

Homosexual Behavior in Simians: A Review of the Prevailing Hypotheses

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Abstract

This paper reviews two hypotheses that attempt to explain the function of homosexual behavior (HB) in simians: the dominance hypothesis and the tension regulation hypothesis. The dominance hypothesis is one in which the socially dominant individual is expected to assume the mounter position over the mountee, presumably reaffirming the hierarchy. In this case, HB belongs in the same function category as threats, supplanting, and groveling. The tension regulation hypothesis postulates that conventionally stressful events will precede HB, thereby preventing health decline and facilitating group unity. The available evidence suggests that neither the function nor frequency of HB is uniform across simian species.

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Sexuality has long been a phenomenon that makes good sense in evolutionary biology. Propagating genes is a must if certain traits are to survive, so an affinity for sex is preferred for maximal offspring production. Two other details pertinent to an individual's fitness is their choice of mate and the time at which they mate with that individual. Mating with a female not in ovulation is a bad choice for a male; not only is he expending energy in such an endeavor but also failing to create offspring. Surely, after studying an evolutionary biology textbook, this male would be a total goon to pursue that female!

For decades, primatologists have observed something interesting: some primate species mate all the time, not only when it directly increases their gene propagation. This is non-reproductive sex. Non-reproductive sex does not directly contribute to an animal's reproductive success; instead, it has an indirect mechanism which leads to an ultimate outcome of reproductive success. What might be termed the proximate benefit to the animal could be one of several things: reconciliation, stress regulation, hierarchical reaffirmation, et cetera. Whatever the proximate benefits may be, the commonality of non-reproductive sex in the primate order suggests that it is adaptive or at least a byproduct of a highly adaptive trait.

To make matters more complicated, some animals engage in homosexual behavior to which history has responded adversely. The 18th century biologist George Edwards referred to these behaviors as "abnormalities", reasoning that the chickens he observed were abnormalized because they were caged (Sommer & Vasey, 2006). Even upon observing this behavior in natural settings, biologists deemed it pathological. The same behavior in cattle was a negative side effect of artificial selection and did not result in infant cattle that could be raised for milk, skins, or meat (Sommer & Vasey, 2006). The frequency at which homosexual behavior was observed in

nature cast these propositions into doubt (Fox, 2001; Geist, 1974, as cited in Roselli et al., 2011; Goodall, 1988, as cited in Fox, 2001). Human homosexuality was met with similar opposition, and the Diagnostic and Statistical Manual of Mental Disorders (DSM) included it as a disorder (Drescher, 2015). According to Drescher (2015), Robert Spitzer, a subcommittee chair who investigated sexual deviations and the characteristics of mental disorders, reported that homosexuality was not a mental disorder because homosexual men and women were not generally distressed nor socially impaired. This, as well as other oppositions to homosexuality as a disorder, led to its removal from DSM II in 1973 (Drescher, 2015).

If homosexual behavior, which from now on will be referred to as HB, cannot be described as pathological, then what is its function? Could HB be considered a beneficial type of non-reproductive sex like its non-reproductive heterosexual counterpart? HB has always been a paradox in evolutionary biology, but many hypotheses have been put forward with hopes of finally putting the case to rest. Although the adaptive value of HB may depend on the species of simian, and the frequency at which HB occurs varies between species, this paper will not be focusing on a single species but many instead.

Homosexual behavior is conservative wording relative to homosexuality; this is purposeful because behavior must be designated as something separate from homosexuality, which is an exclusive predilection for the same sex (Vasey & Duckworth, 2006). Observations find that non-human primates who engage in homosexual sex also engage in heterosexual sex (Muscarella, 2000; Vasey & Duckworth, 2006). This is distinct from human homosexual behavior, which can occur exclusively or not. The reader should note that the evidence presented in this paper is largely inconclusive.

Incest Avoidance

Social behavior is expected to be indiscriminate, between kin and not. Vasey and Duckworth (2006), in observing Japanese macaques (*Macaca fuscata*), found that females do not participate in same-sex consortships with kin. Similarly, Chapais et al. (1997) found that Japanese macaques do not engage in HB with their close kin, but aunts and nieces do. A threshold is proposed to exist because aunts and nieces do not seem to consider each other kin (Chapais et al., 1997). In studying HB in mountain gorillas (*Gorilla gorilla beringei*), Grueter and Stoinski (2016) also found that kin did not participate in homosexual sex, apart from an aunt and niece pair. This incest avoidance plays no functional role between same-sex partners, so why do same-sex kin avoid each other? Some investigators, such as Chapais and Mignault (1991), have found that brother-sister pairs and mother-son pairs engage in sex much more often than same-sex kin, postulating that males are more likely to break incest avoidance than females. Many other investigators confirm the rarity of sex between same-sex kin (Chapais & Mignault, 1991, as cited in Vasey & Duckworth, 2006; Wolfe, 1984, as cited in Vasey & Duckworth, 2006). Nonetheless, heterosexual sex between kin is still largely avoided. Since HB between kin is similarly avoided, the mechanism by which incest is avoided may extend to homosexual incest despite its non-functionality; in other words, homosexual incest avoidance is a byproduct of the selection for non-incestuous heterosexual individuals. If this is not true, then a functionality must exist. This seems implausible, and there is currently no research on a potential functionality for homosexual incest avoidance.

Since incest avoidance in same-sex kin is widely practiced, HB is not a social behavior that is fully generalizable. Huddling, co-sleeping, and grooming, however, are among the social behaviors that occur indiscriminately, between kin and not (Vasey & Duckworth, 2006). Since

kin tend to have similar ranks, could HB be a display of dominance? This would explain why kin do not engage in HB. There are two types of rank reversal: interfamilial and intrafamilial (Seyfarth & Cheney, 2007). As shown by Bergman et al. (2003) in a playback experiment, baboons react more strongly to audio of interfamilial rank reversals than to intrafamilial rank reversals. In this way, it seems that interfamilial rank reversals are considered significant events. This is presumably because a relatively high-ranking individual is being displaced by a low-ranking individual, whereas the ranks within families are similar enough that intrafamilial displacement is nothing over which to make a fuss. In other words, dominating (in this case, mounting) individuals outside of your own family is more substantial than dominating family members. And with that, we will continue to the dominance section of this paper.

The Dominance Hypothesis

Dominance is thought to be expressed by the mounter over the mountee. Grueter and Stoinski (2016) find this potentially problematic because it works under the assumption that the mounter plays the dominant role and that this designation could be open to interpretation. For this section of the paper, that the mounter position is dominant to the mountee position will be assumed because it pervades the literature.

In the dominance hypothesis, HB acts to reaffirm the dominance hierarchy. If this hypothesis is correct, HB would join pant-grunting (Goodall, 1986, as cited in Luef & Pika, 2019), groveling, threatening, supplanting, and other submissive behaviors as a ritual of hierarchical reaffirmation. Grueter & Stoinski (2016), in observing HB in female mountain gorillas, recorded the frequency at which socially dominant females mounted subordinate

females. One of two groups of gorillas supported the dominance hypothesis, but this is attributed to one individual who consistently assumed the mounter position (Grueter & Stoinski, 2016). The other group did not support the hypothesis (Grueter & Stoinski, 2016). Interestingly, the silverback often interfered, apparently upset by the HB (Grueter & Stoinski, 2016). For this reason, copulations often took place in secluded areas, presumably to preclude the silverback's interference (Grueter & Stoinski, 2016). Grueter and Stoinski (2016) evaluate the silverback's odd behavior as a byproduct of a truly valuable behavior: the interference of heterosexual sex, which works to decrease the relative sexual fitness of other males and increase paternity certainty.

Sandel and Reddy (2021) found that male-male sociosexual behavior in chimpanzees (*Pan troglodytes*) could not be explained by dominance relations. In studying Japanese macaques, Vasey et al. (1998, as cited in Vasey & Duckworth, 2006) noticed that consort partners would not assume the same sexual positions; instead, the mounter became the mountee and vice versa, and this alternation occurred throughout the duration of the transient consortship. This was true even for differentially ranked consort partners. Bonobos (*Pan paniscus*) also tend to alternate positions when several sexual contacts are made between two females of similar rank, but in differentially ranked contacts the socially dominant female assumes the mounter position significantly more often (Sommer & Vasey, 2006). Fox (2001), in reporting some of the first sightings of HB in Sumatran orangutans (*Pongo abelii*) in a wild setting, observed that the larger males would assume the mounter position over the smaller males. According to Fox (2001), in orangutans, dominance generally takes the form of larger size relative to the subordinate. These sightings would, therefore, provide evidence for the dominance hypothesis. The evidence is scant, however, owing to the small sample size of two total interactions (Fox,

2001). Though, of course, we would not expect these interactions at all considering orangutans' solitary nature.

Returning to bonobos, their HB is not primarily associated with dominance displays but rather tension regulation and reconciliation (Sommer & Vasey, 2006). These two hypotheses seem to contrast in one fundamental way; one is to reaffirm power, and the other is an effort to seek common ground. For humans, dominance is mal-intentioned, and this leads us to think the two hypotheses irreconcilable among bonobos. According to Sommer & Vasey (2006), female bonobos only assume the mounter position when dominant over their partner; otherwise, like the Japanese macaques, they take turns. In the form of HB, bonobos may reaffirm the dominance hierarchy, but they also simultaneously seem to regulate stress. This aside functions to mention that hypotheses for HB are not necessarily mutually exclusive, even within the same species. With that in mind, we will now discuss tension regulation and reconciliation.

The Tension Regulation and Reconciliation Hypothesis

The tension regulation hypothesis does not exist only for bonobos but also chimpanzees, Hanuman langurs (*Semnopithecus entellus*), and capuchins (*Cebinae*). To find evidence for this hypothesis, we presume that agonistic interactions must precede HB (Grueter & Stoinski, 2016). Sandel and Reddy (2021) report that male chimpanzees participate in HB during stressful events, such as “subgroup reunions and during territorial behavior.” Though HB in chimpanzees does occur, it is much less frequent than in bonobos. Hohmann and Fruth (2000, as cited in Grueter & Stoinski, 2016) found that bonobos engaged in homosexual sex even in absence of any notable agonistic interactions. Though, when agonistic interactions occurred more frequently,

homosexual sex also occurred more frequently (Hohmann & Fruth, 2000, as cited in Grueter & Stoinski, 2016). As stated by Clay and de Waal (2015), this evidence for the tension regulation hypothesis demands further study.

According to Kuroda (1984, as cited in Clay & de Waal, 2015), bonobos that offer sex to food possessors are more likely to be successful in obtaining food than bonobos that do not offer sex. In this way, conflict over food can be reduced and individuals share food that would not otherwise be shared. Chimpanzees also offer sex in return for food (de Waal, 1990, as cited in Manson et al., 1997; Goodall, 1986, as cited in Manson et al., 1997). White-faced capuchin monkeys (*Cebus imitator*), however, do not offer sex in exchange for food (de Waal, 1993, as cited in Manson et al., 1997), though they do participate in food sharing.

Discussion and Future Research

The genus *Pan*, which is composed of chimpanzees and bonobos, has been the focus of the tension regulation section. The dominance section briefly reviewed the most current literature on multiple species of primate, each having weak evidence at best. Strict incest avoidance between same-sex kin, the topic of the first section, is indicative of a purely sexual component to HB; this is especially true for Japanese macaques and potentially mountain gorillas (Grueter & Stoinski, 2016; Vasey & Duckworth, 2006). Though we may be ignorant of an all-encompassing function of HB, one cannot help but wonder whether the function varies across the primate order (Muscarella, 2000); if HB is itself adaptive, that is. Some investigators believe HB to be a byproduct of heterosexual proclivity rather than a product of natural selection in and of itself. Others believe it is adaptive and not a byproduct. It would not be surprising to find proponents of

the byproduct hypothesis who are only aware of HB among species for whom there is little evidence of survival or reproductive benefit. Most are aware of bonobos, about whom there has been much study. With a species like the bonobos in mind, it is much easier to adopt the hypothesis that HB is not a byproduct.

In this paper, the dominance and tension regulation hypotheses were reviewed based on much of the available literature on HB. The incest avoidance section preceded these sections to inform the reader of the ways in which HB is unique among other sociosexual behaviors and to potentially aid the reader in formulating their own hypothesis on this paradox of evolutionary biology. There are many other hypotheses that have not been mentioned thus far. Here are a few prominent ones: 1) The coalition/alliance formation hypothesis (Manson et al., 1997; Vasey, 1996, as cited in Sommer & Vasey, 2006), 2) The paternity confusion hypothesis (Hrdy, 1981, as cited in Manson et al., 1997), and 3) The training-for-heterosexual-sex hypothesis (Chevalier-Skolnikoff, 1976; Grueter & Stoinski, 2016; Sommer & Vasey, 2006). It should be noted that the coalition/alliance formation hypothesis was popular in explaining HB in Rhesus macaques in 2006 (*Macaca mulatta*) (Sommer & Vasey, 2006).

Further investigation is warranted, especially since HB does not appear to have one universal function (Muscarella, 2000). The simians discussed in this paper are all polygamous, so it may be worthwhile to observe HB in monogamous species in which one might expect pair bonding to take place between same-sex individuals. In this case, HB would be rather exclusionary and could potentially illuminate human homosexuality, which is currently shrouded in mystery. The neglected prosimians may shed light on this issue, especially since monogamy is more common among these species. In terms of acquiring more knowledge on non-human primate HB, plenty of studies on simians are yet to be performed.

References

- Bergman, T.J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science* 302, 1234–1236.
<https://www.science.org/doi/10.1126/science.1087513>
- Chapais, B., Gauthier, C., Prud'homme, J., & Vasey, P.L. (1997). Relatedness threshold for nepotism in Japanese macaques. *Animal Behaviour*, 53:533–48.
<https://doi.org/10.1006/anbe.1996.0365>
- Chapais, B., & Mignault, C. (1991), Homosexual incest avoidance among females in captive Japanese macaques. *American Journal of Primatology*, 23: 171-183. <https://doi.org/10.1002/ajp.1350230304>
- Chevalier-Skolnikoff, S. (1976) Homosexual behavior in a laboratory group of stump-tail monkeys (*Macaca arctoides*): Forms, contexts, and possible social functions. *Archives of Sexual Behavior* 5, 511–527. <https://doi.org/10.1007/BF01541216>
- Clay, Z., & de Waal, F. B. (2015). Sex and strife: post-conflict sexual contacts in bonobos, *Behaviour*, 152(3-4), 313-334. <https://doi.org/10.1163/1568539X-00003155>
- Drescher, J. (2015). Out of DSM: Depathologizing Homosexuality. *Behavioral sciences (Basel, Switzerland)*, 5(4), 565–575. <https://doi.org/10.3390/bs5040565>
- Fox, E.A. (2001), Homosexual behavior in wild Sumatran orangutans (*Pongo pygmaeus abelii*). *American Journal of Primatology*, 55: 177-181. <https://doi.org/10.1002/ajp.1051>

- Grueter, C. C., & Stoinski, T. S. (2016). Homosexual Behavior in Female Mountain Gorillas: Reflection of Dominance, Affiliation, Reconciliation or Arousal?. *PloS one*, 11(5), e0154185. <https://doi.org/10.1371/journal.pone.0154185>
- Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female bonobos *Animal Behaviour*, 60. <https://doi.org/10.1006/anbe.2000.1451>
- Hrdy, S.B. (1981). *The Woman That Never Evolved*.
<https://books.google.com/books?hl=en&lr=&id=pICPOwf3lMsC&oi=fnd&pg=PR11&ots=GV1Ohc60rN&sig=2pCU9N3q858UdOo0yhJUVIU05e8#v=onepage&q&f=false>
- Kuroda, S. (1984). Interaction over Food among Pygmy Chimpanzees. In: Susman, R.L. (eds) *The Pygmy Chimpanzee*. The Pygmy Chimpanzee. Springer, Boston, MA.
https://doi.org/10.1007/978-1-4757-0082-4_12
- Luef, E.M., & Pika, S. (2019). Social relationships and greetings in wild chimpanzees (*Pan troglodytes*): use of signal combinations. *Primates* **60**, 507–515.
<https://doi.org/10.1007/s10329-019-00758-5>
- Manson, J.H., Perry, S., & Parish, A.R. (1997). Nonconceptive Sexual Behavior in Bonobos and Capuchins. *International Journal of Primatology* **18**, 767–786.
<https://doi.org/10.1023/A:1026395829818>
- Muscarella, F. (2000) The Evolution of Homoerotic Behavior in Humans, *Journal of Homosexuality*, 40:1, 51-77. https://doi.org/10.1300/J082v40n01_03

- Roselli, C. E., Reddy, R. C., & Kaufman, K. R. (2011). The development of male-oriented behavior in rams. *Frontiers in neuroendocrinology*, 32(2), 164–169.
<https://doi.org/10.1016/j.yfrne.2010.12.007>
- Sandel, A. A., & Reddy, R. B. (2021). Sociosexual behaviour in wild chimpanzees occurs in variable contexts and is frequent between same-sex partners, *Behaviour*, 158(3-4), 249-276. doi: <https://doi.org/10.1163/1568539X-bja10062>
- Seyfarth, R.M., & Cheney, D.L. (2008). Primate social knowledge and the origins of language. *Mind & Society* 7, 129–142. <https://doi.org/10.1007/s11299-007-0038-2>
- Sommer, V., & Vasey, P. L. (2006). Homosexual behaviour in animals.
https://books.google.com/books?hl=en&lr=&id=KXM3F59y1jkC&oi=fnd&pg=PP16&dq=history%2Bof%2Bhomosexual%2Bbehavior%2Bin%2Bprimates%2Bpeer%2Breview&ots=WJXMZqgu0T&sig=xX4wVN6m4QAjFyJF_AUVvl48n7U#v=onepage&q&f=false
- Vasey, P.L. (1996). Interventions and alliance formation between female Japanese macaques, *Macaca fuscata*, during homosexual consortships. *Animal Behaviour*, 52:3, 539-551.
<https://doi.org/10.1006/anbe.1996.0196>
- Vasey, P. L., Chapais, B., & Gauthier, C. (1998). Mounting interactions between female Japanese macaques: Testing the influence of dominance and aggression. *Ethology*, 104, 387–398. <https://doi.org/10.1111/j.1439-0310.1998.tb00077.x>
- Vasey, P.L., & Duckworth, N. (2006). Sexual Reward via Vulvar, Perineal, and Anal Stimulation: A Proximate Mechanism for Female Homosexual Mounting in Japanese

Macaques. *Archives of Sexual Behavior* **35**, 523–532. <https://doi.org/10.1007/s10508-006-9111-x>

Vasey, P.L. (2007). Function and Phylogeny: The Evolution of Same-Sex Sexual Behavior in Primates. *Journal of Psychology & Human Sexuality*, 18:2-3, 215-244, https://doi.org/10.1300/J056v18n02_07

Wolfe, L. D. (1984). Japanese macaque female sexual behavior: A comparison of Arashiyama East and West. *Female primates: Studies by women primatologists*.