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SHORT COMMUNICATION

Pre- and Postconflict Interactions Between Female Japanese Macaques During Homosexual Consortships

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In this paper, I examine whether homosexual behavior in female Japanese macaques functions to reconcile conflicts following the outbreak of aggression. Contrary to the predictions of the reconciliation hypothesis, homosexual interactions between female Japanese macaques did not peak during postconflict periods, as compared to matched control periods preceding the conflicts. In fact, aggressive interactions appeared to inhibit, rather than facilitate, the expression of homosexual behavior among subordinate consort partners. Alternative proximate and ultimate explanations for female homosexual behavior in Japanese macaques are presented.

The functional significance of homosexual behavior in animals, if any, remains the object of debate (Bagemihl, 1999; Vasey, 1995). At an evolutionary level, such behavior has traditionally been interpreted as sociosexual (Wickler, 1967). Within ethological circles, sociosexual behaviors are commonly defined as behaviors that are sexual in terms of their outward form, but enacted to facilitate some type of adaptive social goal or breeding strategy. Contemporary animal behaviorists rarely ascribe sexual motivation to sociosexual interactions. Nevertheless, sexual motivation and social function are not mutually exclusive. Same-sex sexual behavior can be sexually motivated, or occur in a sexual context, and still serve some social function (Wickler, 1967). For example, female rhesus macaques (*Macaca mulatta*) engage in series mounting during close sexual associations called consortships, and researchers believe these interactions are sociosexual in character, namely, they function to facilitate alliance formation among the participants (Fairbanks et al., 1977; Huynen, 1997; Kapasalis & Johnson, 1999). Although Wickler (1967) never explicitly stated it as such, the concept of sociosexual behavior was significant because it suggested a possible adaptive function for what was clearly a nonconceptive sexual act.

Numerous sociosexual functions have been advanced to account for the evolution of homosexual interactions in animals (reviewed in Bagemihl, 1999; Vasey, 1995), among them the notion that same-sex sexual behavior acts as a mechanism to reestablish social bonds following the outbreak of aggression. In bonobos (*Pan paniscus*), for example, genital-genital contact between females increases significantly following agonistic conflicts (including those unrelated to food), compared to preconflict control periods (de Waal, 1987; Hohmann & Fruth,

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2000). Researchers have interpreted this distinct temporal pattern as evidence that female-female sexual activity in bonobos mediates reconciliation (de Waal, 1987; Hohmann & Fruth, 2000), even though the behavior also appears to have a sexual component (de Waal, 1997).

Same-sex sexual contact may function to reconcile conflicts in a number of other primate species as well. Dixson (1977) has argued that female-female mounting in crested black macaques (*M. nigra*) reduces the likelihood of further aggression in a postconflict context. Female-female mounting in pig-tailed macaques (*M. nemestrina*) may mediate reconciliation because, as Oi (1991) reports, it occurs most frequently in postconflict situations.

In this paper, I examine whether homosexual behavior in female Japanese macaques functions to reconcile conflicts following the outbreak of aggression. Japanese macaques represent excellent models for the type of analysis I propose to do here, because females, in certain captive (e.g., Université de Montréal colony: Chapais & Mignault, 1990; Chapais et al., 1997; Vasey, 1996; 1998, 2002 a; Vasey & Gautier, 2000; Vasey et al., 1998; Rome Zoo: Corradino, 1990; Lundardini, 1989; Calgary Zoo: Rendall & Taylor, 1991) and free-ranging populations (Jigokudani: Enomoto, 1974; Oregon troop: Eaton, 1978; Arashiyama-West, Texas: Fedigan & Gouzoules, 1978; Wolfe, 1984; Gouzoules & Goy, 1983; Arashiyama Japan: Takahata, 1982; Wolfe, 1984; Mino-o: Perloe, 1989) routinely engage in homosexual behavior over the course of their life spans. This behavior takes place during consortships—close sexual associations that are temporary, but exclusive. During same-sex consortships, females solicit each other to mount, and to be mounted, using vocalizations and a variety of postural and facial gestures. Single mounts between females are rarely observed. Instead, multiple or series mounting between consort partners is the norm. During mounts, mounters often thrust against mountees who, in turn, commonly reach back to grasp the mounter and gaze intently into her eyes.

In conducting this functional analysis of female homosexual behavior in Japanese macaques, I examined the patterns of same-sex courtship and mounting before and after aggressive interactions between female consort partners. The reconciliation hypothesis predicts that the frequency with which homosexual behaviors are manifested should be very context-specific. Namely, although homosexual behavior may occur outside of a postconflict period, it should be exhibited more frequently following an aggressive incident, as compared to a matched control period preceding the conflict (Veenema, 2000). For example, genital-genital rubbing between female bonobos appears to serve a reconciliatory function within a postconflict context, but females also engage in these types of interactions outside of postconflict situations. They do so when attempting to form close associations with females in groups into which they are transferring (Furuichi, 1989; Idani, 1991) and during periods of social tension associated with food competition and sharing (de Waal, 1987; Furuichi, 1989; Kano, 1980; Kuroda, 1984; Thompson-Handler, 1989; White & Thompson-Handler, 1989). As such, although female Japanese macaques may engage in sexually motivated, series mounting and courtship outside of postconflict contexts, the reconciliation hypothesis predicts that the frequency of these behaviors should peak during postconflict interactions relative to preconflict control periods.

Method

Subjects and Study Site

The study group totalled 37 individuals (18 adult females, ages 3.5-23 years; 5 adult males, ages 4.5-9.5 years; 7 immature females and 7 immature males) housed at the Université de Montréal's Laboratory of Behavioral Primatology (established 1992) near St-Hyacinthe, Québec, Canada. The group was comprised of three unrelated matrilineal lines. The founding members of the study group originated from the Arashiyama West colony of Japanese macaques that were translocated from Arashiyama, Japan, to southern Texas in 1972 (Fedigan, 1991). The study group's age, sex, and matrilineal composition were typical for this species as observed under free-ranging conditions (Yamagiwa & Hill, 1998).

The monkeys lived in five indoor rooms (25 X 15.5 X 3.6 m) and two outdoor enclosures (17 X 16 X 4 m). The rooms and enclosures were furnished with swinging and climbing devices. Animals were fed daily with a mixture of grains, monkey chow, fruit, and vegetables that was distributed in deep wood-chip litter covering the indoor floors. Water was available at will.

Data Collection

All observations were recorded on paper in 30-min time blocks. Observations took place from dawn until dusk (approximately 07:00-16:00 h). I collected 129 h of focal animal data on female homosexual consortships between 17 November 1993 and 13 February 1994, excluding 25-29 December 1993. I collected focal data for both consort partners simultaneously because they were invariably interacting together. When two homosexual consortships occurred simultaneously, I observed the one for which I had the least data.

Definitions

Homosexual consortships occurred when two females engaged in series-mounting (three or more mounts within a 10-min period). These consortships were deemed to have terminated if the two female partners were not in proximity (separated by a distance of more than 1 m) and exhibited no mounting for 10 min. *Sexual solicitations* served to prompt mounting and included pushing, grabbing, head bobbing, screaming, presenting the hindquarters or inclined back, placing one's hands on the hindquarters of another, lip quivering, intense gazing, and body spasms in various combinations.

Aggressive behaviors included open-mouth stare threats, smacking the ground, grunt vocalizations, lunging, chasing, hitting, grabbing, fur pulling, and biting that occurred either singly or in various combinations.

Dominance relationships were determined by the direction of a combination of submissive behavior patterns (displacements, fear grimaces, rapid flights, piercing screams, defensive hunching). Submission had to be unidirectional between two individuals for the recipient of submissive signals to be considered dominant.

Data Analysis

Data were compared across pre- and postconflict periods using the Wilcoxon matched-pairs signed ranks test (Siegel & Castellan, 1988). The *preconflict period* was defined as the 10-min period prior to an aggressive interaction between female consort partners. The postconflict period was defined as the 10-min period following an aggressive interaction between female consort partners.

Average solicitation rates and *average mount rates* were calculated by dividing the number of solicitations or mounts performed by a female by the number of aggressive interactions that female engaged in with her consort partner during a given pre- or postconflict period.

All statistical tests are two tailed. *T* values refer to the smaller of the positive and negative rank sums T_+ and T_- . *T* values are presented in place of *Z* values when sample size is less than 14 (Siegel & Castellan, 1988). Sample size and compositions varied depending on whether subjects performed the particular behaviors during the particular periods under analysis.

Results

Sexual Activity

During the 1993-1994 mating season, two adult females did not engage in sexual activity. All of the others ($N = 16$) were observed to perform sexual solicitations and 15 of these engaged in series mounting during consortships. Focal animal data were obtained for every female that engaged in homosexual consortships, except for one elderly female (age 23) whose consortships were brief and infrequent. Focal data were collected on 21 different homosexual consortships. Focal females ranged in age from 5 to 23. There was no relationship between a female's age and the number of same-sex mounts she performed (Spearman rank correlation, $N = 14$, $r_s = 0.21$, $p = 0.48$).

Dyadic Aggression

A total of 47 aggressive interactions were observed between female consort partners. These aggressive interactions occurred during nine homosexual consortships (Mean \pm SE = 5.22 ± 0.86 ; range: 1-19). The majority (92%) of aggressive interactions involved the dominant female aggressing her subordinate partner. Only one subordinate consort partner, B2, was seen to aggress her dominant counterpart A ($N = 4$ aggressive interactions). None of the aggressive interactions observed among female consort partners occurred over access to food.

Pre- versus Postconflict Interactions

The average rate at which dominant female consort partners performed sexual solicitations did not differ significantly ($T = 5$, $N = 7$, $p = 0.13$) between the preconflict (2.6 ± 0.45) and postconflict (1.7 ± 0.81) periods. Likewise, the average rate at which dominant female consort partners mounted their subordinate counterparts did not differ significantly ($T = 3.5$, $N = 7$, $p = 0.08$) between the preconflict (3.01 ± 0.66) and postconflict periods (1.62 ± 0.68 ; Table 1).

In contrast, the average rate at which subordinate female consort partners performed sexual solicitations was significantly higher ($T = 1$, $N = 7$, $p = 0.03$) during the preconflict (4.04 ± 0.91) compared to the postconflict period (1.42 ± 0.71). Similarly, the average rate at which subordinate female consort partners mounted their dominant counterparts was significantly higher ($T = 0$, $N = 7$, $p = 0.03$) during the preconflict period (2.63 ± 0.43) compared to the postconflict period (1.25 ± 0.62 ; Table 2).

Discussion

Research on a number of primate species, particularly bonobos, indicates that homosexual behavior may function to mediate reconciliation following the outbreak of aggression (de Waal, 1987; Dixson, 1977; Hohmann & Fruth, 2000). In this paper, I examined the value of the reconciliation hypothesis to account for

Table 1

Rate of Sexual Solicitations and Mounts Performed by Dominant Consort Partners During the Pre- and Postconflict Periods.

Consort Pair	Number of Conflicts	Solicitation Rate		Number of Conflicts	Mounting Rate	
		Preconflict	Postconflict		Preconflict	Postconflict
A-B5	1	2	0	1	1	2
A-B2	5	3.17	1.08	4	5	3.25
A3-B2	1	1.67	2	1	1	0
A3-B21	3	1	0	1	2	0
A31-A2	6	3	2	4	5	1.5
A31-B3	1	2.83	0.83	--	--	--
A2-B9	12	4.6	6.2	5	4.2	4.6
B7-C	--	--	--	1	3	0
Mean:	4.14	2.16	1.73	2.43	3.03	1.62
SEM:	1.64	0.46	0.87	0.74	0.71	0.74

Note. Consort pairs are listed in descending order of dominance rank.

Table 2

Rate of Sexual Solicitations and Mounts Performed by Subordinate Consort Partners During the Pre- and Postconflict Periods.

Consort Pair	Number of Conflicts	Solicitation Rate		Number of Conflicts	Mounting Rate	
		Preconflict	Postconflict		Preconflict	Postconflict
A-B2	4	4.25	5.25	4	4.25	4.25
A3-B3	--	--	--	1	3	1
A3-B2	1	2	0	1	2	0
A3-B21	4	2	0.25	4	2.25	0.75
A31-A2	4	4.75	1.25	1	1	0
A31-B3	1	3	1	--	--	--
A2-B9	4	3.29	2.21	8	3.88	2.75
B7-C	1	9	0	1	2	0
Mean:	2.71	4.04	1.28	2.86	2.63	1.25
SEM:	0.65	0.99	0.78	1.09	0.47	0.67

Note. Consort pairs are listed in descending order of dominance rank.

the expression of two dimensions of female homosexual behavior in Japanese macaques, courtship and mounting. Contrary to the predictions of the reconciliation hypothesis, homosexual interactions did not cluster during postconflict periods relative to matched control preconflict periods. Dominant consort partners were as likely to engage in homosexual behavior before an aggressive interaction as after. Subordinate consort partners, on the other hand, were more likely to perform same-sex sexual solicitations and mounts before an aggressive interaction than after. This suggests that aggressive interactions inhibited, rather than facilitated, the expression of homosexual behavior among subordinate consort partners.

In sum, the principle predictions of the reconciliation hypothesis were not supported by this study. I conclude that female homosexual behavior in my study population did not function as adaptation for reconciliation following the outbreak of aggression. These results dovetail nicely with those reported by Vasey et al. (1998) who found that, more often than not, female Japanese macaque consort partners failed to mount or solicit mounts from each other within 1 min of an aggressive interaction. Moreover, they found that in those instances when homosexual mounting did take place within 1 min of an aggressive interaction between consort partners, it often provoked further aggression, rather than reduced it.

Why then do female Japanese macaques engage in homosexual behavior? Previous research indicates that female Japanese macaques, in certain populations, do not use homosexual behavior to impede reproduction by same-sex competitors (Gouzoules & Goy, 1983; Vasey, 1995), form alliances, foster social relationships outside consortships (Vasey, 1996), communicate about dominance relationships (Vasey et al. 1998), or obtain alloparental care (Vasey, 1998). If female homosexual activity in some populations of Japanese macaques is not functional, as the data suggest, then how might we account for this phenomenon?

I have argued previously, that female Japanese macaques engage in homosexual behavior because, in doing so, they obtain immediate sexual reward. Females frequently engage in prolonged and directed clitoral stimulation during same-sex mounting as evidenced by the mount postures they employ and the movements they execute during pelvic thrusts (Vasey et al., 2003). They routinely rub their clitorises against the back of the mountee, or masturbate with their tails during mounting. Of course, my attempt to account for homosexual behavior between female Japanese macaques in terms of proximate sexual reward does not address why the behavior evolved in the first place. In this regard, I have suggested, based on the available evidence, that female homosexual behavior is not an adaptation, rather, it is the *functionless by-product of an adaptation* (Vasey, 1996, 1998, 2002 a, b; Vasey et al., 1998). Functionless by-products of adaptations are characteristics that do not evolve to solve adaptive problems, and thus, do not have a function and are not products of natural selection. Instead, functionless by-products evolve in association with particular adaptations because they happened to be coupled with those adaptations (Buss et al., 1998). Functionless by-products of adaptations cannot be explained in adaptive terms and instead, evolutionary history must be invoked to account for their existence. Explanations that invoke evolutionary history focus on reconstructing the evolutionary steps that lead to a current behavior. This involves understanding the origin of the behavior and how it changed over time (Alcock, 1989).

I have speculated previously that female homosexual behavior as expressed in some populations of Japanese macaques is a functionless by-product of an adaptation, namely, female-male mounting (Vasey, 2002 b). Female-male mounting is routinely observed in certain populations of this species (Gouzoules & Goy, 1983) and, I have suggested that, it is an adaptation that females employ to prompt sexually disinterested or sluggish males to copulate with them (Vasey, 2002 b). In line with this hypothesis is the observation that proceptive females routinely perform mount prompting and mounts in response to movement by desired males away from their immediate vicinity (Vasey, pers. obs., 2002). Once females evolved the capacity to mount, and the capacity to derive sexual gratification during mounts through clitoral stimulation, they could do so just as easily by mounting females, as males. Indeed, at that point in the species' evolution, some same-sex sexual partners might be preferred over certain opposite-sex alternatives (see Vasey, 1998, 2002 a, b; Vasey & Gauthier, 2000) simply because females derive more sexual gratification during interactions with them. Within the context of this evolutionary scenario, female-male mounting can be explained in terms of function and evolutionary history, but female-female mounting can only be explained in terms of the latter.

According to this hypothetical evolutionary history for female mounting in Japanese macaques, females mount potential male mates in order to attract them. As such, is it possible that females mount other females to attract potential male mates, as well? At least two lines of evidence indicate that this functional explanation cannot account for the existence of same-sex mounting between female Japanese macaques. First, female consort partners avoid engaging in homosexual behavior in the presence of males, often attempting to spatially and visually separate themselves from other group members (Gouzoules & Goy, 1983). Second, males that attempt to initiate sexual behaviour with females that are engaged in homosexual consortships are, more often than not, ignored or even attacked and driven away by the consort partners (Vasey 1998, 2002a; Vasey & Gauthier, 2000).

Additional analyses presented here indicate that female Japanese macaques do not use same-sex mounting as practice for female-male mounting. If this were the case, one would expect younger females to engage in more same-sex mounting given their relative sexual inexperience. In reality, however, older, more sexually experienced females in the study population were as likely to engage in same-sex mounting as their younger counterparts.

In conclusion, the proposed evolutionary scenario for female mounting in Japanese macaques outlined above is intended to demonstrate how the perspective of evolutionary history might help us generate testable hypotheses that can help account for the evolution of homosexual behavior, particularly in those cases where the behavior appears to be functionless (Vasey, 2002b). It must be stressed, however, that homosexual behavior is not a uniform phenomenon across species. Instead, multiple motivations, developmental pathways and evolutionary histories underlie the phenomenon we call homosexual behavior and these vary both within and between species (Bagemihl, 1999; Vasey, 1995). As such, attempts to make unifying interspecies generalizations about the nature of homosexual behavior may be misguided and misleading. The study of female homosexual behavior in Japanese macaques may help elucidate at least one developmental and one evolutionary pathway that can lead to the expression of female homosexual behavior.

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