

# The Biogeography and Evolution of Female Homosexual Behavior in Japanese Macaques

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**Abstract** In certain Japanese macaque (*Macaca fuscata*) populations, females routinely engage in same-sex courtship, mounting, and consortship activity. Drawing on behavioral, biogeographic, and genetic research, we suggest that female homosexual behavior may be associated with genetically distinct free-ranging populations of Japanese macaques. In addition, we briefly discuss the implications of this research for the evolution of female homosexual behavior in this species.

**Keywords** Female homosexual behavior · Japanese macaques · Biogeography · Haplotypes

Female Japanese macaque (*Macaca fuscata*), in certain populations, are unusual in that, in addition to engaging in heterosexual behavior, they routinely engage in same-sex courtship and series mounting (with pelvic thrusting) during temporary, but exclusive relationships termed “consortships.” Females compete with males for same-sex sexual partners and will often choose same-sex sexual partners even when given the simultaneous choice of a sexually motivated male alternative (Vasey, 1998). These behaviors do not appear to serve any sociosexual function including: attracting male mates, alliance formation, dominance demonstration, alloparental care acquisition, reconciliation, practice for

heterosexual copulation, and inter-individual tension reduction (reviewed in Vasey, 2006).

Several lines of evidence indicate that female-female mounting, courtship, and consortship activity in Japanese macaques is sexually motivated. First, these interactions mirror male-female sexual behavior in many aspects of their expression. For example, the courtship behavior that females exhibit during homosexual consortships is virtually indistinguishable from that which occurs during heterosexual consortships (Vasey, Rains, VanderLaan, Duckworth, & Kovacovsky, 2008). Similarly, female-female mounting across the ovarian cycle parallels the pattern found for male-female mounting (O’Neill, Fedigan, & Ziegler, 2004). In addition, females exercise incest avoidance with close female kin (Chapais, Gauthier, Prud’homme, & Vasey, 1997) despite the fact that these same kin dyads engage in various forms of social affiliation together, such as grooming (Baxter & Fedigan, 1979). Finally, during most same-sex mounts (78.3%), female mounters engage in vulvar, perineal, and anal stimulation (Vasey & Duckworth, 2006).

This distinctive pattern of female-female consortship activity has been reported in three free-ranging Japanese macaque populations, which are located in the central region of the island of Honshu (Jigokudani: Enomoto, 1974; Mino-o: Perloe, 1989; Arashiyama: Wolfe, 1984). Japanese macaques range across the entire island of Honshu. As such, evidence from free-ranging populations indicates that female homosexual consortship activity is confined to a restricted geographic region within Japanese macaque habitat. This raises the possibility that the unique pattern of female-female consortship activity described above may be associated with genetically distinct free-ranging Japanese macaque populations.

Recent mitochondrial DNA (mtDNA) research on Japanese macaques indicates genetic differentiation into five

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haplogroups all of which occur on the island of Honshu (Kawamoto et al., 2007). The three free-ranging populations in which female homosexual behavior has been observed fall within a single haplogroup (A1), which is exclusive to Honshu. Each of these free-ranging populations is characterized by separate haplotypes (e.g., locations: 36 Yamanouchi, haplotype JN15; 87 Arashiyama, haplotype JN21; 93 Mino-o, haplotype JN35; Kawamoto et al., 2007), of which there are 27 within the A1 haplogroup. Although limited, information on captive Japanese macaque colonies derived from additional areas of Honshu, and in which female homosexual behavior has been observed, corroborates the suggestion that this behavior is exclusively associated with the A1 haplogroup on the island Honshu (e.g., Wakasa-B colony [Primate Research Institute, Inuyama, Japan], location 96 Wakasa, A1 haplotype JN36, Kawamoto et al., 2007; Vasey & Reinhart, 2009). This information strengthens the inference that the distinctive pattern of female homosexual behavior observed in free-ranging Japanese macaque populations may indeed be associated with genetically distinct Japanese macaque populations on the island of Honshu.

Marked geographical variations and concentrations of particular haplogroups are thought to reflect the effects of genetic drift, particularly population bottlenecks and founder events. Japanese macaques are genetically closest to the eastern rhesus macaque (*M. mulatta*; Hoelzer & Melnick, 1996). Research suggests that in the Middle Pleistocene a small subgroup of eastern rhesus macaques migrated eastward from Korea to Japan (Marmi, Bertranpetit, Terradas, Takenaka, & Domingo-Roura, 2004) along a landbridge that resulted from the glacial sea levels being 130–150 m lower than at present (Millien-Parra & Jaeger, 1999). On the basis of palaeogeographic evidence and the propinquity of Japanese macaque genotypes, Marmi et al. (2004) suggested that the small founder population of eastern rhesus macaques dispersed quickly over the Japanese archipelago resulting in an initially homogeneous set of mtDNA genotypes.

These homogeneous genotypes then evolved independently during the late Pleistocene/Holocene in reduced and discrete local populations (Marmi et al., 2004). In light of their habitat requirements (Azuma, 1985), low-lying coastal glacial refugia with temperate vegetation likely facilitated the establishment of genetically distinct Japanese macaque populations. In support of this suggestion, we note that some present-day haplogroups straddle the waterways between islands (Kawamoto et al., 2007), lending weight to the conclusion that genetic divergence began in glacial refugia when sea levels were low, rather than from the geographic isolation of islands. Furthermore, we note that the core area of the A1 haplogroup is located in the central western region of Honshu, a location that is associated with glacial refugia (Tsukada, 1982; Kawamoto et al., 2007). Notably, this region coincides with specific vegetation (e.g. Japanese beech [*Fagus crenata*];

Tomaru et al., 1997) and mammalian fauna (e.g. Japanese sika deer [*Cervus nippon*]; Nagata et al., 1999), which Kawamoto et al. (2007) attribute to local selection pressures within a coastal glacial refugium on the western side of Honshu.

The distinctive pattern of female homosexual behavior observed in some Japanese macaque groups (i.e., sexually, not sociosexually, motivated same-sex series mounting with thrusting, courtship and consortships, along with inter-sexual mate competition and facultative same-sex sexual partner preference) may have evolved in populations living in the core A1 haplogroup area of central western Honshu (e.g., locations: 87 Arashiyama and 93 Mino-o; Kawamoto et al., 2007) once they became geographically isolated in glacial refugia. Females that were behaviorally capable of this distinctive type of homosexual behavior may have then spread from the core A1 haplogroup area following deglaciation and subsequently established populations in higher elevation, inland regions of Honshu (>800 m above sea level (asl), and in some places up to 3000 m asl; e.g., location: 36 Yamanouchi). Terrain and postglacial climate zonation during the late Pleistocene/Holocene may have subsequently facilitated further inter-group differences in the expression of female homosexual behavior through geographic isolation.

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