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Comparative Evidence

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Synonyms

Phylogenetic study of homosexual behavior

Definition

Cross-species comparative analysis of same-sex sexual behavior.

Introduction

If sex is the engine that drives Darwinian evolution, why would a variety of animal taxa invest in nonconceptive sexual behaviors that do not directly contribute to reproduction? This section aims to address this evolutionary conundrum by focusing on the cross-species comparative analysis of homosexual behavior, in an attempt to shed further light upon the origins and evolution of human homosexuality.

Phylogeny of Homosexual Behavior

Despite its apparent lack of fitness benefits, same-sex sexual activity is broadly distributed across the animal kingdom. Descriptive reviews indicate that hundreds of species of mammals, birds, reptiles, amphibians, fishes, insects, spiders, mollusks, nematodes, and other invertebrates engage in extremely diverse homosexual behavioral patterns, including courtship displays, manual-genital, oral-genital, and genital-genital stimulations, and mounting interactions, with pelvic thrusting and even intromission between same-sex partners (Bagemihl 1999). However, the cross-species distribution and expression of same-sex sexual activity is uneven. First, the frequent, prevalent, and enduring occurrence of homosexual behavior in some species contrasts with its seeming absence, or at least obvious scarcity, in others. Second, some species exhibit only female-female or only male-male sexual behavior, whereas other species exhibit both. Third, several proximate and ultimate hypotheses have been proposed to account for the diverse manifestations of same-sex sexual interactions in different species, such as the lack of opposite-sex sexual partners, the pursuit of immediate sexual reward, the practice by immature individuals for heterosexual sex, or the achievement of social goals (e.g., dominance demonstrations, alliance formation, or tension regulation; Poiani 2010; Sommer and Vasey 2006). Only systematic comparative research aiming to quantitatively examine the factors that

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contribute to the emergence and expression of homosexual behavior among animal taxa can provide some solutions to this evolutionary puzzle (Sommer and Vasey 2006; Vasey 2007).

One of the most powerful methodological tools to explore the origins and evolution of biological features is the phylogenetic comparative approach (Martins 1996). By superimposing the phenotypic trait of interest over a robust phylogenetic tree based on molecular data and encompassing many related species, researchers make parsimonious historical inferences about how this trait originated and changed in a step-by-step manner over time. Phylogenetic analyses are particularly useful to reconstruct scenarios for the evolutionary history of behavioral traits, which do not leave any direct fossil traces. They can be used to decide whether similar behavioral patterns are due to common ancestry or the result of independent adaptations to similar environmental pressures (Martins 1996). Such a comparative approach should be relevant to the evolution of homosexual behavior, because it can distinguish adaptive from nonadaptive traits by indicating which ones have predated, accompanied, or followed the modification of some of their structural and functional attributes. Moreover, just like play behavior (cf. Pellis and Iwaniuk 2000), the lack of functional constraints, and thus the flexibility and versatility of same-sex sexual activity, makes it a good candidate for phylogenetic studies. In principle, reconstructing scenarios for the evolution of homosexual behavior requires well-established and often composite phylogenies that are not directly based on sexual characteristics.

Yet, comparative investigations of the evolution of homosexual behavior are extremely rare and limited to birds and mammals. A phylogenetic analysis of the frequency and form of same-sex courtship and mounting behaviors in 80 avian species showed strong associations between such homosexual interactions and both social mating system and developmental mode, but with marked differences between males and females (MacFarlane et al. 2007). More specifically, female-female sexual behavior mainly occurred in socially monogamous species that produce precocial offspring at hatching, whereas the frequency of male-male sexual behavior significantly increased with the degree of polygamy of the species, regardless of the developmental state at hatching. Another study conducted on 93 avian species showed a consistent relationship between sex-specific relative parental care and the frequency of both male and female homosexual behavior: When females provide less care than males, female-female sexual behavior is more frequent, and when males provide less parental investment than females, male-male sexual behavior is more frequent (MacFarlane et al. 2010). Poiani (2010) tackled the daunting task to examine the effect of social, life history, and ecological factors in the frequency of same-sex mounting across 72 bird species and 107 mammal species (including humans). In birds, he found that homosexual mounting was negatively associated with the size of the social unit and positively associated with adult male-biased sex ratio, increased sociality, and increased level of dominance. In mammals, he found that homosexual mounting was negatively associated with social unit size and relatedness between partners and positively associated with polygamy. In both birds and mammals, he found that same-sex mounting was positively associated with social sexual segregation (i.e., spatial distancing between the sexes for part or even most of the year). Comparative tests showed that Poaini's (2010) *Synthetic Reproductive Skew Model of Homosexuality* fit better the avian than the mammalian data set, even though homosexual mounting is more prevalent in mammals than in birds. This suggests that same-sex mounting is more complex in mammals than in birds. The relatively higher prevalence of homosexual behavior in mammals is likely to be associated with a greater degree of sociality, polygamy, and cooperative breeding in this taxon (Poiani 2010). A recent phylogenetic study focusing on nonhuman primates showed that the frequency of same-sex genital contact was positively associated with social complexity, and this effect was stronger in males than in females (Fernandes et al. under revision).

Phylogenetic research on homosexual behavior is still hampered by several types of limitations

that need to be overcome. The first type is both observational and theoretical: The validity of the comparative method rests on the ability of researchers to correctly detect, identify, and record this behavior in their study species when it occurs. This is not trivial because nonadaptive behaviors, such as same-sex sexual activity, are by definition devoid of major fitness consequences and thus tend to be dismissed as idiosyncratic, anecdotal, and not worth of research interest. As a result, the occurrence of homosexual behavior may be underreported in cross-species comparative reviews. The second type of limitation is logical: Absence of evidence is not evidence of absence. Because it is comparatively easier to prove the occurrence of a behavior than its absence, phylogenies of homosexual behavior are likely to contain false negatives (e.g., due to differential research effort when comparing species). The third type of limitation is methodological: The phylogenetic analytical tool kit is broad, and there is no universal consensus on whether the dependent variable (i.e., homosexual behavior) should be dichotomized (i.e., presence/absence) or classified on a frequency scale, divided by sex (i.e., female-female versus male-male sexual behavior) or not, and superimposed on a specific cladogram to control for the evolutionary relatedness across species, as well as how phylogenetically independent contrasts should be calculated (cf. Martins 1996). All these decisions may affect the results of the interspecific comparison and their interpretations. Finally, it is important to remind the reader that these cross-species comparative analyses are based on homosexual *behaviors*, and there is currently very little to no evidence that homosexual *behavior* in nonhuman animals reflects homosexual *orientation*. Rather, it likely reflects animals' potential for bisexual behavior, which exists, for example, in several primate species (Dixson 2012). When considering how results obtained from animal research on homosexual behavior may apply to the evolution of human sexuality, one should keep in mind that although reproductive behaviors in humans and animals likely share some homologous features, nonconceptive sexual behaviors among different species may be analogous. For instance, exclusive same-sex sexual orientation has not been documented in any free-ranging nonhuman primate species. As such, the study of homosexual *behavior* in nonhuman primates may inform us about the evolution of homosexual *behavior* in humans but may shed only limited light as to why exclusive homosexuality evolved.

Conclusion

Overall, cross-species comparative studies suggest that same-sex sexuality is not an evolutionarily uniform phenomenon. Instead, it appears that multiple analogous forms of homosexual behavior have evolved, underlain by different developmental pathways, sociodemographic settings, motivational processes, functional outcomes, and phylogenetic histories both within and between species (Vasey 2007). Therefore, evolutionary explanations of homosexual behavior are contingent on the implementation and full integration of two complementary levels of analysis, namely the phylogenetic (i.e., historical) and functional (i.e., adaptive) perspectives (Vasey 2007). Some forms of same-sex sexual activity may have no adaptive value whatsoever, while others may be nonsexual acts that are executed to serve social functions. As such, we should not expect any one evolutionary explanation for same-sex sexual behavior to account for the diversity of this phenomenon. Indeed, attempts to make unifying interspecies generalizations about the evolution of homosexual behavior may be misguided and misleading.

Cross-References

- ▶ Byproduct Hypotheses
- ▶ Cross-Cultural Studies

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