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Effect of Female-Biased Sex Ratios on Female Homosexual Behavior in Japanese Macaques: Evidence for the "Bisexual Preference Hypothesis"

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Abstract We aimed to explain the frequent and prevalent female homosexual behavior in the context of female-biased operational sex ratios (OSR) and qualified sex ratios (Q) in a free-ranging group of Japanese macaques (*Macaca fuscata*) living at Arashiyama-Kyoto, Japan. Our data included the average availability of sexually mature males during females' putative fertile period (OSR), the ratio of sexually mature males to sexually mature females (Q), as well as heterosexual and female homosexual solicitations and consortships collected during 13 mating seasons from 136 females. Our results did not support the "heterosexual deprivation hypothesis," which holds that female homosexual behavior is attributable to a shortage of male mates. Likewise, our results did not support the "lack of opposite-sex sexual competitor hypothesis," which holds that females have more access to female mates when male sexual rivals are scarce. Of the 11 predictions tested, only one yielded statistically significant results: we found that higher ratios of availability of preferred female partners to preferred male partners were associated with female homosexual consortships rather than female heterosexual consortships. This result supported the "bisexual preference hypothesis," which holds that female homosexual behavior is attributable to female preference for certain female mates relative to certain male mates. We conclude that when a female targets another female as a mate, it is an active choice for a female sexual partner over available male alternatives, rather than a by-default situation that occurs because males are not available as sexual partners, or because females are better able to access female sexual partners due to a scarcity of male sexual competitors.

Keywords Operational sex ratio · Qualified sex ratio · Female homosexual behavior · Bisexual preference · Non-human primates

Introduction

According to a recent review, at least 76 non-mutually exclusive hypotheses have been proposed in the literature to explain the expression and evolution of male and female homosexual behavior in a variety of bird and mammal species, including humans (cf. Table 1.1 in Poiani, 2010). These hypotheses address both proximate and ultimate causes (cf. Tinbergen, 1963). Some of these hypotheses have been tested and consider genetic, endocrinological, neurobiological, immunological, and social explanations, as well as life-history factors (Poiani, 2010). Others seem difficult to test or even disprove, such as the "biological exuberance hypothesis," which holds that the surplus energy produced by some (groups of) organisms is used for non-functional and "extravagant activities," such as homosexual interactions (Bagemihl, 1999, p. 253).

Sex ratio bias is one of the main biodemographic factors invoked to account for high levels of same-sex sexual behaviors in various animal taxa (Poiani, 2010). The absence, scarcity, or unavailability of opposite-sex sexual partners and the availability of same-sex mates during mating periods may create sociodemographic constraints and opportunities leading to an increased expression of homosexual behavior among members of the more abundant sex. This explanation is alternatively referred to as the "heterosexual deprivation hypothesis" (Vasey & Gauthier, 2000), the "outlet for sexual frustration hypothesis" (Yamane, 2006), the "substitute heterosexuality hypothesis" (Bagemihl,

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1999), the "shortage hypothesis" (Bagemihl, 1999), the "best-of-a-bad-job hypothesis" (Poiani, 2010), or a "Hobson's choice" (sensu Fedigan, 1982). In other words, homosexual behavior might be the next best option for individuals that are motivated to engage in sexual activity, but lack opposite-sex mates.

With regard to extreme cases of skewed sex ratios, it seems intuitive to predict that homosexual behavior will be more frequent and more prevalent in single-sex groups (i.e., groups including members of one sex only) than in mixed-sex groups (i.e., groups including members of both sexes). When artificially reared in captive all-male or all-female groups, a variety of animal taxa exhibited increased levels of male or female homosexual activity, respectively (e.g., Trinidadian guppies, *Poecilia reticulata*: Field & Waite, 2004; zebra finches, *Taeniopygia guttata*: Adkins-Regan & Krakauer, 2000; American bisons, *Bison bison*: Vervaecke & Roden, 2006; squirrel monkeys, *Saimiri sciureus*: Talmage-Riggs & Anschel, 1973; rhesus macaques, *Macaca mulatta*: Gordon & Bernstein, 1973). Similarly, "situational" homosexuality is expressed by human males and females under a variety of same-sex settings, such as prisons, boarding schools, and military academies (Anderson, 2009; Ashworth & Walker, 1972; Flood, 2008; Gear, 2005; Hensley, 2000; Kinsey, Pomeroy, & Martin, 1948; Kirkham, 2000; Moodie, Ndatshe, & Sibuyi, 1989). Naturally occurring sexual segregation patterns also generate free-ranging all-male or all-female groups in which male or female homosexual interactions may occur (e.g., domestic goats, *Capra hircus*: Shearer & Katz, 2006; bottlenose dolphins, *Tursiops truncatus*: Mann, 2006; Indian langurs, *Presbytis entellus*: Sommer, Schauer, & Kyriazis, 2006; Japanese macaques, *Macaca fuscata*: Leca, Gunst, & Vasey, 2014a; mountain gorillas, *Gorilla gorilla beringei*: Yamagiwa, 2006).

In free-ranging mixed-sex groups with skewed sex ratios, there is ample observational evidence that members of the more abundant sex have reduced access to members of the scarcer sex, and this may result in an increased expression of homosexual activity. For example, homosexual pairings between male grey0 lag geese (*Anser anser*) are enhanced in flocks with male-biased sex ratios (Kotrschal, Hemetsberger, & Weiss, 2006). Conversely, the formation of female–female pairs in pink flamingos (*Phoenicopterus ruber*) increases when sex ratios are female-biased (King, 2006). Likewise, in some gull colonies (*Larus spp.*) where females outnumbered males three-to-two, female–female pairings were common (Hunt, Wingfield, Newman, & Farner, 1980). Conover and Hunt (1984) experimentally tested the "heterosexual deprivation hypothesis" by removing males, and found that female–female pairs were more frequent in the experimentally manipulated colonies than in nearby control colonies.

There are three reasons why the Arashiyama population of Japanese macaques, near the city of Kyoto, is an ideal non-human primate population for research on the effect of skewed sex ratios on the expression of homosexual behavior. First, in addition to engaging in reproductive interactions (e.g., Huffman, 1992; Vasey, Foroud, Duckworth, & Kovacovsky, 2006; Vasey, Rains, VanderLaan, Duckworth, & Kovacovsky, 2008a), adolescent and adult females in this population routinely exhibit various forms of homosexual activity, including same-sex sexual solicitations and female–female mounting behaviors (Leca, Gunst, & Vasey, 2014c; Vasey, 2002, 2004, 2006; Vasey & Duckworth, 2006; Vasey et al., 2008a; Vasey, VanderLaan, Rains, Duckworth, & Kovacovsky, 2008b). Structurally, sexual behavioral patterns between females are very similar to typical heterosexual ones (Vasey et al., 2008a, b), with same-sex courtship and behavioral variants in mounting postures occurring during temporary, but exclusive, sexual relationships (i.e., consortships; Vasey, 2006). Further, stimulation of the female genital region occurs during both heterosexual and homosexual interactions (Vasey & Duckworth, 2006, 2008). Given this, it is theoretically reasonable to presuppose that homosexual behavior might serve, under certain conditions, as a substitute for heterosexual behavior and vice versa. Second, the ratio of sexually mature males to sexually mature females present in the Arashiyama groups of Japanese macaques is not only much lower than one (i.e., heavily skewed towards females), but it also fluctuates from year to year (Chalmers, Huffman, Koyama, & Takahata, 2012; Fedigan, Gouzoules, & Gouzoules, 1983; Koyama, Takahata, Huffman, Norikoshi, & Suzuki, 1992; Wolfe, 1984). Third, the Arashiyama group of Japanese macaques is one of the longest continuously studied non-human primate populations in the world (Huffman, Fedigan, Vasey, & Leca, 2012). Consequently, the influence of sex ratio fluctuations on sexual behavior can be accessed. Fourth, long-term records of life history traits (including Q) and behavioral data on individually identified monkeys are available from years of collaborative research between observers working at this site (Leca, Huffman, & Vasey, 2012).

Previous observational research on the effect of female-biased sex ratios on female homosexual behavior in Arashiyama Japanese macaques has produced equivocal results. Based on a four-year study, Wolfe (1986) showed that a two-fold increase in the number of sexually mature males was associated with a 27 % decrease in the frequency of female homosexual behavior over a four-year period. Moreover, when females in the Arashiyama-West group (Texas, USA) had access to half as many sexually mature male as those in the Arashiyama-East group (Kyoto, Japan), they formed homosexual consortships almost three times as often (Wolfe, 1986). According to a recent meta-analysis, the percentage of Arashiyama females involved in same-sex mounting decreased linearly as the sex ratio in the group became less female-biased (cf. Figure 8.6 in Poiani, 2010). Taken together, these findings are consistent with the "heterosexual deprivation hypothesis." In contrast, Fedigan and Gouzoules (1978) argued that the number of sexually mature males present in the Arashiyama-West group did not affect the number of females engaging in homosexual consortships. This observation does not support the "heterosexual deprivation hypothesis."

In order to test the effect of sex ratio on female homosexual behavior in Japanese macaques, Vasey and Gauthier (2000) conducted an experimental study on the captive Arashiyama-Montréal group (Canada). They found that female homosexual behavior was more frequent in a test group, heavily skewed toward females (i.e., in which females outnumbered males by 11 to 1) than in a control group, with a female-biased sex ratio more typical of this species (i.e., in which females outnumbered males by 3 to 1). However, a detailed analysis of the sexual behavioral patterns revealed that females in the test group did not engage in homosexual activity simply because they lacked heterosexual alternatives. The sole adult male in the experimental group was often available and motivated to engage in sexual activity, yet females routinely ignored him and formed consortships with each other instead. On the basis of this experiment, Vasey and Gauthier (2000) argued that the scarcity of male rivals (referred to as the "lack of opposite-sex sexual competitor hypothesis") and/or the relative abundance of certain preferred female partners compared to certain preferred male partners (i.e., the "bisexual preference hypothesis") might best account for the increased levels of female homosexual behavior observed in the experimental group. Wolfe (1984) adopted one version of the "bisexual preference hypothesis" by arguing that female Japanese macaques prefer novel female sexual partners over familiar male mates. It is possible that Fedigan and Gouzoules (1978, pp. 494–495) were also arguing for some version of the "bisexual preference hypothesis" when they stated "…homosexual consortships appeared to be part of a larger pattern of female sexual initiative…" and, as such, "…females were not forced to choose other females due to lack of males."

There are several methodological limitations associated with research on the effect of skewed sex ratios on the expression of homosexual behavior (including the research on female homosexual behavior in Japanese macaques). First, long-term quantitative analyses of homosexual behavior under fluctuating sex ratio conditions remain infrequent (but see King, 2006; Kotrschal et al., 2006, for a few notable exceptions). Second, most studies used only one sex ratio variable, the *qualified sex ratio* (Q; also known as the *socionomic sex ratio*), defined as the ratio of sexually mature males to sexually mature females present in the group during a given mating season (cf. Ahnesjö, Kvarnemo, & Merilaita, 2001). To the best of our knowledge, no observational studies of homosexual behavior have considered both Q and the *operational sex ratio* (OSR), defined as the ratio of sexually mature males to sexually receptive females in the group at a given time (cf. Emlen & Orin, 1977; but see Vasey & Gauthier, 2000 for a study of female homosexual behavior under experimentally skewed OSRs). We argue that the combined analysis of Q and OSR is important because Q is a purely demographic variable that may vary across mating seasons but typically remains the same within a given mating season, whereas OSR is both a demographic and physiological variable that may vary both across and within mating seasons. Third, in most studies of homosexual behavior, sex ratio variables were not tested as part of multivariate analyses that included age, dominance rank, relationship quality, and sex-specific relative parental care (e.g., Bagemihl, 1999; Sommer et al., 2006; MacFarlane, Blomberg, & Vasey, 2010; but see Poiani, 2010). Fourth, the meta-analysis mentioned above (cf. Figure 8.6 in Poiani, 2010) only comprised six data points from three different groups of the Arashiyama population of Japanese macaques (namely Arashiyama-West, Arashiyama-East, and Arashiyama-Montréal), and did not distinguish between different female homosexual behavioral patterns (i.e., solicitations, mounts, and consortships). Moreover, it did not include the result obtained by Fedigan and Gouzoules (1978) that did not support the "heterosexual deprivation hypothesis." Finally, there are no reports concurrently testing the three sex ratio hypotheses proposed by Vasey and Gauthier (2000), namely, the "heterosexual deprivation hypothesis," the "lack of opposite-sex sexual competitor hypothesis," and the "bisexual preference hypothesis."

The present study sought to fill these gaps. In order to account for the frequent and prevalent female homosexual behavior in the context of female-biased OSRs and Qs in the Arashiyama-East group of Japanese macaques, we tested a series of predictions related to three non-mutually exclusive hypotheses. First, the "heterosexual deprivation hypothesis" postulates that female homosexual behavior is attributed to a shortage of male mates. In support of this hypothesis, we predicted that, at the individual level, lower OSRs should result in more frequent female homosexual solicitations (Prediction 1a), more frequent female homosexual consortships (Prediction 1b), longer female homosexual consortships (Prediction 1c), and with a greater number of female sexual partners (Prediction 1d). At the group level, we predicted that Q and the percentage of female group members engaging in homosexual consortships should be negatively correlated (Prediction 1e).

Second, the "lack of opposite-sex sexual competitor hypothesis" postulates that females have more access to female mates because male sexual rivals are scarce. At the individual level, we predicted that lower OSRs should result in lower intersexual competition for access to female mates (Prediction 2a), leading to more frequent and longer homosexual consortships and females engaging in homosexual consortships with a larger number of female partners (Prediction 2b). We also predicted that lower OSRs should result in more frequent female homosexual solicitations because, under lower OSRs, females performing homosexual solicitations would be less fearful of male aggression (Prediction 2c). Indeed, previous research showed that female Japanese macaques engaging in homosexual behavior were likely to be aggressed by males (Gunst, Leca, & Vasey, 2015; Vasey, 1998, 2004). For the same reason, and at the group level, we predicted that Q and the percentage of female group members performing female-to-female sexual solicitations should be negatively correlated (Prediction 2d).

Third, the "bisexual preference hypothesis" postulates that female homosexual behavior is attributed to female preference for *certain* female mates relative to *certain* male mates. In support of this hypothesis, we predicted that higher OSRs should result in higher female heterosexual proceptivity (i.e., more frequent female-to-male sexual solicitations directed to a larger number of male targets) because, relatively speaking, there are potentially more preferred male mates (compared to preferred female mates) under such conditions (Prediction 3a). We also predicted that higher ratios of availability of *preferred* (i.e., habitual) female partners to *preferred* male partners should be associated with female homosexual consortships rather than female heterosexual consortships (Prediction 3b).

Method

Study Species and Study Group

Japanese macaques are seasonal breeders and ovulate only during the breeding season (i.e., autumn and winter months). Like other macaque species, they are characterized by a multimale–multifemale mating system (Dixson, 2012). Observations were conducted on the free-ranging provisioned Arashiyama-E troop of Japanese macaques at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan. These monkeys are very well habituated to human presence. The members of the Arashiyama-E troop belonged to 15 separate matrilineages and their exact ages were known. All research methods at this site were approved in accordance with the Guide for the Care and Use of Primates prepared by the Primate Research Institute, Kyoto University. Approval for this research was also obtained from the Animal Welfare Committee at the University of Lethbridge.

During the study periods (1984–1985[1] and 2000–2012), the group size was relatively stable (M number of group members: 142.3 ± 6.8, range 133–154), with a mean of 100.9 ± 2.8 sexually mature females and 17.8 ± 7.2 sexually mature males (Fig. 1). A female was considered sexually mature from the age of 3.5 years, when showing typical physiological and behavioral signs of fertile period. Such physiological signs included reddening of the facial and genital skin, vaginal secretion, and genital swelling and odor. Behavioral signs included sexual proceptivity, receptivity, and attractivity, as evidenced by sexual solicitations directed to or received from potential male or female mates, and heterosexual and homosexual consortship activity (Chalmers et al., 2012; Enomoto, 1974; Enomoto, Seiki, & Haruki, 1979; Nigi, 1976; Vasey & VanderLaan, 2012). Males were considered sexually mature from the age of 4.5 years, when they start to ejaculate and perform sexual solicitations and series mounts directed toward female consort partners (Gunst, Leca, & Vasey, 2013; Hanby & Brown, 1974; Nigi, Tiba, Yamamoto, Floescheim, & Ohsawa, 1980).

Although the group size was stable during the study period, the *qualified sex ratio* (i.e., the ratio of sexually mature males to sexually mature females) was strongly female-biased and varied substantially (up to 65 %) across mating seasons (mean Q 0.18 ± 0.07, range 0.11–0.31; Fig. 2). In other words, the most skewed Q occurred during the mating season when sexually mature females outnumbered sexually mature males by 10–1, and the least skewed Q occurred during the mating season when sexually mature females outnumbered sexually mature males by 3–1. However, these values fall within the range of most free-ranging provisioned groups in this species (Fukuda, 1988; Kurita, 2010; Yamagiwa & Hill, 1998). It is noteworthy that Japanese macaques do not exhibit significantly biased sex ratios at birth; female-biased qualified sex ratios are the result of male emigration from the age of sexual maturity and sex differences in mortality (Koyama et al., 1992).

Procedure and Measures

The data pertaining to *likelihood of fertile period* were collected for each sexually mature female group member. Likelihood of fertile period was ranked from 1 to 5 and based on non-behavioral cues, such as redness of the facial and genital skin, genital swelling, and vaginal secretion producing a pungent urinary genital odor [(1) no cues, (2) low redness of the facial and genital skin, (3) mild redness of the facial and genital skin, and slight genital swelling, (4) high redness of the facial and genital skin, mild genital swelling, slight vaginal secretion, and slight genital odor, (5) high redness of the facial and genital skin, high genital swelling, strong vaginal secretion, and strong genital odor).

Data pertaining to *male-to-female heterosexual solicitations, female-to-male heterosexual solicitations*, and *female homosexual solicitations* were also collected. Such sexual solicitations patterns included body postures (frozen stance and intense gazing, hindquarter presentations, inclined-back presentations, and crouching while screaming), body movements and gestures (lip quivering, head bobbing, ground smacking, hindquarter sniffing, hands-on-hindquarters solicitations, pushing, grabbing, body spasms, and repeated glancing while sitting with 10 m of the target), and sexual vocalizations. Finally, data were collected on *heterosexual* and *female homosexual consortships* (cf. Enomoto, 1974; Enomoto et al., 1979; Vasey et al., 2008b). A *consortship* was defined as a temporary, but exclusive, sexual association between two individuals, and occurred when two individuals engaged in series-mounting (three or more mounts within a 10-min period) separated by inter-mount intervals. Consortships were deemed to have terminated if the two partners were not in proximity (separated by a distance of more than 1 m) and exhibited no mounting for 10 min (cf. Vasey, 2004). Heterosexual consortships involved two opposite-sex partners, and homosexual consortships involved two female partners. Intersexual competition

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[1] This period of data collection, prior to the main 2000-2012 period, was added to extend the longitudinal analysis and provide a more historical perspective on the phenomenon under study.

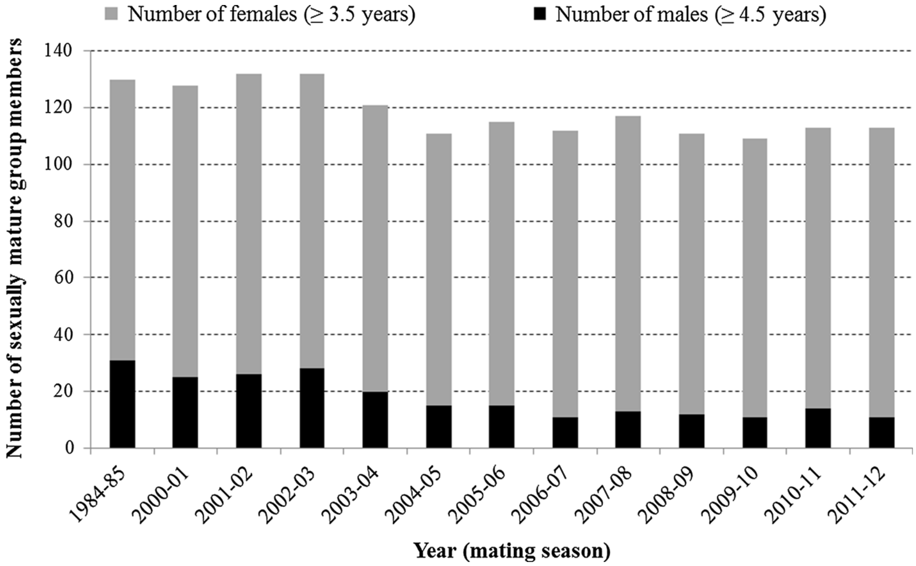

Fig. 1 Number of sexually mature females and male group members during the study period

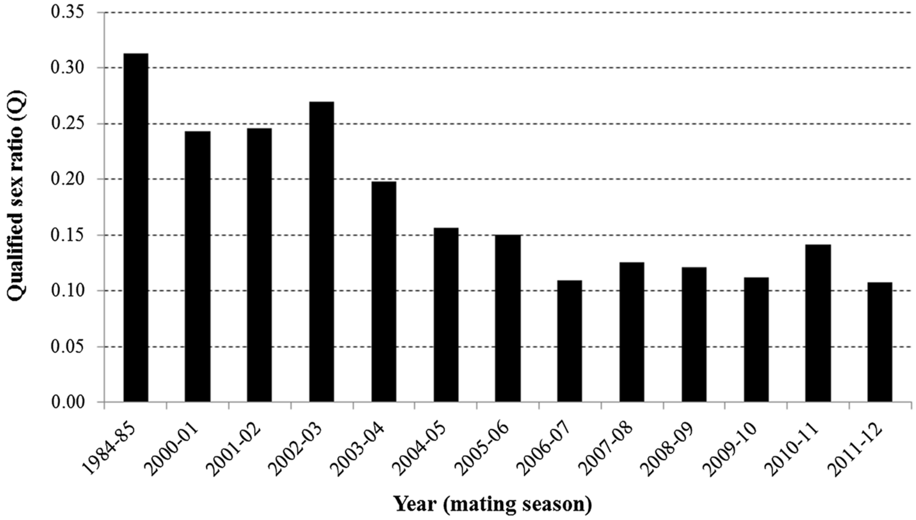

Fig. 2 Qualified sex ratios during the study period

was scored as occurring when a given female received sexual solicitations from opposite-sex and same-sex partners on the same day.

Behavioral data were collected daily from approximately 7:00 a.m. to 2:00 p.m. by using both individual-level and group-level sampling techniques (Altmann, 1974). The former consisted of randomly selected focal-animal sampling of oestrous females (two 30 min-time blocks/female/day, with an interval of at least one hour between the two blocks), during which the frequencies of the aforementioned sexual behaviors were recorded. The latter consisted of daily group scans (approximately every 30 min), during which the occurrences of the aforementioned sexual behaviors were recorded. The identities of the targets or partners were also recorded, except for non-group/peripheral males. The data set was collected during the 1984–1985 mating season and over 12 consecutive mating seasons (between September and January) from 2000 to 2012 by PLV, JBL, NG, and MAH. A total of 213 identified individuals (136 females and 77 males, not including peripheral males) were sampled during this study period. A total of 2851 male-to-female heterosexual solicitations, 2739 female-to-male heterosexual solicitations, 957 female homosexual solicitations, 2332 heterosexual consortships, and 1227 female homosexual consortships were recorded.

Data Analysis

To investigate the effect of female-biased sex ratios on female homosexual behavior, we used three types of analyses. First, in order to test how OSR, in combination with other independent variables, affected heterosexual and homosexual behavior in each female during a given mating season, we conducted a series of multiple regression analyses, each with a different continuous dependent variable.

In each regression, we included eight categorical independent variables to characterize each female during a given mating season. The first variable was nominal and binary: dependent offspring (yes or no). The other seven variables were ordinal: (1) *age class* with five categories (first/second putative fertile period: aged 3–4 years, N = 30 over the 2000–2012 study period; young adult: 5–10 years, N = 82; adult: 11–20 years, N = 85; old adult: 21–27 years, N = 37; and senescent: 28–33 years, N = 9), (2) *matrilineal dominance* with three categories (low-, middle-, and high-ranking), (3) *parity* with three categories (nulliparous, primiparous, and multiparous), (4) *duration of low likelihood of fertile period* (i.e., ranging from 1.5 to 3) with four categories of duration (absence: 0 day, short: 1–10 days, medium: 11–20 days, and long: more than 20 days), (5) *duration of high likelihood of fertile period* (i.e., ranging from 3.5 to 5) with the same four categories of duration, (6) *duration of all likelihood of fertile period* (i.e., ranging from 1.5 to 5) with the same four categories of duration, and (7) *average availability of sexually mature males* with three categories (low: 0–9 males, N = 176; medium: 10–19, N = 396; and high: 20–31, N = 178). To qualify as available, a sexually mature male had to not be engaged in a consortship during a female's putative fertile period(s). The average availability of sexually mature males was considered a good proxy for OSR, as this variable included both male availability and female sexual receptivity. To assess the relative contribution of each independent variable to the regression models, we used the "simultaneous" (or "enter") method (see Field, 2005).

Second, we conducted a group-level analysis in which we used one-tailed Spearman's rank correlation tests to assess the relationship between Q and the percentage of female group members performing homosexual solicitations or engaging in homosexual consortships (i.e., the prevalence of female homosexual behavior) across annual mating seasons. During a given mating season, we distinguished between the percentage of females performing exclusively homosexual solicitations and engaging exclusively in homosexual consortships, and the percentage of females performing both homosexual and heterosexual solicitations and engaging in both homosexual and heterosexual consortships.

In a third individual-based univariate analysis, we used a Wilcoxon signed ranks test to compare the ratios of availability of preferred female partners to preferred male partners during female homosexual consortships and female heterosexual consortships. We defined a *preferred* (female or male) *partner* as an individual that engaged in consortships with, or was solicited by, a given female at least once during three different mating seasons, for a minimum total of three times.

Because all the variables collected during the 2000–2012 study period were not collected during the 1984–1985 study period, the individual-level regression analyses and the Wilcoxon signed ranks tests were conducted by using only the 2000–2012 data set whereas the group-level Spearman's rank correlation tests were conducted by using the 1984–1985 and 2000–2012 data sets. Statistical analyses were performed using the IBM SPSS Statistics 22.0 analytical program. We tested the assumptions and met the requirements of all the statistical tests. Significance levels were set at $\alpha = 0.05$. We did not correct the statistical significance level by considering the number of tests conducted because each of our analyses was motivated by a specific and directional prediction (cf. Table 8), and in that sense, our analyses were not exploratory (cf. Saville, 1990).

Results

Heterosexual Deprivation Hypothesis

When considering the frequency of female homosexual solicitations and the frequency and duration of female homosexual consortships, the best fits were produced by multiple regression models showing non-significant relative contributions of OSR in explaining these dependent variables ($p = .211$, $p = .819$, and $p = .713$, respectively, Tables 1, 2, 3). Each of these three models was composed of a series of retained variables, with different orders of relative contribution, and high Nagelkerke R^2 values. For example, the duration of all likelihood of fertile period contributed the most to explaining the frequency of female homosexual solicitations (with $R^2 = .15$), the duration of high likelihood of fertile period contributed the most to explaining the frequency of female homosexual consortships (with $R^2 = .18$), and the age class contributed the most in explaining the duration of female homosexual consortships (with $R^2 = .14$). This means that the regression models explained 15 % of the variation in the frequency of female homosexual solicitations, 18 % of the variation in the relative frequency of female homosexual consortships, and 14 % of the variation in the duration of female homosexual consortships. These relatively high values showed that the retained variables were good predictors of the frequency of female homosexual solicitations and consortships, and the duration of female homosexual consortships.

Among all the non-significant variables of the three models, OSR showed some of the lowest contributions (Tables 1, 2, 3). There was no significant interaction between independent variables involving OSR. Therefore, lower OSRs did not result in significantly more frequent female homosexual solicitations and consortships and longer female homosexual consortships. Consequently, Prediction 1a–1c were not supported.

When considering the number of same-sex consortship partners per mating season that characterize a given female, the best fit was produced by a multiple regression model showing a non-significant relative contribution of OSR in explaining this dependent variable ($p = .126$, Table 4). Likewise, although other predictors (namely, parity, duration of all likelihood of fertile period, and dependent offspring) contributed 12.6 % of the variation in the number of female partners, OSR showed the lowest contribution of all the non-significant variables. There was no significant interaction between independent variables involving OSR. Therefore, lower OSRs did not result in females engaging

Table 1 Model yielded by a multiple regression analysis, with the frequency of female homosexual solicitations, as a continuous dependent variable

	Order of relative contribution	*t*	*β*	SE	df	*p*
Independent variables retained by the model						
Duration of all likelihood of fertile period	1	−3.33	−2.89	0.86	3	.001
Matrilineal dominance	2	2.61	1.12	0.42	2	.009
Dependent offspring	3	−2.36	−1.69	0.71	1	.018
Age class	4	1.97	2.89	1.46	4	.049
Independent variables not retained by the model						
Parity	n.a.	−1.73	−0.89	0.51	2	.083
Average availability of sexually mature males (OSR)	n.a.	1.25	1.12	0.89	2	.211
Duration of low likelihood of fertile period	n.a.	1.18	0.66	0.55	3	.236
Duration of high likelihood of fertile period	n.a.	−1.07	−0.71	0.66	3	.284

For the model composed of the four retained variables, Nagelkerke $R^2 = .15$, $F(22,736) = 5.79$, $p < .001$

Table 2 Model yielded by a multiple regression analysis, with the frequency of female homosexual consortships as a continuous dependent variable

	Order of relative contribution	*t*	*β*	SE	df	*p*
Independent variables retained by the model						
Duration of high likelihood of fertile period	1	−3.36	−8.34	2.47	3	.001
Matrilineal dominance	2	−3.29	−6.52	1.97	2	.001
Age class	3	−3.02	−7.30	2.41	4	.003
Dependent offspring	4	−2.14	−14.27	6.65	1	.032
Independent variables not retained by the model						
Parity	n.a.	−0.73	−1.73	2.37	2	.465
Duration of all likelihood of fertile period	n.a.	0.61	2.41	3.93	3	.539
Average availability of sexually mature males (OSR)	n.a.	0.22	0.85	3.72	2	.819
Duration of low likelihood of fertile period	n.a.	0.00	0.01	3.16	3	.997

For the model composed of the four retained variables, Nagelkerke $R^2 = .18$, $F(22, 736) = 6.40$, $p < .001$

Table 3 Model yielded by a multiple regression analysis, with the duration of female homosexual consortships as a continuous dependent variable

	Order of relative contribution	*t*	*β*	SE	df	*p*
Independent variables retained by the model						
Age class	1	−2.92	−0.96	0.33	4	.004
Dependent offspring	2	−2.40	−2.19	0.91	1	.016
Matrilineal dominance	3	−2.33	−0.63	0.27	2	.020
Duration of all likelihood of fertile period	4	2.03	1.10	0.54	3	.042
Independent variables not retained by the model						
Duration of high likelihood of fertile period	n.a.	1.88	0.64	0.34	3	.060
Parity	n.a.	0.69	0.22	0.32	2	.489
Duration of low likelihood of fertile period	n.a.	0.38	0.16	0.43	3	.698
Average availability of sexually mature males (OSR)	n.a.	−0.36	−0.18	0.48	2	.713

For the model composed of the four retained variables, Nagelkerke $R^2 = .14$, $F(22, 736) = 5.41$, $p < .001$

in homosexual consortships with a significantly larger number of female partners. Consequently, Prediction 1d was not supported.

At the group level, the correlation between Q and the percentage of female group members engaging in homosexual consortships was not statistically significant, whether we considered the percentage of females engaging exclusively in homosexual consortships during a given mating season (Spearman's rank correlation test, N = 13: $r_s = -0.077$, $p = .401$) or the percentage of females engaging in both homosexual and heterosexual consortships during a given mating season

Table 4 Model yielded by a multiple regression analysis, with a given female's number of same-sex consortship partners per mating season, as a continuous dependent variable

	Order of relative contribution	*t*	*β*	SE	df	*p*
Independent variables retained by the model						
Parity	1	2.51	0.34	0.13	2	.012
Duration of all likelihood of fertile period	2	−2.44	−0.42	0.17	3	.015
Dependent offspring	3	−2.16	−0.43	0.20	1	.030
Independent variables not retained by the model						
Matrilineal dominance	n.a.	1.77	0.21	0.12	2	.076
Duration of high likelihood of fertile period	n.a.	−1.45	−0.27	0.18	3	.145
Age class	n.a.	1.28	0.52	0.41	4	.201
Duration of low likelihood of fertile period	n.a.	1.05	0.16	0.15	3	.293
Average availability of sexually mature males (OSR)	n.a.	0.94	0.23	0.25	2	.346

For the model composed of the three retained variables, Nagelkerke $R^2 = .13$, $F(22, 736) = 4.80$, $p < .001$

Table 5 Model yielded by a multiple regression analysis, with the frequency of intersexual competition as a continuous dependent variable

	Order of relative contribution	*t*	*β*	SE	df	*p*
Independent variables retained by the model						
Duration of high likelihood of fertile period	1	4.15	0.14	0.03	3	<.001
Matrilineal dominance	2	−2.33	−0.06	0.02	2	.018
Independent variables not retained by the model						
Average availability of sexually mature males (OSR)	n.a.	−1.77	−0.08	0.04	2	.076
Duration of all likelihood of fertile period	n.a.	1.51	0.08	0.05	3	.131
Dependent offspring	n.a.	0.89	0.08	0.09	1	.370
Parity	n.a.	−0.55	−0.01	0.03	2	.581
Age class	n.a.	−0.40	−0.01	0.03	4	.689
Duration of low likelihood of fertile period	n.a.	−0.06	−0.00	0.04	3	.949

For the model composed of the two retained variables, Nagelkerke $R^2 = .13$, $F(22, 736) = 5.02$, $p < .001$

($r_s = 0.055$, $p = .429$). Therefore, Prediction 1e was not supported. No female engaged in exclusive homosexual behavior over every mating season during the entire study period.

Lack of Opposite-Sex Sexual Competitor Hypothesis

When considering the frequency of intersexual competition for access to female mates, the best fit (with $R^2 = .13$) was produced by a multiple regression model showing a non-significant relative contribution of OSR in explaining this dependent variable ($p = .076$, Table 5). Therefore, Prediction 2a was not supported.

Since OSR and the level of intersexual competition for access to female mates were not significantly associated, their effects on female homosexual behavior were tested separately. Lower OSRs were not significantly associated with more frequent and longer female homosexual consortships ($p = .819$ and $p = .713$, respectively, Tables 2, 3) or with females engaging in homosexual consortships with a larger number of female partners (Table 4). Although we found statistically significant correlations between the level of intersexual competition for access to female mates and different aspects of female homosexual behavior, the directions of these correlations were all contrary to our predictions: lower intersexual competition for access to female mates was associated with less frequent homosexual consortships (Pearson's rank correlation test, N = 759, $r_p = 0.21$, $p < .001$), shorter homosexual consortships ($r_p = 0.38$, $p < .001$), and females engaging in homosexual consortships with a smaller number of female partners ($r_p = 0.41$, $p < .001$). Therefore, Prediction 2b was not supported. Moreover, there was no significant association between lower OSRs and more frequent female homosexual solicitations ($p = .211$, Table 1). Therefore, Prediction 2c was not supported.

At the group level, the correlation between Q and the percentage of female group members performing homosexual solicitations was not statistically significant, whether we

Table 6 Model yielded by a multiple regression analysis, with the frequency of female-to-male heterosexual solicitations, as a continuous dependent variable

	Order of relative contribution	t	β	SE	df	p
Independent variables retained by the model						
Duration of high likelihood of fertile period	1	−5.42	−4.06	0.74	3	<.001
Duration of all likelihood of fertile period	2	−3.41	−1.88	0.55	3	.001
Duration of low likelihood of fertile period	3	−2.33	−1.18	0.50	3	.020
Independent variables not retained by the model						
Age class	n.a.	−1.82	−2.41	1.32	4	.069
Matrilineal dominance	n.a.	−1.00	−0.38	0.38	2	.317
Parity	n.a.	0.78	0.34	0.43	2	.430
Average availability of sexually mature males (OSR)	n.a.	0.42	0.26	0.64	2	.675
Dependent offspring	n.a.	−0.35	−0.23	0.64	1	.720

For the model composed of the three retained variables, Nagelkerke $R^2 = .34$, $F(22, 736) = 17.22$, $p < .001$

Table 7 Model yielded by a multiple regression analysis, with the number of male targets solicited by a given female per mating season, as a continuous dependent variable

	Order of relative contribution	t	β	SE	df	p
Independent variables retained by the model						
Duration of all likelihood of fertile period	1	−3.96	−0.94	0.23	3	<.001
Duration of high likelihood of fertile period	2	−3.09	−0.70	0.22	3	.002
Age class	3	2.73	0.86	0.31	4	.006
Independent variables not retained by the model						
Duration of low likelihood of fertile period	n.a.	−1.94	−0.29	0.15	3	.052
Matrilineal dominance	n.a.	−1.65	−0.19	0.11	2	.099
Parity	n.a.	−1.18	−0.16	0.14	2	.236
Dependent offspring	n.a.	−0.66	−0.13	0.19	1	.505
Average availability of sexually mature males (OSR)	n.a.	0.17	0.03	0.20	2	.858

For the model composed of the three retained variables, Nagelkerke $R^2 = .32$, $F(22, 736) = 15.44$, $p < .001$

considered the percentage of females who only performed homosexual solicitation during a given mating season (Spearman's rank correlation test, N = 13: $r_s = 0.42$, $p = .075$) or the percentage of females performing both homosexual and heterosexual solicitations during a given mating season ($r_s = 0.01$, $p = .486$). Therefore, Prediction 2d was not supported.

Bisexual Preference Hypothesis

When considering the frequency of female-to-male sexual solicitations and the number of male targets solicited by a given female per mating season, the best fits were produced by multiple regression models showing non-significant relative contributions of OSR in explaining these dependent variables ($p = .675$, Table 6, and $p = .858$, Table 7, respectively). Each of these two models was composed of a series of retained variables, with different orders of relative contribution, and high Nagelkerke R^2 values. For example, the duration of high likelihood of fertile period contributed the most to explaining the frequency of female-to-male sexual solicitations (with $R^2 = .34$, Table 6) and the duration of all likelihood of fertile period contributed the most to explaining the number of male targets solicited (with $R^2 = .32$, Table 7). Such high values showed that the retained variables were very good predictors of the frequency of female-to-male sexual solicitations (34 % of the variation in this variable was explained by the model), and the number of male targets solicited (32 % of the variation in this variable was explained by the model). There was no significant interaction between independent variables involving OSR. Therefore, higher OSRs did not result in significantly higher female heterosexual proceptivity. Consequently, Prediction 3a was not supported.

We found that higher ratios of availability of preferred female partners to preferred male partners were significantly associated with female homosexual consortships (mean ratio 1.61 ± 0.48) rather than female heterosexual consortships (1.44 ± 0.51; Wilcoxon signed ranks test: N = 36, $z = -2.07$, $p = .038$; Fig. 3). Therefore, Prediction 3b was supported.

Discussion

In order to account for relatively high levels of homosexual behavior in the context of skewed operational sex ratios (OSR), we tested three main non-mutually exclusive hypotheses (Table 8). With regards to the "heterosexual deprivation hypothesis," we found no significant effect of OSR on the frequency of female homosexual solicitations, the frequency and duration of female homosexual consortships, and the number of female consort partners at the individual level. Our analyses showed that social and physiological variables (e.g., dominance and duration of putative fertile period) largely explained seasonal variation in female homosexual behavior (Tables 1, 2, 3). In contrast, OSR systematically showed one of the lowest contribution(s) of all the non-significant variables (Tables 1, 2, 3, 4). In other words, lower availability of sexually mature males during periods of increased sexual receptivity in females did not result in higher levels of female homosexual activity. At the group level, we found no significant correlation between Q and the percentage of female group members engaging in homosexual consortships during a given mating season. Taken together, these results did not support the "heterosexual deprivation hypothesis" which holds that female homosexual behavior is attributable to a shortage of male mates.

These findings were consistent with the view that the motiva tion to engage in female homosexual behavior in Japanese macaques is not directly triggered by a lack of opposite-sex sexual partners (Fedigan & Gouzoules, 1978; Vasey, 2006; Vasey & Gauthier, 2000). Rather, at the individual level, the expression of female homosexual behavior is explained in terms of immediate sexual reward and relatively low risk of aggression. On the one hand, immediate sexual reward occurs either because female mounters press or thrust their genital region against the body of male or female mountees or because they stimulate their genital region with their tails during mounts (Vasey & Duckworth, 2006, 2008; Vasey et al., 2006). On the other hand, female homosexual interactions appear to be safer than heterosexual ones, since females (particularly adolescent ones) are less likely to receive severe aggressions by adult males and incur serious injuries when involved in homosexual interactions compared to heterosexual ones (Gunst et al., 2015; Leca et al., 2014c; Vasey, 2006).

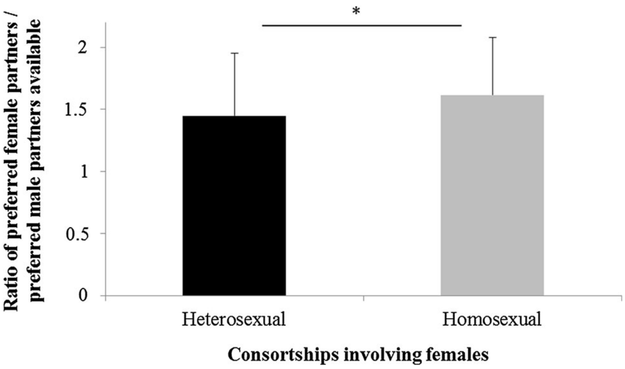

Fig. 3 Ratios of availability of preferred (i.e., habitual) female partners to preferred male partners during female heterosexual versus homosexual consortships (*$p < .05$)

The two free-ranging populations of Japanese macaques, including three separate troops (namely Arashiyama-E, Minoo-F, and Minoo-L: Leca, Gunst, Ottenheimer Carrier, & Vasey, 2014b) in which female homosexual consortships have been reported at the group level fall within a single haplogroup (A1), which is exclusive to central and western Honshu (Vasey & Jiskoot, 2010). Although these three troops have female-biased qualified sex ratios, their sex ratios fall within the range of most free-ranging provisioned troops in this species (Fukuda, 1988; Kurita, 2010; Yamagiwa & Hill, 1998). None of these three troops was characterized by the most heavily skewed Q value reported for Japanese macaques (cf. Fooden & Aimi, 2005). Conversely, in a troop of Japanese macaques on Yakushima island where the sex ratio reaches values close to parity (i.e., $0.92 < Q < 1$: Thomsen & Soltis, 2004), female–female mounting was rare, but it did occur (Leca et al., 2014b). Therefore, neither OSR nor Q, taken alone, can explain the occurrence of female homosexual behavior in this species.

In a recent intergroup comparative study of non-conceptive sexual activity in female Japanese macaques, Leca et al. (2014b) argued that the customary occurrence, high prevalence, and great diversity of female homosexual behavior at Arashiyama may be a cultural practice resulting from combined favorable sociodemographic conditions, namely few resident males, most of them being old, sexually under-motivated, and less aggressive and controlling than the average male Japanese macaques. In most other populations, all the aforementioned sociodemographic conditions are not met, and although several group members may occasionally express female mounting, this behavior does not reach the group-level tradition status. Such findings suggest that group-specific female-biased sex ratios may contribute, to some extent, to the initial expression of female homosexual behavior in Japanese macaques among a small number of individuals. Female homosexual behavior may gradually become more prevalent in provisioned groups of Japanese macaques in part because of increases over time in the qualified sex ratio due to greater food abundance. Following this, female homosexual behavior may become established as a group-wide cultural tradition independent of the original biodemographic drivers of this behavior. Indeed, the present results indicated that intra-seasonal variation in operational sex ratio and inter-seasonal variation in qualified sex ratio did not markedly affect female homosexual behavior in the Arashiyama-E group.

Our results were consistent with research on other animal taxa (including birds, cetaceans, pinnipeds, and other primates) showing that: (1) homosexual activity is not reported in all populations with heavily skewed sex ratios, (2) homosexual activity occurs in numerous populations that have equal (or nearly equal) sex ratios,

Table 8 Proposed explanations for the relatively high levels of female homosexual behavior in the context of female-biased operational sex ratio (OSR) and qualified sex ratios (Q) in the Arashiyama troop of Japanese macaques: hypotheses, predictions, and results

Hypotheses	Predictions	Supported
Heterosexual deprivation: Female homosexual behavior is attributed to a shortage of male mates	Lower OSRs should result in more frequent female homosexual solicitations	No
	Lower OSRs should result in more frequent female homosexual consortships	No
	Lower OSRs should result in longer female homosexual consortships	No
	Lower OSRs should result in females engaging in homosexual consortships with a larger number of female partners	No
	Q and the percentage of female group members engaging in homosexual consortships should be negatively correlated	No
Lack of opposite-sex sexual competitor: Females have more access to female mates when male sexual rivals are scarce	Lower OSRs should result in lower inter-sexual competition for access to female mates	No
	In turn, lower intersexual competition for access to female mates should lead to more frequent and longer homosexual consortships and females engaging in homosexual consortships with a larger number of female partners	No
	Lower OSRs should result in more frequent female homosexual solicitations	No
	Q and the percentage of female group members performing homosexual solicitations should be negatively correlated	No
Bisexual preference: Female homosexual behavior is attributed to female preference for *certain* female mates relative to *certain* male mates	Higher OSRs should result in more frequent female-to-male heterosexual solicitations directed to a larger number of male targets	No
	Higher ratios of availability of *preferred* female partners to *preferred* male partners should be associated with female homosexual behavior rather than female heterosexual behavior	Yes

(3) in many groups with skewed sex ratios, homosexual interactions only occur (or are more common) between members of the sex that is in *shorter* supply rather than in the "surplus" sex, and (4) when homosexual activity occurs in the absence of opposite-sex partners (e.g., in sexually segregated species or in captive settings), it is usually not limited to these contexts and is also expressed in mixed-sex groups (reviewed in Bagemihl, 1999). Thus, although same-sex activity in some species or populations and under certain environmental conditions may be associated with a lack of opposite-sex partners, "the patterns of its occurrence are far more complex than a shortage explanation would indicate" (Bagemihl, 1999, p. 136).

Although our results obtained from female Japanese macaques of all ages did not support the "heterosexual deprivation hypothesis," analyses of the temporal patterns of sexual solicitations showed that, prior to engaging in homosexual activity, 3-year-old females first solicited male partners for copulation (Gunst et al., 2015). However, adult males ignored or rejected most of these young adolescent females' sexual solicitations (Gunst et al., 2015). As the females become older and their homosexual mounting postures become more adult-like, adult females may tend to become first-choice sexual partners associated with pleasurable reward and safer interactions, instead of second-choice partners by young females that fail to attract sexually motivated males (Leca et al., 2014c). Therefore, from a developmental perspective, the "heterosexual deprivation hypothesis" cannot be ruled out for younger females.

With regards to the "lack of opposite-sex sexual competitor hypothesis," we found no significant effect of OSR on intersexual competition for access to female mates at the individual level. In other words, lower availability of sexually mature males during periods of increased sexual receptivity and proceptivity in females did not necessarily result in less rivalry between males and females for the same female sexual partners. Contrary to our predictions, higher intersexual competition for access to female mates was associated with the expression of more female homosexual behavior. This is consistent with previous research showing that same-sex sexual activity among female Japanese macaques may occur even when females are solicited by sexually motivated males (cf. Vasey, 2002, 2004; Vasey & Gauthier, 2000). At the group level, we found no significant correlation between Q and the percentage of female group members performing homosexual solicitations. Taken together, these results do not support the "lack of opposite-sex sexual competitor hypothesis," which holds that an increase in female homosexual behavior is attributable to a relative scarcity of male sexual rivals in the population.

Vasey (1998) found that Japanese macaques routinely engage in inter-sexual competition for female mates. In such cases, males and females directly compete to gain access to female sexual partners. During these interactions, both female participants (i.e., the female sexual competitor and the female that is the focus of competition) can incur injuries that result from male aggression. When the number of male sexual competitors decreases (i.e., when the sex ratio is heavily skewed towards females), the probability for females to be aggressed by males in the context of inter-sexual competition should theoretically decrease and consequently, the frequency of female homosexual interactions should increase (Vasey, 1998; Vasey & Gauthier, 2000). The fact that intersexual competition for access to female mates did not hinder the expression of female homosexual behavior in the Arashiyama-E group may be partly explained by the presence of "mellow males" in this group (cf. Leca et al., 2014b). It has been argued that non-conceptive sexual activity in female Japanese macaques, including female homosexual behavior is more tolerated in groups with less coercive, less controlling, and more affiliative males, leading to lower levels of sex-related aggressiveness (such as consortship intrusion and sexual harassment) by male mates and third-party males (Leca et al., 2014b).

Once again, our findings are consistent with research on a number of bird and primate species showing that individuals not only engage in same-sex activity more or less concurrently with heterosexual activity, but homosexual interactions can also increase as individuals gain access to opposite-sex mates and can decrease in their absence (reviewed in Bagemihl, 1999). This is the exact reverse of what would be expected under the "lack of opposite-sex sexual competitor hypothesis."

With regards to the "bisexual preference hypothesis," higher OSRs did not result in more frequent female-to-male heterosexual solicitations directed to a larger number of male targets. This suggests that the mere increase in the ratio of *any* potential male mates relative to *any* potential female mates is not sufficient to enhance heterosexual proceptivity in female Japanese macaques. In contrast, we found that higher ratios of availability of *preferred* female partners relative to *preferred* male partners were associated with female homosexual consortships rather than female heterosexual consortships. These results support the "bisexual preference hypothesis", holding that female homosexual behavior is attributed to female preference for *certain* female mates relative to *certain* male mates. These preferences are more likely to be expressed as preferred same-sex sexual partners become relatively more abundant in a group. From this perspective, it is not the lack of males per se, which enhances the expression of female homosexual activity, but instead a scarcity of preferred male mates coupled with an abundance of preferred female sexual partners (cf. Vasey & Gauthier, 2000). This conclusion is consistent with the fact that same-sex sexual behavior in female Japanese macaques at Arashiyama does not reflect exclusive homosexuality, but rather is expressed in terms of a bisexual pattern of sexual behavior (Vasey, 2002, 2006).

Overall, we found that female homosexual behavior in the Japanese macaques of Arashiyama cannot be directly explained in terms of lack of heterosexual alternatives or a lack of male competitors. Instead, our findings are consistent with the view that, when a female Japanese macaque targets another female as a sexual partner, it appears to be a true choice rather than a by-default situation that occurs when males are not available as sexual partners, or a situation in which numerous females are available to mate with other females due to a scarcity of male sexual competitors. In other words, for the most part, female Japanese macaques choose same-sex sexual partners even though acceptable opposite-sex alternatives are available and motivated to mate with them (cf. Vasey & Gauthier, 2000), and even when they have to compete with male sexual rivals for access to female mates (Vasey, 1998). Overall, this study offers direct insights into the role of sociodemographic constraints (e.g., interactions between population densities, sex ratios at birth, dispersal patterns, and life history traits—such as age of reproductive maturity, reproductive lifespan, number of offspring—which affect group composition) for understanding mating competition and mate choice, which are key components of sexual selection (cf. Kvarnemo & Ahnesjö, 2002).

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