Human Homosexuality, Transsexuality and Evolution: A Critical Appraisal

J. Roughgarden

Hawai'i Institute of Marine Biology, University of Hawaii; Department of Biology, Stanford University, rough@stanford.edu

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ABSTRACT

Homosexual behavior occurs naturally in many species of mammals. Among primates, homosexuality is an evolutionary innovation originating when the anthropoid lineage split from the prosimian linage, becoming prominent in socially complex old world primates. Many species possess multiple genders: multiple morphs within each sex. Homosexual behavior and transgender expression occur across all present-day human cultures, throughout recorded history, including the Bible, and in Paleolithic drawings and artifacts. A transgender "third sex" has official status in India and its neighbors. Homosexuality became a Western category of personal identity in the mid-1800s. Despite 30 years of research, a gay gene has not been located nor have the brains of homosexual men been shown to resemble the brains of women. The brains of transgender people resemble the brains of the gender they identify with, not with the brains corresponding to their biological sex; this reflects the timing of sex hormones at different stages during fetal growth. Gender identity may exist in the brain as a "cognitive lens" that controls whom to focus on as a developmental "tutor." Transgender identity is the acceptance of a tutor from the opposite sex. Gender identity is developed at birth and sexual orientation develops later during the first few years of infancy. Homosexuality and transgender are too common to be considered genetic diseases. The fertility cost of male homosexuality is as much as 50% in Western culture and often much less elsewhere. The fertility cost of homosexual behavior is not convincingly offset by a fecundity advantage to the mothers of homosexual children. Homosexual behavior is not convincingly selectively neutral. Transgender expression might have evolved through kin selection in some cultures with a third sex. Homosexual behavior is selectively advantageous by producing alliances and partnerships and by promoting cooperation through the reciprocal sharing of pleasure. The homosexual/heterosexual polymorphism may result from frequency-dependent selection between alternative same-sex alliance strategies, with homophobia emerging as a byproduct of competition between these strategies.

INTRODUCTION

This chapter investigates both human homosexuality and transsexuality from an evolutionary perspective. The chapter is broad in scope with three main sections. These consider (1) the extent of homosexuality and transsexuality in both among animals and among humans in present and past cultures; (2) the structural correlates of human homosexuality and transsexuality in both genes and brain structure; and (3) theories for why human homosexuality and transsexuality have evolved.

The chapter is almost unchanged from its presentation as chapter 30 in the first edition of this book, On Human Nature (Roughgarden 2017), except for the correction of typos. However, this chapter has a more accurate title and also contains a Coda after the Summary and before the References sections. This chapter preserves its focus on homosexuality and discusses transsexuality where relevant.

To begin, a major issue is how homosexuality is defined. Indeed, is homosexuality a biological trait at all? Is it homosexuality when two men or two women gaze lovingly at each other across a crowded room, destined never to meet; when a married man with children assumes the superior position atop a willing, hairy, leather-bedecked partner; when a war lord rapes a male prisoner-of-war; when a teenage cabin boy services his ship's captain; when two men or two women partners of 30 years marry at their local place of worship? Is homosexuality some of these, all of these?

Researchers have devised many operational definitions for homosexuality including same-sex genital contact regardless of context or motivation, or a sense of personal identity revealed through interviews. Varied operational definitions of homosexuality affect the repeatability of biological studies of homosexuality.

Ancillary issues arise too. What evolutionary purpose do the external genitals serve? Is homosexual sex a misuse of these organs? Even the gonads, organs whose primary function is the production of gametes, have other functions, such as hormone secretion. What about the external genitals? Is their only purpose to serve as conduits for the heterosexual transfer and receipt of sperm?

Indeed, in mammals, genitals are often signaling organs. In humans, the signaling significance of genitals may underlie why pornography is provocative.

Moreover, the innervation of external genitals in mammals provides a highway to the brain's pleasure centers. Could the reciprocal pleasure from tactile stimulation of genitals in mammals be the counterpart of the reciprocal pleasure birds experience when mutually preening each other's feathers? Are studies of homosexuality missing the point? Perhaps we should be investigating reciprocal physical intimacy in general? Does focusing on reciprocal sexual pleasure while ignoring other forms of reciprocal physical pleasure represent a fetishizing of sex to the exclusion of other functionally equivalent behaviors?

And then there is gender. How many human genders exist? Two? No. India, Pakistan, Nepal, and Bangladesh have three. In these countries, the hijra, a cast-like group of male-to-female transgender people who number over five million members, are formally classified as a third gender on government documents. A sexually intimate relation between a Hijra woman and her male husband might then be considered homosexual, yet also heterogenderal. Among animals too, many species have more than the two morphs associated with the male and female sexes. The multiple morphs, sometimes termed alternative mating strategies, amount to multiple genders of males and females, allowing for a network of same-sex, different gender schemes of courtship, affiliation, and physical intimacy. Can an evolutionary theory of homosexuality ignore its intertwining with gender expression and identity?

An evolutionary theory of human homosexuality is thus a multifaceted enterprise. In the following pages, I will critically review studies that are relevant to one or more possible framings of an evolutionary theory of human homosexuality. Some aspects of this review are partly condensed from Roughgarden (2004).

EXTENT OF HOMOSEXUALITY

This major section of the chapter considers the distribution of homosexuality among animals and across human cultures.

Animals

Fifteen years ago scientists were still in denial about how common homosexuality is among animals. By "homosexuality," for the moment I refer only to same-sex mounting regardless of context and mutual touching of genitals.

In 2000, George Barlow, about to retire, in a summary of his career's work on the biology of cichlid fish wrote, "When animals have access to members of the opposite sex, homosexuality is virtually unknown in nature, with some rare exceptions among primates."

Yet a year earlier, Bruce Bagemihl, out as gay and early in his career, published a 751-page book (Bagemihl, 1999) reviewing unforced same-sex genital contact in the wild in over 300 species of vertebrates. Bagemihl, at the time largely unknown to biologists, received his PhD in linguistics from the University of British Columbia. All his cases were drawn from the peer-reviewed scientific literature. Bagemihl's compilation was followed by another in 2006 (Sommer and Vasey, 2006).

Today, in 2016, the reality of extensive homosexuality among animals is generally accepted among biologists. The 300 known examples of homosexuality in animals, surely an underestimate, reveal much diversity: in some species only males are homosexual, in some only females, in others both sexes; in almost all the homosexuality is mixed in with heterosexuality by the same individual; in some species a small fraction participates in homosexuality; in others, like our closest relative, the bonobo chimpanzee, every animal does (Parish, 1996). Clearly, homosexuality among animals exhibits great contextual variation.

Rather than wondering why an animal is homosexual, the converse may be more interesting. Why is not every animal homosexual, perhaps mixed in with some minimal amount of heterosexuality to ensure reproduction? Indeed, the task of an evolutionary theory of homosexual behavior might be conceived as the need to explain a polymorphism: to account in each species for the ratio of those who do to those who do not employ homosexual behavior.

Homosexuality is widely distributed across many higher taxa and is especially well-documented in birds and mammals, and also in insects. This wide distribution implies that homosexuality has originated many times in the animal kingdom.

Concerning primates, their family tree indicates a pattern. From its base near the ground, the primate tree trunk splits first into the prosimians on one side and the anthropoids on the other side. The prosimian branch, including bush babies, lemurs, and tarsiers, appear to have only incidental same-sex mounting while in heat, and no evidence of a major social role for same-sex courtship. The anthropoid branch splits into two subbranches: the new world primates and the old world primates. The new world primates, including marmosets, tamarins, and the monkeys with prehensile tails, such as spider monkeys, do have some homosexual behavior. In the old world primates though, homosexual courtship becomes prominent. The old world primates, including the macaques (cheek pouch monkeys), baboons, gibbons, orangutans, gorillas, chimpanzees, bonobos, and humans, have the most sophisticated of the primate societies and also the most extensive homosexuality. In these societies, individuals form complex relationships with one another, relationships evidently fostered both with same-sex as well as between-sex sexuality (Vasey, 1995).

The pattern of occurrence of homosexuality across the primate family tree indicates that homosexuality in anthropoid primates, especially in the old world lineages, is an evolutionary innovation originating around 50 million - years ago when the prosimian and anthropoid lineages began their divergence.

Species with multiple genders of males and females are rather common. Documented examples include the North American bull frog, North American plainfin midshipman, and Pacific and Atlantic salmon: two male genders, one female gender; North American bluegill sunfish, spotted European wrasse, cichlid fish from Mozambique, and the Southwestern American tree lizard: three male genders, one female gender; Canadian white throated sparrow: two male genders, two female genders; Southwestern side blotched lizard: three male genders, two female genders, and many others (cf. review in Roughgarden, 2004, pp. 75-106).

In addition, transgender animals have been reported in detail for the sunangel hummingbirds of the Andes from Venezuela through Columbia, Ecuador, Peru, to Bolivia. Male sunangel hummingbirds have colorful feathers on their throats called a gorget. In these species, a "masculine female" is a female with the markings that a majority of the males possess, and a "feminine male" is male with the markings that a majority of the females possess. The investigation of masculine females and feminine males now encompasses 42 species of hummingbirds from five genera, yielding the statistical information about transgender expression in this entire groups of birds (Bleiweiss, 1992, 1999, 2001).

I note in passing that the variation in gender and sexuality now known throughout the animal kingdom and especially well-documented in vertebrates, casts considerable doubt on the accuracy and usefulness of Darwin's (1871) theory of sexual selection. This area of evolutionary biology presents a binary male/female and strictly heterosexual picture of sex and gender roles as universally normal. The form that sexual theory's modification and/ or replacement should take is hotly debated (see, eg, Roughgarden, 2004, 2009, 2015; Roughgarden et al., 2015).

Humans

Turning from animals to people, the subject of homosexuality moves beyond behavior to identity. Homosexuality did not become a category of personal identity until the mid-1800s.

Karl Kertbeny, a Hungarian-German author, published the term "homosexual" (in German) in 1869 and used the term, "heterosexual," in private correspondence the year before (Greenberg, 1988; Katz, 1995; Beachey, 2010). Before this, homosexuality did not exist as a category of personal identity, although ample reference is made to homosexual conduct in writings for many civilizations extending to ancient time.

A wealth of material from ancient Greece pertains to same-sex love and sexuality, including dialogues of Plato, such as the Symposium, plays by Aristophanes, and Greek artwork and vases (Dover, 1978; Halperin, 1990). Homosexual images are even found on European Mesolithic rock art (Nash, 2001). In India, the antecedents of today's third gender, the Hijra, are featured in the Mahabharata, the Kama Sutra, and in some translations of the Ramayana. Signs of Hijra extend to early, even prehistoric, periods of civilization as long ago as 2500 BCE (Zwilling and Sweet, 1996; Penrose, 2001). At more or less the same time, the galli or Cybelean priestesses represented a third gender group that originated in the Neolithic of Anatolia and later spread throughout the Roman empire (Roscoe, 1996; Doniger, 2009; Kueffler, 2001). Gender-variant homosexual people are well represented in the Bible too. Both the Hebrew and Christian Testaments refer at length to eunuchs. In Isaiah 56:3-5, eunuchs are welcomed into the temple. In Matthew 19:11-12, Jesus speaks approvingly of eunuchs, and in Acts 32-40, a eunuch is baptized (Jung and Coray, 2001; Jung and Vigen, 2010). The new world also featured gender-variant homosexual people, referred to as two-spirited or winkte (Williams, 1986; Roscoe, 1991, 1998), the muxe in Zapotec, Mexico, as well as the mahu, fa'afafine, and others throughout Polynesia (Herdt, 1994). Southeast Asia features the waria in Indonesia, the kathoey of Thailand, and the bissu, calabai, and calalai of Sulawesi, among others (Peletz, 2006). Indeed, collectively, the sum of all cultures, today and throughout history, reveal a seemingly endless number of native transgender categories. Moreover, those cultures in which gender identity is associated with genital morphology have an indigenous form of gender reassignment surgery, such as the nirvan among the Hijra, whereas cultures that emphasize work and occupation as the marker of gender identity, such as the two-spirits, do not.

The reason why homosexuality did not exist as a category of personal identity even though homosexual activity and non-binary gender expressions have existed in the human species since prehistoric times is that the techniques of sexual activity, not the sexual identity of the partner, were socially regulated. For example, the famous injunction against homosexual activity from the Holiness Code in the Bible, "You shall not lie with a male as with a woman; it is an abomination" (Leviticus 18:22) specifically condemns sex in which one male partner penetrates the other, particularly anal sex. (Heterosexual sex featured frontal intercourse when seeking conception and anal intercourse when avoiding pregnancy.) In contrast, approved same-sex intercourse among the Greeks was the intercrural or inter-crotch position: the active partner thrusts his penis between the thighs of the passive partner just below the scrotum (Dover, 1978). I have termed this the "missionary position for gay male sex"; it satisfies the letter of the law in Leviticus because a man would not lie with a woman and use the intercrural position with her (Roughgarden, 2004).

Even today, some cultural traditions focus more on the techniques of same-sex activity than on the gender of the participants. For example, in India, kothis are an identity category for receptive partners in sexual encounters with penetrative men who themselves are considered heterosexual often having a wife and children (Chakrapani et al., 2007).

Thus, an evolutionary theory of homosexuality, what it needs to explain, is itself a cultural artifact. A Western perspective might demand an explanation of why same-sex genital contact behavior evolved. Elsewhere, an evolutionary theory of homosexuality might be called upon to explain why a male would assume the subordinate position in intercourse. When Western science purports to explain any deviation from "normal" human sexual conduct, the effort flies in the face of extensive cross-cultural variation in exactly what constitutes normal.

SUBSTANCE OF HOMOSEXUALITY

This major section of the chapter considers the structural correlates of homosexuality and gender identity. First, genes are discussed with respect to homosexuality, then brain structure is discussed separately with respect to homosexuality and to gender identity.

Gay Genes

Being gay and lesbian runs in families. If a man is straight, the chance is only 4% his brother is gay, the same percentage as in the general population. If a man is gay, the chance increases fivefold, to 22%, that his brother is gay or bisexual too. Whether a man is straight or gay has no statistical effect on whether his sister is straight or lesbian (Pillard and Weinrich, 1986). Similarly, if a woman is lesbian, her sister is about twice as likely also to be lesbian than if a woman is straight. Whether a woman is lesbian has a very small or undetectable statistical effect on whether her brother is gay or straight (Bailey and Benishay, 1993; Bailey and Bell, 1993; Dawood et al., 2009). These data show that gay men and lesbian women cluster in families, but they do not say whether shared genes or environment are involved. Gay men and lesbian women cluster independently.

Comparing identical and fraternal twins suggests some genetic component. In one American study, 52% of identical male twins were both gay, while only 22% of fraternal twins were both gay (Bailey and Pillard, 1991). In a later study, 65% of identical male twins were both gay, and 29% of the fraternal twins were both gay (Whitam et al., 1993). Similarly, a study of woman reported that 48% of identical female twins were both lesbian, and only 6% of fraternal twins were both lesbian (Bailey et al., 1993). A British study of males and females combined showed that 25% of identical twins were both homosexual, whereas only 2.5% of fraternal twins were homosexual (King and McDonald, 1992).

These early studies invited twins to participate by placing advertisements in magazines and other sources likely to be seen by gay readers. More recent studies use a preexisting list of twins based on national censuses: Australia (Bailey et al., 2000), United States (Kendler, 2000), and Sweden (Långström et al., 2010). These also show that identical twins are about twice as likely both to be homosexual as fraternal twins. The chance that identical twins are both gay ranges from about 1/4 to 1/2, depending on the study, and is decidedly less than 100%. Thus, even though a genetic component may be present, environmental factors comprise 50-75% of the story.

Despite the aforementioned evidence for a small genetic component to homosexuality, contrary data also exist. The 1991 study already mentioned (Bailey and Pillard, 1991) also showed that an adopted brother of a gay man is twice as likely to be gay, 11%, compared with an adopted brother of a straight man, 5%. So, unless the adoptive parents are somehow selecting babies likely to become gay, something about the environment into which the adopted child is placed is contributing to sexual orientation as much as any genes are.

That homosexuality is to a large degree determined by environmental factors should not be taken as implying that homosexuality is reversible once it has been developmentally attained. Borrowing language from endocrinology, the environment may "organize" the development of behavior, or may "activate" already developed behavioral abilities. Organization is a permanent consequence from a stimulus, whereas activation reverses when the stimulus is removed. Many aspects of an individual's morphology are organized during development by environmental conditions. The resultant morphology is often quite adaptive, even though realized through environmental factors in addition to genetic factors. One may illustrate with an obvious botanical example. A vine of ivy produces small leaves in the sun and large leaves in the shade: these are the adaptive shapes for hot sunny spots and the moist understory, respectively. Once the leaf shape has been organized during development in a certain environment, the shape cannot be reversed, even if the environment changes. Similarly, homosexual capability may be organized to develop in certain social situations for which it is adaptive, and yet once attained, be impossible to reverse.

In addition to pedigree studies mentioned, geneticists have sought the location of the particular genes that contribute to homosexuality. The most famous of these is the study by Hamer and Pattatucci (Hamer et al., 1993, hereafter denoted as HP). HP defines homosexuality as a form of self-identity, irrespective of sexual practice. Hamer states, "As a geneticist, to be blunt about it, I don't really give a damn what label anyone uses, or even what they do, or with whom. I care about what they feel inside" (quoted in Burr, 1996, pp. 179-180). Similarly, Pattatucci states, "I want to know what's on your interior . do you feel that who you are now, your homosexual orientation, has always been part of you, part of who you are . even though your sexual behavior might have been with members of the opposite sex? . That's the important thing. The behavior is irrelevant compared to the core" (quoted in Burr, 1996, pp 235—236)

HP made several points, some controversial:

1. HP confirmed yet again the tendency for Western gay men to cluster in families. The brother of a gay man had a 13.5% of being gay, whereas the brother of a straight man had only the baseline chance of being gay, which in this study was estimated at about 2%.

2. HP claimed that the distribution of men into the categories of straight and gay was nearly absolute: bisexuals were almost completely absent. The authors concluded, "it was appropriate to treat sexual orientation as a dimorphic rather than as a continuously variable trait." This sorting into only two distinct categories is apparently an artifact of present-day social pressures within Western gay and straight communities. The subjects were self-acknowledged homosexual men recruited through the out-patient HIV clinics in the Washington DC area, and through local homophile organizations. Ninety percent of these men said they were nearly exclusively homosexual, and 90% of the straight men said they were nearly exclusively straight too, giving the impression of a clear-cut bi-modality. However, a present-day Western gay man cannot admit to being sexually interested in a woman any more than a present day Western straight man can admit to being sexually interested in a man. HP did not solicit the organizations and magazines that offer safe space for those who do claim a bisexual identity. Moreover, in most cultures, same-sex sexuality is mixed with between-sex sexuality, implying that widespread bisexuality exits (Greenberg, 1988; Herdt, 1994).

3. HP provided demographic data on the life-history of gay men in the United States. The average age of first same-sex attraction was 10 years, 2 years before their average age of puberty at 12. The average age of self acknowledgment was 15 years, and the average age of coming out was 21 years.

4. HP claimed that gayness in males is maternally inherited and linked to the X chromosome. The paper reports that maternal uncles and sons of maternal aunts (first cousins) of a gay man had a 7.5% chance of being gay, higher than the baseline chance of 2%. These purported genetic effects are small. Out of say, 100maternal uncles and cousins of maternal aunts, only about seven are likely to be gay. Although seven is higher than the two who are likely to be gay on the paternal side, the claimed maternal genetic effect is very weak.

5. Building on the premise that some genetic component of gayness is maternally inherited, HP reported that a section on the Xchromosome at the tip of its long armcalled Xq28 was statistically related to gayness, a "gay gene." Out of 40 pairs of gay brothers, 33 shared the Xq28 section of chromosome X, and seven did not. This is an intermediate result. If something on Xq28 were absolutely needed to be gay, then all 40 brothers would share this chunk of DNA, whereas if only 20 brothers shared Xq28, then its random presence would indicate an irrelevance to gayness. The figure of 33 out of 40 is statistically significant, and HP concluded that some gene in the Xq28 region of the X chromosome tends to produce gayness in males. This claim is modest. Although a gene in the Xq28 region is claimed to have some effect, it is clearly neither necessary nor sufficient for gayness in males. HP repeated their study with similar, though somewhat weaker results (Hu et al., 1995).

The HP study was then repeated by a different group, in Canada, using the same overall design (Rice et al., 1999). Advertisements were placed in the Canadian gay news magazines for families in which there were at least two gay brothers. Forty-six families with two gay brothers and two families with three gay brothers were studied. The sexual orientation was confirmed for each subject by direct questions from a "gay interviewer," each subject read gay magazines, volunteered that he was gay, and his self-report was corroborated by interviewing the gay brother. These are behavioral criteria, not testimonials about one's "core identity." Considering the 46 brother-pairs, 23 would be expected to share Xq28 if this section were irrelevant to gayness, whereas all 46 would share their Xq28 if necessary for gayness in males. In fact, only 20 of the pairs shared their Xq28, a number low enough to show that Xq28 is irrelevant to whether a male becomes gay. So, there is no gay gene in the Xq28 region of the X chromosome. The Canadian investigators conclude, "It is unclear why our results are so discrepant from Hamer's original study… Nonetheless, our data do not support the presence of a gene of large effect influencing sexual orientation at position Xq28."

What then could account for the difference between Hamer et al., 1993 and Rice et al. (1999) concerning the gay gene supposedly on the X chromosome at position Xq28? The difference that jumps out is how people were classified as gay to begin with. The Canadian team did not demand that a gay person affirm sexual orientation as a personal identity; sexual practice apparently sufficed, whereas HP insisted that the subject affirm their sexual orientation as a personal identity.

More recently, Mustanski et al. (2005) conducted a full genome scan of sexual orientation in men by genotyping 456 individuals from 146 families with two or more gay brothers using microsatellite markers. These researchers also did not find evidence of any linkage between homosexuality and the X chromosome, but they did pick up traces of linkage to spots on the 7th, 8th, and 10th chromosomes, traces not strong enough to be statistically significant. A follow up by Ramagopalan et al. (2010) also did not find statistically significant evidence of linkage to male homosexuality, and the locations of what little linkage they did detect on chromosome 14 did not coincide with that found by Mustanski et al. (2005). The most recent study in this vein by Sanders et al. (2015) confirms a possible linkage to male homosexuality on chromosome 8 as Mustanski et al. (2005) reported but not on chromosome 14 as Ramagopalan et al. (2010) reported. In any case, linkage to autosomes, whichever is implicated, does not support maternal inheritance. However, Sanders et al. (2015) do claim a comparatively weak linkage to a region of chromosome X which might overlap Xq28. The linkage in all these studies is barely significant, if at all.

How to define homosexuality: whether it is sexual behavior, testimonial of personal identity, or some other criterion confounds genetic studies to this day. Some studies use solely behavior: "[our] survey included no direct question about self-defined sexual orientation. Actual partnered sexual behavior was assessed with two items: lifetime number of opposite-sex and same-sex individuals, respectively, that the respondent had ever 'been sexually together with'" (Långström et al., 2010). Others, like HP, are adamant that sense of personal identity should be the criterion for assessing homosexuality.

Even more recent studies are also failing to confirm a connection between homosexuality and maternal inheritance. Schwartz et al. (2010) report that although male homosexuals had more male homosexual relatives than heterosexual males did, these homosexual relatives were distributed approximately equally on both the maternal and paternal lines. They conclude their results "failed to support the importance of the maternal over the paternal line for male sexual orientation."

Some researchers prefer still another non-behavioral criterion for homosexuality called "psychological sexual orientation." A recent review asserts, "Whereas older studies tended to define sexual orientation behaviorally, most current researchers, ourselves included, define sexual orientation psychologically. Because sexual attraction and fantasy are less likely than behavior to be constrained by societal pressures, psychological sexual orientation is thought to be a more stable and fundamental trait" (Dawood et al., 2009). Despite the claim that "most current researchers" prefer their psychological criterion, the large population study of twins in Sweden just mentioned (Långström et al., 2010) does use solely a behavioral criterion, indicating that little consensus exists among geneticists even today on how to define homosexuality. This situation implies that any ensuing genetic analysis, however technically advanced, is of uncertain value.

It should be added that major difficulties attend any non-behavioral definition of homosexuality, such as any personal identity or psychological criteria just mentioned. The non-behavioral criteria do not involve characteristics that are exposed to natural selection. Natural selection evaluates results, not motivation. An evolutionary approach to homosexuality can address whether the expression of homosexuality is beneficial, not what motivates that expression.

In addition, the personal identity criterion is not applicable to explaining homosexual expression before the mid- 1800s when homosexual identity emerged as a social category. Similarly, the psychological state of those expressing homosexuality in the past is largely unavailable, except perhaps as revealed in provocative gay publications from the Victorian era. Non-behavioral criteria are largely unworkable outside present-day Western settings.

Furthermore, an evolutionary account of homosexuality must address homosexuality not only cross-culturally and through history, but also across species. If homosexuality is defined in terms of personal identity, then no species we know of can be said to possess homosexuality, even though same-sex behavior might be common within it. Similarly, a psychological criterion is impossible to apply to other species, given that little is known (or even knowable) about the psychology of nonhuman animals. Using a non-behavioral criterion for homosexuality isolates its study from the wider community of biologists and reserves its investigation to medical researchers who are automatically pre-committed to a medical model that treats diversity as a pathology.

All in all, 30 years of genetic analysis have shown a possibly small genetic contribution to the development of homosexuality arising from unknown locations in the human genome. These 30 years have also revealed a large environmental contribution, much of which may act to organize the pathways of a person's organic development.

Gay Brains

For 30 years, neurobiologists have sought morphological differences between the brains of homosexual and heterosexual individuals. Much of this work has been motived by the so-called "neurohormonal theory" that posits that homosexuality is caused by unusual sex hormone levels prior to birth. In particular, male homosexuality is posited to depend on low prenatal androgen action and female homosexuality on high prenatal androgen action (Ellis and Ames, 1987). If sex hormone levels influence the development of homosexuality, they must be acting before birth rather than after birth because hormone treatments in adults have failed to influence sexual orientation, and no association has been found between adult hormone levels and sexual orientation (Byne and Parsons, 1993). Focus therefore turns to hormones before birth rather than after birth.

The most famous studies claiming to support the neurohormonal theory pertain to what I have termed a tiny "rice grain of brain" within the hypothalamus called INAH- 3. Allen et al. (1989) reported that INAH-3 is sexually dimorphic, being smaller in females than males. In a highly publicized article, LeVay (1991) confirmed that INAH-3 is sexually dimorphic, and in addition, reported that the size of INAH-3 in gay males was the same as in females. In heterosexual men, this rice grain of brain averages about 1/10 mm3, in heterosexual women, about 1/20 mm3, and in gay men, also about 1/20 mm3. This study would appear to support the gay brain equals female brain theory, with male homosexuality presumably resulting from development under conditions of unusually low prenatal androgen concentration or with unusually weak androgen receptors.

But a follow-up by Byne et al. (2001) looked more carefully into the claims about INAH-3. They observed that the sexual dimorphism between heterosexual males and females pertains not only to the volume of the INAH-3 but also to the number of cells within that volume. Specifically, the volume of INAH-3 in HIV heterosexual mm3 þ males is about 0.11 and in HIV fe males is about mm3, þ 0.07 and the number of their neu rons is about 1900 and 1100, respectively. Now compare the INAH-3 volume in HIV homosexual males: 0.10 mm3, which is actually þ quite close to the HIV heterosexual male volume. In þ addition, the number of neurons in HIV homosexual males significant þ INAH-3 is 1800, a value not ly different from that of HIV heterosexual males and quite different from that of þ females. In short, data simply do not support the claim that the male homosexual INAH-3 resembles the female INAH-3. Byne et al. (2001) conclude "We can neither ascribe any function to INAH-3, nor can we interpret the functional significance of its sexual dimorphism" and that, "sexual orientation cannot be reliably predicted on the basis of INAH-3 volume alone."

Well, if INAH-3 does not connote homosexuality, perhaps another part of the brain does. A small rice grain of nerve cells, a 0.25 mm3 cluster, in the hypothalamus called VIP-SCN also shows sexual dimorphism. After about 10 years of age, males have about 2500 cells, and females about 1000 cells in this cluster (Swaab et al., 1994). VIP-SCN also seems to align with sexuality in males. You may be guessing that gay males have a female-sized VIP-SCN. Nope. Gay males have an even bigger VIP-SCN than straight males, which is in turn bigger than the VIP-SCN of females. So much for the belief that gay men have female brains (Swaab et al., 1995).

Specifically, gay males had a volume of VIP-SCN that was 1.7 times as large, and with 2.1 times as many cells, as straight males. This result directly contradicts the neurohormonal hypothesis for male homosexuality. Homosexual and heterosexual male brains may indeed differ, but homosexual male brains do not differ by being anatomically more female-like than heterosexual male brains are.

Still, the neurohormonal theory for homosexuality just will not die. A review that actually cites the aforementioned studies (Mustanski et al., 2002) manages somehow to conclude, "Evidence consistent with the INAH-3 differences described by LeVay (1991) has been reported in one study (Byne et al., 2001), and these results are compatible with the neurohormonal theory." As just shown however, a close reading of the data in Byne et al. (2001) reveals that this study has been misquoted and that its findings are not compatible with LeVay (1991). It is time to throw in the towel on the neurohormonal theory for the development of male homosexuality.

That said, a postnatal, rather than prenatal, influence of hormones may be involved in differentiating gay and straight brains outside the hypothalamus. Cerebral maturation continues after puberty, especially in boys (Paus, 2005), providing a substrate for effects of social/environmental factors. Savic and Lindström (2008) have shown with PET and MRI scans that homosexual men align with heterosexual women and homosexual women with heterosexual men with regard to features of the cerebrum. Heterosexual men and homosexual women showed a rightward cerebral asymmetry as well as connections from the right amygdala.

Given enough research effort, differences in the brains of gay and straight males will surely accumulate. Consider though, what is the ordinary person-to-person variation in brain structure? Do the brains of politicians and poets also differ? Is some rice grain of Beethoven's brain shared by all composers? Is a different rice grain of Picasso's brain shared by all painters? Are there anatomical markers of ability in performing and graphic arts? Indeed, the part of the brain controlling left-hand fingers is larger in string players than everyone else (Elbert et al., 1995). Political orientation is correlated with brain structure (Kanai et al., 2011), as is musicianship (Bengtsson et al., 2005; Bermudez et al., 2009; Bermudez and Zatorre, 2005; Gaser and Schlaug, 2003; Zatorre et al., 2002) and also the ability to speak Chinese (Crinion et al., 2009). The difference between the brains of homosexual and heterosexual people is like the difference among the brains of any collection of people with diverse capabilities.

Transgender Brains

The inconclusive search for prenatal hormones influencing sexual orientation carried out during the 1990s and earlier have now given way during the 2000s and later to a search for prenatal hormones that organize the brain's development of gender identity. Here, the search for an influence of prenatal hormones is more plausible.

A divergence between genital sex and gender identity theoretically can emerge because an embryo's genitals sexually differentiate at a different time than its brain sexually differentiates (Swaab and Garcia-Falgueras, 2009; Bao and Swaab, 2011). Testosterone during the first 6-12 weeks of embryonic growth leads to the formation of male sexual organs, whereas a lack of testosterone during that period allows the genitals to develop as female sexual organs. In contrast, sexual differentiation of the brain occurs in the second half of pregnancy by the organizing effects of sexual hormones. Hence, the developmental of genitals and the brain are independent and chronologically separated by many months. Therefore, it is plausible to hypothesize that the genitals develop in one hormonal regime and the brain in another, leading to a difference between genital structure and gender identity.

Indeed, many studies are now reporting that the physical brain structure of transgender people more closely resembles the sex they identify with rather than with their genital sex. This match of gender identity with brain sex rather than genital sex is now confirmed for the following: the number of neurons and volume of subcortical nuclei (Zhou et al., 1995; Garcia-Falgueras and Swaab, 2008), cerebral activation by visual erotic stimulai (Gizewski et al., 2009), functional alterations of regional cerebral blood flow (Nawata et al., 2010), and neuronal activation (Schoning et al., 2010), as well as structural differences of gray (Simon et al., 2013) and white matter microstructure (Rametti et al., 2011a, 2011b; Kranz et al., 2014). Saraswat et al. (2015) have contributed a recent review of evidence for a biological under-pining to gender identity. They review data on intersex people, neurohormonal data on brain structure such as that just noted, and also limited data on the genetics of steroid hormones that might be associated with transgender identity.

Moreover, depending on their sexual orientation, some transgender people show hypothalamus activation to odorous steroids intermediate between male and female controls (Berglund et al., 2008). In addition, the brain structure of trans women who are sexually attracted to women is explored with respect to white and gray matter, hemispheric asymmetry, and volumes of the hippocampus, thalamus, caudate, and putamen sections of the brain showing a complex pattern (Savic and Arver, 2011). Furthermore, the structural connectivity networks among different regions of the brains of transgender people differ from both non-transgender males and non-transgender females (Hahn et al., 2015). As before, it is again difficult to contextualize these technical details about brain structure among different people in light of the many differences in brain structure among people more generally.

Taking a synthetic view, I hypothesize that gender identity must develop in the first place as a prerequisite to the later developing of same-gender sexual orientation. I conjecture that gender identity has been attained at or near birth, whereas developing sexual orientation awaits experience during the first few years of infancy after birth (Roughgarden, 2004). This conjecture accords with anecdotes about how stable gender identity can be soon after birth (Colapinto, 2000), whereas the average age of realizing same-sex attraction is about 10 years after birth (Hamer et al., 1993).

But what exactly is "gender identity"? The brain structure studies do not answer this basic question. I have envisioned gender identity as a cognitive lens (Roughgarden, 2004). When a baby opens his or her eyes after birth and looks around, whom will the baby emulate and whom will he or she merely notice? Perhaps a male baby will emulate his father or other men, perhaps not, and a female baby her mother or other women, perhaps not. I imagine a lens exists in the brain that controls who to focus on as a "tutor." Transgender identity then is the acceptance of a tutor from the opposite sex. Degrees of transgender identity reflect different degrees of single-mindedness in the selection of the tutor's gender. Gender expression thus depends both on brain stated which is where the lens is, and on early postnatal experienced because the environment supplies the image photographed through that lens that is developed into brain circuitry. This hypothesis might be tested experimentally. In birds like canaries, males learn their song from male "tutors," often their fathers (Williams, 2008; Belzner et al., 2009). How does a male chick know to listen to his father instead of his mother? Female canaries sing a different song from males. I wonder if an occasional male chick learns his mother's song and an occasional female chick learns her father's song. Such gender-crossing birds would offer a model system to study jointly both transgender behavior and brain structure experimentally.

In summary, the brain structure of transgender people apparently does differ from non-transgender people because, in many details, their brains match the structure of the gender they identify with rather than the sex of their genitals. This presumably reflects the difference in timing of androgen action in early versus late embryonic growth, the different times at which the genitals and brain develop, respectively. In contrast, research shows no convincing evidence that the brain structure of homosexual people has been organized by the action of sex hormones prior to birth: the so-called neurohormonal theory of homosexuality is not true. The slight differences detected in the brain structure between homosexual and heterosexual people are well within the differences that distinguish all persons from one another reflecting their individual aptitudes and training. Thus, the developmental route to attaining transgender capability appears to involve a different androgen level at early versus late episodes prior to birth, whereas the developmental route to attaining homosexual capability is unknown but presumably involves experience during the first 10 years after birth.

Finally, I should alert the reader to the unfortunate language used by investigators of genetic correlates of sexual orientation. Their studies, carried out in medical schools and using pathologizing medical terminology, proceed with the unspoken assumption that homosexual capability is a deleterious trait. Their reports read like those tracing a genetic defect, such as hemophilia through a family pedigree. In fact, whether homosexual capability is deleterious or not is beyond the purview of genetic analysis and lies in the domain of human evolutionary biology, the discipline that considers a trait's function in its natural context.

Similarly, neurological studies of homosexuality and gender identity also convey the unspoken assumption that a heterosexual male/female binary is the normal biological condition for humans, in obvious contradiction with zoological and human cross-cultural data. Transgender people in particular are regularly described by medical researchers as possessing a neurobiological "intersex" condition because their brain structure matches their gender identity rather than their genitals. This terminology lumps transgender people with people possessing a so-called "disorder of sex development", for example, an unusual number of sex chromosomes or insensitive hormone receptors, which lead to genitals that pediatricians consider "too big" or "too small." This is not the place to debate the zoologically uninformed and clinically dubious procedures inflicted by the medical industrial complex upon babies born with unusual genital morphology. The point here is simple: all traits result from some developmental pathway, and all developmental pathways can be described with intimidating Latin and Greek-derived technical terms. An innocuous trait like having ears big enough to attract the ridicule of a cartoon artist (like that of a recent American president) could be described as "macrotia," etymologically derived from "large" in Latin combined with "ear" in Greek. The condition of macrotia undoubtedly results from the action of certain genes, hormones, hormone receptors, etc., all of which could be spun as an intimidating story of developmental pathology. Of course, having large ears is not a pathology, and indeed, it might be especially advantageous in some circumstances. Similarly, if homosexual and transgender capabilities are evolutionarily advantageous, they will, of course, be realized through some biochemical pathway that features some particular timing of growth hormones during embryonic development. Describing that pathway with pejorative medical jargon does not affect whether the trait is in fact valuable and adaptive in its natural context.

The source of natural selection that promotes the evolution and development of homosexual and transgender capability lies in the function of these traits in the cultural contexts where they appear, the subject to which we now turn.

FUNCTION OF HOMOSEXUALITY

This major section of the chapter considers the functions of homosexuality and gender identity among humans in their natural cultural context. Theories for the evolution of homosexuality can be ordered along an axis that expresses an implicit value judgment as to homosexuality's worth. One may start at one extreme with theories that view homosexuality as completely deleterious, then move to theories that view homosexuality as deleterious in some circumstances and beneficial in others, then continue on to theories that view homosexuality as neutral and inconsequential, finally culminating at the other extreme with theories that view homosexuality as an adaptive trait mutually benefiting all participants. Subsections of this section present the major types of theories ordered along this deleterious-to-advantageous axis, and sub-subsections within these further describe important subtopics. In its entirety, this major section of the chapter presents a comprehensive look at all the varieties of theories presently available about why homosexuality and transgender identity have evolved.

Homosexuality Deleterious in All Circumstances: A Genetic Disease

This subsection pertains to theories for the evolution of homosexuality that assume homosexuality is unequivocally deleterious. The first sub-subsection considers the population-genetic relation between how common a genetically based trait is and how deleterious it is. The next sub-subsection presents a sample of theories that assume homosexuality is some type of pathology.

Criterion for a Genetic Disease

Until recently, researchers have taken for granted that homosexuality is a deleterious trait because it supposedly leads to lower reproduction by homosexuals compared with heterosexuals. Hence, researchers have traditionally looked for theories, often far-fetched, to explain how a deleterious trait can somehow become common through evolution.

To begin, we ask, is homosexuality in fact a genetic disease? Even if a gay gene does not exist, or if the influence of genetics on the development of homosexuality is limited and/or complicated, it is important to see what conditions must be satisfied before homosexuality could be considered a genetic disease. A genetic disease is a genetically determined condition that is deleterious at all times and under all conditions. Could homosexuality be considered a genetic disease?

Genetic diseases are automatically rare in the population because they are continually being weeded out by natural selection. The degree of rarity for a genetic disease is set by a balance between two rates: the rate at which the bad gene arises by mutation and the rate of elimination by natural selection. This level of rarity is called a mutationeselection equilibrium. A formula from population genetics expresses the connection among three numbers: how common a disease gene is, how deleterious it is, and how often it is regenerated by mutation from healthy genes.

Suppose, hypothetically, a population consists initially of straight individuals, and a mutation arises for same-sex attraction (a gay gene). Let the average net reproduction by a straight individual be standardized to 1 and the average net reproduction of a gay individual be defined as 1-*s*. The *s* might be called the coefficient of deleteriousness. The bigger *s* is, the more deleterious it is to be gay. If *s* is 1, an average gay individual does not reproduce at all, which would be equivalent to reproductive sterility or lethality. If *s* is 0, an average gay individual reproduces just as much as an average straight individual, which would mean that being gay was not deleterious at all. An *s* between these extremes would indicate that an average gay individual does reproduce, but not as much as a straight individual does, so being gay is partially deleterious. The phrase "net reproduction" means that one takes account not only of how many offspring an individual produces (fecundity) but also the probability of living to reproductive age (survivorship). For example, if the number of offspring that an individual of reproductive age produces is 2, and if the chance of living long enough to reach reproductive age is ½, then the net reproduction by the individual is 1. ("Net reproduction" here is synonymous with what is usually called "Darwinian fitness" in the population-genetic literature.)

If the mutation rate producing a bad gene balances the rate that natural selection is eliminating the bad gene, then the frequency of births carrying the gay gene, *b*, works out to equal about *v/s*, where *v* is the mutation rate (for details see, eg, Roughgarden, 2004, pp 281–282, 446–447).

A typical mutation rate, *v,* is one in a million. So if gays do not reproduce at all (*s* = 1), they would be very rare, ¼ say around one in million, that is, each gay individual would be a new mutation. Indeed, almost-lethal traits like Huntington disease are present in frequencies of 5 per 100,000 births, hemophilia A at 1 birth per 8500, and so forth, very rare. Gay and transgender people are nowhere close to being this rare.

The formula relating *b* to *v/s* can be rearranged to predict how deleterious a trait must be given how common it is. Upon rearranging the formula, a trait's degree of deleteriousness, *s*, given how common it is, *b*, and the mutation rate, *v*, works out to be *v/b*.

According to 2011 demographic information on lesbian, gay, bisexual, and transgender people in the United States (Gates, 2011), 3.5% of adults in the United States explicitly identify as lesbian, gay, or bisexual (LGB), and an estimated 0.3% of adults identify as transgender. Thus, approximately 9 million Americans identify as LGBT, a figure roughly equivalent to the population of New Jersey. Moreover, those who report any lifetime same-sex sexual behavior and/or any same-sex sexual attraction are substantially more common than those who explicitly identify as LGBT. Indeed, 8.2% report that they have at some point in their life engaged in same-sex sexual behavior, and 11% acknowledge at least some same-sex sexual attraction.

Let us use a nominal value of 1 in 20 (5%) as the frequency of gay people. How deleterious is it to be gay, given that gays are this common? Taking a mutation rate of 1 in a million divided by 0.05 yields a coefficient of deleteriousness, *s*, of only 0.00002. That is, the degree of overall deleteriousness for being gay must be infinitesimal.

Similarly, take a nominal value of 1 in 300 (0.3%) as the frequency of transgender people. How deleterious is it to be transgender? Taking the mutation rate of 1 in a million divided by 0.003 yields an s of 0.0003, which is also infinitesimal.

Although one can fiddle with the value of the mutation rate or use a more accurate formula to describe the mutation-selection equilibrium than the simple heuristic of $b \approx v/s$, the conclusion is inescapable that gay and transgender people are 10,000 times more common than would be consistent with assuming that being gay or transgender express a trait deleterious under all conditions.

Candidate Genetic Diseases

That said, researchers have conjured no shortage of theories that cast homosexuality as a pathology. Blanchard has been especially energetic in this effort (Jannini et al., 2010; Blanchard and Klassen, 1997; Blanchard, 2008), proposing that homosexual men who have older brothers owe their homosexuality to an autoimmune disease acquired from their mother. The rationale for this suggestion comes from the so-called "birth order effect" among gay men.

Blanchard and Bogaert (1996) calculated that each additional older brother increases a male's odds of homosexuality by 33%. Bogaert (2006) found that biological brothers increase the odds of homosexuality in later-born males, even if they were reared in different households, whereas stepbrothers or adoptive brothers have no effect on sexual orientation. This suggests that the birth order effect is caused somehow by prenatal conditions.

To explain the birth order effect, Blanchard and Bogaert (1996) formulated what they call the maternal immune hypothesis. According to this hypothesis, cell or cell fragments from a male fetus enter the maternal circulation during childbirth. The mother's immune system recognizes these male substances as foreign and starts producing antibodies against them. The mother's antibodies then cross the placenta into a subsequent male fetus. When absorbed by the male fetus, these antibodies somehow influence the sexual differentiation of the fetal male brain in a female direction so that the individual will later be attracted to men rather than women. Blanchard acknowledges, however, that because half or more of all homosexual men have no older brothers, other causes must account for at least half of existing homosexual men.

Two problems arise in the autoimmune disease theory of male homosexuality. First, as we have seen, brains of male homosexuals do not resemble the brains of females regardless of whether that resemblance is supposed to have been caused by prenatal hormones or by prenatal antibodies.

Second, the autoimmune theory of male homosexuality is a developmental theory, not an evolutionary theory. Evolutionarily, it does not matter how the birth order effect is produced, what matters is what the advantage is for more younger brothers to be homosexual than older brothers. The autoimmune theory of homosexuality does not address the evolution of homosexuality. It merely casts the development of homosexuality in pathological sounding language. And the theory is incomplete because the connection between maternal antibodies to a male fetus and the brain structure of subsequent male offspring is left dangling mysteriously.

Other disease theories for the development of human homosexuality are regularly given by researchers to the news media. A scientist who declined to be quoted by name stated to the science writer, Chandler Burr, that homosexuality was caused by a mitochondrial gene or a bacterium transmitted exclusively through females. He went on to brag, "homosexuality may be a type of bacterial infection we've just never encountered before, one that we may eventually be able to eradicate with an antibiotic" (Burr, 1996, pp. 257–259).

These homosexuality-as-a-disease theories all spring from an uncritical acceptance of homosexuality as universally deleterious. If one accepts that premise, one is forced to conjure up scenarios whereby a deleterious trait can become as common as homosexuality is. The widespread uncritical acceptance of homosexuality as deleterious by the medical community explains why so many foolish disease theories of homosexuality keep popping up.

Homosexuality Deleterious in Some Circumstances and Beneficial in Others

This subsection pertains to theories for the evolution of homosexuality that assume homosexuality is deleterious in some circumstances and beneficial in others, or has positive consequences in addition to negative consequences. The first sub-subsection considers what the cost is to being homosexual in terms of lower fertility. The next two sub-subsections present two different theories for how homosexuality may offer other, possibly indirect, fertility benefits that may compensate for its fertility cost.

Fertility Cost of Homosexuality

If not always deleterious, perhaps homosexuality is somehow occasionally beneficial, directly or indirectly. This contingent benefit might offset some of its presumed deleteriousness and account for homosexuality being much more common than it would be if it were simply a genetic disease.

Direct evidence is surprisingly scanty as to how deleterious homosexuality actually is for fertility, setting aside for the moment the impact of homosexuality on survival.

For lesbian women, a 1988 US survey reported that the mean number of children born to women with homosexual experience was 1.2 compared to a mean of 2.2 for women without homosexual experience (Essock-Vitale and McGuire, 1988). A 1994 survey reported that 67% of lesbian women were mothers, compared with 72% for straight women (Yankelovich Partners, 1994). A 1995 study of contemporary British women showed bisexual women have a higher fecundity to age 25 and no significant difference in lifetime fecundity compared to heterosexual women (Baker and Bellis, 1995). Thus, lesbian and bisexual woman apparently have about the same or higher reproduction than straight women.

For gay men, the 1994 study showed that 27% were fathers, compared with 60% for straight men (Yankelovich Partners, 1994). Of 655 homosexual and bisexual men in contemporary Japan, 83% have offspring (Isomura and Mizogami, 1992). A 1997 investigation surveyed 256 homosexual men in Australia who were older than 49 years of age. Of these about 63% were or had been married and about 56% had children (Van de Ven et al., 1997). Clearly, gay men are not reproductively sterile.

However, King et al. (2005) asked male attendees at two central London clinics for sexually transmitted infections to complete anonymous questionnaires. They compared offspring production from 403 white gay males with 301 white straight males. But the study excluded bisexual men. Not surprisingly, they found that gay males in this sample of people on the average produced only 0.002 offspring, whereas the straight men produced 0.36 offspring.

Schwartz et al. (2010) recruited a sample of 894 straight males and 694 gay males from 16 gay-themed festivals and eight general community festivals in the United States and Canada. Gay males produced on the average about 0.2 offspring and straight males about 0.6.

Clearly, no one really knows what the impact of homosexuality on fertility is. It is difficult to obtain a representative sample of people. Those still in the closet and those who are bisexual are not as likely to turn up at gay pride events or AIDS clinics as those who are out and sexually active in the gay community (cf. Gates, 2012). This will lead to an underestimate of the fertility of homosexual people.

Furthermore, the fertility cost of homosexuality clearly depends on the culture in with the behavior takes place. An extreme example comes from Melanesia where homosexual behavior is well known. About 10-20% of Melanesian societies require all men to participate in homosexual as well as heterosexual sex (reviewed in Herdt, 1994). Obviously homosexual behavior there not only involves no cost, but to the contrary, failure to share in homosexual behavior is deleterious.

Studies that deliberately omit bisexual people from their survey samples commit a particularly serious mistake with regard to the evolution of homosexuality. Hypothetically, if exclusive homosexuality represents a genotype homozygous for a gay gene, bisexuality a genotype heterozygous with both the gay gene and a straight gene, and exclusive heterosexuality a genotype homozygous for the straight gene, then the course of evolution of homosexuality, and whether a polymorphism exists, depends on knowing the average net reproduction by all three genotypes of individuals, not only two of the types. Similarly, for more complex genetic mechanisms, the net reproduction for all the genotypes associated with any particular genetic mechanism must be known if the course of evolution based on that mechanism is to be predicted.

Moreover, Western national surveys of LGBT people consistently and clearly show that bisexual people are about as common as gay and lesbian people (Gates, 2011), contrary to the presumption often expressed by gay researchers that bisexuals are rare (eg, Hamer et al., 1993). What is going on is that bisexual people are not socially organized around their sexuality to the extent that gay people are, so survey protocols that sample primarily gay venues amplify the gay component of the LGBT population while underestimating the bisexual component.

What then, if anything, can be said about the impact of homosexuality on fertility? In the Western cultures that have been sampled, it seems fair to summarize that homosexuality in males might involve a reduction of say, 50%, in fertility relative to heterosexuality.

To explain homosexuality's evolution, a 50% reduction in fertility would need to be compensated somehow by a doubling of the probability of survival if the net reproduction of homosexuals is to match that of heterosexuals. Today's society in many countries is certainly not kind to the survival and health of gay and lesbian people (eg, Dean et al., 2000), but the matter may have been entirely different during human evolutionary history. The possibility that homosexuality may increase survival through building alliances and partnerships, and thereby compensate for the fertility cost of homosexuality, is taken up in detail later in "Homosexuality Promotes Alliances and Partnerships". Here, the next sub-subsections focus on possible fertility benefits that might compensate for the fertility cost of homosexuality.

Fertility Benefit of Homosexuality: Sex-Antagonistic Pleiotropy

Although the fertility cost of homosexuality may be compensated by increased survival, other possible avenues for compensation exist too. One idea receiving current attention is that the gay gene functions to increase any individual's sexual attraction to men. The gene is supposed to cause females to seek heterosexual mating more than females lacking the gene, yielding more offspring. As a side effect, the gene is also supposed to lead males to seek more homosexual mating than males lacking the gene, yielding fewer offspring. Thus the gene is beneficial in females and deleterious in males. This genetic mechanism for evolution is called sex-antagonistic pleiotropy.

The theoretical possibility of sex-antagonistic pleiotropy accounting for male homosexuality has been explored using mathematical models by Gavrilets and Rice (2006) and Camperio Ciani et al. (2008). The applicability of this mechanism to humans has been proposed by Camperio Ciani and colleagues in a series of papers (Camperio Ciani et al., 2004, 2009; Iemmola and Camperio Ciani, 2009) and in *Drosophila* by Hoskins et al. (2015).

In a sample of homosexual and heterosexual people drawn from Northern Italy, Camperio Ciani et al. (2004) found that the mothers of male homosexuals had on the average about 2.7 offspring, whereas the mothers of heterosexual males had on the average about 2.3 offspring. Camperio Ciani et al. (2009) extended their samples to include bisexual men. Here, they found that the mothers of homosexual men had on the average 2.6 offspring, the mothers of bisexual men had on the average 2.7 offspring, whereas the mothers of heterosexual men had on the average 2.1 offspring. These results are consistent with the hypothesis that homosexuality results from genes that promote a general sexual attraction to males by any individual regardless of sex.

Camperio Ciani et al. (2008) found in their mathematical models that the enhanced male sexual attraction trait required a certain minimal genetic system: the genetics for the trait must consist at least of two loci with two alleles at each locus, and at least one of the loci must be located on the X chromosome. If the trait was determined by a single locus, either autosomal or X-linked, or by two loci neither of which is on the X chromosome, then the predicted evolutionary process would not agree with their data.

Four objections might be raised to this sex-antagonistic pleiotropy hypothesis for humans. First, the size of the difference between the fecundity of mothers of homosexual males and mothers of heterosexual males is not very big. An increase of only 0.5 extra offspring produced by mothers of homosexual males may not be enough to compensate for the 50% loss of fertility in her homosexual children.

Second, although Camperio Ciani's et al.'s (2004) data showed evidence of maternally inherited genetic factors favoring male homosexuality, other studies do not. Schwartz et al. (2010) are explicit: "none of our findings supported the hypothesis that maternal inheritance of male sexual orientation was a more significant factor than paternal inheritance." They go on to say, "the lack of elevated 'transmission' of male sexual orientation in the maternal line in the current study supports the notion that hereditary contributions to male sexual orientation do not predominantly reside on the X chromosome, but instead primarily reside elsewhere, that is, on the autosomes."

Recall, too, this chapter's previous discussion concerning Hamer et al.'s (1993) study claiming a gay gene is on the X chromosome. That study has not been confirmed, and Mustanski et al.'s (2005) whole-genome scan and others found little or no evidence of genes for homosexuality on the X chromosome, or elsewhere for that matter. Thus, Camperio Ciani's findings about maternal inheritance of homosexuality are apparently not general, undercutting their requirement for a gay gene on the X chromosome.

Third, no direct information about behavior itself is available. Do mothers of homosexual children actually show an elevated sexual attraction to men compared with mothers of heterosexual children? Camperio Ciani and colleagues do not survey any of the women implicated in their hypothesis, only men. So far as the women are concerned, we must content ourselves solely with statistics on their "fecundity." No one actually asks the women themselves to see whether those with more homosexual children are in fact more attracted to sex with men than the mothers of solely heterosexual children. On reflection, mothers of a gay child may have more children than mothers without any gay children for many reasons having nothing to do with an elevated sexual attraction to men. The mother of a gay child may have an additional child to have grandchildren. Or the social dynamics within large families might promote situations where being homosexual is adaptive.

Fourth, resting an explanation for a trait as widespread as homosexuality on the peculiar properties of a specific genetic mechanism is dubious theoretically. If an increase in the degree of sexual attraction by females to males is adaptive, natural selection need not shackle this trait to a deleterious trait in males. Beyond the two primary loci for elevated sexual attraction to males in the Camperio Ciani et al. (2008) model, a third locus might be introduced, a modifier locus (eg, Feldman, 1972), whose alleles alter the extent to which the primary genes are expressed in males. Modifier genes will then increase to reduce any deleterious impact in males of a trait that is beneficial in females. The genetic mechanism that Camperio Ciani et al. (2008) relies upon is not structurally stable to an increase of genes that would alter the genetic system itself, removing the peculiar properties that enable male homosexuality to be interpreted as a deleterious side effect of a gene that is beneficial to females.

Fertility Benefit of Transgender: Helpers at the Nest

Another way to compensate for the fertility cost of homosexuality is for the gene to increase the fertility of relatives. If a homosexual person augments the fertility of a close relative, the person theoretically can compensate for their own fertility cost by propagating the genes contained in the offspring of their close relatives. This hypothesis is a version of what evolutionists term kin selection.

By this theory, gays and lesbians are similar to avian helpers at the nest, offspring who stay around their nuclear family to help in raising brothers, sisters, and cousins who then go on to do the reproducing (Wilson, 1975, 1979). When initially proposed, this theory broke new ground by valuing the contributions to family and society that gay and lesbian people might potentially make and was a step forward in de-pathologizing same-sex sexuality. However, a limitation of this theory to begin with is that it does not explain why helpers who remain as part of an extended family would specifically be gay or lesbian.

Important though this suggestion has been historically, helping at the nest does not appear to hold the answer to why homosexuality has evolved in humans. In a 2001 study (Bobrow and Bailey, 2001), 66 homosexual and 57 heterosexual men were recruited using advertisements in free urban alternative and gay publications. The name of the city is not mentioned, but it is presumably Chicago because that is where the investigators were located. Based on questionnaires, homosexual men were no more likely than heterosexual men to channel resources toward family members. To the contrary, heterosexual men tended to give more financial resources to siblings than homosexual men. Furthermore, homosexual men were somewhat more estranged from family members, especially from fathers and oldest siblings than heterosexual men.

A follow-up study in 2005 (Rahman and Hull, 2005) found similar results based on 60 homosexual and 60 heterosexual men recruited from East London and Essex. Questionnaires revealed no significant differences between heterosexual and homosexual men in general familial affinity, generous feelings (willingness to provide financial and emotional resources), and benevolent tendencies (such as willingness to baby-sit).

In contrast to the studies from urban Western settings, evidence supporting kin selection theory does come from transgender people in Samoa.

Like other Polynesian cultures, Samoan culture features a third gender for male-to-female transgender people, called the fa'afafine (pronounced, fah-ah-fah-fee-nay). They often are "strikingly feminine" and can easily pass as women in public by wearing make-up, jewelry, women's clothing, feminine hairstyles, and speaking with a feminine voice, and moving in a feminine manner (Bartlett and Vasey, 2006). As Schmidt (2003) explains, drawing on her own field work and that of Poasa (1992) and Besnier (1994), parents identify fa'afafine when they are children because of a propensity for feminine tasks. Families do not equate this early preference for feminine labor with sexual orientation. Upon reaching adulthood, sexual relations with men are seen as a consequence of being fa'afafine rather than as a defining criterion for inclusion in the category. Fa'afafine have traditionally been, and generally still are, identified by their labor preferences not sexual preferences. Furthermore, fa'afafine do not identify as gay because this is interpreted as indicating a straight man having sex with another straight man. Thus, sexual relations between fa'afafine and straight men would be described as homosexual and heterogenderal. This fact means that evidence of kin selection found for fa'afafine pertains primarily to the evolution of transgender expression: any implications for the evolution of homosexuality are incidental.

In Samoa, child-care activity is largely a feminine gender role activity (Vasey and VanderLaan, 2009). When their children are infants, Samoan mothers take primary responsibility for child care. New mothers are surrounded by kinswomen who take care of her other children while she rests and recovers. Infants are often handed over for extended periods of time to the care of an older female relative, usually a sister or a cousin. Some women offer specialized child-care activities, such as massaging infants and small children to cure muscular soreness. Grandmothers often feed children if mothers are away. In addition, aunts and grandmothers often instruct young girls in handicrafts and other work.

Vasey et al. (2007) gave questionnaires to 38 selfidentified fa'afafine and 43 self-identified straight men in Independent Samoa. Vasey et al. (2007) found that the fa'afafine and straight men did not differ in their overall generosity and allocation of financial resources toward kin, nor did they differ in general neediness or financial resources obtained from kin. However, fa'afafine did carry out a suite of activities pertaining to their family's child care more than the straight men did: babysitting for an evening, babysitting on a regular basis, taking care of the children for a week while their parents are away, buying toys for the children, tutoring the children, helping to expose the children to art and music, contributing money for day care, contributing money for the children's medical expenses, and contributing money for the children's education. A follow-up study (Vasey and VanderLaan, 2009) supplied questionnaires to 136 self-identified fa'afafine, 182 self-identified straight men, 40 women without children, and 89 mothers. In this study the fa'afafine had the highest willingness to carry out the suite of child-care activities, higher even than the mothers, the women without children and the straight men in the sample.

Readers who refer back to the papers by Vasey and colleagues may be confused by the terminology used. Vasey describes the child-care activities by the fa'afafine as "avuncular," a word that means uncle-like even though the activities themselves are exactly the same as those used by women while carrying out their child-care responsibilities. The activities might better be described by the word, "materteral" which means aunt-like because the fa'afafine are performing in a feminine work role in accordance with why they identify as fa'afafine to begin with. By focusing on the biological sex of the fa'afafine rather than their gender expression, Vasey is considering them as uncle-like even though their behavior is aunt-like, erasing their gender identity in favor of a sexual identity.

There is a backstory to Vasey's gender identity: erasing language. Vasey subscribes to a controversial typology of transgendered people introduced by Blanchard (1989). By this typology, all transgender women belong to two distinct non-overlapping classes: heterosexual cross-dressing men (CD-trans) and homosexual men (H-trans). Blanchard envisions that CD-trans women are heterosexual men pursuing a cross-dressing sexual fetish to the extreme of having a vagina surgically constructed in them. He envisions that the H-trans women are homosexual men seeking to improve their attractiveness for sex with men. In the Blanchard typology, bisexuals do not exist; they are homosexuals in self-denial. In addition, gender identity does not exist; transsexual claims to identifying with the gender opposite to their sex are delusions.

Research from the Blanchard perspective comes primarily from faculty at three institutions: The Clarke Institute of Psychiatry in Toronto (now absorbed into the Center for Addiction and Mental Health), the psychology department of Northwestern University, and more recently the psychology department in the University of Lethbridge. Vasey is from Lethbridge.

The Blanchard typology ignited 20 years of vitriolic controversy, largely because of its proponent's incendiary animus toward transgender people. (For a history of the disputes, see http://ai.eecs.umich.edu/people/conway/conway. html and http://www.tsroadmap.com/info/bailey-blanchardlawrence.html). The Blanchard typology is increasingly discredited among academics (Moser, 2010; Nuttbrock et al., 2011; see also Smith et al., 2005). Hence, the interpretation favored in this paper is that transgender expression does exist as a primary trait, and not as the derivative of some sexual drive. Therefore, the evidence for kin selection among the Samoan fa’afafine is regarded as pertaining to the evolution of transgender expression, not to the evolution of homosexuality. The sexual orientation of the fa'afafine is taken to be a by-product of the fa'afafine's social expectations, consistent with the ethnographic studies on Samoa.

The case for kin selection favoring the evolution of transgender expression among the fa'afafine has not yet been made quantitatively. Although the contribution of the fa'afafine to child care undoubtedly increases the reproduction from their families, as evidenced by the larger family sizes of families with fa'afafine compared to families without, it is not clear if this effect is large enough to fully compensate for the fertility cost of the homosexuality that the fa'afafine practice.

The generality of a kin selection theory for the evolution of transgender expression as in the fa'afafine is not clear. The Hijra in India, for example, are generally cast out from their extended families and instead join collectives managed by a Hijra guru (Nanda, 1999). On the other hand, transgender people, such as the two-spirited women of some Native American nations do participate to some extent in women's labor roles but also have unique social roles, such as mediating disputes between men and women and acting as shamans (Herdt, 1994; Roscoe, 1991, 1998).

Although the importance of fa'afafine child care has been discussed in the literature with regard to kin selection, reflecting the early formulation originating with Wilson (1975), a contemporary quantitative analysis of the fa'afafine contribution to reproduction might best be framed in terms of family selection, or multilevel selection (Wilson and Wilson, 2007). Indeed, the social roles of third-gender people that go beyond helping in child care, and extend to mediating disputes and to leading religious ceremonies that bind people together, might produce tribes that prosper more than tribes lacking such social glue. Differential success of tribes with and without third-gender people might form the basis for a multilevel selection theory for the evolution of transgender expression. Such transgender expression might include homosexuality as a side effect. The sex in such situations would be homosexual and heterogenderal.

A theory emphasizing the value of helping in child care and thereby increasing family size needs to explain why such care is offered specifically by transgender people. Why could not anyone else provide the help, say other women, or the men: why a transgender woman specifically?

As a possible answer, I first conjecture that the gender role whereby child care is primarily the women's responsibility is an ancient and preexisting condition. Next, suppose an increase in size of the female labor pool is favored through multilevel selection on families, despite the constraint of an underlying 50:50 biological male-to-female sex ratio. In this situation, evolution can add to the female labor pool by tuning the amount and timing of the delivery of prenatal hormones to produce a female identifying individuals from within the male pool. This allows the production of more people carrying out female labor tasks rather than male tasks despite the population biological sex ratio remaining fixed at 50:50. That is, the phenotypic male-to-female sex ratio is free to vary even though the biological sex ratio remains 50:50.

Homosexuality Selectively Neutral

This subsection pertains to theories for the evolution of homosexuality that assume it is costless, a harmless by-product of other activities that are adaptive. A sub-subsection presents a well-known case with Japanese macaques and another sub-subsection presents the population-genetic criterion for a trait to be neutral with respect to natural selection.

Japanese Macaques

This harmless by-product view of homosexuality, first stated most clearly by Futuyma and Risch (1984), has been further developed and applied to the case of female homosexuality in Japanese macaques (Vasey, 1998). After reviewing and dismissing possible functions of homosexuality in female Japanese macaques, Vasey concludes the females carry out homosexuality for its sheer pleasure. He writes, although "sexual pleasure was selected for because it motivates individuals to engage in fertile sex… sexual pleasure is not specific to reproductive sex but can be satisfied by many non-reproductive sexual outlets as well."

All Japanese macaque females participate in what are called female-female consorts. These are short-term relationships (STRs) that last for less than an hour up to four days. During this time, the two females mount each other frequently with genital-genital contact. When not having sex together, they huddle, sleep, and forage together, groom each other, and defend each other from challenges. For the duration of their STR, a pair is monogamous. After a few days though, they re-assort and form new STR's with one another.

Female Japanese macaque back each other up while together in an STR. The lower ranking member of an STR increases in rank temporarily because of her partner's support (Vasey, 1996). This temporary increase in rank ends when the STR dissolves. The mountings are bidirectional and mutually pleasurable, and they show no sign of a dominance or submissiveness within the relationship (Vasey et al., 1998).

According to the theory that homosexuality is selectively neutral, homosexuality does not disappear during evolution because homosexuality is harmless. Female macaques have lots of offspring, and they do participate in heterosexual mating whenever they need some sperm. Homosexuality does not apparently interfere with their reproduction, so how could natural selection remove this harmless behavior?

Thus, by chance, according to the selective neutrality theory, homosexuality has drifted over the course of evolution into prominence in some species, while remaining nearly absent in others. Or, in some species, chance has genetically linked homosexuality to certain important genes and homosexuality has "hitchhiked" into prominence on the coattails of those genes. Homosexuality is viewed as beneath natural selection's radar screen and subject only to the winds of passion.

Do Japanese macaques have lots of free time to hang around? Is every day another day in paradise, an endless party filled with evolutionarily meaningless play? Why should macaques be so lucky, while the rest of us poor sods have to work for a living? Actually, homosexual interaction would seem to occupy far too much time in the lives of female macaques to be evolutionarily incidental. So, is homosexuality plausibly a selectively neutral trait?

Criterion for Selective Neutrality

Evolutionary theory offers a quantitative rule of thumb for whether homosexuality can be a selectively neutral trait. If the strength of natural selection against the trait as measured by *s*, the coefficient of deleteriousness, is less than the reciprocal of the population size, then the trait is neutral; it cannot be touched by natural selection. Conversely, if *s* is greater than the reciprocal of the population size, the trait is deleterious and will tend to be removed by natural selection resulting in a selection/ mutation equilibrium, as previously discussed.

If *s* is less than the reciprocal of the population size, indicating that the gene for homosexuality is neutral, then the strength of genetic drift, the ever-present random fluctuation of gene pool frequencies, exceeds the strength of the natural selection against the gene. That is, if homosexuality is selectively neutral, any small "signal" of natural selection is buried in the ever-present "noise" of the gene pool's random fluctuations.

For example, if the population size of Japanese macaques is 50, the reciprocal of the population size is 1/50, or 0.02. Suppose the average net number of offspring left by non-homosexual females is scaled to 1.0, and the average net number of offspring left by homosexual females is

0.99. Then *s*, the coefficient of deleteriousness, is 0.01. In this case, homosexuality is selectively neutral. However, if the homosexual females have even a little bit fewer offspring than the homosexual females because of wasting time in homosexual mounting, say homosexual females leave 0.95 offspring to every one left by a non-homosexual female, then *s* is 0.05, which is greater than the reciprocal of the population size. In this case, homosexuality would not be neutral and would evolve to be present at low frequency in a mutation/selection equilibrium. Thus, for homosexuality to be evolutionarily neutral, females who do, and who do not, participate in short-term homosexual relationships need to have an almost exactly identical average life-long net reproduction, which seems highly improbable.

Vasey (in comment following Kirkpatrick, 2000) reiterates his belief that human homosexual behavior is a neutral by-product of direct selection for heterosexual sexual pleasure, that homosexuality is expressed solely for sexual gratification. As such, Vasey claims that homosexual behavior has no evolutionary function and simply will not be selected against, presuming it does not interfere with the participants' heterosexual efforts. Vasey allows, however, that homosexual behavior could be co-opted to serve a socio-sexual role, such as alliance formation (an exaptation). As such, Vasey envisions that homosexuality may then come under positive selection because of its beneficial effects on fitness. The problem with this seemingly appealing theory is that the initial condition is improbable. That is, selectively neutral traits do not patiently await, so to speak, to be pressed into duty for some adaptive function. A time-consuming behavior like homosexuality as practiced in the Japanese macaques would almost surely not have been neutral to begin with. Instead, if homosexuality has evolved as an offshoot from heterosexuality, then it will have been advantageous immediately without passing through an intermediate state of selective neutrality awaiting to be adaptively rescued.

To the contrary, homosexuality in Japanese macaques is apparently beneficial now and always has been. Indeed, all females do participate in homosexual STRs. If there is a benefit to homosexuality, the coefficient of deleterious, s, is negative. The reason why homosexuality might be beneficial in Japanese macaques is that the fate of a female who decides not to participate in homosexual STRs would seem bleak because she is likely to be kicked out of the group and left to die soon thereafter. If participating in STRs is necessary for inclusion in female social groups, then those who are not homosexual would be at a selective disadvantage. In this species female same-sex sexuality is what I am calling a social-inclusionary trait (Roughgarden, 2004).

Homosexuality Selectively Advantageous

This subsection pertains to theories for the evolution of homosexuality that assume homosexuality is a positive adaptation for its participants. For these theories, the commonness of homosexuality is no problem whatsoever. Indeed, the problem with these theories is to explain why everyone is not homosexual. Two sub-subsections offer different types of theories for why homosexuality is adaptive.

Homosexuality Promotes Alliances and Partnerships

Two papers in 2000 advance the hypothesis that homosexual behavior is advantageous by promoting bonding in varying circumstances.

Greenberg (1988) classifies homosexual behavior into three types. One is transgenderal exemplified by the fa'afafine, Hijra, and so forth, as previously discussed in "Fertility Benefit of Transgender: Helpers at the Nest". That is what I term homosexual and heterogenderal. Instead, this section focuses on homosexuality that is both homosexual and homogenderal. In this regard, Greenberg distinguishes two types: adult-peer (which he calls egalitarian) and the patron/client (which he calls transgenerational). Adult-peer homosexuality is type most common in contemporary discourse about gay marriage; both partners are nearly the same age, and they belong to the same generation. However, patron/client homosexuality is evidently the most common type of homosexuality cross-culturally and throughout history.

Muscarella (2000) focuses on the value of homosexual behavior in male patron/client relationships which he states, "has been a persistent feature of the human species since recorded history." Continuing, Muscarella (2000) writes, "The long history of institutionalized homosexuality between higher status and lower status males," usually of different ages by five years or more, produces "relationships [that] tend to socialize the youths into the adult male role, nurture and protect the youths and provide the basis for life-long friendships, social alliances and social status… Social status, a reflection of political strength and alliances, appears to have played a large role in the evolutionary history of human male reproductive success."

For women, Muscarella (2000) suggests that homosexuality provides bonds of friendship that lead to mutual assistance in raising children, assuming paternal assistance is absent in primitive societies. Here too, homosexuality is hypothesized to provide higher reproductive success.

These conjectures about how homosexuality evolved feedback to determining the type of environment in which homosexuality develops during infancy. Muscarella (2000) writes, "Homoerotic behavior may be evoked as a normal response to placement in an environment which closely resembles the environment in which it evolved and was adaptive in the evolutionary past."

Kirkpatrick (2000) generalizes the discussion about homosexuality leading to alliances beyond a focus on the patron/client. He writes, "If homosexual behavior also serves non-conceptive functions, such as the maintenance of same-sex alliances (long-term supportive relationships) that aid in resource competition or in cooperative defense, then homosexual behavior will be under positive selection…Homosexual behavior is a survival strategy, not a reproductive strategy."

Kirkpatrick (2000) mentions many examples. I have condensed his account as follows: "Pair-bonds between adult-peer males in many societies of native North America reduced variance in food intake and provided for cooperative defense. Males become companions in hunting, in war, and in fortune and have a right to food and lodging in each other's cabin. Within 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. In precolonial Tahiti and Hawaii, the clients of powerful patrons gained prestige, as did clients in classical Athens and 15th-century Florence. In ancient Crete, men without same-sex sexual partners were at a social disadvantage. Same-sex sexual partners of the Japanese samurai gained both martial training and land. In classical Athens and in Tokugawa Japan, same-sex alliances were thought to be more dangerous to entrenched interests than female-male alliances. And lest one think of homosexual and heterosexual relationships as antagonistic, both female exchange marriage and homosexual behavior integrate with each other in Melanesia to link individuals in complex chains of mutual dependency and obligation. Among the Etoro, a patron's ideal client is his wife's younger brother, effectively linking wife and client in a hetero/homosexual threesome marriage in which one co-spouse is reproductively active."

Tantalizing clues also exist that homosexual behavior becomes expressed more in complex rather than simple societies. Homosexual behavior occurs more often in agricultural than in hunter-gather societies, and more often in larger social groups (Barber, 1998). Homosexual behavior may also be more frequent when political networks rather than independent individuals are empowered, and it may be expressed more in industrial nations after their demographic transition, that is, the shift in a population's demography from high reproduction to high survival following industrialization (Dickemann, 1993).

A difficulty faced by a theory of homosexuality as a form of alliance building is that male-male alliances can be built without using sexuality. This brings me to my own contributions pertaining to the evolution of homosexuality (Roughgarden, 2012a).

Physical Intimacy Promotes Cooperative Coordination

My hypothesis is that it is specifically the physical intimacy in homosexuality that is important, not sex, *per se*. I conjecture that the research focus on the sexual aspect of homosexuality merely reflects our fetishizing of sex and not what is important about homosexuality.

Instead, I hypothesize that genital-genital contact is a special case of physical intimacy that pertains uniquely to mammals who happen to have genitals filled with pleasure sensing neurons and who happen to use their genitals for signaling and social purposes other than the exchange of gametes in heterosexual mating. Indeed, I hypothesize that mutual grooming in mammals, mutual preening in birds, even calling together in chorus, also fulfill a similar function to the physical intimacy of homosexuality.

And what function is that? The reciprocal exchange of pleasure in these behaviors provides coordination to cooperative activities in a way that allows a pair of animals (or people) that have a potential conflict of interest to arrive at a cooperative outcome rather than a competitive outcome.

Darwin (1872) reviewed the facial and bodily expressions of many animals, especially mammals, and frequently mentioned how pleasure is expressed. He writes, "With the lower animals we see the same principle of pleasure derived from contact in association with love. Dogs and cats manifestly take pleasure in rubbing against their masters and mistresses, and in being rubbed or patted by them. Many kinds of monkeys . delight in fondling and being fondled by each other, and by persons to whom they are attached" [31, pp. 215-216]. Darwin also recognized pleasure through song: "We can plainly perceive, with some of the lower animals, that the males employ their voices to please the females, and that they themselves take pleasure in their own vocal utterances" [31, pp. 87-88]. The pleasure associated with physical and vocal intimacy that Darwin describes is the key feature to my concept of teamwork.

I have further hypothesized that the act of cooperation itself is pleasurable. As a human analogy, consider the difference in pleasure between making an "Alley-Oop pass" in basketball compared with making two foul shots, both of which yield the same two points. Of course, every member of a basketball team feels some pleasure when two foul shots are successful, but the pleasure experienced is even greater if the two points are obtained with a beautiful acrobatic pass followed by a teammate's dunk at the basket. This is invariably followed by high-fives all around. A similar point could be made about the pleasure of scoring a goal during regulation play in soccer compared with scoring a goal during sudden death overtime.

Together with colleagues, I have published game-theoretic mathematical models showing how cooperation attained via the reciprocal exchange of pleasure, including homosexuality, leads to cooperative solutions to games that involve conflicts of interest between the parties (Roughgarden et al., 2006; Akçay et al., 2009; Akçay and Roughgarden, 2011; Roughgarden, 2012b).

Finally, I would like to remark on what might explain the polymorphism in sexual orientation: the ratio of gays to straights? Indeed, a problem if homosexuality supplies advantages becomes why is everyone not homosexual, as in bonobos and Japanese macaques. The polymorphism between straights and gays may be maintained by frequency-dependent selection between two alternative strategies of within-sex relations, each of which provides survival or reproductive advantages. Members of the straight morph may build alliances based on a meritocracy and/or the exchange of power, and members of the gay morph may build alliances based on the exchange of pleasure. Either strategy, if common enough, would be subject to increase when rare by the other, leading to a polymorphism.

Furthermore, the conflict likely to occur between these alternative morphs for same-sex relations is possibly the basis of homophobia. Alliances based on the exchange of pleasure may threaten to subvert alliances based on the exchange of socially constructed concepts of merit and power. Same-sex pleasure-based alliances would then be subject to suppression seemingly justified with a disparaging narrative propounded those with the power to define normalcy.

SUMMARY

1. Homosexual behavior occurs naturally in many species of mammals, and also in insects. Among primates, homosexuality is an evolutionary innovation originating when the anthropoid lineage split from the prosimian linage, and it becomes particularly prominent in the complex societies of the old world primates.

2. Many species possess multiple genders: multiple morphs within each sex.

3. Transgender species have been documented, especially in hummingbirds.

4. Homosexual behavior and transgender expression is documented across all present-day human cultures, throughout recorded history, including the Bible and other religious texts, and in Paleolithic drawings and artifacts.

5. A transgender "third sex" exists in many cultures, and it has official status in India and its neighbors.

6. Homosexuality became a Western category of human personal identity in the mid-1800s.

7. Investigators employ many inconsistent definitions of homosexuality.

8. Gay and lesbian people cluster in families.

9. Despite 30 years of research, a gay gene has not been located in the human genome.

10. Despite 30 years of research, the brains of homosexual men have not been shown to resemble the brains of women.

11. The brains of transgender people resemble the brains of the gender they identify with and not with the brains corresponding to their biological sex.

12. The brains of transgender people develop reflecting the timing of sex hormones at different stages during fetal growth.

13. Gender identity may exist in the brain as a "cognitive lens" that controls who to focus on as a developmental "tutor." Transgender identity is the acceptance of a tutor from the opposite sex.

14. Gender identity has developed by the time of birth, and sexual orientation develops later during the first few years of infancy.

15. Homosexuality and transgender are too common to be considered genetic diseases.

16. The fertility cost of male homosexuality is as much as 50% in contemporary Western culture and much less or nonexistent in other cultures.

17. The theory that the fertility cost of male homosexual behavior is offset by a fecundity advantage to the mothers of homosexual children has weak or no supportive evidence.

18. Transgender expression, but not homosexual behavior, might have evolved through kin selection in cultures with a third sex, such as the fa'afafine of Samoa.

19. It is improbable that homosexual behavior is selectively neutral.

20. Homosexual behavior appears to be selectively advantageous because it produces alliances and partnerships.

21. Homosexual behavior may be a special case of various forms of physically intimate behavior that promote cooperation through the reciprocal sharing of pleasure.

22. The homosexual/heterosexual polymorphism may result from frequency-dependent selection between alternative same-sex alliance strategies: alliances based on a socially-constructed meritocracy and alliances based on a mutual exchange of pleasure. Homophobia might be a byproduct of competition between these types of alliances.

CODA

Ten years have passed since this chapter was written for the first edition of this book. I think the landscape of conceptual issues covered in the original chapter remains largely accurate although additional examples of same-sex behavior in animals have accumulated (Monk et al 2019). Also, Monk et al (2019) introduce and defend the hypothesis that indiscriminate mating is a primitive condition followed by derived specialization to same-sex sexuality and between-sex sexuality. A program seeking evolutionary explanations for same-sexuality in animals lives on and by extension also with humans.

I have recently published a deep-dive review contrasting a sexual-selection to a social-selection approach for explaining sexual reproduction in animals (Roughgarden 2026). Two observations from that review seem worth reiterating here, both of which have also been alluded to in the first edition's chapter.

First, any program for evolutionarily explaining homosexuality per se seems destined to fail for the simple reason that the trait is not well defined. In humans homosexuality has variously been defined as genital-genital contact, same-sex love and feelings of identity, all leading to non repeatable and incomparable results. And in animals, two male beetles mounting may be equivalent to two male elephants mounting, but who can to say? Ad hoc definitions of homosexuality can be devised for particular studies, but homosexuality is not well defined across species and contexts and likely never will be.

I think research programs instead should focus on affiliative behaviors in general, regardless of the detailed form the behavior takes, whether mutual grooming, preening, genital touching, or reciprocal calling. Research can then focus on the circumstances where cooperation rather than competition is beneficial and how to coordinate the cooperating individuals with one another and how to distribute their joint fitness earnings. Studies could investigate how the reciprocal exchange of pleasure provides information about each partner's state and willingness to continue cooperating. The behavioral mechanisms for the exchange of pleasure would vary among species. Those having genitals already used for signaling and enervated with ample pleasure neurons could employ genital-genital contact to exchange information, whereas species with advanced auditory capabilities could use duetting and other vocalizations to exchange the information. I think this type of broader research program shows more promise that continuing with studying the evolution of homosexuality, per se.

Second, even posing the question about how homosexuality has evolved brings value-loaded cultural baggage. As noted in the original chapter, historically speaking, homosexuality is a new category of identity, having been coined in Germany in the mid 1800's. Asking about the evolution of homosexuality prior to that would be a meaningless question even in Europe, not to mention other cultures that employ different identity categories and customs for sexuality. Asking science to explain homosexuality enacts a modern Western script for the subjugation of minorities, as though there's something anomalous that needs to be understood. And today's Western culture deploys the artillery of medicine and biotechnology to adjudicate is normal and what is abnormal and diseased, turning science into a political project of oppression. Widening the evolutionary inquiry about same-sex sexuality to the class of all affiliative behaviors involving the reciprocal exchange of pleasure restores the topic to the domain of objective science.

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