

Female Homosexual Behavior in Japanese Macaques

Homosexual behavior occurs in several animal species for various reasons. Often the homosexual behavior is sociosexual in that it appears sexual outwardly, but in fact serves an adaptive social goal. In the Japanese macaque (*Macaca fuscata*), however, female homosexual behavior does not seem to have an adaptive social purpose, but rather is a behavior primarily sexual in motivation. In some populations of macaque, females will court, mount, and compete for female partners. Most females engage in both heterosexual and homosexual activity over the course of their life, each mating season, and sometimes a single day. Female Japanese macaques appear to be bisexual in preference, preferring certain same-sex partners to certain opposite-sex partners as well as certain opposite-sex partners to certain same-sex partners.

In Japanese Macaques, female homosexual behavior occurs within the context of “temporary but exclusive” consortships, lasting from an hour to over a week. During a consortship, females solicit their partners for sex on average every couple of minutes, with mounting occurring slightly more frequently on average than every two minutes (Vasey 2002). Both mounters and mountees solicit mounting behavior. Mountees perform hindquarter or back presentations. In hindquarter presentations, the potential mountee stands on all fours, orienting her perineum towards the potential mounter. In back presentations, she sits with her back inclined and oriented towards the potential mounter. Hands-on-hindquarter solicitations are performed by potential mounters, who grasp or place both hands on the hindquarters of the potential mountee. This behavior is similar to male mount attempts, which the female can refuse by leaving or not assuming the proper mount position (Soltis, Thomsen, and Takanaka, 2001). In heterosexual behavior, mounting occurs in the pattern of an ejaculatory mount preceded by a series of non-ejaculatory mounts (Soltis *et al*, 1997).

Mounting, usually a male-specific behavior, is expressed by females in a variety of ways, including double foot-clasp mounts, sitting mounts, standing mounts, reclining mounts. Each of these can be performed with or without pelvic thrusts. In double foot-clasp mounts, the mounter grasps above the mountee's ankles with her feet and has her hands on the mountee's back, so that the mounter's groin region is in contact with the mounter's perineum. The double foot-clasp mount is also the normal mount for males mounting females (Wolfe 1978). In sitting mounts, the mounter sits on the mountee's back, so that her perineum is in contact with the lower back of the mountee. In standing mounts, the mounter stands behind the mountee with her knees slightly bent and grasps the mountee's lower back with her hands; her groin region is in contact with the mountee's perineum. In reclining mounts, the mounter lays ventrally on the mountee's back, grasping fur on the mountee's upper back with her hands and the mountee's lower legs with her feet. "Females frequently engage in prolonged and directed clitoral stimulation during same-sex mounting either by rubbing their clitorises against the back of the mountee or by masturbating with their tails while mounting" (Vasey and Pfaus, 2005).

With eight types of mounting, female Japanese macaques exhibit a much greater variety of mount postures than males. "Some of the most common types of mount postures employed by females were never exhibited by males. Females performed fewer pelvic thrusts per mount than males, but they executed more pelvic movements per mount, as well as, greater variety and complexity of movement. In addition, the qualitative style of pelvic mounting that females employed differed, in general, from that of males" (Vasey, Foroud *et al*, 2006). This difference suggests that females engaging in homosexual mounting want to maximize genital stimulation, resulting in different mount types from males due to different architecture of genitals.

Homosexual consortships by two females could be interrupted by a male with interest in one of the females as a sexual partner. In this situation the other female and the male are said to be in intersexual competition. The male intrudes by approaching and making sexual solicitations to the focus of competition as well as being aggressive towards the female competitor. Responses of the females to this behavior include ignoring the male until he leaves, moving away from the male, separating and rejoining later to continue the consortship, or ending the consortship. The challenged female could also respond with a counterchallenge, aggression directed at the intruding male and approaches and solicitations directed at the other female (Vasey, 2004). After the intersexual competition ended, the female who was the focus of the competition would either choose the female competitor, the male competitor, or neither. In 120 intrusions observed, 92.5% of the time the female chooses the female competitor. (Vasey, 2002)

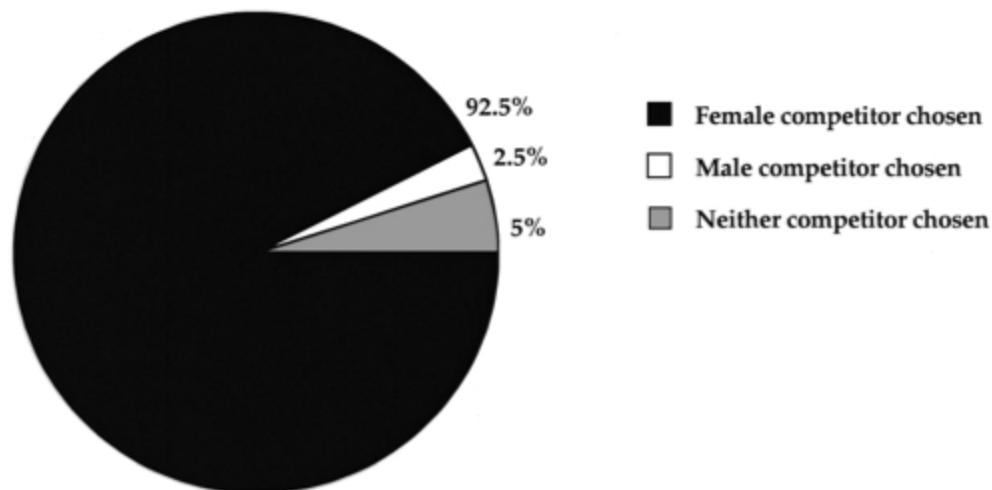


Figure 1. Choice of competitors by foci of competition following intersexual competition interactions.

In some species, female-female mounting behavior serves an adaptive social function, as part of a breeding strategy, for example. However, in Japanese macaques it appears that homosexual behavior is a sexual behavior, rather than a sociosexual one.

Whether these interactions more closely represent nonsexual female interaction or sexual male-female interaction provides a clue to the nature of this behavior. Hypotheses as to the function of this behavior can also be tested. Some potential adaptive social functions of homosexual consortships between females include attracting male mates, impeding reproduction by same-sex competitors, forming alliances inside or outside the mating season, communicating about dominance relationships, obtaining alloparental care, reducing social tension associated with incipient aggression, practicing for heterosexual sexual activity (i.e., female–male mounting), or reconciling following conflicts (Vasey and Pfaus, 2005).

Homosexual consortships seem to match much more closely the characteristics of male-female consortships than nonsexual female-female social interactions, such as grooming, co-sleeping, huddling, and interventions. For example, like heterosexual behavior, homosexual behavior is never observed outside of the fall-winter mating season of Japanese macaques. When a female engages in homosexual behavior, her face and perineum reddens, indicating increased sexual receptivity. Female homosexual behavior occurs in temporary but exclusive sexual pairings. Both partners solicit sex from each other, in a manner that appears identical to heterosexual solicitations. Also, mountees do not struggle against the mounter, but facilitate mounts by clasping the mounter and gazing into her eyes, a pattern that occurs in many heterosexual mounts (Vasey 2002).

The homosexual consortships have much in common with heterosexual mating, but also contrast with nonhomosexual female-female interaction. Females avoid homosexual contact with close kin; consortships are never seen between mothers and daughters, sisters, and grandmothers and granddaughters. “This pattern could not be explained either in terms of kin not being simultaneously in estrus, kin avoiding affiliative interactions in general, or

non-kin utilizing the tension-reducing effect of estrus to affiliate exclusively with each other” (Chapais and Mignault, 1991). Close kin such as mothers and daughters, however, frequently engage in social behaviors such as grooming, etc., with each other.

Interestingly, aunts and nieces do engage in homosexual interactions, suggesting that they do not recognize each other as kin, at least for the purpose of sexual interactions (Chapais, Gauthier *et al*, 1997)

While in a homosexual consortship, female macaques are very likely to intervene in a conflict on behalf of their partner. Outside of these consortships, it is rare for these same females to support each other. Additionally, within consortships there is a dramatic increase in the occurrence of interventions in which the target of aggression ranks higher than the macaque on whose behalf her partner is intervening. Again, this rarely happens outside the context of homosexual consortships. Nonkin females will intervene if the target of aggression ranks lower than both the supporter and recipient of support, but not otherwise. A third disparity between homosexual female-female interaction and social female-female interaction is seen in grooming. In a consortship, dominant partners groom the subordinate partners significantly more often than the other way around. Outside of consortships, grooming is generally directed up the hierarchy among female macaques. Finally, while in consortships, females are almost exclusively in proximity with their nonkin partners. Outside of consortships, female Japanese macaques spend most of their time with close kin. Taken together, these differences show that homosexual consortships do not match the patterns of normal female social behavior in Japanese macaques. They are characterized by rank reversals, particularly for dominant partners, as seen in Figure 2 (Vasey, 1996).

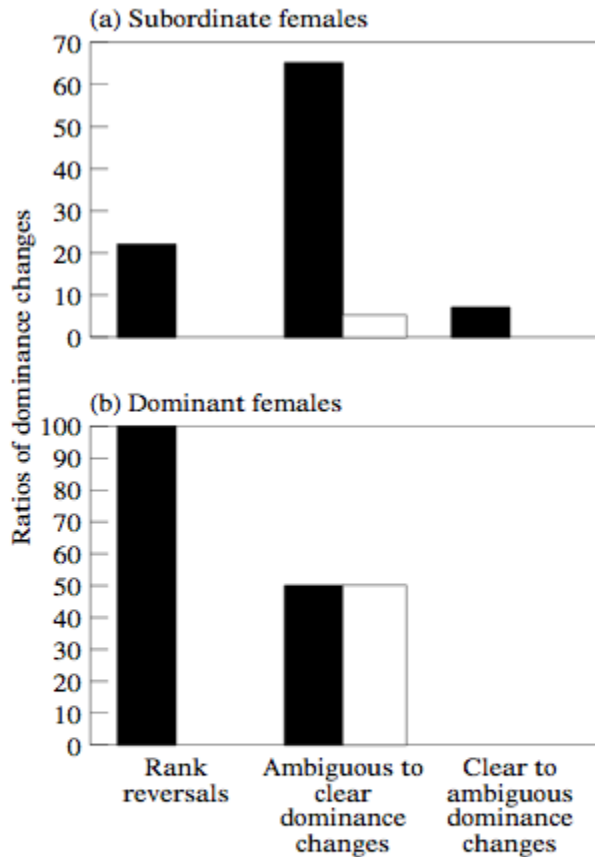


Figure 2. Ratios of dominance changes during the consortship period. For each particular type of dominance change, ratios were calculated as increases or decreases in dominance divided by the total number of opportunities for dominance change. ■: dominance increases; □: dominance decreases.

Though female macaques in a homosexual consortship will intervene for each other in conflicts, a female will not intervene for her partner's offspring in a conflict. In fact, females will even intervene against the partner's offspring in a conflict. Female macaques also do not groom their partner's young, even when they are in close range. This behavior suggests that females are not motivated to enter in consortships to acquire alloparental care.

Another proposal is that female homosexual behavior functions to attract male sexual partners. This is contradicted by the tendency of

consorting females to separate themselves from the rest of the group. If males do not know this behavior is happening, it cannot serve to attract them. Female consortships also often happen after conception, when acquiring a male mate would serve no reproductive purpose. And perhaps most convincingly, when females are interrupted by a male, they will ignore or even threaten him (Vasey 2002).

There is also the possibility that female homosexual behavior could be used to form alliances between macaques. If this were the case, high-ranking consort partners should be preferred, as they are more valuable allies. Research shows an "absence of preference for

high-ranking consort partners, coupled with the bi-directional flow of most affiliation within consortships[, suggesting] that choice of same-sex partners was principally based on mutual sexual attraction and not on their potential utility as allies” (Vasey 1996).

Consortships do promote the formation of alliances between the partners— it is seen that partners are more likely to intervene in conflicts for each other than otherwise— but it seems this is not the express purpose of engaging in homosexual behavior.

Female homosexual behavior might also serve to communicate about rank and reduce social tension. If this were true, the rank of two partners should be demonstrated in the roles they take in the mounting. Additionally, same-sex mounting should occur more often when there is an incidence of aggression, serving the purpose of reducing threat of escalation. This is not the case. Dominant and subordinate partners both take turns mounting, and being mounted. Even when each different mount type is analyzed separately, neither partner mounts significantly more often. Also, dominant partners do not perform hands-on-hindquarter solicitations more often than subordinate partners, nor do subordinate partners perform hindquarter or back presentations significantly more than dominant partners do. As to the question of regulating social tension, less than 1% of all mounts, solicitations, and presentations occurred within one minute of an aggressive interaction between consort partners (Vasey 2002).

Another explanation for homosexual behavior is that it occurs simply for a lack of opposite-sex partners. Opposite sex partners might be scarce, entirely absent, or uninterested in sexual activity, leaving females to turn to homosexual interactions. To test this, an experiment was done in which the majority of males were removed from a group of macaques and observational data was collected. With fewer males, female homosexual interactions did increase significantly. However, it does not appear this was because they

lacked male mates. The remaining male frequently solicited the females for sex, and they would often ignore him and engage in same-sex interactions instead. However, the majority of these same females would sometimes engage in heterosexual consortships with the male at some point in the study, indicating that they found him an acceptable mate. This evidence suggests female macaques do not engage in homosexual behavior merely because there are no acceptable males present (Vasey 2002).

It appears that female Japanese macaques engage in homosexual behavior for sexual reasons rather than sociosexual motivations. That the behavior is sexually motivated is supported by the diversity of mount types observed, while the lack of support for any of the adaptive social goals commonly seen behind homosexual behavior in other species suggests that in Japanese macaques, female homosexual interactions are not sociosexual behavior. Additionally, female macaques sometimes prefer same-sex partners to opposite-sex partners, as shown in the results of intersexual competition and experimenting with skewed sex ratios.

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