The Evolution of Human Homosexual Behavior¹

by R. C. Kirkpatrick

Homosexuality presents a paradox for evolutionists who explore the adaptedness of human behavior. If adaptedness is measured by reproductive success and if homosexual behavior is nonreproductive, how has it come about? Three adaptationist hypotheses are reviewed here and compared with the anthropological literature. There is little evidence that lineages gain reproductive advantage through offspring care provided by homosexual members. Therefore, there is little support for the hypothesis that homosexuality evolved by kin selection. Parents at times control children's reproductive decisions and at times encourage children in homosexual behavior. There is therefore more support for the hypothesis of parental manipulation. Support is strongest, however, for the hypothesis that homosexual behavior comes from individual selection for reciprocal altruism. Same-sex alliances have reproductive advantages, and sexual behavior at times maintains these alliances. Nonhuman primates, including the 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. Homosexual emotion and behavior are, in part, emergent qualities of the human propensity for same-sex affiliation. Adaptationist explanations do not fully explain sexual behavior in humans, however; social and historical factors also play strong roles.

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And if there were only some way of contriving that a state or an army should be made up of lovers and their loves, they would be the very best governors of their own city . . . and when fighting at one another's side, although merely a handful, they would overcome all men.

PLATO, The Symposium

The brother-in-law is ally, collaborator, and friend.
... In the same band, the potential brother-in-law,
i.e., the cross-cousin, is the one with whom, as an
adolescent, one indulges in homosexual activities
which will always leave their mark in the mutually
affectionate behaviour of the adults.

CLAUDE LÉVI-STRAUSS, The Elementary Structures of Kinship

Homosexual behavior has existed throughout human history and in most, perhaps all, human cultures (e.g., Blackwood 1986a, Greenberg 1988, Duberman, Vicinus, and Chauncey 1989). Cross-cultural and historical studies qualify the breadth of homosexual experience, while medical studies, primarily from the contemporary West, quantify its depth. The Melanesian example of homosexual behavior is well known, with 10 to 20% of Melanesian societies requiring all men to participate in homosexual as well as heterosexual sex (reviewed in Herdt 1984a). In southern China at the turn of the last century, 100,000 women joined a marriage resistance movement that included, for many, lifelong homosexual partnerships (Sankar 1986). And Mpondo miners of South Africa in the first half of the 20th century commonly entered into "mine marriages," forgoing sexual liaisons with nearby township women (Moodie, Ndatshe, and Sibuyi

Homosexual behavior is much more systemic than the above isolated examples might suggest (table 1). In Pacific Island societies other than in Melanesia, such as Tahiti and Hawaii, homosexual behavior was common prior to Western influence (Gunson 1964, Morris 1990). In native North America, at least 137 societies had institutional roles for transgenders (berdache) commonly associated with homosexual behavior (Callender and Kochems 1983, Williams 1986, Roscoe 1987, Lang 1998). Homosexual behavior has also been common in societies of native South America (reviewed in Greenberg 1988; Murray 1995*a*, *b*), Asia (e.g., Hinsch 1990, Leupp 1995), precolonial Africa (reviewed in Sweet 1996), and premodern Europe (e.g., Dover 1989, Rocke 1996). In Ford and Beach's (1951) world sample, homosexual behavior is normative in 64% of the societies with available data (n = 76), at least for certain classes of individuals.

Studies over the past 70 years in contemporary soci-

had their origin in a seminar on human mating led by S. Hrdy many years ago. I am grateful for her continuing encouragement and the encouragement of P. S. Rodman to develop these ideas.

TABLE 1 Selective Overview of Geographical Distribution and Forms of Homosexual Behavior

Continent/Society	Form	Female or Male?	Juvenile or Adult?	Concurrent with Hetero- sexual Behavior?	Frequency in Total Population	Reference
Africa						
Siwah (Libya)	Patron/client, including "lending" of sons among promi-	M	J, A	Yes	~95%[?]	I
Azande (Sudan)	nent men M: patron/client among warriors; F: within polygynous	F, M	J, A	Yes	Common	2
Dahomey (Nigeria)	marriages Among adolescent peers, predicts rit- ual best friend of adults	F, M	J, ?A	?	Common	3
Mpondo (South Africa)	Patron/client; client receives aid in household formation	M	A	Yes	Common	4
Europe						
Classical Athens	M: patron/client; F: reported but little described	F, M	J, A	Yes	Common	5
Early Roman empire	M: state-sanctified marriages; F: appar- ently much the same as male	F, M	J, A	Yes	Common [?]	6
Dinaric (Serbia)	Within sworn	M, ?F	?A	?	Unknown	7
Florence, 15th century	friendships Patron/client across class, also among peers within guilds	M	J, A	Yes	> 50%[?]	8
Americas						
Lakota (U.S.A.)	Men in conventional marriages sponsor transgender "berdache"	M	A	Yes	Unknown	9
Mohave (U.S.A.)	Same-sex marriage be- tween transgenders and those of con- ventional gender	F, M	A	Yes	Limited	10
Nambikuara (Brazil)	Among classificatory	M	J	No?	Common [?]	II
Yanomamo (Venezuela)	brothers-in-law Among peers, prior to heterosexual marriage	M	J	No	> 50%	12
Oceania						
Precolonial Tahiti	Within sworn friendships	M	J, A	Yes	Common	13
Arunda (Australia)	Among cross-cousins, following exogamy rules of heterosex- ual behavior	F, M	J	No	Common	14
Big Nambas (Melanesia)	M: patron/client; F: common but little described (appar- ently among peers)	F, M	J, A	Yes	~100%	15
Marind-anim (Melanesia)	Adult male serves as mentor, ideally to sister's adolescent son	M	J, A	Yes	~100%	16

TABLE I (Continued)

Continent/Society	Form	Female or Male?	Juvenile or Adult?	Concurrent with Hetero- sexual Behavior?	Frequency in Total Population	Reference	
Sambia (Melanesia)	Adult male serves as mentor, ideally to wife's younger brother	М	J, A	Yes	~100%	17	
Asia							
China, 700–400 B.C.	Patron/client; client receives social prestige and politi- cal power	M	A	Yes	Unknown	18	
China, A.D. 1865–1965	Sworn alliances in marriage resistance of 100,000 women	F	A	No	Limited	19	
Japan, 16th, 17th century	M: patron/client, common in both rural and urban ar- eas; F: little described	F, M	J, A	Yes	> 50%[?]	20	
Pukhtun (Pakistan)	More pleasurable than heterosexual behavior because of male-female antagonism	M	Ј, А	Yes	Unknown	21	

SOURCES: 1, Cline (1936); 2, Evans-Pritchard (1970); 3, Herskovits (1938); 4, Moodie, Ndatshe, and Sibuyi (1989); 5, Dover (1989); 6, Boswell (1980); 7, Tomasic (1948); 8, Rocke (1996); 9, Williams (1986); 10, Lang (1998); 11, Lévi-Strauss (1943); 12, Chagnon (1966); 13, Gunson (1964); 14, Roheim (1933, 1950); 15, Deacon (1934); 16, van Baal (1966); 17, Herdt (1984b); 18, Hinsch (1990); 19, Sankar (1986); 20, Schalow (1989), Leupp (1995); 21, Lindholm (1982).

eties quantify homosexual behavior over time (table 2). In a selected sample of U.S. women in the 1920s (n =2,200), approximately 23% had homosexual sex (Davis 1929). Similarly, in Kinsey et al.'s (1953) sample of U.S. women in the late 1940s (n = 2,601), 20% had homosexual sex. In Kinsey, Pomeroy, and Martin's (1948) sample of U.S. men over age 20 (n = 2,830), 37% had orgasmic sex with other men, 10% were primarily homosexual for three years between ages 16 and 55, and 4% of Caucasians were exclusively homosexual after adolescence. In a representative sample of U.S. men in 1970 (n = 1,450), 20% had orgasmic sex with other men, 7% after age 19 (Fay et al. 1989).

In the Darwinian view of natural selection, individuals should seek to maximize reproductive success. Humans are a sexually reproducing species, and children result only through mating with members of the other sex; homosexual acts do not appear to aid reproduction. Homosexual behavior is too widespread to be a fluke or an aberration, but evolutionists in particular should be puzzled by its ubiquity. One could look at homosexual behavior as a value-free activity, such as grooming, but few societies do. In fact, much significance is attached to homosexual relations.

Why is homosexual behavior so widespread? How could it have evolved? Attempts by evolutionary biologists to reconcile homosexual behavior with natural selection have assumed that homosexual behavior is negative for individual fitness and therefore must be maintained by indirect selection. The theories of kin selection and of parent-offspring conflict, in particular, have been the focus of adaptationist explanations. In the kin-selection hypothesis, homosexuals altruistically forgo reproduction to assist the offspring of relatives (Wilson 1975, Weinrich 1987a). In the parental-manipulation hypothesis, children are manipulated by parents to forgo reproduction, become homosexual, and assist the offspring of relatives (see Trivers 1974, Ruse 1988). A third hypothesis, presented by Hutchinson (1959) and called "balanced polymorphism," suggests that homosexual behavior is retained because it co-occurs with a second trait under positive selection. Hutchinson does not describe this second trait, although he suggests that it might involve rates of development.

I propose a fourth possibility: that direct, positive selection for homosexual behavior occurs because of its nonconceptive benefits (see fig. 1). Heterosexual behavior serves nonconceptive functions such as the maintenance of long-term bonds (Morris 1967, Wilson 1975, Small 1995). If homosexual behavior also serves nonconceptive functions, such as the maintenance of samesex alliances (long-term supportive relationships) that

TABLE 2
Proportions for Homosexual Behavior Reported in Contemporary Societies, Primarily from the West

Study Population		n (Women)	Men			Women			
	n (Men)		Exclusive Homosexual	Bisexual	Sum	Exclusive Homosexual	Bisexual	Sum	Reference
U.S. nonrandom									
samples									
United States	_	2,200	-	_	-	n.r.	n.r	23.0°	I
United States ^b	III	_	n.r.	n.r.	27.0°	_	_	_	2
United States	2,830 ^d	2,601	n.r.	n.r.	37.0°	n.r.	n.r.	20.0	3
U.S. random samples									
United States	1,450	_	n.r.	n.r.	20.3	_	_	_	4
Los Angeles	_	298	_	_	_	1.0	3.0	4.0	5
United States	1,288	674	$0.8^{\rm e}$	5.4°	6.2e	0.3 ^e	3.3°	3.6e	6
United States	3,324		I.I	1.2	2.3	_	_	_	7
United States	1,401	-	0.7	4.9	5.6	_	-	-	8
European random samples									
Norway	~3,150 ^f	~3,150 ^f	0.6	2.9	3.5	0.8	2.2	3.0	9
France	9,928	10,127	0.7	2.4	3.I	0.6	2.0	2.6	10
France	1,506	788	0.7 ^e	10.0 ^e	10.7 ^e	0.1°	3.2 ^e	3.3°	6
United Kingdom	8,384	10,492	0.2	5.0	5.2	0.1	2.5	2.6	11
United Kingdom	1,137	696	I.I ^e	3.4°	4.5°	0.5 ^e	1.6e	2.1 ^e	6
Other societies, non-random samples									
Arab Near East ^{b,g}	113	_	n.r.	n.r.	38.0	_	_	_	12
Colombia ^b	n.r.	n.r.	3.0^{h}	15.0h	18.0 ^h	n.r.	n.r.	12.0^{h}	13
Thailand ^b	173	_	0.6	16.3	16.9	_	_	_	14
Thailand	983	1,285	0.2	3.1	3.3	0.9	0.3	1.2	15
Thailand ⁱ	n.r.	-	n.r.	n.r.	25.6	-	-	-	16
Median			0.7	4.9	8.5	0.6	2.4	3.3	
Mean			0.9	6.3	14.2	0.5	2.3	7.0	

SOURCES: I, Davis (1929); 2, Finger (1947); 3, Kinsey, Pomeroy, and Martin (1948), Kinsey et al. (1953); 4, Fay et al. (1989); 5, Essock-Vitale and McGuire (1988); 6, Sell, Wells, and Wypij (1995); 7, Billy et al. (1993); 8, Smith in Diamond (1993); 9, Sundet et al. (1988); 10, ACSF (1992); 11, Johnson et al. (1994); 12, Melikian and Prothro (1954); 13, Ardila (1986); 14, Whitam and Mathy (1986); 15, Sittitrai et al. in Diamond (1993); 16, Nopkesorn et al. in Sittitrai and Brown (1994).

NOTE: Both median and mean numbers are unweighted and therefore bias totals toward U.S. and European samples.

aid in resource competition or in cooperative defense, then homosexual behavior will be under positive selection. In terms of the biological distinction between sexual and somatic reproduction, homosexual behavior is a *survival* strategy, not a *reproductive* strategy. If this is the case, homosexual behavior will be best explained by reference to the costs and benefits of reciprocal altruism (*sensu* Trivers 1971).

After a brief review of correlates of human homosexual behavior, predictions of the kin selection, parental-manipulation, and alliance-formation hypotheses are compared with the ethnographic literature. (Although my intent is to incorporate the homosexual behavior of women and men equally, examples in the literature are biased toward men.) Limited reference to nonhuman primates is made in the course of a consideration of the evolution of homosexual behavior in hominids. In this review, sexual behavior is defined (after Vasey 1995) as genital contact or genital manipulation by individuals who have begun development of secondary sexual characteristics. By this definition, ephebophilic interactions (those involving pubescent adolescents) can be sexual,

^aMean of married and unmarried samples.

^bCollege students.

^cOrgasmic sex.

dAge 21 years and older.

^eBehavior in past five years (i.e., not lifetime behavior).

^{63%} return of 10,000 postal questionnaires; see also Veierod et al. (1997).

^gApproximately 90% from Lebanon, Syria, Jordan, and Iraq.

hAverage of four cities; selected sample estimates homosexual:bisexual ratio.

ⁱMilitary conscripts, age 21.

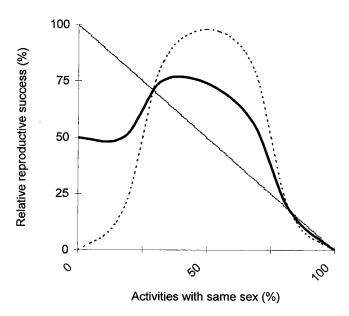


Fig. 1. Curves for reproductive success both from sexual activities and from somatic (survival and maintenance) activities. The curve for sexual reproduction (thin solid line) assumes a monotonic decrease in fecundity with reduced proportion of heterosexual activities. The curve for somatic reproduction (dotted line) assumes a sigmoidal increase in survival and maintenance with increased same-sex alliances to the midpoint, after which increases in same-sex alliances lead to a decrease in reproductive success. (The decrease results from the inability to sustain heterosexual alliances and thereby take advantage of the sexual division of labor and of the long-term bonds typically necessary for successful child rearing.) Averaging the two curves (heavy solid line) shows that the best strategy for net reproductive success is alliances with both sexes. If, within particular cultural systems, homosexual behavior is useful for maintaining same-sex alliances, it is then adaptive to include a moderate level of homosexual behavior in one's sexual repertoire.

while pedophilic interactions (those involving prepubescent children) cannot. A "homosexual" has sex only with the same biological sex, while a "heterosexual" has sex only with the other biological sex. A person with a sexual history including both sexes is "bisexual." Bisexuality is as of much interest as homosexuality per se; the term "nonheterosexuals" refers to bisexuals and homosexuals together, and the term "homosexual behavior" refers to individual acts of both bisexuals and homosexuals.

These behavior-based definitions are more restrictive than those typically found in the literature. Behaviorbased categories are, however, more logically defensible and no less verifiable than assigning bisexuals to the homosexual or heterosexual categories. Behavior is also a better classifier than self-identification. In a sample of contemporary U.S. women (n = 1,384), 17% had homosexual sex, yet only 5% defined themselves as gay or bisexual; for men (n = 1,335) the numbers were 22% versus 9% (Janus and Janus 1993). Although intentionality may differ between individuals who identify themselves as gay and as straight, the a priori assumption should be that their behaviors arise from the same source. Behavior-based categories allow for comparisons across cultures—and species—while categories based on self-identification do not. Behavior-based categories further allow for objective comparison with the performance measure of reproductive success. The use of restrictive definitions in this review at times leads to the testing of predictions about homosexuals with data for nonheterosexuals (i.e., homosexuals and bisexuals together). This is, unfortunately, unavoidable because of inconsistency among researchers in dividing the continuum of human sexual behavior.

Correlates of Homosexual Behavior

Any behavior to be explained by evolution must have inherited components. This is not to argue for direct genetic determinants of sexuality. Culture can be a powerful, consistent way of transferring traits between generations (Boyd and Richerson 1985); behavioral polymorphisms need not be genetically based and may result from mixed strategies within an individual's lifetime (Maynard Smith 1982). Recent research addresses the possibilities of biological and cultural influences on homosexual behavior. Clearly, homosexual behavior has statistically significant correlates, at least in contemporary Western societies.

GENES

Individuals who identify themselves as homosexual or bisexual are found in particular family lines (reviewed in Bailey and Bell 1993, Pattatucci and Hamer 1995, Pillard 1996). Monozygotic twins have concordance for nonheterosexuality at about twice the rate of dizygotic twins, suggesting some genetic influence on the findings on family aggregation (e.g., Bailey et al. 1993, Whitam, Diamond, and Martin 1993; cf. Hershberger 1997). Further, there may be chromosomal concordances in nonheterosexuals who are brothers (Hamer et al. 1993). The chromosomal studies have been particularly contentious (see Risch, Squires-Wheeler, and Keats 1993, Byne 1995); initial findings have been replicated by Hamer and colleagues (Hu et al. 1995), but replication has eluded independent researchers (Rice et al. 1999).

Twin studies also suggest the importance of environmental factors. Bailey and Pillard (1991; see also Buhrich, Bailey, and Martin 1991), for example, found that 52% of the monozygotic co-twins (n = 56) of male nonheterosexuals were also nonheterosexual, while only 22% of dizygotic co-twins (n = 54) were also nonheterosexual. Eleven percent of adopted brothers (n = 57) were nonheterosexual, compared with 9% of nontwin related brothers (n = 142). A large portion of homosexual behavior must therefore be free from the influence of genes and of the uterine environment, or monozygotic twins would have greater concordance and adopted brothers and nonadopted nontwin brothers—who share no genetic material—would have greater differences in homosexual behavior.

HORMONES

Data are contradictory concerning hormonal and developmental differences between those who engage in homosexual behavior and those who do not (reviewed in Small 1995, Byne 1995, LeVay 1996). Differences in prenatal hormones between self-identified homosexual and heterosexual men are implicated by small statistically significant differences in fingerprints (Hall and Kimura 1994). (Fingerprints complete development by the fourth month of pregnancy and are quite heritable.) However, there are no apparent differences in the androgen receptors of self-identified homosexual and heterosexual men, and this weakens the case for differences in hormone exposure (Macke et al. 1993). There may be differences in brain morphology and associated differences in visuospatial ability between homosexuals and heterosexuals (reviewed in LeVay 1996, Sanders and Wright 1997), but any such differences are quite small and have almost complete overlap in range (Byne 1995, 1996; Wegesin 1998). The inconclusiveness of the available evidence for hormonal correlates to homosexual behavior is given a balanced treatment by Small (1995).

Several longitudinal studies suggest that gender-atypical children grow up to be homosexual (e.g., Green 1987, Zuger 1988). In some Western societies, children identified by parents as gender-atypical tend to identify themselves as homosexual as they become adolescents; many self-identified homosexuals recall a gender-atypical childhood (Whitam and Mathy 1986, 1991; Zucker 1990). However, twin studies suggest that sexual orientation does not covary with gender nonconformity (Bailey and Pillard 1991). Further, many populations known for male homosexual behavior do not have a reputation of effeminacy (e.g., the samurai of feudal Japan [Leupp 1995], the knights of feudal Europe [Greenberg 1988; cf. Gilmour-Bryson 1996], the Yanomamo of South America [Chagnon 1966]].

It remains possible that sexual orientation has a complex, dependent relation with the development of gender identity. Prenatal hormones contribute to differences in gender characters, and certain gender characters may tend to co-occur with homosexual behavior (reviewed in LeVay 1996). If a link exists between sexual orientation and gender identity, however, we know remarkably little of its details. Studies of gender identity and sexual orientation typically lack strict controls for study groups. Determining cause and effect is confounded by societal preconceptions of gender identity (Corbett 1998). While many self-identified homosexuals recall a gender-atypical childhood, for example, so do many self-identified heterosexuals (Byne in Small 1993). Gender nonconform-

ity is neither necessary nor sufficient for homosexual behavior.

ENVIRONMENT

Homosexual behavior is correlated with social and demographic variables. Military service increases the likelihood of homosexual behavior by 50% (19% of 570 males versus 12% of ~880 males, Yates-corrected χ^2 = 12.6, d.f. = 1, *p* < 0.001 [Fay et al. 1989:348 n. 30]). Public school attendance in England doubles the likelihood of adolescent homosexual behavior (Johnson et al. 1994). Homosexual behavior also correlates with birth order, at least in U.S. and Canadian men: the likelihood that a man will engage in homosexual sex increases with the number of older brothers he has (reviewed in Blanchard and Bogaert 1996a, b). Blanchard and Bogaert (1996a, b) hypothesize that prenatal hormones mediate this effect, with immune response in mothers becoming stronger with each male child. The postuterine environment might also influence the correlation between birth order and homosexual behavior, however. The different opportunities presented to boys in different positions within family hierarchies is an alternative, psychological explanation for this correlation (Sulloway 1996:488 n. 36).

Human homosexual behavior aggregates in particular lineages, relates to birth order, and depends in part on one's social network, and some cultures encourage it while others do not. What is most striking about correlates of homosexual behavior is the small amount of variation explained by any single factor. Genes, hormones, childhood experience, and adult experience are multivariate and interact to produce multivariate life histories. Present evidence suggests that homosexual behavior is weakly, if significantly, correlated with numerous traits, some genetic, some developmental, and some experiential. Subtle increases in propensity for homosexual behavior on a broad range of fronts create an array of human experience. There may be certain constellations of traits that lead to a greater or lesser propensity for an individual to participate in a greater or lesser proportion of homosexual acts. Sexual behavior and emotion are continuous variables, not dichotomous ones (Ellis, Burke, and Ames 1987, McConaghy, Buhrich, and Silove 1994). Focus on slight differences in modal tendencies due to single, isolated factors obscures the fundamental continuity between homosexual, bisexual, and heterosexual experience.

This implicitly suggests that it is a mistake to divide individuals into "constitutional" versus "facultative" homosexuals (e.g., Bell, Weinberg, and Hammersmith 1981). Such a division is, in essence, an extreme position in the general "nature" versus "nurture" debate. For most mammals, social behaviors are based on a range of constitutional propensities interacting with a range of facultative opportunities; behaviors are condition-dependent and not typically fixed in individuals within populations but fluid as individuals' life histories accumulate. Sexual orientation is not bimodal (contra LeVay

1996; e.g., see Johnson et al. 1994). Admittedly, the data are not clear on whether there is one type of human sexuality that ranges from homosexual to heterosexual or two types of sexuality—homosexual and heterosexual—that blur only when facultative opportunities do not match constitutional desires. However, while it is unclear whether sexual orientation is a dichotomous variable, it is clear that sexual *behavior* is a continuous one. And, as Small (1995:149) notes, "[A] strategy isn't a strategy if it's rarely implemented; it's just an unfulfilled wish. And evolution doesn't recognize unfulfilled wishes. In other words, what people say they want is not important, it is what they get that is of real significance [to natural selection]."

Kin Selection and Parental Manipulation: Predictions and Evidence

Humans have few children over a lifetime and invest heavily in each child. Reproductive success and lineage survival therefore depend more upon the quality and quantity of child care than on gross number of children. If a homosexual sufficiently increases the reproductive success of kin, then the genetic material transmitted to the next generation via kin and held in common with the homosexual by virtue of relatedness may offset the homosexual's lack of offspring. This may come from direct support of offspring, direct support of the lineage, or indirect support by not producing competitors to the lineage's designated heirs.

Wilson (1975) suggests that if homosexuals in nontechnological societies function as helpers, kin selection can maintain genes for homosexuality. Alternatively, nonreproductive individuals may increase the reproductive success of parents, but the inclusive-fitness gains may not be enough to offset the losses to nonreproductive individuals themselves (Alexander 1974, Trivers 1974). If so, parents may manipulate selected offspring to forsake sexual reproduction, become homosexual, and assist in raising siblings or the offspring of siblings. An implicit assumption of the proponents of both hypotheses has been that most individuals engaging in homosexual behavior are homosexuals and therefore homosexuality is the behavior to be explained.

Kin selection and parental manipulation are confounded with regard to homosexuality because the two hypotheses have a number of predictions in common. Dickemann (1995) joins the two under the more general hypothesis of "inclusive fitness" and suggests that since one need not be homosexual to assist kin, "the inclusive fitness hypothesis is a hypothesis about celibacy and nonreproduction. Whether and when celibates are homosexual ... are subsidiary questions" (Dickemann 1995:174). Three central predictions of both hypotheses are (1) that homosexual behavior reduces individual reproductive success, (2) that lineages with homosexuals have greater reproductive success than lineages without,

and (3) that homosexual behavior is typically seen in individuals of low reproductive potential.

REDUCED INDIVIDUAL REPRODUCTIVE SUCCESS

Present information is equivocal on the prediction of reduced reproductive success for individuals. Homosexuals do not, by definition, have offspring, but most people who engage in homosexual behavior are bisexual (see, e.g., table 2). There is as yet no compelling evidence that the number of surviving offspring or even fecundity is limited by homosexual behavior as seen in the majority of individuals practicing it.

Many individuals who engage in homosexual behavior have children. In a sample of contemporary British women (n = 3.180), bisexuals have significantly higher fecundity to age 25 and no significant difference in lifetime fecundity when compared with heterosexuals (Baker and Bellis 1995). Of approximately 265 homosexual and bisexual men over 30 years old in contemporary Japan, 83% have offspring (Isomura and Mizogami 1992). Quinn (1996) provides data for lifetime fecundity (within the confines of marriage) for 13 men, all 19th-century Mormons known to have participated in consensual homosexual sex. On average, 2.1 children were born to these men, with a range of o to 9. (Comparison of these numbers with a general sample of 19th-century Mormons could test for statistical differences.) In some societies, many individuals—probably most individuals—who produce children also engage in homosexual sex (e.g., 15th-century Florence [Rocke 1996], 17th-century Japan [Schalow 1989, Leupp 1995], Melanesia [Herdt 1984*a*]).

There are limited data in support of this prediction, however. In Davis's (1929) sample of married U.S. women (n = 1,000), those having "intense emotional relationships" with other women tend to be childless more often than women without such relationships (39% of 18 women versus 21% of 982 women, Yates-corrected χ^2 = 2.40, d.f. = 1, p = 0.121). (Only 8 of the 18 women reporting "intense emotional relationships" are known to have had homosexual sex [see Davis 1929: chap. 11, table 41.) In a random sample of contemporary U.S. women (n = 298), the mean number of children born to women with homosexual experience is 1.2 versus a mean of 2.2 for women without homosexual experience (significance not reported [Essock-Vitale and McGuire 1988). In some societies homosexual behavior is tolerated only so long as procreative duties are fulfilled (e.g., 17th-century Fujian, China [Ng 1989], contemporary Thailand [Jackson 1989]), suggesting that parents may oppose homosexual behavior when it reduces a lineage's reproductive success.

INCREASED REPRODUCTIVE SUCCESS FOR LINEAGES

If homosexuality occurs because of lineage benefits at the expense of homosexuals themselves, there will be greater offspring survival in lineages with homosexuals. Although there are no studies showing such ultimate differences, the proximate mechanism presumably would be more or better aid to kin's offspring from homosexuals than from heterosexuals or celibates.

The data here are weak and not directly to the point. The most that can be said is that individuals engaging in homosexual behavior at times help their families. In the marriage resistance movement of southern China, two or three individuals would sometimes swear friendship, and this often led to homosexual behavior (Sankar 1986). Women in the movement were relatively wealthy from work in the silk industry and regularly sent wages back to their natal families; some parents encouraged daughters to join the sisterhood as a means of increasing lineage income. A different source of lineage support might be betrothal payments in homosexual marriages (e.g., 17th-century Fujian [Ng 1989], the Azande of Sudan [Evans-Pritchard 1970]). In the Siwah of Libya, boys commanded a higher betrothal price than girls (Maugham in Murray 1997). In native North America, transgenders could provide lineage support through their roles as matchmakers and as mediators of disputes; they also had access to restricted technologies such as basket making and pottery, and this provided them material gain (e.g., the Navaho of North America [Hill 1935]).

Data are unavailable, however, on the amount of care given by homosexuals to the offspring of kin. Arguments in support of this prediction rely on the *potential* of homosexuals to aid their lineages. Even if it can be shown, for example, that North American transgenders received benefits in their roles, this is not the same as benefit to kin (Dickemann 1995).

TYPICAL APPEARANCE IN INDIVIDUALS OF LOW REPRODUCTIVE POTENTIAL

If individuals forgo reproduction for the benefit of kin (altruistically with kin selection, under duress with parental manipulation), these individuals should be those with a low probability of producing offspring directly. Factors associated with reproductive potential include birth order, biological sex, and demographic sex ratios. The data provide some support for this prediction. Birth order clearly has implications for the role one takes (or is assigned) in one's lineage. Also in keeping with this prediction, current information suggests more male than female homosexual behavior. There are as yet no systematic studies to show that demographic skews lead to homosexual behavior, however.

Birth order. Particularly in societies with unigeniture, sanctioned reproduction is reserved for those of high birth order (e.g., 15th- and 16th-century Portugal [Boone 1988]). Individuals of low birth order presumably have less opportunity for successful reproduction (e.g., in the priesthood, the military). Self-identified male homosexuals in the United States and Canada tend to have more older brothers than do self-identified male heterosexuals (Blanchard and Bogaert 1996a, b), and this implicitly supports the prediction that homosexuality correlates with low reproductive potential. Gender-role "reversal" of some individuals engaging in homosexual acts is com-

mon in some societies—although this role reversal does not apply to their heterosexually married partners (e.g., North and South America [Williams 1986; Murray 1995a, b; Lang 1998], precontact Hawaii [Morris 1990]]. Therefore, it is of interest that among the Lache of Colombia and in societies of the West Indies in the 1800s, sons of very low birth order were at times raised as daughters (Métraux and Kirchhoff 1948, Waitz in Greenberg 1988). Further, later-born females apparently are more likely to be raised as sons among the Kaska of North America (Honigmann 1954). Such reports are potentially in keeping with the prediction that low birth order is correlated with homosexual behavior, particularly for males.

Biological sex. Males have greater variance in reproductive success than do females (Trivers 1972), and if homosexuality results from low reproductive potential there should be more male than female homosexuals. This may be the case. Roughly twice as many males report homosexual behavior as do females in the contemporary United States, the United Kingdom, and France (Sell, Wells, and Wypij 1995; see also table 2). Cross-culturally, male homosexual behavior is reported more frequently than female homosexual behavior (e.g., classical Athens [Dover 1989], 16th- and 17th-century Japan [Leupp 1995], native North America [Callender and Kochems 1983, Lang 1998]). This may be due in part to reporting bias (Herdt 1984a, Blackwood 1986b). Reduced homosexual behavior in females may also result from greater social control of female sexuality (Small 1995). In contemporary Britain, women and men report similar levels of homosexual attraction, but women report only half the level of homosexual behavior (Johnson et al. 1994). The control of female sexuality is variable across cultures, however, and there are as yet no data indicating a negative correlation between female homosexual behavior and the control of female sexuality.

Demography. Several writers suggest that less-powerful males engage in homosexual behavior primarily because more-powerful males have multiple wives and thus reduce the availability of other-sex mates (e.g., Lévi-Strauss 1943, Wilson 1959, Evans-Pritchard 1970). A study of 70 cultures randomly drawn from the Human Relations Area Files (HRAF) does not, however, find polygyny correlated with male homosexual behavior (Barber 1998). It has also been suggested that organized homosexual behavior in Melanesia may relate to imbalanced sex ratios or the spatial segregation of the sexes, but no systematic comparisons have been made (Davenport 1977, Herdt 1984a; see also Knauft 1987, Spain 1992). The implicit assumption is that homosexual acts occur only when heterosexual opportunities are absent, but the data do not support such an assumption. Polygynous males in the Big Nambas of Melanesia have many male lovers, at times preferring them sexually to their wives (Deacon 1934). Homosexual behavior is also reported as more compelling than heterosexual behavior in numerous societies, including the Pukhtun of Pakistan, migrant miners of several societies in South Africa,

and the classical Athenians (Lindholm 1982, Moodie, Ndatshe, and Sibuyi 1989, Dover 1989).

Differentiating the Kin Selection and Parental Manipulation Hypotheses

The hypotheses of kin selection and of parental manipulation differ in the mechanisms they envision (Trivers 1974). With kin selection, individuals should become homosexual of their own accord. With parent-offspring conflict, homosexuality is induced when parents channel resources or socialize offspring in ways that make them less competitive in reproductive roles.

There is only anecdotal support for the prediction that parents manipulate selected offspring to take nonreproductive roles and to become homosexual. Clearly, parents judge their children's reproductive value (e.g., colonial India [Dickemann 1979], 17th-19th-century Germany [Voland 1989]) and at times encourage children in homosexual behavior. Parents in 15th-century Florence encouraged homosexual relations between their sons and the leaders of influential lineages, apparently to increase their political power (Rocke 1996). This is similar to paternal involvement in the selection of male patrons for sons in classical Athens and in Melanesia. Parents also manipulate selected offspring to take nonreproductive roles—castrating sons to qualify them for positions as eunuchs in the Byzantine court, for example (Ringrose 1996). In native North America, parents played significant roles in the selection of children for apprenticeship as transgender shamans, although typically claiming such selection as a response to the child's innate disposition (Williams 1986; cf. Callender and Kochems 1983). Mohave transgenders were foretold by mothers' dreams, for example (Devereux 1937). Among the Araucanians of South America, male transgender shamans are "generally chosen for this office when they are children, and a preference is always [shown] to those, who at that early time of life discover an effeminate disposition" (Falkner 1935:117 [1774]). Data are absent, however, on whether nonreproductive, homosexual children significantly help the other children of their lineage.

Alliance Formation: Predictions and Evidence

The hypothesis of alliance formation through reciprocal altruism provides predictions that clearly distinguish it from both kin selection and parental manipulation. As pointed out by Trivers (1985:198), "the sexual and romantic side of homosexual relations would seem to interfere with kin-directed altruism: insofar as one is sexually attracted to another individual, one will naturally be inclined to invest some resources in intrasexual competition to gain this individual's favors. Should the relationship blossom into a love relationship, it will be natural to devote some of the same resources and energy that would go into a loving heterosexual relationship."

Contests for the resources at stake in intrasexual competition—such as material goods or social support—allow direct selection to act upon the propensity for homosexual behavior. Predictions of this hypothesis include (1) that same-sex alliances aid survival and subsequent sexual reproduction, (2) that homosexual behavior aids in alliance formation, and (3) that bisexuality is more common than homosexuality. (An implicit assumption of this hypothesis is that bisexuality is the behavior to be explained.)

IMPORTANCE FOR INDIVIDUAL SURVIVAL

If homosexual behavior has fitness benefits due to samesex alliances, those alliances must help individuals establish and maintain households and, consequently, help offspring reach reproductive age. Data are limited on how same-sex alliances influence reproductive success. Individuals who engage in homosexual acts receive benefits applicable to their reproductive lives, however. This prediction is strongly supported in that same-sex alliances are important in networks that aid in survival and, potentially, marriage exchange.

Among the K'ekchi' Mayans of Belize, men with samesex alliances in agricultural labor have significantly more children surviving past six months because of increased productivity (Berte 1988). (Berte does not specify the mechanisms by which K'ekchi' Mayan males maintain their alliances, although precolonial Mayan culture condoned homosexual behavior among unmarried men and may still today [Greenberg 1988; see also Reina 1959, Gossen 1974, Sigal 1997].) For the Azande and other African societies with polygynous marriages, Blackwood (1986b) suggests that female homosexual behavior helps negotiate alliances that extend trade networks and enhance economic security. Alliances in the marriage resistance movement of southern China were fundamentally about mutual economic support (Sankar 1986); same-sex unions of the early Christian era were designed to create socioeconomic units, solemnized in religious vows and civil contracts (Boswell 1994). (Sexual behavior was clearly a part of some of these alliances, although population proportions are unknown. Pair-bonds between (non-transgender) males in many societies of native North America reduced variance in food intake and provided for cooperative defense. As described by the 18th-century missionary Lafitau (in Katz 1976:289), "they become companions in hunting, in war, and in fortune [and] they have a right to food and lodging in each other's cabin."

Within age-graded ("patron/client") same-sex alliances in Melanesia, the younger client provides labor in the fields (and sexual services) while the older patron provides food and education (Marind-anim [van Baal 1966]; Big Nambas [Deacon 1934, Guiart 1953], Kiman [Serpenti 1984]). In precolonial Tahiti and Hawaii, the clients of powerful patrons gained prestige (Gunson 1964, Morris 1990), as did clients in classical Athens and 15thcentury Florence (Dover 1989, Rocke 1996). In ancient Crete, men without same-sex sexual partners were at a

social disadvantage (Boswell 1980). Same-sex sexual partners of the Japanese samurai gained both martial training and land (Leupp 1995). In classical Athens and in Tokugawa Japan, same-sex alliances were thought to be more dangerous to entrenched interests than femalemale alliances (Boswell 1980, Leupp 1995).

Same-sex alliances with homosexual behavior often have exogamy rules and rituals similar to heterosexual marriages (e.g., Roheim 1933, Gunson 1964, Evans-Pritchard 1970, Ernst 1991). This suggests that same-sex alliances and heterosexual marriages are complementary. Lévi-Strauss (1943) treats as equivalent alliances based on the "reciprocal sexual services" of sister-exchange marriage and alliances based on homosexual behavior by classifactory brothers-in-law. Both female-exchange marriage and homosexual behavior in Melanesia link "individuals and groups in complex chains of mutual dependency and obligation" (Lindenbaum 1984:345). Among the Etoro, for example, a patron's ideal client is his wife's younger brother, effectively linking wife and client in a sororal/fraternal "polygynous" marriage in which only one co-spouse is reproductively active (Kelly 1977). Among both the Jaqaj and the Onabasulu of Melanesia, homosexual alliances increase marriage exchange rights to the women controlled by one's partner (Boelaars 1981, Ernst 1991; see also Herdt 1984a).

AID IN THE FORMATION OF SAME-SEX ALLIANCES

The prediction of aid in the formation of same-sex alliances receives support, with the strong caveat that homosexual behavior is not required for alliance formation. In some cultures, same-sex relationships that entail rights and responsibilities and are solemnized by public ceremonies or wealth exchange appear to be celibate (e.g., the Lovedu of southern Africa [Krige 1974], the majority of 19th-century Mormons [Quinn 1996]). Same-sex alliances often do involve sexual behavior, however. Homosexual behavior by adolescents appears to predict alliances as adults among the Dahomey of Nigeria, the Nambikuara of Brazil, and the Barasana of Colombia (Herskovits 1938, Lévi-Strauss 1943, Hugh-Jones 1979; see also Sorensen 1984). Homosexual behavior also occurs as part of sworn friendships among the Khoisan of South Africa and the Dinaric of Serbia (Schapera 1930, Tomasic 1948).

Sexual emotion can reinforce long-term supportive relationships (e.g., the Azande [Evans-Pritchard 1970]). Among the Kiman of Melanesia, homosexual behavior stops after adolescence but "nevertheless, a lifelong emotional relationship often results from homosexual relationships" (Serpenti 1984:305); this also appears to be the case for the Onabasulu (Ernst 1991). (Homosexual behavior does not appear to influence emotional ties at East Bay in Melanesia, however [Davenport 1977].) Among the Sambia, homosexual behavior occurs among initiates in a regional cohort of loosely joined militias. The Sambia are headhunters, often at war with neighboring groups; Herdt (1984b) argues that their homosexual behavior solidifies bonds that are vital for mutual defense.

BISEXUALITY MORE COMMON THAN HOMOSEXUALITY

While the alliance-formation hypothesis predicts that self-motivated homosexual behavior typically enhances survival, it also predicts that homosexuality per se will be maladaptive in Darwinian terms. The alliance-formation hypothesis therefore predicts that bisexuals should outnumber homosexuals.

The data strongly support this prediction. Most individuals who engage in homosexual behavior are, in practice, bisexual (e.g., Melanesia [Herdt 1984a], 17th-century Fujian [Ng 1989], classical Athens [Dover 1989], contemporary United States [Kinsey, Pomeroy, and Martin 1948, Kinsey et al. 1953). Literary and biographical sources from 17th-century Japan and court records on sodomy accusations in 15th-century Florence suggest that the majority of the men in these two societies may have been bisexual (Schalow 1989, Leupp 1995, Rocke 1996). Across two millennia of records from China, individuals known for homosexual activity are typically known for heterosexual activity as well (Hinsch 1990). In native North America, the majority of those engaging in homosexual sex were not transgenders (whose sexuality remains unclear) but gender-typical individuals who clearly were bisexual (Callender and Kochems 1983; Williams 1986, 1992a); the same is true with regard to Tahiti (Herdt 1997).

Also in keeping with this prediction, homosexual emotion exists apart from homosexual behavior. Between 8 and 12% of Western men and women have homosexual attraction, though not behavior, after age 15 (Sell, Wells, and Wypij 1995; see also Davis 1929; Laumann et al. 1994: fig. 8.2; Pattatucci and Hamer 1995). Among both Australian and Malaysian medical students, most homosexual attraction is felt by those whose behavior is predominantly or exclusively heterosexual (McConaghy, Buhrich, and Silove 1994). This continuum of experience is implicit in the "sentimental effusions" reported by Lévi-Strauss (1943) and others (e.g., Hugh-Jones 1979) when discussing same-sex sexual behavior that seems, to these investigators, to be unrelated to sexual gratification.

Discussion

HOMOSEXUAL BEHAVIOR IN HUMANS

In a Popperian sense, hypotheses cannot be proven, only soundly disproven. Further, even if it is shown that a particular behavior is adaptive, this falls short of showing that it is the product of natural selection (Caro and Borgerhoff Mulder 1987). In the final analysis, the available evidence does not allow rejection of any of the three hypotheses reviewed here (table 3). Kin selection and parental manipulation remain least satisfying, however, if only because the data are inadequate to test their central predictions. There is no strong evidence that homosexual behavior, as seen in the majority of individuals

TABLE 3 Predictions and Support for Three Evolutionary Hypotheses of Human Homosexual Behavior

Prediction	Support
Kin selection and parental manipulation 1. Homosexual behavior reduces individual reproductive success. 2. Homosexuals provide more or better aid in raising offspring than do heterosexuals or celibates. 3. Homosexual behavior is seen predominantly in individuals of low reproductive potential.	Equivocal Insufficient data Moderate
Parental manipulation 1. Parents manipulate selected offspring to forgo reproduction, become homosexual, and aid in the rearing of siblings or the offspring of siblings.	Limited
Alliance formation (reciprocal altruism) 1. Same-sex alliances aid individual survival. 2. Homosexual behavior aids the formation of same-sex alliances. 3. Bisexuality is more common than homosexuality.	Strong Moderate Strong

practicing it, reduces average reproductive success. There is no evidence for increased reproductive success in lineages with homosexual members. Although present information does not allow refutation, these two hypotheses clearly do not have strong explanatory power. In particular, there is no evidence that homosexuals provide greater service than celibates. A fundamental question remains why natural selection would select homosexual nonreproductives when asexual nonreproductives would seem more efficient (Trivers 1985, Dickemann 1995). (Developmental processes may make a switch from "homosexual" to "heterosexual" easier than one from "asexual" to "sexual.")

Nonreproductive offspring that are altruistic to siblings will always benefit their parents' reproductive success before reaching the threshold of benefit to their own (Trivers 1974). Parental manipulation is therefore more likely than kin selection if only because the threshold is lower. Parents manipulate children to accept nonreproductive roles; individuals who accept nonreproductive roles potentially aid kin. With the possible exception of Native American transgenders, however, there is little evidence that (presumed) nonreproductive individuals are predominantly homosexual. The clergy in the early Christian era probably engaged in no more homosexual behavior than the laity, for example (Boswell 1980, Greenberg 1988). Present information rather suggests that parental evaluation of offspring reproductive potential results in other behaviors, such as sex-biased infanticide, shunting of selected offspring to high-risk strategies (e.g., military service), or encouragement to form polyandrous households (Dickemann 1979, 1993; Voland 1989; Durham 1991).

Alliance formation is the hypothesis that best explains the observations in the historical and ethnographic literature. It does not depend on homosexual behavior's being detrimental to reproductive success or even require that lineages benefit. Same-sex alliances help individuals survive and subsequently reproduce, same-sex alliances are expressed sexually at times, and bisexuality is more common than homosexuality. Further, alliance formation best explains the curious disjunction between the facultative expression of homosexual behavior and its genetic and developmental correlates. In many societies, people engage in homosexual behavior primarily at certain stages of life, such as during adolescence or prior to heterosexual marriage, and then switch to relatively exclusive heterosexual behavior as adults or soon after household formation. This may be because same-sex alliances aimed at somatic reproduction are more important early in life and female-male alliances aimed at sexual reproduction more important later. Also, the alliance-formation hypothesis is relatively parsimonious in that it does not posit a separation between the homosexual behavior of humans and that of nonhuman primates, in which homosexual behavior is seen as one component of adaptive life histories (e.g., de Waal 1995).

Reciprocal altruism often develops in long-lived, mutually dependent animals with repeated contact (Trivers 1971). When there is competition for social resources, it is important to prevent rivals from forming alliances with one's partners (Harcourt 1989). Bonds involving reciprocal exchange of lineage members, ritual ceremonies, and sexual emotion may help negotiate exclusive rights to alliance partners—which may explain the intense jealousy found in same-sex sexual partnerships (e.g., the Khoisan [Schapera 1930], the Big Nambas [Deacon 1934], 17th-century Japan [Schalow 1989]). Layton (1989:435) suggests that "reciprocal altruism [explains] ... much human action conducted in the idiom of kin" and that social kinship terms identify partners for reciprocal exchange. This corresponds well to social kinship terms that regulate homosexual partnerships in many societies (e.g., the Nambikuara [Lévi-Strauss 1943], the Marind-anim [van Baal 1966]).

The currencies and the costs and benefits of reciprocal altruism are complex. There are age-specific, sex-specific, and culture-specific constraints to reproductive value, and these will vary with demographic and ecological conditions. The costs and benefits of altruistic acts are also influenced by asymmetrical limitations to reproductive success. Alliances within and between age/

sex classes may therefore take different forms. In alliances among peers, the currencies of reciprocal altruism appear the same, and payoffs probably occur within short periods (i.e., over a number of years). In alliances between older patrons and younger clients, the currencies appear asymmetrical, and payoffs may span generations. The patron receives labor, the prestige of maintaining a social institution, and sexual gratification; the patron has, presumably, already established a household and is within a reproductive system designed to ensure potential for fertilizations. The client is limited by access to both the knowledge and the resources that will allow establishment of a household. Nonreproductive sex is low-cost because the client is unlikely to be accepted socially as a member of the reproductive population. That patron/ client alliances are more common in males than in females (Herdt 1997) may reflect greater intrasexual competition in males, with alliances holding reciprocal obligations such as access to mates (e.g., the Yanomamo [Chagnon 1982]).

Selective pressure for alliances might occur when assisted labor increases individual productivity or when there is strong competition for defensible resources. Increased fecundity can be detrimental to reproductive success when producing additional children *now* provides less benefit than investing in children already produced or amassing resources to support children one has a high probability of producing in the future (e.g., Hill and Kaplan 1988). This leads to the prediction that same-sex alliances will be seen in societies where investment in offspring is more strongly correlated with reproductive success than is raw number of offspring. Such societies include those with heavy sanctions on illegitimacy, those in predictable environments, and those in environments at carrying capacity.

Culture is probably a more immediate influence on homosexual behavior than ecology, but the expression of homosexual behavior may be influenced, in part, by ecological variables (cf. Dickemann 1993). In societies where labor increases productivity, same-sex alliances may be based on considerations of labor (e.g., the Big Nambas [Deacon 1934]). In societies where status is relatively salient, alliances may be structured by status differentials (e.g., 15th-century Florence [Rocke 1996]). Lindenbaum (1987) suggests that homosexual behavior in Melanesia is positively correlated with low population density, a marker of low-productivity habitats. In 70 cultures drawn randomly from the HRAF, homosexual behavior occurs significantly more often in agricultural than in hunter-gatherer societies and more often in larger social groups (Barber 1998). This implicitly supports Dickemann's (1993) prediction that homosexual behavior will be seen more often when political networks rather than independent individuals are the prime social force. If patterns of social organization and alliance formation are predicted by ecological variables (Dickemann 1979, Flinn and Low 1986), then homosexual behavior should vary predictably with ecology. If, for example, certain forms of cousin marriage are predicted by ecological conditions that regulate male needs for coalitions (Flinn and Low 1986), male homosexual behavior should be predicted by such conditions (cf. Layard 1959, Lindenbaum 1987). Again, if polygyny is predicted by ecological conditions and if female homosexual behavior strengthens economic security within polygynous marriages, female homosexual behavior should be predicted by such conditions.

In some instances, alliances may be not between the patron and the client but between the patron and the client's parent, particularly if the patron is high in status (see Harcourt 1989). Parents in 15th-century Florence and in Siwah, Libya, in the early 20th century may have used their adolescent sons' sexuality to establish bonds with more powerful households (Rocke 1996, Murray 1997; see also Cline 1936). Among the Azande, the samesex lover fulfilled kin obligations to the lover's parents (Evans-Pritchard 1970). When alliances result in the transfer of wealth to parents (e.g., betrothal payments in 17th-century Fujian [Ng 1989]), parents have an incentive to manipulate offspring alliances; they use children for their own purposes. As Hart and Pilling (1960:15) note, "in Tiwi culture daughters were an asset to their father, and he invested these assets in his own welfare. He therefore bestowed his newly born daughter on a friend or an ally, or on somebody he wanted as a friend or an ally." Parents in Tokugawa Japan sold both sons and daughters into indentured prostitution (Leupp 1995). In some Melanesian societies, initiation begins before puberty and is more properly considered pedophilic than ephebophilic, at least in its initial stages (e.g., the Sambia [Herdt 1984*b*]).

In many societies, alliances are maintained without sexual behavior. Sexualization of alliances might be anticipated when commitment of social partners is particularly important or competition for partners particularly severe. Sex can be a way of conferring pleasure presumably a currency of long-term supportive relationships—and may signify to one's partner and to others a high level of affiliation and exclusivity. Insofar as maintaining an alliance has significant costs in terms of time, displays of commitment are adaptive because of the cost (cf. Zahavi 1975). Homosexual acts become powerful symbols of loyalty and affiliation. It remains unclear why sex is used to negotiate alliances that do not hold direct conceptive benefits. However, for some mates—including humans—sex is rarely for procreation (Wrangham 1993, Small 1995, Manson, Perry, and Parish 1997). Wrangham (1993) estimates for bonobos that only 1% of copulations are conceptive. Sexual behavior and emotion can therefore be appropriated to establish and maintain alliances. Sexual behavior is not indispensable to same-sex alliances. Homosexual behavior is not at a selective disadvantage, however, as long as enough heterosexual matings ultimately occur, on average, to provide the individual with the average number of surviving offspring. Particularly in societies requiring heterosexual marriage, it is unlikely that homosexual behavior results in a net decrease to an individual's reproductive success (Weinrich 1987*b*).

HOMOSEXUAL BEHAVIOR IN THE HUMAN ANCESTOR

Human homosexual behavior shows similarity across broad geographic regions. Organized homosexual behavior in Melanesia is thought to have originated in a culture that reached Melanesia perhaps 10,000 years ago (Herdt 1997). Widely divergent cultures across the Americas have a broadly similar although by no means unitary way of incorporating transgender homosexual behavior (Williams 1986, Lang 1998), and this suggests that the original human migrants into the Americas 12,000 years ago had similar cultures. Homosexual behavior appears to have been part of the human behavioral repertoire at least since the beginning of the Holocene.

In some species of nonhuman primates, homosexual behavior occurs at least as frequently as heterosexual behavior (reviewed in Vasey 1995). Abnormal captive conditions can induce homosexual behavior but do not explain the majority of observations. The strongest adaptive explanation of homosexual behavior in nonhuman primates is the maintenance of social relationships (Vasey 1995). In olive baboons at Gilgil, males use alliances in aggressive disputes; a primary form of expression of these alliances is holding the testes of alliance partners (Smuts and Watanabe 1990). In the Japanese macaques at Arashiyama, imbalances in demographic sex ratio explain some female-female homosexual behavior, but this behavior also predicts alliances (Wolfe 1986, Vasey 1996). These alliances appear primarily to maintain exclusive sexual access to same-sex partners [Vasey, personal communication].)

In bonobos, homosexual behavior is integral to exchange networks that link sex with food (White 1989, Parish 1994). Immigrant bonobo females also use sex to solidify alliances with high-ranking resident females (Idani 1991). In gorillas at Virunga, homosexual behavior (including anal intromission) occurs between age-graded pairs in all-male units; silverbacks defend blackback sexual partners from the approaches of other silverbacks (Yamagiwa 1987). This intrasexual competition for samesex mates is precisely the type envisioned by Trivers

Interpretation of current evidence concerning early hominids suggests that their success was based on alliances with individuals of both sexes (Foley 1989). The genus Homo has extensively expanded its geographic distribution over evolutionary time, presumably, in part, because of behaviors such as cooperative hunting and gathering, the separation of male and female spheres, and greatly enhanced transfer of knowledge between generations. If such speculation is reasonably correct, then same-sex alliances almost certainly were key in hominid evolution. This should result, over evolutionary time, in a psychological predisposition for same-sex affiliation (cf. Trivers 1971). In nonhuman primates, homosexual behavior is part of a complex network of reciprocal exchange. The great apes and humans all show homosexual behavior (Vasey 1995). We can never know the specific social behaviors of extinct hominids, but it is safe to speculate that homosexual behavior was part of their social repertoire. If sexual behavior indeed strengthens affinity and if sex in anthropoid primates is rarely for procreation, there is no a priori reason to assume that sexual behavior will be confined to one type of alliance or another.

SOCIAL FORCES AND FACULTATIVE SEXUAL BEHAVIOR

In terms of natural selection, homosexual behavior is a benign trait in most instances and becomes adaptive within certain social contexts. Social conditions on broad historical fronts will alter the costs and benefits of behaviors such as alliance formation and homosexual behavior. This explains, for example, why homosexual behavior is adaptive primarily in Melanesian societies with a history of using this behavior in alliance formation (cf. Herdt 1984a). Homosexual behavior has been adaptive in classical Athens, in 17th-century Japan, among the Nambikuara of Brazil and the Azande of Sudan, and in many other cultures because it has been a social institution with few if any sanctions. Costs and benefits of alliances and of particular sexualities will depend on the dominance hierarchies within families and within societies.

Most individuals conform to social norms, and there is wide cross-cultural variation in level and form of homosexual behavior. This is not to suggest that sex is entirely malleable. Studies trying to "teach" sexual arousal to Western adults have only weakly modified objects of desire (reviewed in O'Donohue and Plaud 1994; see also Letourneau and O'Donohue 1997). Prepubertal gender socialization (e.g., of biological males raised as females) typically does not counteract pubertal hormonal changes leading to attraction to the other sex (reviewed in LeVay 1996; cf. Byne 1996). And although public school attendance in Britain doubles the likelihood of adolescent homosexual behavior, it does not predict adult homosexual behavior; the sexual socialization in British public schools does not have long-standing behavioral effects (Johnson et al. 1994). Still, humans are quite plastic in conforming to social institutions. In some societies of Melanesia, in 17th-century Japan, and in classical Athens, men have been expected to find men sexually attractive, and on the whole they have done so (Herdt 1984b, Schalow 1989, Dover 1989). Tokugawa Japan and Ming China had rich, centuries-long homosexual traditions. These traditions were slowly supplanted after extended contact with foreign cultures (Hinsch 1990, Leupp 1995). The relation between learning processes and sexual behavior is weakly understood. Individuals with a strong propensity for either homosexuality or heterosexuality (e.g., the rare Sambia men who do not marry [Herdt and Stoller 1990]) may find it difficult or impossible to conform to social norms. Freud (1905) contends, however, that neither homosexuality nor heterosexuality is learned; it is bisexuality that is forgotten.

To address how or whether bisexuality is "forgotten" would require greater understanding of the development of sexual identity, how erotics are learned, and why sexual desires may become disconnected from sexual practices. The hypothesis that homosexual emotion and behavior are tools for alliance formation suggests that human sexuality has elements common to the sexuality of all primates. The interplay of biological propensities toward particular sexual desires with societal influences toward particular sexual practices, however, may well lead to areas that are distinctly human.

Conclusion

At present, we cannot rule out any of the three hypotheses on the evolutionary origins of homosexual behavior. This will be possible only after data are collected on how varying degrees of bisexuality influence reproductive success and on the reproductive success of lineages with homosexual members. Hypotheses for the evolution of homosexuality will remain of limited explanatory power, however, as long as they focus on the reproductive functions of the sex act. Sexual behavior is useful in arenas other than the production of children. Homosexual behavior is a form of exchange and, outside conception, is traded in the same currencies as heterosexual behavior.

It seems doubtful that there are special genes, levels of hormones, or family dynamics that are exclusive to homosexuals or to heterosexuals. Similarly, there are no fixed social or ecological correlates. There are different constellations of human experience, and these constellations lead to greater or lesser propensities to form longterm alliances with members of the same sex. Broad social and cultural constraints further influence decisions of whether or how to use sexual behavior as a means of securing and maintaining these alliances. Within a basic bisexual potential, some individuals will fall at homosexual and heterosexual extremes. That social conditions play such a strong role in sexual behavior shows that culture influences sexuality in ways that evolutionary biology has yet to fully incorporate. An adaptationist framework is useful for explaining some aspects of sexual behavior but not all.

The evolution of human homosexuality is tied to the benefits of same-sex affiliation. Natural selection favors same-sex affection; it must be fundamental for both sexes to desire bonds with partners of both sexes. All men, to varying degrees, have the ability and desire to form affectionate ties with other men. Women have a corresponding ability and desire to form affectionate ties with other women. Attraction to members of the same sex and expression of that attraction is in no way contrary to or an alternative for attraction to members of the other sex. Homosexuality is an emergent quality of individual selection for same-sex affiliation and has been a part of the human experience, perhaps all primate experience, since its inception.

Comments

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Kirkpatrick's analysis offers a compelling hypothesis regarding the evolutionary origins of homosexual behavior and strengthens the argument for the cultural "origins" of human sexualities. Typically, anthropologists highlight marriage, kinship, and heterosexual bonds as the social "glue" of preindustrial societies, while same-sex alliances are deemed of little importance to larger cultural processes. Such alliances deserve much more attention. Cultural anthropology has yet to explore if there are differences between same-sex alliances and intimate sexual friendships. This does not, however, detract from Kirkpatrick's argument about the importance of intimate friendships to larger cultural processes. By drawing a comparison between conjugal partners and same-sex alliances, Kirkpatrick presses the point that sexual relations in the two cases arise for some of the same reasons (i.e., to strengthen the bond between two individuals and improve their positions in the community). This argument is important because it suggests that homosexual behavior is simply a form of sexuality, not an aberrant or "negative" behavior. Further, it gives the lie to the bimodal model of sexuality and should encourage us to avoid thinking in either/or terms.

One question about Kirkpatrick's proposition is whether women's same-sex relations fit the model. Kirkpatrick states rightly that the literature is biased toward men. Among the many reasons for this is that male observers assumed that heterosexually married women only engaged in heterosexual behavior; they were also generally unable to find out otherwise (see Blackwood and Wieringa 1999). In arguing against the model of parental manipulation, Kirkpatrick points out that "most people who engage in homosexual behavior" are bisexual and produce children. Women's sexuality is extremely pertinent on this point, since the cultural evidence suggests that in most cases same-sex relations between women occur within the context of marriage (Blackwood 1986b). In matrilineal societies nonreproductive women are strongly discouraged, and bisexual behavior is common as long heterosexual bonds produce heirs (see Blackwood 1998). Further work needs to be done on the relation between cultural ideologies of reproduction and women's homosexual behavior. Several examples that fit the model of same-sex alliances in addition to the one that Kirkpatrick mentions are the mummy-baby relations of teenage Lesotho girls (Gay 1986) and bond friendships (motsoalle) of women in Lesotho (Kendall 1999, Nthunya 1997), as well as the senior-junior (matron-client) relations of Afro-Caribbean working-class women in Suriname (Wekker 1999).

Having said this, I want to point out some problems.

Kirkpatrick takes sketchy and uneven data to construct an empirical basis for his proposition. Cultural data on sexual practices are notoriously biased and incomplete, especially with regard to women, which means that any conclusions drawn must necessarily be provisional, as Kirkpatrick acknowledges. Even more problematic is that sexual behavior is not everywhere culturally meaningful in the way Kirkpatrick assumes it is. A transman (female-to-male) in the United States does not consider himself as engaging in "homosexual" behavior when he makes love to a woman (see Cromwell 1999). Similarly, the Native American two-spirit person ("berdache" in the older literature) cannot be subsumed within a "samesex" model, since in many cases the two individuals involved are differently gendered (see Jacobs, Thomas, and Lang 1997). Among other things, this problem raises questions about his tracing of "homosexual" behavior to the beginning of the Holocene, which is based on the evidence of transgender behavior among Native Americans.

Whether same-sex relations are a "survival strategy" for reproductive success remains a question for me. Kirkpatrick does not mention any study that has compared groups with same-sex alliances versus those without them. Further, the prediction that same-sex alliances will be more likely in societies where material investment in offspring is high is contradicted by the examples from foraging societies such as the Australian Aborigines and the !Kung San. What is of greatest value in the essay is its emphasis on the importance of cultural processes to the formation of sexual behaviors. Whether or not individuals are able to survive and reproduce because of same-sex alliances, it is clear that social groups and communities survive and become more stable and productive because of these relationships. Kirkpatrick's argument offers a refreshing view that moves the study of sexual origins from a myopic obsession with sex acts and their products to the cultural dimensions of sexual relations.

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How could it happen that a vice that, if it were general, would destroy human kind, and that is an infamous offense against nature, should however be so natural?

VOLTAIRE, Dictionnaire philosophique, 1764

Kirkpatrick's well-researched paper is a considerable advance over previous "Darwinian" attempts to explain "homosexuality." In particular, his focus on behaviors rather than identities is helpful. However, the paper suffers from a certain schizophrenia. On the one hand, the author's commitment to the search for a single adaptive function and a single origin, resulting from direct selection, allies him with the early pathologists such as Krafft-Ebing and their modern sexologist descendants. All of these commit the reifying fallacy, assuming that every label indicates the existence of a discrete entity out there, with unitary nature and origins. In the same way, Kirkpatrick reifies behavioral acts, while in contrast most of his data and many of his conclusions point in a precisely opposite direction.

There is no evidence that same-sex sexual acts per se are under direct selective pressure any more than is masturbation, anal sex, bestiality, pedophilia, vaginal entry from the front or rear, or any other sexual practice. Sexual desire, arousal, orgasm (especially in men), and male ejaculation, all basic mammalian capacities, are selectively maintained through production of offspring. But these capacities are not specific to reproduction, as Kirkpatrick admits. The high human and especially male sex drive, maintained by its guarantee of reproduction, is available for elaboration in socially condoned, prohibited, or ignored forms for social, emotional, and physiological satisfaction. It is not necessary that each individual engage in "enough heterosexual matings" as long as some parents and kin do so. There is no need to posit (and absolutely no evidence for) a separate human prehistory of homosexuality. Our mammalian and primate inheritance of high sex drive and aseasonality is patent. Kirkpatrick's prehistorical speculations reveal a lack of understanding of prehistoric population movements and the nature of culture areas.

It is a common "Darwinian" fallacy to assume that all components of a behavioral act are under equal selective pressure. This leads to treating behavioral acts as discrete adaptive units when in fact they usually have both adaptive and nonadaptive or neutral components. Language, for example, aids in survival and reproduction, but not all linguistic acts provide direct reproductive gain. There is no direct selection for, nor are there genes for, the creation of poetry. The direct, genetically inherited components of homosexuality are those listed above, common to all sex acts.

Thus the search for a predictive hypothesis is misplaced, and the present analysis collapses into a series of reviews of some of the ways in which same-sex relations are employed for familial and social ends. (Casual and sub rosa acts receive less attention [cf. Reeves. quoted in van Praunheim 1980:164-66; Zeeland 1996].) Such investigations are more effectively carried out under the familiar rubrics of "kinship and marriage," "alliance formation," etc., always recognizing that the form of the innate sex drive in each sex plays some role in determining its social expression and use. Beyond that, only briefly addressed here, are the general classes of socioeconomic structure, which show commonalities in forms of same-sex relations and social attitudes that are currently under active investigation by historians and anthropologists of sex and gender. While individual propensity remains a mystery, it will be better understood through advances in the study of internal family dynamics, the most difficult and most needed area of developmental psychology.

Franz Boas insisted, no doubt because of his training in the physical sciences, that all human events are multiply caused, and Freud insisted that human psychic states are "overdetermined." We have forgotten our forebears. The social context in which most Western "scientific" research on homosexuality (in contrast to historical and cultural anthropological work) has occurred is one of belief in and a consequent search for genetic mechanisms governing much of human behavioral diversity—a bias that is reinforced by often naive and widely popularized "Darwinian" hypotheses, often masquerading as fact, which underplay the profound environmental influences on human behavioral capacities. This is aggravated by the tendency of some individuals of variant identities to claim genetic differences as a means to self-validation. Meanwhile, heterosexual "Darwinians" covertly assume that "heterosexuality" is natural, essential, selected, and therefore genetically based. Avoiding overt statement of this hidden assumption, they evade the necessity of searching for a gene for heterosexuality. What if no such thing could be found?

Once distracting assumptions about the "evolution and origin" of specific sexual practices are cleared away, we may focus on a far more intriguing and significant fact: sexual reproduction (i.e., heterosexual acts) and hence reproductive success in humans depend not on some innate instinct but solely on the undirected, "polymorphous perverse" drive for sexual release, with its concomitant capacities, the vagaries of childhood sex/ gender identity formation, desire for emotional relations, the emotional and strategic calculations of future parents, and the coercive force of social rules and concepts. In brief, the continuation of our species depends on the sex drive and social processes alone. (This statement is oversimple, as some subsidiary propensities, such as attraction to young children, may play roles.) The nonhuman primate data reviewed by Kirkpatrick point clearly in this direction. Surely it is time, finally, for evolutionary anthropologists to consider this.

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Alliance theories of kinship like Lévi-Strauss's are concerned with how men make alliances with other men beyond their immediate kin by giving or exchanging women. Kirkpatrick puts a new spin on this argument by arguing that same-sex alliances can also be held together more directly by leaving the mediating opposite-sex party out of the deal and giving or exchanging homosexual services.

Both cross-cultural evidence collected by ethnographers, especially in societies which encourage some forms of homosexual behavior, and evidence collected by psychologists and others regarding individual variation in homosexual orientation are relevant here. I believe there is some support for Kirkpatrick's thesis in the first body of evidence but very little in the second. A reasonable conclusion would be that homosexuality is (at least) two different phenomena, with different causes.

Kirkpatrick himself comes close to this conclusion when he notes "the curious fracture between the facultative expression of homosexual behavior and its developmental and genetic correlates," but in most of the paper he tries to push a single explanation of homosexual behavior, and the explanatory overreach weakens his argument.

Research on sexual orientation by psychologists and others has produced a strong consensus on several points. Homosexual orientation, especially in men, is a relatively immutable aspect of personality whose roots can often be traced to well before the onset of puberty. The best predictor of future homosexual orientation is childhood gender nonconformity. Feminine boys—who prefer to play with girls and to play girls' games, who avoid playing with boys or playing boys' games, who may enjoy cross-dressing, and who are commonly recognized as gender-nonconforming by other children and by adults—are vastly more likely to be homosexual when they grow up than other boys, and similarly for masculine girls (Bailey and Zucker 1995). In Green's (1987) prospective study, about 80% of markedly feminine boys grew up to be homosexual or bisexual (but not necessarily markedly feminine) by age 18, compared with just one boy in a nonfeminine control group who grew up to be bisexual. There is also a substantial heritable component to sexual orientation (Bailey and Pillard 1991, Bailey et al. 1993), and while there is a nonheritable component as well, it must be kept in mind that this component includes things like uterine physiology (which may explain birth-order effects) and sheer chance and that efforts to identify systematic postnatal environmental causes of homosexual orientation (as opposed to temporary situational homosexual behavior) have turned up virtually nothing.

Kirkpatrick makes several weak arguments to minimize the importance of childhood gender nonconformity in the ontogeny of homosexuality. He states that men in cultures that promote homosexual behavior are not notably feminine, which even if true is irrelevant to intracultural variation, and cites Bailey and Pillard's failure to find correlations between feminity and homosexuality within twin pairs, again of marginal relevance. His comment that "gender nonconformity is neither necessary nor sufficient for homosexual behavior" is just another way of saying the correlation between the two is less than 1.0, which is not surprising given the mosaic nature of sexual development.

Kirkpatrick is unconvincing in arguing that whatever selective advantages accrue to homosexually reinforced alliances are sufficient to account for the maintenance of heritable homosexuality. In the United States, among the 1–3% of adult men who report same-sex relations with other men in the last 12 months, most have had little or no adult heterosexual experience (Rogers and Turner 1991). The 2–4% of men who identify themselves as homosexual or bisexual report much lower rates of fatherhood than other men (27% vs. 60% in one major recent survey) (LeVay 1996). These men are only a fraction—albeit a large one—of the 4–8% of men with some

adult homosexual experience (perhaps 10-20% if adolescent experience is included) (Rogers and Turner 1991), but there is no evidence that men with both heterosexual and homosexual experience have substantially higher fitnesses than completely heterosexual men—that bisexuality is maintained by stabilizing natural selection against extreme heterosexual and homosexual orientations. Similar associations between childhood gender nonconformity, adult homosexual orientation, and low rates of marriage and fatherhood are noted in many societies (Williams 1986, Whitam and Mathy 1986).

Given the evidence on childhood gender nonconformity and homosexual orientation, a more likely evolutionary explanation for the persistence of heritable homosexuality is sexually antagonistic selection. Although it is commonly assumed that natural selection optimizes female and male traits independently, this is often not the case: selection for optimal traits in females often favors genes that incidentally lower fitness when expressed in males and vice versa (Rice 1992, Lessells 1999). Hamer notes preliminary evidence consistent with sexually antagonistic selection among gay men and their sisters (Hamer and Copeland 1998). Whether this accounts for some homosexuality or not, there is little evidence—as opposed to mere assertions—that the socially encouraged homosexual behavior shown by many men and women under some circumstances in some cultures has the same causes as the deeply rooted homosexual orientation that persists in a small but significant minority even in strongly antihomosexual cultures and even in the face of great social penalties.

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Kirkpatrick's theory is seminal and important. It helps to fill a large gap in the literature on the evolution of homosexual behavior and will contribute to the impetus necessary to generate more theoretical and empirical work in the area. I agree with his recommendation of a behavior-based definition in the evolutionary study of homosexual behavior. It is parsimonious and separate from the variously defined concept of sexual orientation (Shively, Jones, and DeCecco 1984), which has been described as lacking construct validity (Gonsiorek and Weinrich 1991). It will increase the reliability of the reporting of behavior as homosexual and, as Kirkpatrick states, make comparisons easier across species and cultures. Once the evolution of a disposition to engage in homosexual behavior is understood, it may contribute to the study of sexual orientation.

Kirkpatrick may be criticized for a lack of data to support predictions 1 and 2 of his theory—that same-sex alliances are important to individual survival and that homosexual behavior aids the formation of same-sex alliances. However, at this time, such criticism cannot be reliably interpreted as a genuine weakness in the theory. Rather, the lack of supporting data can be viewed as the result of a long history in the biological and social sciences during which research to gather such data was discouraged. Recently published work has documented prejudice, distortion, and active suppression of data regarding homosexual behavior and other types of sexual diversity in biology (Bagemihl 1999), primatology (Vasey 1995), cultural anthropology (Herdt 1997), physical anthropology and archeology (Taylor 1996), and evolutionary psychology (Muscarella 1999).

The third prediction of Kirkpatrick's theory regarding the greater incidence of bisexuality than homosexuality is supported by a vast and growing literature in history, anthropology, and sexology. There is a consistent and pervasive pattern of bisexual behavior in humans across the history of the species; however, this behavior may have origins other than those hypothesized by Kirkpatrick.

In my own work in evolutionary psychology (Muscarella 1999, n.d.) I have posited that hominid juveniles and young adults may have undergone a period of sex-segregated social peripheralization as do the young of other primates. A capacity to engage in homosexual behavior with peers and higher-status conspecifics may have been adaptive because, as Kirkpatrick also hypothesizes, it reinforced alliances which contributed directly to individual survival and indirectly to reproductive success. The views of Kirkpatrick and myself are consistent with Vasey's (1995) speculation that homosexual behavior may have evolved as an exaptation—that is, that it originated as a neutral variation and was acted upon by natural selection because it enhanced reproductive success.

Kirkpatrick speculates that the greater incidence of homosexual behavior in males may be due to a relationship between greater variance in male reproductive success and low reproductive success resulting in homosexuality. I have speculated (Muscarella n.d.) that there may have been greater selection pressure on males to engage in homosexual behavior because hominid male reproductive success was probably closely linked to dominance status in the social hierarchy (Fox 1971, Zillman 1984). Males who could use homosexual behavior as social manipulation in alliance formation may have climbed the social hierarchy more effectively and thus obtained better and perhaps quicker access to females. However, I agree with Kirkpatrick that we cannot rule out the effects of social control on female homosexual behavior.

Kirkpatrick notes that alliances within and between age- and sex-classes can be expected to take different forms. Throughout recorded history, the vast majority of homosexual behavior has been transgenerational (Greenberg 1988, Rind 1998) and, when of the peer type, predominantly between subadults (Greenberg 1988). These patterns may be related to the evolutionary history of the behavior and useful in guiding evolutionary hypotheses.

I agree with Kirkpatrick that both cultural and ecological forces can act upon the behavioral disposition to create a variety of manifestations of homosexual behavior. Homosexual behavior may be more likely under conditions similar to those in which it evolved, and this assumption could be incorporated into empirical tests of evolutionary hypotheses. Contrary to what would be predicted by Kirkpatrick's theory, many close-knit organizations of men are known to exhibit high levels of homophobia. However, research suggests that high levels of homophobia in men may be a defense against their unrecognized homoerotic feelings (Adams, Wright, and Lohr 1995). In the context of Kirkpatrick's theory, a high level of expressed homophobia in male groups could be interpreted as a unique cultural manifestation of evolutionarily motivated homoeroticism.

Kirkpatrick notes that homosexual behavior is not necessary for alliance formation, and his theory may be criticized because it does not account for the preponderance of strong alliance formation without homosexual behavior. However, he is only trying to address the evolutionary origins of homosexual behavior. Homosexual attraction and behavior may have played a much greater role in alliance formation among prelinguistic hominids. The chimpanzee and bonobo models suggest that hominids probably relied on intense and highly physical interactions conducive to sexual arousal to establish and maintain alliances. Human alliances are based predominantly upon linguistically mediated and reinforced concepts such as shared purpose, fidelity, and responsibility, which obviate the need for the physical expression of motives and feelings.

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I applaud Kirkpatrick's attempt to examine homosexual behavior within an evolutionary framework. Nevertheless, I remain unconvinced as to the validity of his hypothesis that human homosexual behavior is under direct, positive selection because it functions in a facultative manner to reinforce same-sex alliances.

In evaluating any adaptive hypothesis, it must be established whether the characteristic under consideration is a distinct trait or simply one expression of a more generalized trait (Futuyma and Risch 1984). Regarding this point, Kirkpatrick comments that the "data are not clear on whether there is one type of human sexuality that ranges from homosexual to heterosexual." If human sexuality is a "continuous" and "fluid" variable as he argues, then perhaps his attempt to compartmentalize homosexual behavior and explain it within an adaptationist framework are inappropriate.

This issue aside, homosexual behavior and alliance formation may well be correlated without the former's being an adaptation for the latter. In Japanese macaques, for example, females which engage in homosexual behavior frequently form alliances. They do not, however, engage in homosexual behavior for the express purpose

of alliance formation. Instead, mutual sexual attraction and gratification appear to be the basis on which they acquire and maintain same-sex sexual partners (Vasey 1996, Vasey, Chapais, and Gauthier 1998). To some, the issue of what motivates homosexual behavior may seem like a red herring. After all, natural selection should favor homosexual behavior, irrespective of the participants' motivation, if the behavior promotes fitness-enhancing alliances. Nevertheless, if humans, like female Japanese macaques, typically choose same-sex sexual partners on the basis of "sexual emotion" as Kirkpatrick seems to imply, then associations with useful allies, let alone powerful ones, would occur only as often as mutual sexual attraction existed between such individuals. The variability inherent in such a system of ally choice would seem to indicate that homosexual behavior in humans was not designed by natural selection as an adaptation for alliance formation.

In contrast, among bonobos young females immigrating into a new community appear to target dominant resident females (i.e., potentially powerful allies) for homosexual sex (Idani 1991). The specificity of this partner choice suggests that homosexual behavior, as manifested by immigrant female bonobos, may have been modified by natural selection to act as an adaptation for alliance formation.

The differences between human and bonobo homosexual behavior outlined above underscore an important point: primate homosexual behavior is not a uniform phenomenon. Instead, multiple motivations, functions, and effects underlie this behavior, and these vary both within and between species. Any attempt to explain primate homosexual behaviors in terms of one "prime mover" such as alliance formation will likely prove to be a chimera.

To my mind, a more parsimonious and unifying evolutionary explanation for human homosexual behavior is that it is a neutral, concomitant by-product of direct selection for a more generalized trait (Futuyma and Risch 1984, Vasey 1995) such as sexual pleasure (Abramson and Pinkerton 1995). In line with this reasoning, it will frequently be manifested for no other reason than sexual gratification. In such cases, homosexual behavior will have no evolutionary "function" (sensu Gould and Vrba 1982). So long as such interactions do not interfere with the actors' reproductive efforts, they will not be selected against. As part of a pool of neutral behavioral variation homosexual behavior could, however, be co-opted to serve any number of sociosexual roles (e.g., alliance formation, reconciliation) that might incidentally augment the participants' fitness. In such cases, homosexual behavior could best be described as an "exaptation," that is, a characteristic which was not built by natural selection for the fitness-enhancing role that it currently serves but instead was co-opted for that role (Gould and Vrba 1982). Although exaptations are not the products of direct selection, they may eventually come under positive selection because of their beneficial effects on fitness, at which time secondary adaptive modifications will occur.

At several points in his article, Kirkpatrick seems to

espouse elements of this "by-product hypothesis." He states, for example, that "sexual behavior and emotion can ... be appropriated to establish and maintain alliances" and that "in terms of natural selection, homosexual behavior is a benign trait in most instances and becomes adaptive within certain social contexts" (emphasis mine). I think that the validity of Kirkpatrick's 'alliance hypothesis" would have been greatly strengthened had he addressed its merits relative to the "byproduct hypothesis" presented here and elsewhere (Futuyma and Risch 1984, Vasey 1995, Abramson and Pinkerton 1995).

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At long last the anthropological profession is beginning to pay attention to same-sex love, a form of human behavior that is quite widespread across cultures but has been singularly ignored in anthropological writing. Kenneth Read, in analyzing the avoidance of cultural studies of homosexuality, concluded that this avoidance came from many anthropologists' personal uncomfortableness with the topic. Either consciously or unconsciously, he wrote, they accepted "Western attitudes toward homosexual behavior as a sensitive subject which, though it is probably as prevalent as witchcraft, is morally distasteful" (1984:215–17). Read posited that, in contrast to the situation with other "savage" behaviors, anthropologists could find no cultural "justification for homosexual behavior. It was far easier, for example, to excuse infanticide (a custom also abhorrent by Western standards) since it could be shown to have a rational basis in some demographic situations: it 'produced' something. But homosexuality did not 'produce' anything."

This brings us to the efforts of more recent scholars to show that homosexual behavior does, in fact, produce something of value to cultures. Kirkpatrick makes a substantial contribution to this effort, and I agree that all of hypotheses he suggests for the evolutionary origin of homosexual behavior may apply. One hypothesis or another may best explain particular individuals. These alternatives of kin selection, parental manipulation, or alliance promotion are not opposites, and one or more of them may be present in certain cultures. However, what gets lost in all of this discussion of evolutionary advantage is the simple fact that, for primates, the stimulation of genitals is pleasurable.

To note pleasure as a principle for human behavior seems beyond the abilities of some anthropologists, at least as far as this is reflected in anthropological writings. Sexual behavior is most often relegated to "gutter" language which cannot be part of a serious discourse. That sexual pleasure is a major concern of human life and underlies much of social relations within and between groups is therefore widely ignored.

What is missing in Kirkpatrick's analysis is simple

desire. Not everything has to be explained in terms of social function. Individual desires in nonsexual matters vary enormously; some people prefer scrambled eggs with coffee, while others like poached eggs and tea. Given this reality of variation, why would we expect sexual desires to all be the same? If there is an evolutionary advantage at work here, it is the advantage of variation.

The question, then, is not why certain individuals enjoy participating in sexual pleasure with another person of the same sex but why certain individuals would limit this pleasurable activity of genital stimulation solely to the other sex. As Kirkpatrick points out, if the evidence suggests that most people in most cultures (for which we have information) can enjoy sex with both sexes, then a bisexual potential is the true human norm. If genital stimulation feels good, in and of itself, then why do we like particular types of persons to do it to us but not others? We need much more research on the variability of sexual desire before such questions can be answered.

What is even more important for anthropologists to understand is why a minority of cultures stigmatize this pleasurable genital stimulation between persons of the same sex. Thus, as I have written elsewhere (Williams 1997), it is not homosexual behavior which most needs to be analyzed by anthropologists but homophobia. We have ignored our responsibility and our role of pricking the bubbles of assumptions about what is "normal" behavior propounded by the other social sciences, which base their analysis solely on modern Western culture. We ignore our professional responsibility if we do not publicize the reality of human individual and cultural variation on attitudes toward same-sex love.

In contemporary society fundamentalist Protestant and Catholic churchmen commonly state that "the only purpose of sex is reproduction." Anthropologists above all others need to publicize the falsity of this statement. There are many purposes of sex, far more complex than procreative concerns. As Kirkpatrick emphasizes, a major factor in sexual involvement is alliance formation. While kinship theorists have shown how heterosexual marriage leads to widening circles of mutual dependence and reciprocity obligation, it only stands to reason that sex between males and between females can also produce intimate bonds that aid survival. Sexual involvement with friends and relatives produces overlapping circles of intimate involvement that complement reciprocity networks (Williams 1992b, c).

If Kirkpatrick is right about the importance of alliance formation as a motivator for sexual behavior, then the implications are astounding. First, as Kirkpatrick points out, the modern Western notion of separate innate homosexual and heterosexual categories of persons does not explain the sexuality of many humans and nonhuman primates. If sexually relating to both males and females offers an advantage over an exclusive orientation to only one sex, how then are we to explain the establishment of compulsory heterosexuality in premodern European and Euro-American cultures and then the rise of exclusive homosexuality in the modern world?

Let me suggest another hypothesis to account for the rise of compulsory heterosexuality: it helped to maximize population increase for competing European nation-states that wanted to expand their political and economic dominance in Europe and into colonial empires around the world. In this expansionist value system any form of nonprocreative sex (for example, masturbation, birth control, abortion, oral sex) becomes stigmatized in favor of penile-vaginal sex as the only acceptable form of sex for everyone. This hypothesis could explain why the most expansionist modern nation-states (for example, the United States, Nazi Germany, and the Soviet Union) and the most expansionist missionary-oriented Christian churches (for example, Catholics, Mormons, and fundamentalist Protestants) are associated with severe discrimination against homosexuality. That is, homophobia is, to a great extent, a product of expansionist missionary imperialism. This hypothesis could also explain why Japan, once one of the world's most accepting cultures of same-sex love (Watanabe and Iwata 1989), has become so homophobic in the period since it began its expansionist empire. Social pressure to reproduce also explains why such high percentages of Japanese bisexuals and homosexuals marry heterosexually and have children. In the post-1945 world, as colonial empires have started falling apart and population growth is no longer the prime need, sanctions against nonprocreative sexuality have declined. Nonimperialistic European nations like those of Scandinavia and (after 1950) Holland have not surprisingly led the way in repealing laws against homosexuality.

Given the compulsory heterosexuality of the Western-dominated contemporary world, exclusive homosexuality may be a reaction against it. Many people repress their same-sex desires and identify themselves as heterosexuals but others who feel strong same-sex attractions either become depressed or suicidal or rebel against the repression. The rebels flip over to the other extreme to identify themselves as homosexuals/gays/lesbians/transgenders/queers. There are many reasons that particular individuals construct identities of sexual minorities, but in the anonymity of large cities becoming a member of a sexual underground can offer subcultural identification that can assist psychological functioning.

What this suggests is that, in order to get beyond a binary division of society, it will be necessary for people to destigmatize bisexuality. Anthropologists can be at the forefront of this effort, breaking down prejudices by teaching about the reality of human sexual variation. Of course, we must be careful not to substitute a compulsory bisexuality for everyone, since even nonhomophobic cultures have a minority of individuals who remain totally other-sex-oriented or totally same-sex-oriented (see Williams 1986). The message must be the reality and advantage of human variation.

Another astounding perspective is Kirkpatrick's suggestion that same-sex attractions strengthen warrior-hoods. Contrary to claims by the U.S. Armed Forces that homosexuality is incompatible with military service, a cross-cultural perspective would suggest that same-sex

intimate bonding leads to stronger mutual defense. While many nations are abandoning discrimination against gay and lesbian soldiers, it may take an anthropologist to suggest that policies suppressing sex between soldiers may in fact be counterproductive to defense effectiveness. Recognition of sex as a means of building stronger alliances may be tacitly accepted, and this would avoid the huge expenditure currently borne by the U.S. military in its efforts to investigate and dismiss homosexuals from its ranks.

Kirkpatrick's perspective also challenges Western prejudice against intergenerational sexual bonding between men and boys. It is not surprising to find intergenerational male relationships to be so common among cultures that are accepting of same-sex love, because institutionalizing such age patterns leads to greater access to resources and knowledge acquisition for the younger partner. While unfortunately little is known of a womangirl sexual relationships, extensive cross-cultural surveys of man-boy patterns include Bullough (1976), Greenberg (1988), Gregersen (1983), Karsch-Haack (1975[1911]), Murray (1992), Weinrich and Williams (1991), and Williams (1998). Individual cultures which accepted man-boy sexual relationships include ancient Greece (Dover 1978), feudal China (Hinsch 1990), Melanesia (Herdt 1981, 1984c, 1987), and East Africa (Evans-Pritchard 1970).

In fact, such intimate bonds were often the basis for a culture's educational system. Rather than educating youths in schools, many cultures have structured education in terms of individual apprenticeships. For example, in premodern Japan Buddhist monks and their student novices commonly developed sexual relationships that were socially accepted (Watanabe and Iwata 1989). Likewise, in medieval southwestern Asia, the Mamluks of the sultanate governments were forbidden to have sex with females but commonly had boys as sexual partners. The adult Mamluk would educate the boy as his apprentice, to take on his administrative duties as he reached old age. For over a thousand years, this system was largely responsible for government administration in areas ranging from Egypt to Turkey, as each successive generation of apprentices matured and took boys as its trainees and sexual partners (Hardman 1990, Williams 1998).

For those cultures that are concerned about controlling pregnancies among females outside of marriage, encouraging young males to establish same-sex relationships has the added advantage of allowing youths a sexual outlet while also preventing female out-of-wedlock births and prostitution. That many cultures allow a same-sex outlet for pubescent, adolescent, and young adult males at the height of their sexual drive also seems to be a realistic measure to preserve social order (Williams 1986, 1992b, c, 1996, 1998). Perhaps this is why intergenerational relationships are so much more institutionalized for males than for females. In the current climate of large population increases throughout much of the world, it seems sensible for anthropologists to publicize these ancient and indigenous population control mechanisms

that function to delay heterosexual marriage until mature adulthood.

What is most important is that anthropologists take a leading role in countering ignorant claims that the only purpose of sex is reproduction. If we do not say again and again that sexual behavior is multipurposed and highly variable, then we are allowing a major distortion of reality to continue. As Kirkpatrick points out, hominid evolution involves more than simply passing along genes; it also requires strategies for survival through alliances with others. For highlighting the important role of sexual relationships in promoting alliances between individuals of the same sex, Kirkpatrick deserves our thanks.

Reply

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In the friendship I speak of, our souls mingle and blend with each other so completely that they efface the seam that joined them, and cannot find it again. If you press me to tell why I loved him, I feel that this cannot be expressed, except by answering: Because it was he, because it was I. . . . neither of us reserved anything for himself, nor was anything either his or mine.

M. DE MONTAIGNE, "Of Friendship"

Is it not reasonable to anticipate that our understanding of the human mind would be aided greatly by knowing the purpose for which it was designed? G. C. WILLIAMS, Adaptation and Natural Selection

I thank the commentators for their perceptive reviews of my argument's strengths and weaknesses. As I read their comments, they have three main concerns: (1) weakness of the data and of my methodology, (2) lack of attention to alternative explanations, and (3) the role of scientific authority in social policy.

Data and methodology. Blackwood praises the article for showing same-sex alliances as important in larger cultural processes. She finds the data generally weak, however, and I agree that the article is an interim assessment. Muscarella also finds the data weak for the predictions that same-sex alliances are helpful to individual survival and that homosexual behavior is part of same-sex alliances. He generously suggests that this is because data on homosexual behavior are primarily qualitative. Dickemann notes that I concentrate on longterm relationships with little review of the "casual and sub rosa," but long-term relationships are more prevalent in the cross-cultural and historical literature.

Blackwood, Muscarella, Williams, and Vasey all de-

scribe limits to my analysis of alliance formation. Blackwood suggests a crucial test: comparing societies with same-sex alliances and those without them. Melanesia provides a "natural experiment"; societies with systemic homosexual behavior exist alongside and are not outcompeted by societies without such behavior. (I would also note Blackwood's insight that my term "patron/client" is not inclusive enough.) Muscarella points out that the alliance-formation hypothesis would not predict the homophobia we see in some close-knit groups of men. I agree that this is a weakness of the hypothesis and think Muscarella may be correct in hypothesizing that this arises, in part, from repressed homophilia (displayed so convincingly in Adams, Wright, and Lohr 1996). Homosexual behavior may also promote pair bonds (notwithstanding the casual and sub rosal that may threaten the cohesiveness of the larger group. Muscarella also raises the tantalizing idea that sex is a symbol and therefore analogous to language. If this is the case, then nonprocreative sex may have been relatively important to prelinguistic humans; I had not thought to take my argument so far or to align it so closely with bonobo sexuality. (Dickemann is, of course, correct to point out the connection between the nonprocreative behavior of humans and of other mammals; my discussion of nonhuman primates was not meant to imply "a separate human prehistory of homosexuality.") Williams raises the interesting prediction that it should be colonial powers that most repress homosexuality; typically at carrying capacity (Crosby 1986, Ponting 1991), they may therefore force procreation to fuel colonialist expansion. His prediction differs from mine that societies at carrying capacity may be relatively tolerant of homosexual behavior. Colonial powers are often aggressive in their expansion, and if homophilia increases military effectiveness this might counterbalance a push for compulsory heterosexuality. Vasey raises a more fundamental point: finding a correlation between homosexual behavior and alliance formation is not the same as showing that homosexual behavior results from the adaptive benefits of alliances. I recognize this and say so in the opening paragraph of my discussion.

Jones suggests that homosexual behavior is "at least" two phenomena with two separate causes. In essence, my position differs from his only in the number of paths we see leading to homosexual behavior. Logically, there is a difference between homosexual behavior that *stops* when other-sex partners are available and homosexual behavior that *continues* when other-sex partners are available. In my judgment, however, categorizing homosexual behavior as either "facultative" or "constitutional" is an unjustifiable reduction. The evidence rather points to a broad range of interacting factors that produce innumerable pathways to homosexual behavior. Blanchard and Bogaert (1997), for example, describe the potential separate contributions of just two of these factors: family aggregation and number of older brothers. Isolating facultative and constitutional aspects of homosexual behavior and ignoring the interaction between them and the variance in their components would seem a principal reason that models of homosexual behavior have failed to approach the richness we observe. Posner's (1992) cost/benefit analysis of homosexual behavior further supports the idea that sexual behavior results from a range of individual predispositions interacting with a range of individual circumstances. I believe that Williams's comment on this issue is fundamentally correct: the bimodality of homosexual and heterosexual identity in Westernized societies is the result of social pressure.

My dissatisfaction with the deterministic facultative/ constitutional dichotomy leads to an ambivalence about incorporating issues of gender nonconformity into my argument, also noted by Jones. In rejecting most uses of gender nonconformity in the understanding of homosexual behavior (e.g., Green 1987, Zucker 1990), I am not denying the importance of gender to sexuality. Rather, I am expressing dissatisfaction with the concepts and techniques this approach has used. Even if sexual behavior is closely tied to feminine or masculine predispositions, I remain unconvinced that a focus on the extremes will explain much about the range. A framework that reduces homosexual behavior to a discussion of "feminine" boys and "masculine" girls is incomplete. Boyhood femininity and girlhood masculinity may cooccur with later homosexual identity. As Corbett (1998) notes, however, we have yet to learn of nonproblematic childhood gender nonconformity; we have only learned of children taken to gender-identity clinics by parents. Zucker says that the primary reason parents bring children to his clinic—one of the largest in the world—is that they "don't want their kids to be gay" (quoted in Burke 1996:100). Many researchers of gender nonconformity seem to mistake conformity for health. Green, for example, says, "You've got to get these mothers out of the way. Feminine kids don't need their mothers around" (quoted in LeVay 1996:100). My fear, perhaps unjustified, is that the science surrounding gender nonconformity is colored by activism against homosexuality.

In contrast to Jones, who suggests that I should divide homosexual behavior *more* finely, Dickemann and Vasey suggest that I have already divided sexual behavior too finely. They consider my categories of "homosexuals," "bisexuals," and "heterosexuals" inappropriate. As I read their comments, they suggest that my analysis would be stronger using the categories "procreative behavior" and "nonprocreative behavior." This point is well taken—the issues of appropriate levels of analysis and whether to categorize individuals or behaviors are common in dialogues concerning evolutionary explanations of behavior-yet it seems to me that "people who have sex with the same sex" is a logically distinct category from "people who have sex with the other sex" and both are distinct from "people who have sex with both sexes." Certainly, there will be overlap between various schemes. Within the "heterosexual" and "bisexual" categories, there will be individuals who also have nonprocreative sex. I fail to see a contradiction between these two schemes, however, and remain unconvinced that one scheme should be valued above the other.

Dickemann and Vasey suggest that, having reified homosexual behavior, I have attempted post hoc adaptive explanations. There is, of course, some truth to this. Adaptive explanations are always "historical narratives" (Mayr 1983); this is simply the way this type of analysis is done. Only after we have failed to explain a phenomenon adaptively are we justified in using explanations that are less testable. The hypotheses I used were chosen for their theoretical merit; they were not designed, post hoc, to mirror (weakly) the complex reality of homosexual behavior. I agree with Vasey that exaptation may be a useful concept in analyzing nonprocreative sex and that homosexual behavior did not evolve "for" long-term alliance formation any more than nonprocreative heterosexual behavior evolved "for" long-term pair bonds. Still, the intuition remains that natural selection acts on predispositions for same-sex social relations. This, it seems to me, is one of the "subsidiary propensities" referenced generally by Dickemann. (I would not expect selection for alliance formation without regard to the partner's sex. Gender differences—weakly biological and strongly social—make women and men very different types of partners.) Humans are complex, as are other organisms, but it remains the goal of science to "cut nature at its joints." It is valid to infer adaptive causes for behavior. The challenge is, in Mayr's (1983:329) words, to chart a course "between a pseudoexplanatory reductionist atomism and stultifying nonexplanatory holism."

Alternative hypotheses. My objective has been to use hypothesis testing to compare multiple alternatives rather than to advocate any particular hypothesis or theory. Almost universally, the commentators find that I have failed in this task. Upon reflection, I agree that I may have promoted the alliance-formation hypothesis too strongly. However, kin selection, parental manipulation, and reciprocal altruism are the three most powerful adaptive explanations for mammalian social behavior (Wilson 1975, Trivers 1985). Kin selection and parental manipulation have already been explored in relation to homosexuality (e.g., Weinrich 1987a, Ruse 1988, Dickemann 1995, McKnight 1997 [the Freudian argument on homosexuality is also closely allied with the parental manipulation hypothesis]). Reciprocal altruism has not, and I therefore felt it useful to explore its strengths.

Dickemann, Jones, and Vasey point out that to search for a single cause of homosexual behavior is to search, in Vasey's term, for a "chimera." Williams notes that adaptive hypotheses are not mutually exclusive and that different individuals will be subject to different selective pressures. Models will interact at the level of individual circumstance. I approach this issue, briefly, in the article's discussion section when mentioning parental interest in alliances. Jones is correct, however, that my attempt to explore reciprocal altruism fully has limited the complexity and therefore the strength of my overall argument.

I realize that there are many avenues for further testing of the hypotheses I present. For example, if homosexuals work to benefit kin, then male and female homosexual behavior may be expected to split with residence pattern (that is, we would expect more homosexual behavior in the philopatric sex, although this could possibly be forestalled by incest-avoidance mechanisms). Reciprocal altruism would predict homosexual behavior to be more common in the nonphilopatric sex (cf. Manson, Perry, and Parish 1997). Werner (in Greenberg 1988) indeed finds a weak correlation $(r^2 = 0.25)$ between acceptance of male homosexuality and patrilocality for 20 select societies, although Greenberg severely questions Werner's methods.

I made a conscious decision to focus on the three central theories of social evolution. While this approach has limits, it is legitimate and has important benefits. It is not meant to detract from the research avenues detailed by the commentators. I would agree with Jones, for example, that there is support for the hypothesis of sexually antagonistic selection, both theoretically (e.g., Getz 1993) and in the real world (e.g., the findings of Hamer et al. 1993 that male homosexuality may be passed through the female line). Although somewhat more complex than Hutchinson's (1959) hypothesis of balanced polymorphism, sexually antagonistic selection is completely in keeping with it. (McKnight 1997 reviews additional hypotheses allied with balanced polymorphism.)

Dickemann, Vasey, and Williams hypothesize that sexual pleasure explains much of sexual behavior's variance. "Simple desire," in Williams's words, is the trait under selection and confers evolutionary advantage. This "pleasure hypothesis" clearly is an important line of research to pursue. Jones suggests, however, that individuals have sexual orientations; Williams too raises the question of preference for particular partners. Preference is not explained, nor is it expected, by a generalized sexual response. As I understand the pleasure hypothesis, we should expect relatively equal proportions of heterosexual and homosexual acts within individual life histories, within societies, or, at the very least, within large collections of societies. Yet this is not the case.

Dickemann and Vasey clearly recognize that selection for generalized sexual response is an incomplete explanation. The pleasure hypothesis starts with the premise that all anyone really wants is good sex. Well, ves. But what is "good sex"? And what is the relation between "proximate" good sex and "ultimate" good sex? Blackwood notes that sex is part of larger cultural processes; Dickemann points out that family dynamics and social concerns strongly influence the avenues allowed for sexual pleasure. Posner (1992) suggests dividing the category of "nonprocreative sex" into two subcategories: "hedonistic" and "sociable." These distinctions might add much to the pleasure hypothesis.

In its barest form, the pleasure hypothesis is limited because it ignores the entire literature on mate choice. Why do we find some mates more compelling than others? Mate choice is a system of valuation; more valuable mates are often those who potentially will increase one's reproductive success (Betzig 1988, Borgerhoff Mulder 1988). Mate choice is clearly a part of many, if not most, homosexual relationships. Exogamy rules regulate the choice of partners in homosexual relationships among the Sambia of Melanesia and the Nambikuara of Brazil, for example (Herdt 1984b, Lévi-Strauss 1943). In patron/ client and matron/client alliances, the client is, in effect, choosing a "model" (sensu Boyd and Richerson 1985); clients should avoid poor models by practicing mate choice. This is fundamentally what occurs in the "tests" given to prospective patrons by prospective clients described by Ihara (1972 [1687]) and Ng (1989). I believe this speaks to Vasey's point that "by-products" of a generalized sexual response can come to be under positive selection. Both Muscarella and Vasey note that exaptation has no fundamental conflict with the adaptive hypotheses presented in the article.

The pleasure hypothesis is a proximate explanation and fails to explain why pleasure is maximized. It would seem that natural selection should ultimately favor sexual energy that was sharply focused, not broadly dispersed. Genetic mechanisms, developmental processes, family dynamics, and social forces are also proximate explanations. I generally agree with the commentators on proximate responses but remain unwilling to forgo some attempt to analyze ultimate results. The question that interests me is not so much how sexual variation comes about as why it persists. Is it because sexual pleasure has general benefits or because nonprocreative sexual behavior has specific benefits? I am skeptical that sexual behavior can be reduced solely to proximate responses, just as I am skeptical that it can be explained solely by ultimate results. Family dynamics and social forces are the sum of individual actions and must have some relationship—however weak—to adaptive, evolutionary functions. This is why humans have been strikingly successful over evolutionary time. My argument on alliance formation reviews potential functions of same-sex alliances and therefore reasons to expect a psychology of same-sex affiliation. This in no way conflicts with a generalized sexual response that leads to a variety of sexual relationships. The best course, in my view, is to use homosexual behavior as an example of nonprocreative sex that identifies and informs issues of sexual behavior in general, such as the varied processes by which sexual energy is harnessed for evolutionary gain.

Science and society. Williams is most explicit in noting that, to use a feminist phrase, the personal is political. He sees the article in the context of efforts to show that homosexual behavior produces "something of value." Blackwood finds that it supports the view that homosexuality is not "aberrant." Other commentators also find a political edge in the article, allying it with the work of "early pathologists" (Dickemann) or finding that it uses "mere assertions" (Jones) instead of judgments. The conventional wisdom is that any inquiry into homosexual behavior must be tied to a political agenda.

A key point of the article, recognized by Blackwood and Williams, is that, for humans, sex is not solely for procreation. This, I believe, is a scientific fact, not in itself a political statement. Yet questions of how and why societies come to make a fetish of procreation are, in part, political analyses. Another key point recognized by

Blackwood and Williams is that the nonprocreative benefits of homosexual and heterosexual acts are identical. This subsumes homosexual behavior under the more general discussion of, in Williams's words, the "many purposes of sex, far more complex than procreative concerns." This also has political implications.

As the above quotation from Green illustrates, we all have preconceived notions and our own agendas. Categorizing people according to their sexual practices is typically not a neutral description but a political or social decision to prioritize particular behaviors. Such decisions influence behavior in both gross and subtle ways, just as biological propensities influence behaviors in both gross and subtle ways. There is an ill-defined zone in which the social and the biological are indistinguishable. The questions become under what social conditions certain biological differences become the salient characteristics of sex and how social conditions alter our perceptions of biological differences. Such questions arise on both the level of society and the level of the individual. But this does not obscure the fundamental point that biological research is an inappropriate foundation for social attitudes and policies.

Research cannot be separated from the social context in which it occurs; I am aware of the discourse on the political uses of scientific authority (e.g., LeVay 1996, Laslett et al. 1996, Rosario 1997, Murphy 1997). Clearly, a gay identity influences my perceptions. But this should not alter the scientific analysis of my ideas. The idea that human sexuality is not driven solely by pleasure or that it does not result blindly from genetic predisposition may at first challenge preconceived notions. My reading of the evidence, however, leads to the hypothesis that much homosexual behavior is driven by emotion and that this emotion is maintained by its adaptive consequences. (This is not to imply that emotional ties result in egalitarian relationships.) I believe that scientific analysis, of which this paper is an imperfect start, will support this hypothesis. Yet certainly I agree with Futuyma and Risch (1984:157) as they write, "Science is not science unless its conclusions are examined as critically when they conform to our personal beliefs as when they oppose them."

In the end, I believe that my arguments are more modest than the commentators suspect. In the article, I clearly say that I find adaptive explanations to be incomplete. Implicit in the article is my sense that homosexual behavior may be subject to "cultural evolution" (sensu Boyd and Richerson 1985) as much as "biological evolution." My findings can be reduced to several short sentences. Women are affectionate to other women and men are affectionate to other men. There are biological and social processes that influence variance in affiliation and the sexualization of affiliation. Homosexual and heterosexual behaviors are biological equivalents in terms of their nonprocreative uses. Some alliances will grow to the point at which pairs of individuals become, to follow Montaigne's metaphor, "seamless souls." In the context of evolution, this fundamentally shifts selection away from the individual and toward the bonded pair. For the individual, this shift is profoundly adaptive.

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