 11 infrequently. Hence, the majority of primate species rarely exhibit homosexual behavior. What they do exhibit, in fact, is non-reproductive behavior. For instance, in nearly every population there is a group of non-breeders. In species with a harem, one male has access to the females in the harem to the exclusion of all other males. In other species, often only the highest-ranking male mates with females (Alcock 1984). But even in a heterosexual species without harem, males and females do not mate all the time. For a great number of species mating has never been observed despite hundreds or thousands of hours of observation. Often males and females live in separate groups. Young animals up to 3 - 5 years do not breed. Male baboons have been observed copulating a pregnant or lactating female, a non-reproductive behavior.

The range of homosexual contact among the primates include oral-genital contact, mutual genital manipulation and anogenital contact with intromission; however, anogenital contact that was observed between male partners happened primarily in captive situations (Kempf 1917, Carpenter 1942, cited in Nadler 1990, Morris 1970, Thornton and Goy 1986). Homosexual behavior appears to be less characteristic of monogamous, polyandrous and polygynous primates, and more common among multimale, multifemale and all-male groups (Carpenter 1942, Gartlan 1974, Yamagiwa 1987).

There are a few theories for primate homosexual behavior. It should be re-emerged that most theories deal with captive animals. One theory holds that exposure to androgen levels more characteristic of the opposite sex may result in homosexual behavior. Some studies, where castration was used, indicate that male-male mounting increases significantly when androgen levels are at normally occurring lower ranges (Loy et al. 1984), and other studies claim that homosexual mounting is not associated with elevated levels of androgens (Gouzouls and Goy 1983).

The second theory of the hormonal hypothesis for primate homosexual behavior holds that sex-atypical androgen levels that are experienced prenatally organize the brain according to the opposite sex pattern, thereby predisposing the individual to exhibit homosexual mounting in adulthood (Birke 1981). To investigate this theory, primatologists have experimentally simulated the conditions of hormonal excess in the prenatal development, by treating pregnant females with excess doses of testosterone, which induces pseudohermaphroditism in their female infants (Young et al. 1964, Eaton et al. 1973). These studies indicate that pseudohermaphroditic females that are one year old consistently engage in more homosexual mounting than control animals of similar age do (Young et al. 1964, Goy and Phoenix 1971). However, in the light of their abnormal prenatal development, ambiguous genital morphology and potentially different socialization, these pseudohermaphrodites are not the best models for investigation the relationship between prenatal testosterone exposure and homosexual behavior (Goy and Phoenix 1971, Vassej 1995).

Two sociobiological hypotheses for homosexual behavior are similar in character, in that both attempt to explain the functional significance of female-female mounting. For example, Parker and Pearson (1976) propose that female homosexual mounting functions to increase the reproductive success of the mounting female. By mimicking the copulatory pattern of rival males, the mounting female can attract dominant male sexual partners and increase her chances of insemination. Because female mountees do not gain access to the male sexual partner, they behave altruistically for the benefit of the female mounter. The authors argue that such mountees' behavior can evolve via kin selection or reciprocal altruism. The other sociobiological theory is proposed by Tylor (Nadler 1990), who suggested that female homosexual mounting represents a form of intrasexual competition that minimizes the probability that rivals are inseminated. Mounting females may reduce the mountee's receptivity and access to male partners by providing alternative sexual stimulation. Also, the mountee's probability of insemination is reduced, which would decrease the number of future competitors for the mounter.

Homosexual behavior between immature primates or between an immature and a mature individual is frequently observed during play, and some studies suggested that homosexual behavior expressed during play may function as practice for adult heterosexual copulation (Hamilton 1914, Bingham 1928, Baldwin 1969). Numerous other studies suggested a relationship between social tensions and homosexual behavior. Kuroda (1980: 190), for example, suggested homosexual behavior among bonobos to be a mechanism to reduce tension during periods of close proximity in the same food patch. De Waal (1987) argued that when mechanisms for regulating aggression fail, bonobos can use homosexual behavior to reestablish social bonds.

Another theory for primate homosexual behavior is dominance-assertion hypothesis (Nadler 1990). It is argued that such interactions reaffirm the dominance hierarchy and thereby reduce aggression. Mounting is a display of dominance, and being mounted is a display of submission. Smuts and Watanabe (1990), for example, interpret these interactions among the baboons as dominance negotiations during which the participants flesh out their relationships. Here is de Waal's (1996) account on baboons which illustrate this dominance-negotiation hypothesis, but it should be mentioned that studied subjects do not engage in real sexual behavior:

Perhaps the best known form of negotiation among primates is the way adult male baboons greet other males in their troop. ..One male will typically walk up to another with a rapid, swinging gait. He looks the other straight in the eye with some friendly expression, such as lip smacking, which makes it absolutely clear that he only wants to initiate a greeting. To communicate intention is essential, given the fierce rivalry of males over females and the formidable canines with which males can cause a deep gash in a split second.

The encounter itself follows a certain protocol that varies with the kind of relationship the two males have. Often, the other welcomes the approach with a similar friendly expression, and one male presents his rear end while the other touches or grasps his hips. They may then proceed to mounting, or, if they really get intimate, one male may fondle the other's scrotum or pull at his penis. Known as 'diddling', it is a sign of tremendous trust. The contact lasts only a few seconds, after which the two males separate again. Male baboons do not seem comfortable enough in each other's presence to associate or groom; their predominant modes of interaction are fighting and greeting (de Waal 1996: 191).

De Waal (1996) stated that the same behavior has been noticed in other colonies; there too, encounters are found to be extremely tense, occasionally erupting into fights. The reason is that male baboons often serve to test and confirm who is on top: the dominant male will be the mounter. Greetings like this seem to be a way of assessing intention; a male who used to elicit presentation in another, learns from the other one if their previous roles are still working, and if not, a serious challenge may result. Because tensions remain under control in the majority of greetings, the advantage of this kind of information exchange is that matters can be often worked out without physical fight and confrontation. This pattern is used most by the youngest, most pugnacious males, since they are the most preoccupied with dominance:

Take Alexander and Boz, two devoted allies. On one occasion Boz heard Alexander scream from 50 meters away, hurried over to the spot, and jumped without hesitation on the back of his buddy's attacker. Alexander would have done the same thing for Boz. This alliance served them so well that every day, first thing in the morning, the two males would go through a series of intimate

greetings so carefully balanced that one would think they were keeping count. Boz would present to Alexander to let him touch his genitals, while both gazed into the other's face and lipsmacked. Two minutes later Alexander would present to Boz for the reverse procedure. If they were agreeing on something, the symmetry of their encounters made it evident that it was on mutual support and shared profits for the fresh day, not on who could push around whom (de Waal 1996: 192).

Similarly, Smuts and Watanabe argued that "the genital touching that sometimes occurs in greetings perhaps serves to enhance the truth value of whatever these males are 'saying' to each other within the formally circumscribed context of greeting. Lacking articulate speech, and unable to swear oaths, perhaps male baboons make a gestural equivalent by literally placing their future reproductive success in the trust of another male. Such risky gestures may help to enhance whatever verity is presumed in the greeting because they impose a potential cost on the presenting male" (Smuts and Watanabe 1990: 169).

Yet another explanation to animal homosexuality is proposed by Alcock (1984): the by-product/side effect model proposes that homosexual behavior is a result of the powerful drive to have sex. The mechanism of this model is based on the principles of heterosexuality. In mammals, females must carry their young through pregnancy, therefore restraining their potential number of offspring. Males need only supply sperm, and may have no further cost or time investment in their offspring. Males can produce sperm efficiently continually and hence father many offspring. A male mammal's reproductive success is enhanced as it inseminates more females, thus ensuring a larger number of offspring. Since a female cannot produce a higher number of offspring through increased copulation it is of no benefit for a female to copulate with a number of sexual partners. Instead, a female increases her fitness through selecting the best possible father for her offspring, thus increasing the fitness and chance for survival in her young. During evolution males have obtained behavioral traits to compete with other males for more frequent copulation with a number of sexual partners and thus greater reproductive success. This "super-sexuality" has consequently evolved in males which causes them to attempt for a maximum number of copulations with a broad range of partners and that their "imperfect sex recognition" when in such a state of heat leads them to mount males as well as females (Alcock 1989). It may be that in fact, animal "homosexuality" is a misnomer, and really refers to bisexuality or the behavior of mounting with animals of both sexes. This theory is well-supported by observations of sexual behavior in the animal kingdom.

Homosexual behavior is observed more in all-male groups, both among free-ranging and captive animals. Demographic patterns and group sex-ratios can influence social and sexual behavior. A detailed study by Yamagiwa (1987) illustrates this argument. Yamagiwa studied for 11 months six unre-

lated males of Virunga mountain gorillas, in Zaire; due to the small group size and high cohesiveness of these group members, the author was able to record almost all agonistic and nonagonistic interactions which occurred among them at the time studied. For mountain gorillas, it is characteristic that both males and females commonly emigrate from their natal groups, but only females immigrate into other groups; males travel alone for a long period of time after emigration, and sometimes form their own groups by taking one or more young females from other groups. The group studied was formed after the collapse of a former group when the leading male and female were killed by poachers, and the rest of the females transferred to neighboring groups. All the members of the group studied spent about 90% of their day time feeding and resting; however, during play time, some activities ended in homosexual contact: "Some of them resulted in mounting with pelvic thrusts in the same manner as observed in copulation between males and females of the bisexual groups" (Yamagiwa 1987: 12). Male-male mounting was observed 98 times during this study, where the elder ones usually mounted the younger ones. Mounting occurred in both ventro-ventral and dorso-ventral positions, with both males emitting copulatory vocalizations, and sometimes the mounters emitted a deep sigh at dismounting as if they had ejaculated. However, signs of ejaculation were observed only twice during the time studied. Yamagiwa stated that strong competition for sexual partners among this all-male group resulted in frequent aggression, increased social tension and sometimes violent fights between them. He wrote,

The male-male mounting observed in the present study was not caused by high social tension or stress among the males. It occurred in both the resting and feeding phases, and did not occur in the situation of high social tension... These observations suggest that male-male mounting is probably not used to decrease the high social tension among male gorillas. On the contrary, such mountings in a sexual context reduced the inter-individual distances and increased the social tension between the silverbacks. This resulted in frequent aggression and sometimes violent fights between them (Yamagiwa 1987: 23).

As an explanation for male gorillas' homosexual behavior, Yamagiwa argued that this kind of sexual behavior is due to the inaccessibility of females. In general, male gorillas, even in bisexual groups have infrequent sexual activity. Male gorillas rarely joined bisexual groups after emigration from their natal groups; the reason for this is related to the stronger inter-male competition for females between groups than that within groups. Several other authors presumed that the males who did stay in their natal groups after maturity were the sons of leading males; on the other hand, the female gorillas are sexually active only 1 to 3 days in each 25 to 40-day cycle. Although bisexual groups of mountain gorillas usually include more than one female, their number is still low—the average number per group is 3.4. Also, females with young infants have a

long period, about three years, of sexual inactivity. Thus, male gorillas participate very infrequently in sexual activities, and males who travel alone or live in all-male groups have "virtually no chance to do so" (ibid.: 25). In this situation, male gorillas engaged in homosexual behavior. Yamagiwa's findings are supported by another study: one of the groups of mountain gorillas monitored in Virunga recently became an all-male group, and the males of the group have begun to show homosexual behavior (Wilson, cited in Yamagiwa 1987: 26). Yamagiwa also argued that, in present times, instead of traveling alone and trying to obtain a female, male gorillas more often form all-male groups:

However, since aggression is the main tactic employed by a resident male against others to prevent their association with his females, lone travel has become more risky for maturing males in recent situations. Males who have attempted to gain female mates have faced severe counterattacks from their silverbacks. Human disturbance (mainly poaching) has prevented these males from traveling widely in the Virunga forest. Such changes have probably forced maturing males to form or join all-male groups instead of traveling alone. Although the formation of an all-male group may prevent maturing males from positively participating in reproduction, it may protect them from hazards within bisexual groups and in their lone travels, and contributes to the preservation of fertile males for future group formation (Yamagiwa 1987: 28).

The data from the available literature on animal homosexual behavior point out that even if there is a biological basis for homosexual behavior, the genes in question were not selected by natural selection by virtue of their contribution to homosexuality. As Wright (1994: 385) argued: "If there is a gay-gene that has spread to a sizable part of the population, it probably was having some effect other than homosexual inclination in the environment in which it spread". In reviewing the literature on homosexual behavior among non-human animals, the conclusion can be made that there is no exclusive homosexual behavior among animals. As we seen, homosexuality occurs more often in all-male, multi-male and multifemale groups. The Mountain gorillas' example clearly illustrates this point. Deprived of females, males may engage in some forms of homosexual behavior, and in this way animal homosexual behavior is comparable indeed to the situation that the human polygynous system creates (Cvorovic 2001).

In fact, among non-human animals in general, what looks like homosexual behavior may often be more correctly categorized as infantile play, dominance-submission behavior or poor discrimination. For instance, male and female frogs of some species look alike even to other frogs. When a male frog grasps another male, the grasped male utters a release call, which apparently means: "let go, and find yourself a real female" (Williams 1966: 47, Berman 2003). Overall concern about the "gay gene—being born that way" question implies that the answer should have moral consequences. Nevertheless, it is very unlikely that some genes, or a gene, were selected by natural selection by

virtue of their contribution to homosexuality. Moreover, the naturalness of homosexuality is irrelevant: the primary interest should be in behavior, how individual animals behave, not genes.

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**HOMOSEKSUALNO PONAŠANJE KOD NE-HUMANIH PRIMATA:
KRITIČKI PREGLED LITERATURE**

U ovom radu ponuđen je kratak pregled literature o seksualnom ponašanju ne-humanih primata. Reprodukcijska i seksualna ponašanja od vrhunske su važnosti i u biološkim i u društvenim naukama. Iz ovog razloga, homoseksualno ponašanje predstavlja veliki izazov onima koji tvrde da se darvinizam može sa jednakim uspehom primeniti u obe grupe nauka. Odnosi sa istim polom javljaju se među najrazličitijim vrstama životinja. Međutim, na osnovu postojeće literature i podataka, moguće je da veći deo onoga što deluje kao homoseksualnost zapravo igra među mladuncima, posledica nesposobnosti razlikovanja, ili odnos dominacije i podređenosti.