Homosexual Behavior in Primates: A Review of Evidence and Theory

Paul L. Vasey[1]

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Homosexual behavior is defined as genital contact, genital manipulation or both between same-sex individuals. Available data indicate that this behavior is phylogenetically widespread among the anthropoid primates, but totally absent among prosimians. The majority of the 33 species that demonstrate homosexual behavior do so rarely, but for a substantial number (N = *12) it appears to be a more common pattern under free-ranging conditions. I summarize data on homosexual behavior as it relates to form, living condition, age, sex, social organization, and ecological context, and discuss hormonal, demographic, and sociosexual theories for primate homosexual behavior. Among adult primates, the behavior is not the product of abnormal excesses or deficiencies in androgens. Prenatal excesses of androgens may have some effect on the expression of female homosexual behavior, but these effects might vary over the life span, and data are equivocal at present. Demographic processes that result in skewed sex ratios can favor the expression of homosexual behavior in a population, which causes intraspecific variation. I examine several sociosexual explanations, including (a) proceptivity enhancement, (b) receptivity reduction, (c) dominance assertion, (d) practice for heterosexual copulation, (e) tension regulation, (f) reconciliation, and (g) alliance formation. An evolutionary scenario highlights the transformations this behavior underwent during the evolution of the anthropoid primates. I suggest exaptation as a theoretical framework for interpreting homosexual behavior and conclude that future consideration of sexual selection among primates should address homosexual components of this process.*

KEY WORDS: homosexual behavior; sociosexual behavior; hormones; demography; exaptation.

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[1] Département d'anthropologie, Université de Montréal C. P. 6128, succ. Centre-ville, Montréal, Québec, H3C 3J7 Canada.

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INTRODUCTION

Academic interest in homosexual behavior among nonhuman primates (hereafter primates) dates to the beginning of this century (Hamilton, 1914; Kempf, 1917; Nadler 1990). Much of this research focused on caged subjects; consequently, homosexual behavior was characterized as an abnormal product of captivity, unlikely to be found in nature. Accordingly, such research often seemed to be motivated by the perceived need for a cure to eliminate a behavioral problem. Following these initial investigations, primatological research on the subject dwindled until the early 1960s when a link between hormonal imbalances and same-sex mounting was sought, echoing the notion of homosexual behavior as a curable abnormality (Young *et al.*, 1964).

With the emergence of sociobiology, a paradigmatic shift occurred that resulted in homosexual behavior being viewed not as an abnormality, but instead as the product of evolutionary processes and explicable in adaptive terms. The sociobiological perspective generated many adaptive hypotheses for this behavior, but was much less successful in establishing supporting evidence (Wilson, 1975; Parker and Pearson, 1976; Kirsch and Rodman, 1982; Tyler, 1984; Ruse, 1988; Dickemann, 1993). Despite decades of scholarly investigation under various paradigms, primate homosexual behavior remains poorly documented and poorly understood.

I aim first, to summarize the data on primate homosexual behavior, and second, to examine the theories that have been used to explain this data. There can be little doubt that this behavior has been overlooked by most primatologists. Thus, I hope that an exhaustive review of the subject will awaken research interest. Research on this subject may play an important role in modifying theoretical debates surrounding sexual selection, and thus contribute to a deeper understanding of primate social relationships and social systems. Moreover, such research has obvious sociopolitical implication for humans because animals are often used as a gauge for measuring what constitutes natural or abnormal behavior worthy of legal protection or persecution (Boswell, 1980; Weinrich, 1980; Haraway, 1989; Travis and Yeager, 1991).

TERMINOLOGY

The subjectivity involved in defining homosexual behavior according to context, function, and motivation has been repeatedly called into question and criticized as ignoring the multifaceted nature of these interactions (Hanby, 1974; Reinhardt *et al.*, 1986; Srivastava *et al.*, 1991). By focusing specifically on the motor patterns of homosexual behavior, a less subjective definition presents itself (Vasey and Chan, 1992). Hence, for the purposes of this discussion, I consider genital contact or genital manipulation, or both between individuals of the same sex to be homosexual behavior. I label all behaviors that are homosexual in form homosexual herein, regardless of function and context or the actors' ages and motivation. Excluded from this range of possibilities is genital inspection of infants by their care givers. Homosexual behavior can result in genital stimulation—erection, ejaculation, orgasm—of one or both individuals, but such stimulation is not a defining criteria of the behavior.

The term homosexuality refers to an erotosexual preference for same-sex partners, which may be manifested behaviorally or cognitively (Whitam, 1983). For example, by engaging in homoerotic fantasy, humans could be considered homosexual in preference or orientation, even if they do not engage in homosexual behavior. At present, primatology lacks a methodology by which the cognitive aspects of primate sexuality could be assessed. Hence, I deal only with behavior and makes no claim concerning the cognitive realms of primate erotosexual preference and orientation. As such, primate homosexual behavior is the focus of this paper and not primate homosexuality or homosexual primates.

The very breath of this definition allows homosexual behavior to be defined in species-neutral terms (Rodseth *et al.*, 1991). This facilitates more objective cross-specific comparisons, which aid in the construction of evolutionary models for the behavior. Some would argue that the term homosexual is so laden with cultural meaning that it is in no sense whatsoever a neutral term. However, if one can talk about a species exhibiting heterosexual behavior—a term equally loaded (Haraway, 1989)—then one can talk about that species exhibiting homosexual behavior (Weinrich, 1980).

DATA COLLECTION

I gleaned data from published reports on captive and free-ranging primates, as well as personal communications with several primatologists. Where appropriate, I refer to my own observations of homosexual interactions among female *Macaca fuscata* at the Laboratory of Behavioral Primatology of the Université de Montréal. Few studies have been directed specifically at the question of primate homosexual behavior. Hence, the bulk of data are from studies that catalogue other behaviors over an extended period of time. Often, homosexual behaviors were mentioned only in passing. Some of the species listed herein as not demonstrating homosexual behavior will likely be shown to do so as information on this subject accumulates.

RESULTS

The Form of Homosexual Behavior

Homosexual behavior among primates most commonly takes the form of ventrodorsal mounting with thrusting. Ventroventral mounting has also been observed between same-sex individuals (Bingham, 1928; Hanby and Brown, 1974; Fox, 1977; Fischer and Nadler, 1978; Savage-Rumbaugh and Wilkerson, 1978; Wolfe, 1979; Kano, 1980; Harcourt *et al.*, 1981; Thompson-Handler *et al.*, 1984; de Waal, 1987; Yamagiwa, 1987; Kitamura, 1989; Edwards and Todd, 1991). Homosexual and heterosexual mounts often appear indistinguishable and are accompanied by similar vocalizations and patterns of social behavior such as grooming and synchronized movement. Oral-genital contact and mutual genital manipulation between same-sex individuals has also been reported (Struhsaker, 1967; Kollar *et al.*, 1968; Thompson, 1969; Wolfheim and Rowell, 1972; Weber, 1973; Chevalier-Skolnikoff, 1974, 1976; Gartlan, 1974; Owens, 1976; Dixson, 1977; Fox, 1977; Maple *et al.*, 1977; Coffin, 1978; Fischer and Nadler, 1978; Rijksen, 1978; Akers and Conaway, 1979; Bernstein, 1980; Makwana, 1980; Maple, 1980; Wrangham in Weinrich, 1980; Hoage, 1982; de Waal, 1987). Anogenital contact with intromission has been observed between male partners, primarily in captive situations (Kempf, 1917; Carpenter, 1942; Morris, 1970; Chevalier-Skolnikoff, 1974, 1976; Erwin and Maple, 1976; Maple *et al.*, 1977; Rijksen, 1978; Thornton and Goy, 1986; Bound *et al.*, 1988). Savage-Rumbaugh and Wilkerson (1978) described clitoral intromission between female *P. paniscus*.

Males sometimes exhibit penile erection during homosexual interaction (Ploog *et al.*, 1963; Shadle *et al.*, 1965; Struhsaker, 1967; Tokuda *et al.*, 1968; Hanby and Brown, 1974; Leresche, 1976; Dixson, 1977; Fox, 1977; Maple *et al.*, 1977; Kano, 1980; J. J. Moore and R. W. Wrangham in Weinrich, 1980; Thompson-Handler *et al.*, 1984; de Waal, 1987; Kiamura, 1989), and ejaculation occasionally occurs (Kempf, 1917; Gordon and Bernstein, 1973; Hanby, 1974; Erwin and Maple, 1976; Fox, 1977; Rijksen, 1978; Makwana, 1980; Maple, 1980; Slob and Schenck, 1986; Yamagiwa, 1987; Edwards and Todd, 1991). Orgasm, between female partners has been implied also (Chevalier-Skolnikoff, 1974, 1976; Goldfoot *et al.*, 1980; Wolfe, 1984; Enomoto, 1990). Overall, the sexual repertoires of primates engaging in homosexual interaction appear highly varied and flexible.

Phylogenetic Distribution

Homosexual behavior is phylogenetically widespread among anthropoid primates, occurring in 33 species (Table I). In striking contrast, total absence of this behavior characterizes the prosimians (A. Jolly and S. K. Bearder, personal communication, 1992). Apart from prosimians, however, species that demonstrate homosexual behavior occur in every family of the primates. The widespread nature of this behavior among anthropoids should not overshadow the fact that it appears to be totally absent among some well-studied anthropoid species: *Alouatta* spp., *M. sylvanus*.

Captive vs. Free-Ranging Populations

Of the 33 primate species that exhibit homosexual behavior, 13 do so under both captive and free-ranging conditions (Table I). Seven species have been observed to engage in homosexual interactions only under free-ranging conditions, whereas 13 species have been observed to do so only in captivity (Table I). Regarding the latter, with the exception of *P. troglodytes*, none of them has been studied extensively under free-ranging conditions. This lack of data may have created a false impression that their homosexual behavior is restricted to captivity.

In the vast majority of cases, homosexual behavior reflects a normal facet of the sexual repertoire of primates, not an abnormal response to captivity. Since some species engage in homosexual activity under free-ranging conditions, but fail to do so in captivity, caging sometimes seems to inhibit this behavior instead of promoting it. The expression of homosexual behavior in captivity should not automatically be labeled abnormal, particularly when it is demonstrated by free-ranging members of the same species. Some primates, for which free-ranging data are lacking, engage in homosexual interactions in captivity in the absence of abnormal conditions such as greatly skewed sex ratio and human induced social disturbance (*C. jacchus*: Rothe, 1975; *L. rosalia*: Hoage, 1982; *M. silenus*: Skinner and Lockard, 1970; Table I). In such cases, this behavior may represent a species-typical pattern that will eventually be observed among free-ranging individuals. Although homosexual behavior *can* be associated with abnormal captive situations, they account for a small fraction of observations, and robust evidence exists for homosexual behavior under free-ranging conditions.

Table I. Homosexual Behavior in Primates[a]

	Living Condition	Grouping Pattern	Sex Class	Age Class		Frequency		Sexual Content		Sources
				Male	Female	Male	Female	Male	Female	
Platyrrhini Callitrichidae										
Callithrix jacchus	C*	?	F	n/a	2	n/a	1*	n/a	?	Rothe (1975)
Leontopithecus rosalia	C*	7?	M	2	n/a	2*	n/a	N	n/a	Hoage (1982)
Sanguinus fuscicollis	C	7(9)	M/F	?	?	1	1	Y	Y	Shadle *et al.* (1965)
Sanguinus midas	C	?	F	n/a	?	n/a	1*	n/a	Y*	Christen (1974)
Sanguinus nigricollis	C	?	M/F	?	?	1	1	Y	Y	Shadle *et al.* (1965)
Sanguinus oedipus	C	7?	M/F	?	?	1	1*	?	?	Moynihan (1970)
Cebinae										
Cebus capucinus	F	10	M	2	n/a	1*	n/a	Y*	n/a	Rose, personal communication (1992)
Cebus olivaceus	F	4	M/F	2	3	1*	1*	?	?	Robinson, personal communication (1992)
Saimiri sciureus	C/F	5	M/F	1	1	2*	2*	Y*	Y	Baldwin (1969); DuMond (1968); Talmage-Riggs and Anschel (1973); Denniston (1980)
Catarrhini Cercopithecinae										
Cercocebus atys	C	?	M/F	?	?	1*	2*	?	?	Bernstein (1970)
Cercopithecus aethiops	C/F	5(4)	M/F	1	?	2*	1*	Y*	?	Struhsaker (1967); Bernstein (1970)
Miopithecus talapoin	C/F	5	M/F	3	3	1*	1	N	N	Scruton and Herbert (1972); Wolfheim and Rowell (1972); Rowell (1973)
Erythrocebus patas	C/F	3	M/F	4	3	1*	1*	?	N	Gartlan (1974); Loy, personal communication (1993)
Macaca arctoides	C	5	M/F	1	1	2*	2*	Y*	Y*	Chevalier-Skolnikoff (1974, 1976); Bernstein (1980)

Macaca fascicularis	C	5	M	1?	n/a	2*	n/a	?	n/a	Thompson (1969)
Macaca fuscata	C*/F	5	M/F	1	1	1-3*	1-3*	Y*	Y*	Hanby *et al.* (1971); Hanby (1974); Hanby and Brown (1974); Eaton (1978); Fedigan and Gouzoules (1978); Wolfe (1979, 1984, 1986); Takahata (1982); Gouzoules and Goy (1983)
Macaca mulatta	C/F	5	M/F	1	3	1-3*	1-3*	Y*	Y*	Carpenter (1942); Altmann (1962); Gordon and Bernstein (1973); Fairbanks *et al.* (1977); Akers and Conaway (1979); Chan personal communication (1991)
Macaca nemestrina	C*/F	4	M/F	1	1	3*	3*	?	N	Evans (1967); Tokuda *et al.* (1968); Bernstein (1970); Oi (1990, 1991)
Macaca nigra	C	?	M/F	4	3	2*	2*	Y*	Y*	Dixson (1977)
Macaca radiata	F	5	M/F	1	?	3*	1?*	Y*	?	Simonds (1965); Makwana (1980)
Macaca silenus	C*	5	M/F	1	1	1?*	1?*	Y	?	Skinner and Lockard (1979); Bound *et al.* (1988)
Macaca tonkeana	F	?	M/F	3	3	2*	2*	?	?	Thierry (1986)
Papio cynocephalus	C/F	5	M/F	1	1	1-3*	1-3*	?	N	Maxim and Buettner-Janusch (1963); Owens (1976); Smuts and Watanabe (1990)
Papio hamadryas	C/F	8(2)	M/F	4	?	1*	1*	N	Y	Zuckerman (1932); Kummer (1968); Leresche (1976)
Theropithecus gelada	C/F	8(2)	M/F	4	3	2*	1*	Y*	?	Bernstein (1975); Wrangham in Weinrich (1980)

Table I. Continued

	Living Condition	Grouping Pattern	Sex Class	Age Class		Frequency		Sexual Content		Sources
				Male	Female	Male	Female	Male	Female	
Colobinae										
Nasalis larvatus	F	8(5)?	M/F	2	3	1*	1*	N	N	Yeager (1990)
Presbytis entellus	F	4	M/F	1	1	3*	3*	Y	Y*	Weber (1973); Sommer (1988); Srivastava *et al.* (1991)
Hominoidea										
Hylobatidae										
Hylobates lar	F	6	M	4	n/a	1*	n/a	Y*	n/a	Edwards and Todd (1991)
Symphalangus syndactylus	C	6	M	1	n/a	2?*	n/a	Y*	n/a	Fox (1977)
Pongidae										
Gorilla gorilla	C*/F	9	M/F	4	3	3?	2?*	Y	Y*	Coffin (1978); Fischer and Nadler (1978); Harcourt *et al.* (1981); Nadler (1986); Yamagiwa (1987)
Pan paniscus	C/F	1	M/F	1	1	2–3*	3*	Y*	Y*	Kano (1980, 1992); Kuroda (1980, 1984); Thompson-Handler *et al.* (1984); de Waal (1987); Furuichi (1989); Kitamura (1989); Enomoto (1990); Idani (1990, 1991)

Pan troglodytes	C	1	M/F	2	1	1	1	?	?	Kohler (1925); Bingham (1928); Kollar *et al.* (1968)
Pongo pygmaeus	C/F	11	M/F	2	3	1*	1*	N	Y*	Morris (1970), Rijksen (1978); Maple (1980); Nadler (1990)

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[a](1) Living Condition: C = caged; F = free-ranging; C* = group composition of the animals had not been disrupted six months before or any time during the study and the sex ratio is between 0.5–2 males per female.

(2) Grouping Patterns: Definitions from Smuts *et al.* (1986, pp. 501–505); 1 = community with individuals foraging partly independently; 2 = community with breeding units foraging partly independently; 3 = large group, one resident adult male; 4 = large group, variable number of resident adult males; 5 = large group with more than one resident adult male; 6 = monogamous pairs; 7 = monogamous pairs and polyandrous groups; 8 = small groups with one resident adult male; 9 = small group, variable number of resident adult males; 10 = small group with more than one resident adult male; 11 = solitary individuals.

(3) Sex Class: M = Male; F = Female.

(4) Age Class: Age classes observed to engage in homosexual behavior: 1 = various combinations of immature and/or mature individuals; 2 = immature; 3 = adult; 4 = immature males with adult males.

(5) Relative Frequency of Expression: 1 = Rare: (a) Homosexual behavior occurred approximately 5% or less frequently as heterosexual behavior, or (b) the behavior was described in an anecdotal fashion so that concrete conclusions about frequency are impossible; 2 = Occasional: (a) Homosexual behavior occurred approximately 6%–24% as frequently as heterosexual behavior, or (b) constituted part of a developmental phase that all individuals of an age/sex class experience; 3 = Frequent: (a) Homosexual behavior occurred approximately 25% or more frequently than heterosexual behavior; asterisk: indicates that this frequency value occurred in the presence of opposite-sex individuals.

(6) Sexual Content of Homosexual Interactions: Y = Yes; N = No; ? = Uncertain; Y* = homosexual interactions with sexual content occurred in the presence of opposite-sex individuals.

Frequency

Primate homosexual behavior is highly variable in frequency of expression. It ranges from total absence (*Alouatta* spp., *Macaca sylvanus*) to levels that approach or even surpass heterosexual behavior: *Macaca radiata* (Makwana, 1980); *M. fuscata* (Wolfe, 1986), *M. nemestrina* (Oi, 1990, 1991); *Presbytis entellus* (Srivastava *et al.*, 1991); *Pan paniscus* (de Waal, 1987). With few exceptions quantitative measures of the frequency with which this behavior occurs inter- and intraspecifically relative to heterosexual behavior are not documented. Consequently, to approximate the frequency of homosexual behavior in the 33 anthropoid, I employ broad categories: rare, occasional, and frequent (Table I). I divided each species by sex in order to elucidate sex differences that might exist in the frequencies of homosexual behavior.

Of the 28 species in which females engage in homosexual behavior, 16 do so rarely, 6 occasionally, and 6 frequently. Of the 31 species in which males engage in homosexual behavior, 13 do so rarely, 9 occasionally, and 8 frequently. Hence, the majority of primate species demonstrate homosexual behavior rarely. However, for 12 species, homosexual behavior is occasional or frequent in one or both sexes under free-ranging conditions. If one includes captives that are not affected by skewed sex ratio or human-induced social disturbance, the number of species that demonstrate homosexual behavior occasionally or frequently increases to 15 (Table I). Why interspecific and intraspecific variation in the frequency of homosexual behavior exists remains largely unclear and deserves the attention of future researchers.

Age Differences

Homosexual behavior is often thought to be a developmental phase restricted to or more common among immature individuals. Nevertheless, it has been observed in all age classes of primates. In 24 of the 27 species for which information is available, adults engage in homosexual behavior (Table I). Therefore, it is neither indicative of nor restricted to immature primates, nor is it uncommon among adults.

Sex Differences

I examined homosexual behavior for sex differences according to three behavioral parameters: presence or absence; sexual content, and frequency of expression. When homosexual behavior occurs within a primate species it is typically demonstrated by both sexes. This is true for 26 of the 33 species (Table I). The few exceptions to this pattern probably represent a lack of relevant data rather than a biologically significant phenomenon.

There is no evidence that the homosexual interactions of one sex are more overtly sexual in nature than those of the other. Using criteria modified from Fedigan (1982), I deemed a homosexual interaction partially sexual in nature if series mounting, consorting, and/or directed genital stimulation occurred in an nonaggressive context. An erection or ejaculation or both is further evidence for sexual content in the homosexual interaction of males. Where information is available for both males and females of a species ($N = 14$), in the majority of cases ($N = 12$) both sexes engage in homosexual behavior that is partially sexual in nature (Table I).

Although the majority ($N = 20$) do not exhibit sexual differences in the frequency with which homosexual behavior is expressed, a substantial number (13) of species do. As for the latter, it appears more frequently in males of 9 species and in females of 4 species (Table I). These sexual differences in frequency of expression may represent species-typical patterns, but factors such as living condition, group composition, and seasonality can affect intraspecific levels of this behavior. More careful documentation of the frequency of male and female homosexual behavior are needed before one could state that such differences are characteristic of a species vs. the focal subjects.

Social Grouping Pattern

Although several researchers have suggested that homosexual behavior may be restricted to particular types of grouping patterns, it occurs in all the major primate social systems (Smuts *et al.*, 1986; Table I). However, homosexual behavior appears to be less characteristic of monogamous, polyandrous, and polygynous primates, and more common among multimale, multifemale groups. In the former, sexual partners remain bonded for prolonged periods of time, and consequently, selection of a same-sex partner would have a devastating impact on the individuals' reproductive success. Thus, selection should act to constrain sexual activity to heterosexual interaction among species whose grouping patterns mitigate multiple sexual opportunities with many partners. There is also evidence that homosexual behavior is more common among primates that inhabit all-male groups (Carpenter, 1942; Gartlan, 1974; J. J. Moore and R. W. Wrangham in Weinrich, 1980; Yamagiwa, 1987).

Ecological Context

The interplay between ecological adaptation and social behavior is a particularly active area of research in primatology, yet virtually nothing is known about how ecological context affects homosexual behavior. Primatologists have remarked on a close temporal relationship between feeding and homosexual behavior, suggesting that dietary adaptation be causal (Hanby, 1974; Dixson *et al.*, 1975; de Waal, 1987; Kano, 1980; Kuroda, 1980; Savage-Rumbaugh and Wilkerson, 1978; Thompson-Handler *et al.*, 1984; Yamagiwa, 1987; Furuichi, 1989; White and Thompson-Handler, 1989; Edwards and Todd, 1991). For example, White and Thompson-Handler (1989; White, 1989) note that genitogenital rubbing between female *P. paniscus* is positively correlated with food patch size. White (1989) states that female *Pan paniscus* appeared to enter a patch, assess the amount of available food, and genitogenital rub accordingly. Wrangham (1993) argues that a primary factor favoring homosexual behavior in *P. paniscus*, but not *P. troglodytes* is that the former exploits both fruit and herbaceous vegetation, and thus experiences less intraspecific feeding competition. Consequently, individual *P. paniscus* are able to forage together in large groups, a social pattern that may favor the expression of homosexual activity (Wrangham, 1993). Until primatologists have more precise means by which to model the complex interactions between behavior and ecological adaptation, question as to why some closely related species exhibit homosexual behavior while others do not will remain unresolved.

SOCIAL AND BIOLOGICAL THEORIES FOR PRIMATE HOMOSEXUAL BEHAVIOR

Hormones and Homosexual Behavior

Because human can not be manipulated readily and observed directly, other primates have been used extensively as referential models for understanding the developmental influence of hormones on the expression of behavior. Although the majority of primate hormonal studies were not designed with the specific goal of investigating homosexual phenomena, this has not deterred speculation as to the implications of this research for its etiology.

Homosexual behavior has long been characterized as sex-role atypical for the actor, and thus the result of developmental processes more inherent to the opposite sex (Birke, 1981; Futuyma and Risch, 1984; Byne and Parsons, 1993). Consequently, the discovery that exposure to androgens plays a central role in the differentiation of male and female morphological characteristics led some researchers to hypothesize that exposure to androgen levels more characteristic of the opposite sex may result in homosexual behavior (Birke, 1981; Gartrell, 1982; Ruse, 1988). It has been hypothesized that females that exhibit homosexual behavior have a physiological excess of androgen, whereas their male counterparts have androgen deficiencies. On the basis of this conceptual framework, two categories of hormonal hypotheses for homosexual behavior have been generated: (1) those implicating abnormalities in adult hormonal levels and (2) those implicating hormonal abnormalities during prenatal development.

Abnormal Adult Hormone Hypothesis

The relevant primate data on the relationship between adult hormonal status and homosexual behavior come from three types of studies: (1) those that monitor gonadally intact, group-living individuals, (2) those that compare intact and gonadectomized individuals, and (3) those that treat both intact and gonadectomized adult individuals with excess doses of androgen.

Some studies of group-living *Macaca fuscata* and *M. mulatta* indicate that male–male mounting increases significantly when androgen levels are at normally occurring lower ranges (Loy *et al.*, 1984; Rostal *et al.*, 1986). However, similar studies of male *M. arctoides* and *M. mulatta* showed no such correlation (Gordon *et al.*, 1978; Nieuwenhuijsen *et al.*, 1987). Hence, while lower testosterone levels can be associated with male homosexual behavior in free-ranging macaques, higher levels are also compatible with the behavior. Studies of group-living female primates are more consistent, revealing that homosexual mounting is not associated with elevated levels of endogenous androgens (Akers and Conaway, 1979; Ruiz de Elvira *et al.*, 1983; Gouzoules and Goy, 1983; Turner *et al.*, 1989; Srivastava *et al.*, 1991).

Castration studies provide a means by which androgen production can be halted, following which the hormonally deficient, castrated individuals can be compared to gonadally intact individuals. The study by Loy *et al.* (1984) employed this methodology and showed that male *M. mulatta* castrated as juveniles demonstrate significantly higher levels of homosexual masturbation and mounting in adulthood versus intact males. These results seem to support the interpretation that deficiencies of endogenous androgen promote male homosexual behavior. However, as Loy *et al.* (1984) point out, apart from any hormonal considerations the relative lack of females in the castrated males' group may have promoted their increased tendency toward homosexual behavior. Moreover, a more appropriate methodology might have been to castrate the males following puberty. As such, these findings may reflect a lack of exposure to pubertal sex hormones rather than a deficiency in adult hormones *per se*.

To date, the research that reveals the most about abnormal hormonal levels and adult homosexual behavior has entailed injecting subjects with excess doses of androgens. The expression of homosexual behavior in intact (Phoenix *et al.*, 1968; Goy and Resko, 1972) or ovariectomized captive adult female *M. mulatta* (Eaton *et al.*, 1973; Phoenix and Chambers, 1982; Pomerantz *et al.*, 1986) is not significantly influenced by excess androgen. Excess androgen treatment of adults appear only to intensify patterns of sexual behavior that already exist, instead of inducing the expression of entirely novel ones (Goy and Resko, 1972; Thornton and Goy, 1986).

It seems reasonable to conclude that homosexual behavior among adult primates is not the product of abnormal excesses or deficiencies in androgens. Furthermore, the idea that normal androgen production in adult males or females is incompatible with homosexual behavior is not supported by the data. Although there are some data that support the idea that male homosexual behavior is associated with naturally occurring lower testosterone levels, there are an equal number of studies that contradict such findings.

Prenatal Hormonal Hypothesis

The second category of hormonal hypotheses for primate homosexual behavior posits that sex-atypical androgen levels that are experienced prenatally organize the brain according to an opposite sex pattern, thereby predisposing the individual to exhibit homosexual mounting in adulthood (Young *et al.*, 1964; Birke, 1981; Byne and Parsons, 1993). If this reasoning is correct, homosexual behavior might be more frequent among males that exhibit deficiencies of prenatal androgen and in females that exhibit excesses of prenatal androgen.

To investigate the prenatal hormonal hypothesis, primatologists have experimentally simulated the conditions of hormonal excess in the prenatal environment by treating pregnant female *M. mulatta* with excess doses of testosterone, which induces pseudohermaphroditism in their female infants (Goy and Resko, 1972). These pseudohermaphroditic *M. mulatta* are genetic females that possess ovaries, but unlike normal females they also possess a well-developed penis, an empty scrotum, a disrupted ovarian cycle, and no vaginal orifice (Young *et al.*, 1964; Eaton *et al.*, 1973). Behavioral differences between the pseudohermaphrodites and the normal females are argued to result from differential prenatal exposure to androgens. Research indicates that pseudohermaphroditic females that are <2 years old consistently engaged in more homosexual mounting than control females of similar age do (Young *et al.*, 1964; Goy and Phoenix, 1971).

Another strategy in trying to establish a link between excess prenatal androgens and homosexual behavior among female primates is to investigate sensitivity to exogenously administered androgen. Theoretically, females that are exposed to excess prenatal androgens should be neurologically predisposed toward greater androgen sensitivity in adulthood. Behaviors affected by circulating androgens, which presumably include homosexual behavior, should manifest themselves more rapidly in these females. Therefore, if pseudohermaphroditic females are given excess androgen, they should exhibit homosexual behavior more readily than normal females do.

Goy and Resko (1972) indicated that when pseudohermaphroditic female *M. mulatta* were injected with testosterone as adults, they demonstrated no consistent increase in mounting of other females. Working with ovariectomized individuals, Eaton *et al.* (1973), Phoenix and Chambers (1982), and Pomerantz *et al.* (1986) employed a similar methodology, but with contrasting results. They treated ovariectomized females and ovariectomized pseudohermaphrodites with TP (testosterone propionate) and then pair-tested them with ovariectomized estradiol-primed females. Pomerantz *et al.* (1986) found that following testosterone treatment homosexual mounting increased significantly among ovariectomized pseudohermaphrodites relative to ovariectomized females. In contrast, Eaton *et al.* (1973) and Phoenix and Chambers (1982) found no consistent difference in the frequency of homosexual mounting between the ovariectomized females and pseudohermaphrodites either before or after the administration of TP. In sum, the evidence that prenatal exposure to excess androgen predisposes a female toward testosterone sensitivity is limited to the one study by Pomerantz *et al.* (1986). Differences in the subjects' patterns of socialization, age, gonadal status, testosterone doses, and test schedules may be partially responsible for the differing results obtained across these studies.

The contradictory results and limited number of pseudohermaphrodite studies make generalizations difficult. Despite the need for future testing of the prenatal hormonal hypothesis, the methodological practice of employing pseudohermaphrodites as models for primate homosexual behavior is questionable. Free-ranging primates engage in homosexual behavior, sometimes at higher frequencies than the pseudohermaphrodites, and they do so independent of excessive androgen treatment or gonadal removal. In light of their abnormal prenatal environment, their ambiguous genital morphology, their disrupted ovarian cycle, and their potentially different socialization pattern (Fedigan, 1982; Ruse, 1988), the pseudohermaphrodites are dubious models for investigating the relationship between prenatal testosterone exposure and homosexual behavior as expressed by normal female primates.

Perhaps the most important idea to arise from these studies, and one that deserves further investigation, is the suggestion that prenatal exposure to excess androgen may result in differential affects over the life span (Phoenix and Chambers, 1982), and therefore have no direct effect on adult homosexual behavior. Thus, young pseudohermaphroditic females that engaged in more homosexual mounting than normal females (Young *et al.*, 1964; Goy and Phoenix, 1971), may not do so in adulthood.

Demography, Sex Ratios, and Homosexual Behavior

The influences of demographic patterns and group sex ratios are important variables affecting social behavior. For example, it seems intuitive that individuals living in unisexual groups would engage in relatively more homosexual interactions than those living in bisexual groups. Indeed, homosexual behavior has been observed in all-male groups, both in captive situations (Shadle *et al.*, 1965; Moynihan, 1970; Gordon and Bernstein, 1973; Slob and Schenck, 1986; Bound *et al.*, 1988) and under free-ranging conditions (Carpenter, 1942; Gartlan, 1974; J. J. Moore and R. W. Wrangham in Weinrich, 1980; Yamagiwa, 1987).

Research by Wolfe (1979, 1984, 1986) is unique in its detailed description of demographic effects on the expression of homosexual behavior by a primate species over time. She compared demographic trends and frequency of homosexual behavior between females in two populations (Arashiyama West and Arashiyama B) of *M. fuscata*. Of the sexually active Arashiyama West females, 78% engaged in homosexual behavior, whereas only 27% of Arashiyama B females did. Sexually mature females of the Arashiyama West troop had access to approximately half the number of sexually mature males that Arashiyama B females had. Wolfe (1984, 1986) argues that this difference in sex ratios accounts, in part, for the higher frequency of homosexual behavior among the Arashiyama West females. This hypothesis is further supported by Wolfe's (1986) comparison of her 1973–1974 data for the Arashiyama West population with that of Gouzoules and Goy (1983) from 1977. During this period the number of sexually active females that engaged in homosexual behavior decreased significantly from 78% to 51%, and this decrease was accompanied by an significant increase in the number of sexually mature males per female.

While Wolfe's research provides strong support for the influence of demographic variables on the expression of homosexual behavior, it must be stressed that even when males are well represented in a population, some female *M. fuscata* continue to exercise individual partner preference by engaging in homosexual consorts (Fedigan and Gouzoules, 1978; Fedigan, 1982; Takahata, 1982; Wolfe, 1984, 1991). Hence, while demographic processes appear to be very important, taken alone they provide only a partial explanation for the existence of homosexual behavior.

Sociosexual Explanations of Homosexual Behavior

Proceptivity-Enhancing and Receptivity-Reducing Hypotheses

Two sociobiological hypothesis for homosexual behavior—the proceptivity-enhancing hypothesis (Parker and Pearson, 1976) and the receptivity-reducing hypothesis (Tyler, 1984)—are similar in character, in that both attempt to explain the functional significance of female–female mounting. 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. Accordingly, the authors argue that female homosexual behavior can evolve via kin selection or reciprocal altruism.

Tyler (1984) 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. In this manner, the mountee's probability of insemination is reduced, which would decrease the number of future competitors for the mounter. Furthermore, limiting the mountee's copulations would guard against male sperm depletion, and this would increase the mounting female's own chances of being inseminated.

Based on these hypotheses, two shared predictions should hold: (1) female homosexual behavior should occur only in the presence of males and (2) only when females are fertile. Furthermore, if the proceptivity-enhancing hypothesis is correct, females should cease homosexual activity following the solicitation of sexually motivated males, whereas if the receptivity-reducing hypothesis is true, female's should not solicit other females to mount them.

These are the only sociobiological hypothesis for homosexual behavior that have been explicitly addressed using primate data. None of the predictions are supported. First, female homosexual behavior in *Presbytis* *entellus* often occurs when males are definitely out of sight, and consorting female *Macaca fuscata* often attempt to spatially and visually separate themselves from their group (Gouzoules and Goy, 1983; Srivastava *et al.*, 1991). Second, female homosexual behavior in these species commonly occurs following conception (Fedigan and Gouzoules, 1978; Gouzoules and Goy, 1983; Wolfe, 1979, 1984; Srivastava *et al.*, 1991). Third, inconsistent with the proceptivity-enhancing hypothesis is the fact that males often appear disinterested in females engaged in homosexual behavior, and consorting females tend to ignore or threaten any male that solicits them (Wolfe, 1984; Srivastava *et al.*, 1991; Vasey, in preparation). Fourth, in contradiction to the receptivity-reducing hypothesis, females of these two species actively solicit other females to mount them (Wolfe, 1979; Chapais and Mignault, 1991; Srivastava *et al.*, 1991). In conclusion, the proceptivity-enhancing and receptivity-reducing hypotheses are not supported and should probably be abandoned as explanatory models for homosexual behavior in primates.

Dominance-Assertion Hypothesis

Homosexual interaction among primates have a long history of being interpreted as ritualized dominance interactions (Nadler, 1990). It is argued that such interactions reaffirm the dominance hierarchy and thereby reduce aggression. Accordingly, mounting is a display of dominance, while being mounted is a display of submission (Wickler, 1967). While there are undoubtedly numerous circumstances of homosexual mounting that can be interpreted primarily as dominance interactions, the overall situation appears considerably more complex (Hanby, 1974; Reinhardt *et al.*, 1986).

Few studies report a strict relationship between dominant individuals mounting subordinates individuals of the same sex (Carpenter, 1942; Talmage-Riggs and Anchel, 1973; Leresche, 1976). By contrast, numerous studies document that while dominant individuals mounted more often, the mounting of a dominant by a subordinate individual is not uncommon, depending on the social context (Altmann, 1962; Simonds, 1965; Tokuda *et al.*, 1968; Travis and Holmes, 1974; Dixson *et al.*, 1975; Rothe, 1975; Makwana, 1980; Gouzoules and Goy, 1983; Reinhardt *et al.*, 1986; de Waal, 1987; Yamagiwa, 1987; Smuts and Watanabe, 1990; Cordischi *et al.*, 1991; Oi, 1991; Srivastava *et al.*, 1991). Still other studies show no consistent relationship between rank and mounting position (Christen, 1974; Hanby, 1974; Bernstein, 1975, 1980; Owens, 1976; Dixson, 1977; Eaton, 1978; Akers and Conaway, 1979; Ruiz de Elvira *et al.*, 1983; Thompson-Handler *et al.*, 1984; Bound *et al.*, 1988; Furuichi, 1989; Kitamura, 1989; Chapais and

Mignault, 1991; Rendall and Taylor, 1991; Oi, 1991). Some of these studies document that subordinate individuals mount dominant individuals following agonistic interactions, which is the exact opposite of what one would expect if interpreting these homosexual mounts as dominance displays. Furthermore, mounts by dominant individuals are sometimes associated with affiliative behavior and solicitations, which would indicate sexual interest in a heterosexual context.

The ambiguity of homosexual mounts in relation to rank has led many researchers to abandon a strict dominance interpretation. This is not to say that some homosexual interaction do not involve elements of dominance; however, this would not preclude the existence of other sociosexual roles, nor would it preclude a sexual element in such interactions. Smuts and Watanabe (1990) suggest that a more productive way to interpret these interactions may be as dominance negotiations during which the participants flesh out their relationships. Hence, while dominance is probably an important component of some primate homosexual behavior, it can only partially account for these complex interactions.

Practice for Heterosexual Copulation Hypothesis

Homosexual behavior between immature primates or between an immature and a mature individual is frequently observed during play, often involving rough and tumble interaction (Evans, 1967; Struhsaker, 1967; Baldwin, 1969; Wolfheim and Rowell, 1972; Hanby, 1974; Hanby and Brown, 1974; Dixson *et al.*, 1975; Rothe, 1975; Owen, 1976; Maple *et al.*, 1977; Thompson-Handler *et al.*, 1984; Nadler, 1986; de Waal, 1987; Enomoto, 1990; Yeager, 1990; Edwards and Todd, 1991). It has been hypothesized that play behavior functions to facilitate social and motor development. Thus, Hamilton (1914), Bingham (1928), Baldwin (1969), and Chevalier-Skolnikoff (1976) suggested that homosexual behavior expressed during play interactions may function as practice for adult heterosexual copulation. Some laboratory evidence supports this conclusion.

Research on captive, isosexually reared male *Macaca arctoides* (Slob and Schenck, 1986) and *M. mulatta* (Bercovitch *et al.*, 1988) indicate that a lack of heterosexual experience during immaturity does not necessarily affect the expression of competent heterosexual copulation during adulthood. Nonetheless, among macaques, adequate opportunity to engage in mounting when young is necessary for competent performance of heterosexual copulation in adulthood (Goy and Wallen, 1979). While the presence of mounting partners is essential during immaturity for the development of competent heterosexual copulation, the actual sex of immature mounting partners appears to be irrelevant. Hence, these isosexual studies could be marshaled as evidence that homosexual behavior among immature primates can serve as practice for adult heterosexual interactions. However, given the rapid learning abilities of primates, it seems unlikely that homosexual behavior among immature individuals serves merely as practice for adult heterosexual copulations. Moreover, with age, homosexual behavior diminishes during play and is exhibited more frequently in other social contexts by adult individuals. Hence, although there is probably some truth in this hypothesis, its explanatory value is limited.

Tension-Regulation Hypothesis

Numerous authors have noted that a relationship exists between social tension and anthropoid homosexual behavior (Carpenter, 1942; Ploog *et al.*, 1963; Evans, 1967; Struhsaker, 1967; Thompson, 1969; Wolfheim and Rowell, 1972; Gordon and Bernstein, 1973; Hanby, 1974; Dixson *et al.*, 1975; Erwin and Maple, 1976; Gartlan, 1974; Travis and Holmes, 1974; Bernstein, 1975, 1980; R. W. Wrangham and S. B. Hrdy in Weinrich, 1980; Oi, 1990, 1991; Yeager, 1990). Researchers studying *P. paniscus* have been particularly active in investigating this relationship, especially as its relates to interactions involving food.

Homosexual behavior frequently occurs between *P. paniscus* individual feeding at the same food site, where signs of tension over food are apparent (Kano, 1980; Kuroda, 1980, 1984; Thompson-Handler *et al.*, 1984; de Waal, 1987, 1989; Furuichi, 1989; White and Thompson-Handler, 1989). Kuroda (1980, p. 190) interprets homosexual behavior among *P. paniscus* to be a mechanism to reduce tension during periods of close proximity in the same food patch. He argues that it "works to calm anxiety or excitement, to dissolve inter-individual tension," and "thus to increase tolerance, which makes food sharing smooth." In support of this hypothesis, individuals entering an occupied patch are more likely to acquire food after engaging in homosexual interactions (Kuroda, 1984; de Waal, 1987; Furuichi, 1989). Moreover, genitogenital rubbing between female bonobos is positively correlated with food patch size, which presumably reflects the amount of time individuals spend in close proximity competing for resources (White and Thompson-Handler, 1989).

In accordance with the data on *P. paniscus*, research on *Papio cynocephalus* (Owen, 1976), *Macaca nemestrina* (Oi, 1991), and *M. nigra* (Dixson, 1977) also suggests a close temporal association among homosexual behavior, increased interindividual tolerance, and reduced aggression during periods of tension or excitement. These observations lend considerable support to the tension-reduction hypothesis and should be pursued among other primate species.

Reconciliation Hypothesis

de Waal (1987) demonstrates that when mechanisms for regulating aggression fail, *P. paniscus* can use homosexual behavior to reestablish social bonds. Homosexual mounts among captive *P. paniscus* increase significantly within a 15-min period following an agonistic conflict unrelated to food. Aggressors were more likely to initiate homosexual contact with their victims than vice versa, which de Waal (1987) interprets as reconciliation attempts by the aggressor. Kano (1980) also observed homosexual interactions among males following aggressive interactions. Even in the midst of agonistic interactions, homosexual behavior between female *P. paniscus* terminates the conflict (Furuichi, 1989). Although other species such as *Macaca nemestrina* (Oi, 1990) and *M. nigra* (Dixson, 1977) may also reconcile conflicts via homosexual behavior, further studies will be necessary to discern whether this behavioral pattern occurs extensively outside *P. paniscus*.

Alliance-Formation Hypothesis

The possible relationship between homosexual behavior and alliance formation was initially detailed by Fairbanks *et al.* (1977). They observed high levels of homosexual behavior between female *Macaca mulatta* in newly formed groups containing many unfamiliar individuals. They hypothesized that under such conditions, homosexual behavior may restore social bonds in the context of group social instability. Fairbanks *et al.* (1977, p. 248) state,

> In a natural troop, consort bonds between a male and a female are rapidly formed and broken, in contrast to typical female-female relationships, which are based on long-term familiarity . . .In the absence of the normal mechanisms for assuring female-female bonds, a few members of each group . . .turned to the behavior pattern of the sexual consort relationship for rapid bond formation. The females who could form the first bonds joined in coalitions against their undefended peers and attempted to drive them from the group. This division of the social group into "bonded females" and "strangers" was apparently the first stage in the formation of a new group.

At first glance it seems unlikely that the experimental situation created by Fairbanks *et al.* (1977) has any parallel under free-ranging conditions. Nonetheless, a number of free-ranging species demonstrate homosexual behavior in situations involving less extreme social instability such as intergroup contact and transfer (Carpenter, 1942; Struhsaker, 1967; Gartlan, 1974; S. B. Hrdy in Weinrich, 1980; Thompson-Handler *et al.*, 1984; Furuichi, 1989; Yeager, 1990; Idani, 1990, 1991; Kano, 1992).

However, it is unlikely that as a mechanism for alliance formation homosexual behavior is restricted solely to conditions involving social instability. For example, in a discussion of female homosexual behavior among *M. fuscata* Fedigan (1982, p. 43) stated,

> . . .females who had engaged in homosexual consorts during the mating season were likely to remain affinitively bonded (friends) throughout the year in contrast to male-female consort pairs which were not translated into year-round bonds. Since sexual partners are almost always unrelated, these friendships cross-cut matrilineal lines and are a potential source of alliance and bonding in addition to kin ties.

Chapais and Mignault (1991) argue that at least during the consort period, subordinate female *M. fuscata* can enjoy alliance support provided by their dominant nonkin partners. Such alliance support may result in the subordinate female temporarily outranking all individuals between herself and her dominant female sexual partner.

The study by Smuts and Watanabe (1990) on male *Papio cynocephalus* is the most detailed examination to date demonstrating a relationship between male–male alliance formation and homosexual behavior. Males that mounted and manipulated each other's genitalia more frequently formed the most cohesive and successful alliances against other males. Often, as if to reaffirm their alliance bond, two males would engage in homosexual behavior just before challenging a rival (also see Owen, 1976). The most intensely bonded males encouraged behavioral symmetry in their relationship by actively soliciting each other for mounts and genital fondling. Smuts and Watanabe (1990) suggest that males permit potential rivals intimate contact with their genitalia in order to demonstrate a willingness to accept risk, and thus, genuine interest in forming a reciprocal alliance in spite of the short-term cost they entail.

Evidence of a relationship between homosexual behavior and alliance formation among other species is suggested by an increasing body of data. In *Pan paniscus*, sexual behavior between females promotes alliance formation which allows partners to monopolize food sources and deter male harassment (Kano, 1992; Parish, in press) or to gain entry into a new group (Furuichi, 1989; Idani, 1990, 1991). Furthermore, among *Theropithecus gelada* and *Presbytis entellus*, males engage in homosexual behavior during attacks on resident males, which may affirm the attacking males' alliance (Wrangham and Hrdy in Weinrich, 1980). Similarily, among *Papio hamadryas*, male homosexual behavior has been linked to alliance formation and, in turn, to acquisition of female mates (Colmenares, 1991).

DISCUSSION

The phylogenetically widespread nature of primate homosexual behavior indicates that it is not a historically recent phenomenon, but one that can be traced back at least to the Oligocene, during the evolutionary diversification of the Anthropoidea. In striking contrast to anthropoids, prosimians are characterized by no homosexual behavior. On the basis of the extant primates, one can infer that increasing behavioral flexibility characterized the Oligocene anthropoid primates, relative to their prosimian ancestors and contemporaries. One facet of this increasing behavioral flexibility is the decoupling of sexual behavior from mere reproduction. In other words, with increasing behavioral plasticity, reproductive behavior was appropriate for diverse sociosexual purposes unrelated directly to fertilization. The term sociosexual refers to behavior that is sexual in form and that fulfills some social role (Wickler 1967). One consequence of this expanded sexual repertoire among anthropoid primates was the evolution of sociosexual interaction between same sex partners, in short, homosexual behavior.

The two major groups of anthropoid that predominated during the Oligocene, the New World and the Old World primates, were characterized by geographic isolation throughout their separate evolutionary histories (Conroy, 1990). In keeping with their distinct evolutionary trajectories, extant members of these two groups demonstrate different patterns of homosexual behavior. Consider, for example, that (1) none of the modern platyrrhines demonstrate frequent homosexual behavior, (2) none of them engage in extended homosexual interactions or consorts, and (3) their homosexual behavior appears restricted to play and dominance interaction (Table I). Thus, although platyrrhine sexual behavior has been decoupled from a strictly reproductive context, their homosexual behavior remains largely constrained in terms of frequency, form and sociosexual role.

Homosexual behavior among catarrhine primates appears to be an elaboration on the more basic platyrrhine pattern. The origin and evolution of frequent and more complex homosexual interactions involving consort bonding, reconciliation, tension regulation, and alliance formation appeared during the evolution of catarrhine primates. Unambiguous homosexual mate choice, as well as intra- and intersexual competition for same-sex sexual partners are other features that distinguish this group from the platyrrhines (Yamagiwa, 1987; Vasey, in preparation).

Exclusive homosexual behavior appears to be absent among nonhuman primates, but cross-cultural data indicate that it is expressed by a small percentage of people across numerous societies worldwide (Whitam, 1983). This indicates that at some point during or after the late Miocene–early

Pliocene certain hominid or protohominid individuals evolved the behavioral potential to engage in exclusive homosexual behavior and consort bonding.

Despite the widespread nature of homosexual behavior among primates and its long evolutionary history, there exists no satisfactory theoretical framework for interpretation. Not surprisingly, questions of fundamental theoretical importance such as whether homosexual behavior is adaptive (Ruse, 1988), neutral (Futuyma and Risch, 1984), or maladaptive (Gallup and Suarez, 1983) remain the subject of debate. Among primates, it does not appear to be maladaptive because there is no evidence indicating that it interferes with the actors' reproduction (Fedigan and Gouzoules, 1978; Wolfe, 1979, 1984; Gouzoules and Goy, 1983; Srivastava *et al.*, 1991). Despite some very compelling research demonstrating the adaptive advantages of homosexual behavior (Fairbanks *et al.*, 1977; de Waal, 1987; Smuts and Watanabe, 1990), there are numerous instances for which it appears to be adaptively neutral.

These seemingly contradictory observations of adaptive and neutral homosexual phenomena might be partially resolved if we abandon the view that it is the product of direct selection (Wilson, 1975; Parker and Pearson, 1976; Kirsch and Rodman, 1983; Tyler, 1984; Ruse, 1988; Dickemann, 1993). Alternatively, primate homosexual behavior could be a neutral, concomitant byproduct of selection for other trait(s), as yet undefined (Futuyma and Risch, 1984). As part of a pool of neutral variation, homosexual behavior could be co-opted to serve any number of sociosexual roles that might incidentally augment the actors' reproductive success (Vasey and Chan, 1992). From this theoretical perspective, instances of homosexual behavior that serve a fitness-enhancing sociosexual role could be described as exaptations *sensu* Gould and Vrba (1982). Exaptations are characteristics that were not built by natural selection for the fitness-enhancing roles that they currently serve, but instead, were co-opted for them (Gould and Vrba, 1982). Although exaptations are not the products of direct selection, they may eventually come under selection due to their positive effects on fitness, at which time secondary adaptive modifications will occur. However, not all homosexual behavior serves a sociosexual role that is potentially fitness enhancing. Primates frequently engage in homosexual interaction simply for sexual gratification; therefore, exaptation cannot characterize all homosexual behavior. In such cases, selection against the behavior may not occur because it does not interfere with reproduction, and it falls within a tolerable range of neutral behavioral variation.

As an exaptation, primate homosexual behavior may be regarded as trivial vis-à-vis the evolution of primate societies. Previous theoretical models of social evolution have focused on heterosexual behaviors, especially male–male competition for female mates and female choice of male mates, and how they interact with ecological factors to produce various social systems (Wrangham, 1986). However, homosexual mate choice, and intra- and intersexual competition for same-sex mates are salient features of some species, especially catarrhine primates living in multimale and multifemale groups, and all-male groups. Perhaps such homosexual interactions influence patterns of heterosexual copulation, which, in turn, could effect the combinations of genes that are contributed to the next generation. Several primatologists have commented on the important roles homosexual mate choice and intrasexual competition for same-sex mates play in structuring primate social relationships (Fairbanks *et al.*, 1977; Yamagiwa, 1987; Lunardini, 1989; Idani, 1990, 1991). Our understanding of social evolution would improve if future discussions of sexual selection included homosexual components of this process.

By defining the boundary that separates other primates from humans, primatologists mold society's ideas of human nature (Fedigan, 1986; Haraway, 1989; Zihlman, 1987). Although the first reports of homosexual behavior among primates were published >75 years ago, virtually every major introductory text in primatology fails to even mention its existence. Insofar as nature is often the popular criteria for crafting moral and social policies (Boswell, 1980; Weinrich, 1980; Haraway, 1989; Travis and Yeager, 1991), one might be left with the impression that homosexual behavior is a recent abnormality unique to humans, and thus outside natural order. Nevertheless, there exists robust evidence that homosexual behavior, and by extension, other nonreproductive sexual behaviors, are the products of a long evolutionary history that occurred independent of human culture. While homosexual behavior is widespread among our primate relatives, aggression specifically directed toward individuals that engage in it appears to be a uniquely human invention.

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