Evolution of Homosexuality

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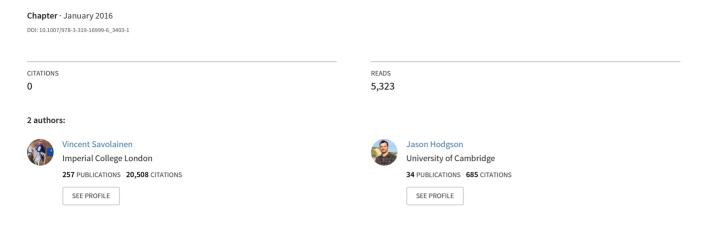
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Evolution of Homosexuality

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Synonyms

Biological exuberance

Definition

Study of transmission of same-sex sexual behavior across animal species and humans.

Introduction

Sexual behavior takes multiple forms across organisms, and although it has evolved for reproduction, it also serves other social purposes. The evolution of sex has also led to sexual dimorphism, meaning that there are morphologically and behaviorally distinct male and female genders. Across species, males usually have sex with females (heterosexuality); however, this is not always the case, and there are numerous possible variations. For example, many animals possess the sexual organs of both genders either simultaneously or at different times of their lives. Earthworms first mature as males and then lay eggs and fertilize those after copulating with another male. Despite both animals having the male gender at the time of copulation, biologists describe such cases as hermaphroditic rather than homosexual. Clownfish start their life as males and develop into females when the group matriarch dies. In this case, biologists refer to them as sequential hermaphrodites rather than transgenders. However, nonreproductive sexual behavior has been observed between members of the same sex (homosexuality, HS) in numerous species including our own. So, is "true" HS common in nature, and why?

Natural History of Homosexuality

In birds and mammals, there are numerous reports of homosexual behavior, which may or may not involve a sexual act, but can include courtship, pair-bonding, and coparenting. These have been observed in geese, flamingos, gulls, oyster-catchers, warblers, dolphins, deer, zebras, giraffes, and others (Bagemihl 1999). At least 93 species of birds engage in HS (MacFarlane et al. 2010). Same-sex mounting is commonly observed in a wide variety of mammals such as gazelles, sheep, and elephants, and this has been attributed to expression of dominance or hormonal malfunction during rut (Bagemihl 1999).

Homosexual sex is particularly developed in primates. Interestingly, HS is more predominant in primate lineages more closely related to

humans than in more distant taxonomic groups such as lemurs. In new-world monkeys (platyrrhines), such as squirrel monkeys, homosexual behavior seems limited to play and dominance interactions. In contrast in apes and old-world monkeys (catarrhines), homosexual sex is common and complex, involving consort bonding, reconciliation, tension regulation, and alliance formation (Vasey 1995). Among apes, pygmy chimpanzees (bonobos) are famous for the large variety of sexual acts that they perform, including genito-genital rubbing, fellatio, and manual masturbation across all genders (De Waal and Lantin 1998). Bonobos are bisexual, and this is thought to contribute to group cohesion (De Waal and Lantin 1998). Common chimpanzees also engage in homosexual sex, for example, with about a third of mountings occurring between males (Bagemihl 1999) (Fig. 1). In mountain gorillas, which live in groups dominated by fewer males than in chimpanzees, sexual behavior between females is widespread (Grueter and Stoinski 2016). Other catarrhine examples of HS include baboons, macaques, and langurs (Bagemihl 1999). However, after bonobos, homosexual behavior is probably most common in humans and has been documented by anthropologists worldwide, across cultures and time periods (Table 1).

In all these examples, bisexuality may be the norm, as those individuals involved in HS often also take part in reproductive sex. However, there are also numerous exceptions, for example, about 15 % of male graylag geese are strictly homosexual (Kotrschal et al. 2006). There is increasing evidence that HS is common in nature; however, scientists and the public at large have only learned about it relatively recently, perhaps because the reporting of such behaviors had been previously censored due to societal and religious taboos.

Is Homosexual Behavior a Darwinian Paradox?

Homosexual behavior has often been considered a "Darwinian paradox." This is because, intuitively, a genetically influenced focus on nonreproductive sex to the detriment of reproductive sex should reduce evolutionary fitness (i.e., reduce an individual's number of descendants), and any such genetic variants should eventually go extinct (Kirkpatrick 2000). However, twin studies indicate that heritability of homosexuality is ca. 30 % in men and up to 60 % in women (Kirk et al. 2000). Note, however, that these values may be inflated, because twin studies generally estimate the broad-sense heritability, which includes several components of genetic variance,

Evolution of Homosexuality, Fig. 1 Several male chimpanzees mounting one another before intergroup encounter, Kibale forest, Uganda (Photo Aaron Sandel)

Evolution of Homosexuality, Table 1 Homosexuality across human cultures (Modified from Kirkpatrick 2000)

Continent	Society	Female or Male?	Juvenile or Adult?	Bisexual?	Frequency
Africa	Libya	M	J, A	Yes	95 %
	Sudan	F, M	J, A	Yes	Common
	Nigeria	F, M	J, A	Unknown	Common
	South Africa	M	A	Yes	Common
Europe	Classical Athens	F, M	J, A	Yes	Common
	Early Roman empire	F, M	J, A	Yes	Common
	Dinaric (Serbia)	F, M	A	Unknown	Unknown
	Florence, 15th century	M	J, A	Yes	>50 %
Americas	Lakota (USA)	M	A	Yes	Unknown
	Mohave (USA)	F, M	A	Yes	Limited
	Nambikwara (Brazil)	M	J	No	Common
	Yanomamo (Venezuela)	M	J	No	>50 %
Oceania	Precolonial Tahiti	M	J, A	Yes	Common
	Arundo (Australia)	F, M	J	No	Common
	Big Nambas (Melanesia)	F, M	J, A	Yes	100 %
	Marind-anim (Melanesia)	M	J, A	Yes	100 %
	Sambia (Melanesia)	M	J, A	Yes	100 %
Asia	China, 700–400 BC	M	A	Yes	Unknown
	China, 1865–1965	F	A	No	Limited
	Japan, 16th, 17th century	F, M	J, A	Yes	>50 %
	Putunukhtu (Pakistan)	M	J, A	Yes	Unknown

as opposed to the narrow-sense heritability, which only includes the statistically additive effects of genes. Nevertheless, the fact that there is some heritability of HS indicates that there is a genetic component underlying such a widespread behavior. Thus, the discrepancy between simple evolutionary expectations and the observed nature and prevalence of HS warrants explanation; but is homosexuality really an evolutionary paradox?

Among variable traits, homosexual behavior stands out, because the fitness consequences of preferring same-sex sexual partners seem obvious since these pairings never result in offspring. Also, widespread cultural taboos that consider HS to be "unnatural" likely draw extra attention to it. However, there are at least two reasons why the seeming paradox of HS might be an illusion. First, the fitness consequences of HS are largely unknown and may be greatly overstated. Second, sexual preference is not a binary trait with clear homosexual and heterosexual states. Rather it is a continually variable quantitative trait, maybe

involving the interactions of many genes (Bailey et al. 1993), and ranging from exclusively homosexual attraction through all degrees of bisexuality to exclusively heterosexual attraction (Sell 1997); for simplification, Kinsey scored sexual behavior from 0 (strictly heterosexual) to 6 (strictly homosexual) (Kinsey 1948). It is not unusual for continuously variable traits to have fitness costs at the phenotype extremes rather than in the middle range (Lande 1976).

HS can only be a paradox if the genetic factors that predispose individuals towards homosexual behavior have real fitness costs. Although there are reasons to doubt whether there are actual fitness costs to homosexuality, quantifying fitness in long-lived natural populations is extraordinarily difficult (Kingsolver et al. 2001). First, in social species nonreproductive sexual behavior is common even in heterosexual pairings. This is especially true in humans, where females remain continuously sexually receptive throughout the nonfertile phases of their cycle, and even while

pregnant (Gangestad and Thornhill 2008). In humans and other primates, nonreproductive sex (including homosexual sex) is thought to have important social implications (De Waal and Lantin 1998; Gangestad and Thornhill 2008; Vasey 1995). Thus, there may also be fitness costs to extreme heterosexuality due to reduced sociality, as well as fitness costs to extreme homosexuality due to lost mating opportunities. If so, some intermediate phenotype may be optimum. Second, there is some evidence that the genetic variants that predispose to HS increase fitness in those who have the genes but not the phenotype. Support for this has been found in genetically identical twins where one is homosexual and the other heterosexual. In such twins, the heterosexual members have a greater number of opposite-sex sexual partners compared to identical twins who are both heterosexual (Zietsch et al. 2008). In this scenario, there is no evolutionary paradox so long as the lost reproductive success of homosexuals with the predisposing genes is balanced by increased reproductive success in heterosexuals with those same genes.

Furthermore, the fact that HS is not entirely heritable also points towards significant amounts of phenotypic variance being nongenetic and due to environmental variation (maybe up to 70 % in men; (Kirk et al. 2000)). Nongenetic variation needs little or no adaptive explanation even if there are fitness costs. This variance in quantitative traits is generally known to be a combination of direct effects of environment on individual phenotypes plus developmental noise, much of which may be practically unavoidable (Lande 1976).

Finally, even if there have been real fitness costs to homosexual behavior, this alone does not make the behavior unique or in particular need of biological explanation. Most traits that vary within humans are heritable and many of these will have fitness differences according to trait expression. For example, stature in humans is highly heritable (90 %) (Macgregor et al. 2006), and taller (but not extremely tall) men have greater reproductive success (Pawlowski et al. 2000). Similarly, physically attractive people have greater reproductive success than unattractive people (Jokela 2009). Yet, neither biologists nor the general public wonder why there are still short, less attractive people. It might be supposed that there is excess focus on HS compared to, say, stature, because the effects on reproductive success are more direct. However, this is not necessarily the case. For example, erectile function/dysfunction is a variable trait with clear reproductive implications. Yet, there has been almost no interest among researchers or the general public in why natural selection has not eliminated erectile dysfunction (Cellerino and Jannini 2005). The long-term maintenance of genetic and phenotypic variation in quantitative traits despite stabilizing selection or fluctuating directional selection has long been recognized (Lande 1976; Lande 2008), and it is likely that the focus on HS as an evolutionary paradox is largely driven by cultural taboos against the behavior, rather than any real unique biological perplexity.

Biological Models of the Prevalence of Homosexual Behavior

The seeming Darwinian paradox of homosexual behavior has led to the development of several biological models to explain its prevalence. Most models fall into two broad categories: genetic and epigenetic models. Genetic models typically explain the persistence of a hypothetical "HS" gene variant (allele) through some indirect evolutionary advantage for that variant. Epigenetic models explain homosexual behavior as a result of heritable changes in gene expression patterns due to chemical modifications that occur to the DNA of developing organisms. These models each make clear predictions; however, there is only limited support for any of them.

Kin altruism selection. This model is based upon William Hamilton's kin selection theory and suggests that homosexuals forego their own reproduction in order to altruistically aid in the rearing or reproductive efforts of relatives (Kirkpatrick 2000). Kin selection theory only

predicts altruistic behavior when the reproductive benefits to the recipient are greater than the product of the cost to the altruist and the degree of relatedness. Because the costs of completely foregoing reproduction are quite high, this model predicts that only individuals of low phenotypic quality with low personal reproductive potential should adopt the strategy. It also predicts that the behavior will be more common in males because of the greater variance in male reproductive success. There is little direct support for the kin selection model. Also, it is not clear why foregoing reproduction to aid relatives would necessitate HS (Kirkpatrick 2000).

Overdominance selection. Overdominance selection proposes that men who are heterozygous for a hypothetical "HS" allele are heterosexual and have increased fitness over homozygotes for the "HS" allele (who are homosexual), as well as over homozygotes for the "non-HS" allele (who are also heterosexual). The same applies to women. In this scenario, the increased fecundity of heterozygotes maintains the "HS" allele in the population at a frequency that is determined by the relative fitness of the three genotypes. With overdominance selection, it is expected that the "HS" gene will be found on a nonsex chromosome (autosome), because it is easier to maintain overdominance polymorphisms at equilibrium on those autosomes rather than sex chromosomes (Gavrilets and Rice 2006). There is currently scant evidence for the overdominance selection hypothesis.

Sexually antagonistic selection. In sexually antagonistic selection, a hypothetical "HS" allele would result in an evolutionary cost when expressed in men (i.e., they would have fewer offspring) but would be counterbalanced by an advantage when expressed in females (i.e., more offspring), or *vice versa* (Gavrilets and Rice 2006). In this scenario, it is hypothesized that an "HS" allele would be either masculinizing or feminizing when expressed in either sex. A masculinizing "HS" allele would increase the fitness of males, but decrease the

fitness of females by causing HS, and a feminizing "HS" allele would do the opposite. Under the sexual antagonistic model, it is expected that genes influencing HS would be found on the X chromosome more often because there are a wider range of relative fitness scenarios under which polymorphism can be maintained compared to the autosomes, and this is one possible way in which this model can be distinguished from overdominant selection (Gavrilets and Rice 2006). Limited evidence in support of the model comes from the finding that markers on the X-chromosome influence male homosexuality in humans (Hamer 1993).

Bisexual advantage. Another model is proposed here for the maintenance of homosexual behavior based on the idea of stabilizing selection or fluctuating directional selection; this new model is called "bisexual advantage." This model extends aspects of homosexual alliance formation discussed above in primates, along with a quantitative genetics approach to trait evolution. Sexuality is a continuously variable and heritable trait that ranges from exclusively homosexual attraction to exclusively heterosexual attraction. Numerous genetic loci would contribute small additive amounts to the overall heritability of this quantitative sexual trait. It is hypothesized that the optimum trait value with respect to reproductive fitness is intermediate and thus in the bisexual range (maybe between Kinsey's 1–3 scores). Individuals with fully homosexual attraction (Kinsey's 6 score) would fail to reproduce and be selected against, while individuals with fully heterosexual attraction (Kinsey's 0 score) would also have fewer offspring. This may be because such individuals are poor at forming social alliances (Kirkpatrick 2000), or it may be for some yet unknown reason. Indeed, such a pattern where both phenotype extremes are disadvantaged is thought to be the most common among quantitative traits and is due to stabilizing selection or fluctuating directional selection (Lande 1976; Lande 2008). The bisexual advantage

model predicts that (i) some degree of bisexual attraction is more common than exclusive homosexual or heterosexual attraction, (ii) sexual attraction is fluid and changes depending upon social context (i.e., the environmental component), (iii) many genetic loci weakly influence sexual attraction, and (iv) there are no genetic loci that strongly influence sexual attraction. The bisexual advantage model is perhaps the most conservative genetic explanation for the persistence of homosexual behavior because sexuality would then follow the pattern of the vast majority of quantitative traits where intermediate phenotypes are favored (Lande 1976). Note that this model is compatible to a degree with the sexually antagonistic model, if (i) possessing one copy of a "HS" allele contributes to some, but not exclusive, homosexual behavior and (ii) this allele goes to fixation in the population (i.e., every individual of the population has a copy of this allele in their genome (Savolainen and Lehmann 2007)).

There is some behavioral as well as genetic support for this bisexual advantage hypothesis. First, good estimates of the frequency of bisexuality do not exist; however, the majority of human and nonhuman animals that participate in homosexual sex also participate in reproductive sex (Kirkpatrick 2000; Vasey 1995). Second, the expression of homosexual behavior is known to be condition-dependent in humans. For example, having spent time in the US Navy or in a British boarding school increases the likelihood of having had homosexual experience (Kirkpatrick 2000). Finally, genomic surveys looking for genes that influence sexual attraction have failed to find any loci that strongly predict homosexuality (Sanders et al. 2014). Instead, genome-wide scans have identified relatively few loci associated with HS, each with relatively small effect, leaving the majority of the heritability of homosexuality unexplained. This is the expected pattern if most of the heritability is contributed by loci with too small of an effect to be detected in genome-wide scans (Yang et al. 2010), suggesting that sexuality is a quantitative trait, and the majority of loci influencing sexuality are yet to be discovered.

Paternal and maternal effects. In an epigenetic model of HS, so-called epigenetic marks (changes in DNA packaging such as DNA methylation or histone tail modifications) influence sensitivity to androgen hormones by the developing genitals and brains, and therefore also influence gender preference and identity (Rice et al. 2012). In animals such as humans, male and female sex chromosomes (XY and XX, respectively) have characteristic epigenetic marks that canalize development accordingly. When discordant epigenetic marks are passed trans-generation, a child may develop a cellular mosaic whereby genital development will match the appropriate sex chromosome but brain development for sexual preference will be canalized towards the opposite gender by the epigenetic marks. Put simply, a mother may pass onto her son discordant epigenetic marks causing the development of female sexual preference and resulting in male HS. The same logic applies to the father of a lesbian daughter. This epigenetic model of HS has advantages over genetic models: It is compatible with the relatively low concordance of HS in identical male twins (30 %; (Kirk et al. 2000)) and with the fact that genomic association studies have failed to find strong genetic markers for HS (Rice et al. 2012; Sanders et al. 2014). The model has also clear testable predictions, although the practicalities of such studies would be impaired by requirements to work with postmortem or fresh human stem cells (Rice et al. 2013). Nevertheless, those predictions include: (i) there are XX- and XY-specific epigenetic marks in the stem cells of developing heterosexuals; (ii) there are XX- and XY-discordant epigenetic marks in the stem cells of developing homosexuals; and (iii) some of these discordant epigenetic marks are trans-generationally inherited and therefore will be shared with higher frequencies by identical twins when at least one is HS, but not necessarily the other one (Rice et al. 2013).

Conclusion

Homosexual behavior is common throughout the animal world and has often been considered an evolutionary paradox. The existence of the supposed paradox is likely a confluence of the assumption that those who engage in HS fail to reproduce, coupled with cultural disapproval of homosexual behavior. Some of this confusion may also stem from the fact that most researchers have considered sexuality to be a binary trait with either homosexual or heterosexual trait states. If sexual preference is a continuous trait influenced by many different genes of small effect, or some epigenetic marks canalizing a "mosaic" development, then the persistence of homosexual behavior is not particularly surprising. In fact, it may be the case that some degree of bisexuality is actually an evolutionary optimum phenotype in many species, including humans.

Cross-References

▶ Ancient Homosexuality
▶ Female Homosexuality and Bi-Sexuality
▶ Genetic Component of Homosexuality
▶ Homosexual Receptivity
▶ Homosexuality
▶ Homosexuality Paradox
▶ Hormonal Component of Homosexuality
▶ Lesser Known Theories of Homosexuality
▶ Non-Western Homosexuality
▶ Prenatal Influence on Homosexuality

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