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Comparative Development of Heterosexual and Homosexual Behaviors in Free-Ranging Female Japanese Macaques

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Abstract We used cross-sectional focal data collected in adolescent and adult females to elucidate the comparative development of heterosexual and homosexual behaviors in female Japanese macaques (*Macaca fuscata*) living at Arashiyama, Japan, in a group where adult females routinely exhibit sexual interactions with both males and females. Our data fully or partially supported most of our predictions (20 out of 30) related to the "learning hypothesis," which postulated that adolescence would serve to provide young females with a period in which to practice, and gradually acquire, three types of adult female-like heterosexual and homosexual behavioral patterns, namely sexual solicitations, sexual mounts, and spatio-temporal coordination during consortships. However, there were marked differences in the development of heterosexual and homosexual behaviors. The percentage of homosexual mounts was significantly higher in adolescent than in adult females. Of the fully or partially supported predictions, 13 of 15 pertained to heterosexual activity whereas only seven of 15 pertained to homosexual activity. A number of sexual behavioral patterns (e.g., demonstrative solicitations, range of solicitation patterns and mounting postures, and grasping behavior during consortships) emerged earlier and developed faster when directed to females than when directed to males. We explain such differences in terms of risk of male aggression, males' disinterest in adolescent females' sexual solicitations, presence of motivated same-sex sexual partners, social facilitation, and sexual reward.

Keywords Learning hypothesis · Adolescence · Sexual solicitation · Mounting · Consortships · Primates

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Introduction

The normal development of sexual behavior in immature individuals depends upon the early (pre- and post-natal) exposure of their developing brains to two types of appropriate environments during critical periods. First, an endocrine hormonal environment with specific hormonal stimuli (e.g., testosterone, estrogens, and progesterone) is needed that organizes and activates neural mechanisms, which, in turn, mediate sexual behavior (i.e., the "organizational/activational hypothesis"). Second, a social environment with particular social stimuli (e.g., interactions with the mother, other adults, and peers) is needed that contributes to experiential processes supporting learning (i.e., the "learning hypothesis:" Dixson, 2012; Poiani, 2010).

Primates are characterized by the longest juvenile period in relation to life span of all mammals (Pereira & Fairbanks, 1993). According to the "learning hypothesis," prolonged juvenility is associated with behavioral patterns (e.g., foraging techniques) that necessitate acquiring a proportionally large amount of information and/or skills to reach adult competence before individuals become reproductively mature (Gunst, Boinski, & Fragaszy, 2010; Ross & Jones, 1999). When applied to sexual behaviors, the "learning hypothesis" is often rephrased as the "practice for heterosexual sex hypothesis," which holds that mounting interactions, including same-sex mounting, allow immature individuals to learn copulatory skills that are essential later in a heterosexual context (Dagg, 1984; Harlow, 1965; Pfaus et al., 2012; Poiani, 2010; Vasey, 1995). The "practice for heterosexual sex hypothesis" has been marshaled as an explanation for same-sex mounts in immature individuals in a variety of animal taxa (Gunst, Leca, & Vasey, 2013; Leca, Gunst, & Vasey, 2014a; MacFarlane, Blomberg, Kaplan, & Rogers, 2007; Vasey, 1995; Wallen, 1996). Thus, because vital and complex behaviors are expected to develop gradually during immaturity, we should find a developmental trajectory toward mature sexual

behaviors in species that exhibit complex sexual patterns, with young individuals showing behavioral precursors of fully adult sexual behavioral patterns.

In immature male primates, several lines of evidence suggest that the gradual development of mounting behavioral patterns and partner preferences reflects physical maturation, physiological changes, sensorimotor practice, and social experience (Dixson, 2012). First, research on cercopithecine monkeys (including macaques and baboons) showed that the "double foot-clasp mounting posture," typically performed by adult males, is a complex behavioral pattern that develops during the juvenile period and is strongly affected by hormonal and experiential factors (Gunst et al., 2013; Harlow, 1965; Wallen, 1996). This posture consists of grasping the mountee's calves with their feet and is the only mounting posture that allows for penile intromission during mount series in a dorso-ventral position in many species of Old World monkeys (Dixson, 2012). However, during infancy and juvenescence (0–2 years) and even later during adolescence (3–4 years), early mounting attempts by males were often characterized as being "disoriented," "improperly oriented" or "incomplete" (Gunst et al., 2013; Hanby & Brown, 1974; Owens, 1976).

Second, adolescent male macaques gradually learned penile intromission behavior during mounting. As they gained experience, their mount series patterns increasingly resembled those of adults (Hanby & Brown, 1974; Michael & Wilson, 1973; Wolfe, 1978). Moreover, before achieving intromissions, adolescent males directed their mounts to males and females whereas after achieving intromissions they mounted almost exclusively female partners (Wallen, 2001). Thus, it is likely that growing males learned the rewarding stimulus properties of intromissions after accomplishing full heterosexual intercourse for the first time (Wallen, Zehr, Herman, & Graves, 2003).

Third, the failure of immature male macaques reared in socially restricted conditions to correctly perform double foot-clasp mounts is likely explained by a lack of social opportunities that are required to develop active cooperation and sensorimotor coordination between the two partners involved in the mounting interaction (Wallen, Goldfoot, & Goy, 1981; Wallen et al., 2003). Fourth, the timing of selection of females as mounting partners by these immature males appeared to be dependent upon the presence of adult females in the group. When present, males were found to mount females more than males as soon as 1 year of age whereas peer-raised males (i.e., without their mothers, other adult females or female peers) did not develop a preference for females until 4 years of age (Goy, Wallen, & Goldfoot, 1974). Taken together, these studies clearly show the need for a period of maturation and practice, as well as an adequate social environment, in the development of adult-like sexual behaviors and sexual partner preferences in immature males.

Adolescence is a key phase for understanding the ontogeny of sexuality in female primates. In mammals, including primates, there is growing interest in the possibility that puberty and adolescence may represent an additional critical phase (or sensitive period) for the steroid hormone-dependent organization of sexual behavior during brain development (Schulz, Molenda-Figueira, & Sisk, 2009). During adolescence, most females experience their first estrus period (i.e., a phase of increased female sexual proceptivity, receptivity, and attractivity to males) and engage in their first sexual interactions (Dixson, 2012). The development of sexual behavioral patterns during female adolescence may involve a change in the frequency of a sexual behavior, a modification of the form of a sexual behavior typical of juvenile females, the appearance of new behaviors not observed in the sexual repertoire of juvenile females or a variation in the range of sexual partners. However, the developmental progression of female sexual behavior from infancy through adolescence and into adulthood has rarely been articulated.

There have been few quantitative studies on the development of sexual behavior and mate choice in non-human primate females (but see Eaton, Johnson, Glick, & Worlein, 1985; Hanby & Brown, 1974; Hashimoto, 1997; Perry & Manson, 1995; Wolfe, 1978; Woods & Hare, 2011). Like young males, adolescent female primates showed some form of ineptness in their sexual encounters and exhibited immature sexual behavioral patterns (Scott, 1984; Wolfe, 1978). In macaques, mounts received by adolescent females were made difficult by their inability to arch their backs and male mounters appeared to be pushing down the females' lumbar area with their hands in an attempt to improve the posture of the female (Wolfe, 1978). Even though such poorly executed sexual behaviors may entail lower costs during adolescence than during fully mature sexual life (Scott, 1984), they also show the need for an early period of rehearsal of sexual behavioral patterns and mate choice in immature females (Perry & Manson, 1995). Interestingly, although mounting behavior is a male-typical behavior, in many species females mount occasionally, while in a few others female mounting occurs quite commonly (Baum, 1979; Dixson, 2012; Sommer & Vasey, 2006; Vasey, 1995). As is the case with immature males, mounting by immature females is often characterized as immature in its expression (Scott, 1984; Wolfe, 1978). For example, mounts performed by young female gorillas have been described as "mechanically difficult" (Fischer & Nadler, 1978). The nascent expression of mounting behavior by immature female primates suggests that early practice of behavioral precursors is necessary before fully adult patterns of sexual behavior can be performed.

The free-ranging Arashiyama group of Japanese macaques (*Macaca fuscata*) located northwest of Kyoto city, Japan, is an ideal non-human primate population for developmental research on sexual behavior because, in addition to engaging in reproductive sexual interactions (e.g., Pavelka & Fedigan, 1999; Vasey, Foroud, Duckworth, & Kovacovsky, 2006; Vasey, Rains, VanderLaan, Duckworth, & Kovacovsky, 2008a), adult females in this group routinely exhibit various forms of homosexual,

heterosexual, and solitary non-conceptive sex, including same-sex solicitation and mounting behaviors (Vasey, 2002, 2004, 2006; Vasey & Duckworth, 2006; Vasey et al., 2008a; Vasey, VanderLaan, Rains, Duckworth, & Kovacovsky, 2008b), female–male mounting (Gouzoules & Goy, 1983; O'Neill, Fedigan, & Ziegler, 2004; Vasey & Duckworth, 2008), and masturbation (Wolfe, 1979). Structurally, homosexual behavioral patterns in adult females are very similar to typical heterosexual behavior (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). Although same-sex mounting among adult females is common at Arashiyama (but not at other sites: Vasey & Jiskoot, 2010), it does not seem to serve any obvious sociosexual function (Vasey, 2006). Instead, its expression is associated with immediate sexual reward, which occurred via genital stimulation (Vasey & Duckworth, 2006; Vasey & VanderLaan, 2012). At Arashiyama, Vasey (2006) hypothesized that adult females might mount adult males to restrict males' movement, focus males' attention, and prompt males to mount them (see also Beach, 1968).

Some previous studies have documented the development of sexual behavioral patterns in adolescent female Japanese macaques (Eaton et al., 1985; Hanby & Brown, 1974; Wolfe, 1978). However, there are two methodological limitations associated with these findings. First, some authors (cf. Hanby & Brown, 1974; Wolfe, 1978) did not use the focal-animal sampling technique to collect their behavioral data, which is the only technique that provides undisputable hourly frequencies of behaviors, provided random selection of the focal subjects (Altmann, 1974). Instead, they used the all-occurrence (i.e., behavior-dependent) sampling technique, which may result in biased frequencies, depending on the degree to which a behavior is both visible and conspicuous (Martin & Bateson, 1993). Second, most of these studies lacked clear distinctions between: (1) the different age and sex classes of subjects (Hanby & Brown, 1974; Wolfe, 1978), (2) the mounts performed and the mounts received (Hanby & Brown, 1974; Wolfe, 1978), and (3) the different contexts of mounts (Eaton et al., 1985; Wolfe, 1978).

A recent study of the development of sexual behaviors in female Japanese macaques living at Arashiyama showed that infant and juvenile females (aged one and two years) did not engage in sexual behavior of any kind (Leca, Gunst, & Vasey, 2014b). That study also showed that adolescence served to provide females with a period in which to practice adult female-like sexual behavioral patterns and, in that sense, supported the "learning hypothesis" (Leca et al., 2014b). However, the study by Leca et al. (2014b) did not distinguish between heterosexual and homosexual behaviors. No previous research has focused on adolescent female homosexual behavior and, as such, the manner in which such behavior develops is unknown. Moreover, how such behavior relates to females' heterosexual behavior needs to be detailed.

In the present study, we used cross-sectional focal data collected in adolescent (3 and 4 years) and adult females (ranging from 7 to 21 years) to elucidate the comparative development of heterosexual and homosexual behaviors in female Japanese macaques at Arashiyama. A recent study showed that female Japanese macaques, including adolescent females, received more severe aggression from adult males and incurred more serious injuries when engaged in heterosexual interactions than when engaged in homosexual interactions (Gunst, Leca, & Vasey, in press). Because severe aggression is more likely to be life-threatening on smaller-bodied adolescent females than on larger-bodied adult females and because female homosexual interactions seem to be safer than heterosexual ones (see also Vasey, 2006), we expected higher percentages of homosexual solicitations, mounts, and consortships in adolescent females than in adult females.

In addition, we tested a series of predictions pertaining to three types of homosexual and heterosexual behavioral patterns in females, namely sexual solicitations, sexual mounts, and spatio-temporal coordination during consortships. The predictions relate to age differences in the appearance, frequency, and form of various sexual behavioral patterns, as well as the range of sexual partners exhibited (Table 1). Our predictions were informed by what we know about the sexual solicitations, mounting, and consortships of adult female Japanese macaques at Arashiyama (Vasey, 2006).

Method

Study Species, Study Group, and Sampled Subjects

Japanese macaques are seasonal breeders and ovulate only during the breeding season (i.e., autumn and winter months: Shimizu, 2012). Like other macaque species, they are characterized by a multi-male/multi-female 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 Arashiyama group of Japanese macaques is one of the longest continuously studied non-human primate populations in the world (Huffman, Fedigan, Vasey, & Leca, 2012). Long-term genealogical and behavioral records on individually identified monkeys are available from years of collaborative research between observers working at this site (Leca, Huffman, & Vasey, 2012). The exact age of all group members was known.

During the study period, the Arashiyama group comprised eight resident adult males (≥5 years), 93 adult females (≥5 years), eight individuals aged 4 years (three males and five females), eight individuals aged 3 (three males and five females), 11 individuals aged 2 (seven males and four females), seven yearling

Table 1 Development of sexual behaviors in female Japanese macaques: hypotheses and predictions

Hypotheses	Predictions
1. Sexual solicitations	1a. Due to the need to practice the performance of sexual solicitations, their frequency should increase with age
	1b. Likewise, the range of solicitation patterns should increase with age
	1c. As females become older and learn more effective patterns of sexual solicitations, they should perform more demonstrative solicitations (e.g., hindquarter presentation) and less non-demonstrative solicitations (e.g., glancing)
	1d. As females become older and better able to assess the potential threat of aggression from others, they should perform more solicitations involving body contact with their targets (e.g., grabbing) and less non-contact solicitations (e.g., intense gazing)
	1e. As females become older and learn to select individuals more willing to engage in sexual interactions, the turnover of solicited targets should decrease
2. Sexual mounts	2a. As adult females routinely perform mounting behavior at Arashiyama, and because acquiring mounting skills requires practice, the frequency of mounts should increase with age
	2b. As females become older and acquire mounting skills, the frequency of complete mounts should increase
	2c. As females become older and learn to associate mounting behavior with pleasurable genital stimulation, the frequency of mounts with pelvic thrusting should increase
	2d. As females become older and learn to associate different mounting postures with different forms of genital stimulation, the range of complete mounting postures should increase
3. Spatio-temporal coordination during consortships	3a. As females become older and learn to court and mount more effectively, the duration of consortships should increase with age
	3b. The time spent in body contact during inter-mount intervals should increase with age because this would facilitate efficient series mounting
	3c. The time spent in dorso-ventral orientation during inter-mount intervals should increase with age because this position facilitates efficient series mounting
	3d. The time spent performing grasping behavior during inter-mount intervals should increase with age this behavior facilitates efficient series mounting
	3e. The time spent moving during inter-mount intervals should decrease with age because this behavior inhibits efficient series mounting
	3f. The frequency of ambiguous mounting initiations should decrease with age as females learn how to perform complete mounts

individuals aged 1 (four males and three females), and seven infants between 0 and 1 year (five males and two females). These values fall within the range of most free-ranging provisioned groups in this species (Yamagiwa & Hill, 1998). Males aged 1–3 years were referred to as juvenile males. 1- and 2-year-old females were referred to as juvenile females (i.e., post-infant and pre-estrus females) whereas 3- and 4-year-old females were referred to as adolescent females (i.e., 3-year-old females showing cues of first estrus and 4-year-old females showing cues of second estrus: cf. Nakamichi & Yamada, 2010; Pereira & Altmann, 1985). Thus, sex differences in the manner in which males and females were ascribed to particular age classes reflected sex differences in their respective patterns of sexual development.

These individuals belonged to 15 separate matrilineages. All ages mentioned in this study were rounded down to the nearest age. Because May was the peak month of birth at Arashiyama (Koyama, Takahata, Huffman, Norikoshi, & Suzuki, 1992) and because our observations were conducted during the fall and winter seasons, individuals reported as aged 0, 1, 2, 3, and 4 years were actually aged 0.5, 1.5, 2.5, 3.5, and 4.5 years, respectively. The number, age, and sex of sampled females are shown in Table 2. We randomly selected five adult females, aged 7, 10, 11, 15, and 21 years to compare with the five 3-year-old and five 4-year-old females. These five adult females were representative of adult female Japanese macaques of Arashiyama, with regards to the degree of heterosexual and homosexual activity exhibited and the range of sexual behaviors performed (Leca et al., 2014b; Vasey et al., 2006, 2008a, b). All research methods were approved in accordance with the Guide for the Care and Use of Primates prepared by the Primate Research Institute, Kyoto University.

Measures and Procedure

All the study subjects were sampled in October 2010-January 2011 and October 2011-March 2012 by NG who knew the

Table 2 Age and number of females sampled, with mean and total observation time

Age (years or class)	Number of individuals sampled	Total observation time (h)	Mean (±SD) observation time (h) per individual	Total observation time (h) during estrus period	Mean (±SD) observation time (h) per individual during estrus period
3	5	70.1	14.0 ± 0.1	17.5	3.5 ± 1.0
4	5	72.2	14.4 ± 0.2	14.5	2.9 ± 1.9
Adult	5	70.5	14.1 ± 0.1	21.5	4.3 ± 0.4

identities of all group members. Each individual was sampled only during one of these two study periods. The sampling technique was continuous pen-and-paper focal-animal sampling (Altmann, 1974). The typical daily duration of individual focal samples consisted of two consecutive blocks of 30 min. The visibility conditions were generally excellent. However, in the rare cases when the focal individual was lost during the first 30 min-time block, the focal sample was discarded. When the focal individual was lost during the second 30 min-time block, only the first 30 min-focal sample was retained. The focal individual was selected, independently of its activity, from an ordered list of possible focal individuals. The list was prepared in advance and assured that all individuals had equal sampling opportunities every week. The same focal individual could not be selected twice and sampled more than 1 h on the same day.

During focal follows, the following behaviors and interactions were continuously recorded: (1) *demonstrative sexual solicitations* performed by females. Demonstrative sexual solicitations included specific body postures (frozen stance and intense gazing, or "bird-dogging": Fedigan, 1982, hindquarter presentations, inclined-back presentations, and crouching on the ground or against a branch while screaming), body movements and gestures (lip quivering, head bobbing, ground smacking, hindquarter sniffing, hands-on-hindquarters solicitations, pushing, grabbing, and body spasms), and sexual vocalizations; (2) *non-demonstrative sexual solicitations* performed by females. Non-demonstrative sexual solicitations included following the target and sitting between 5 and 10 m away from it for at least 5 min while glancing at it repeatedly; (3) *sexual solicitations with body contact* performed by females, such as hands-on-hindquarters solicitations, pushing, and grabbing whereas *non-contact sexual solicitations* included all other solicitation patterns that could be performed by females from a distance; (4) *mounting behaviors* received and performed by females; and (5) *non-sexual consortship activities,* such as resting, foraging, moving, grooming interactions, playful interactions, and agonistic interactions (approach/avoidance events and aggressions with or without physical contact) (cf. Enomoto, 1974; Enomoto, Seiki, & Haruki, 1979; Fedigan, 1982; Vasey et al., 2008a). The identities of the non-focal individuals (males or females) involved in these interactions were also recorded and whether they were *performers* (i.e., partners) or *recipients* (i.e., targets) of these behaviors.

We also recorded the following six mounting postures (cf. Hanby & Brown, 1974; Vasey et al., 2006): (1) *improperly oriented mounts* in which the mounter crouched, stood or lied against a partner, readjusted his or her position by changing hand and foot grips, and thrusted at any portion of the partner's body other than the hindquarters or back, (2) *single or no foot-clasp mounts*, in which the mounter grasped from behind the mountee's back with its hands, while either standing bipedally with his or her feet on the ground and his or her knees slightly bent, or standing with one foot on the ground and the other grasping the mountee's hind limb, (3) *sitting mounts* occurred when the mounter sat on the mountee's back in a jockey-like position, while grasping the mountee's upper back with his or her hands and the mountee's lower back with his or her feet, (4) *reclining mounts* occurred when the mounter laid ventrally on the mountee's back, using his or her feet to grasp the mountee's legs above the ankles and his or her hands to grasp fur on the mountee's upper back, (5) *ventro-ventral mounts* occurred when the two participants embraced each other with their arms and legs, with chest-to-chest and belly-to-belly contact, facing each other in a standing, sitting, or lying position, and (6) *double foot-clasp mounts* involved the mounter grasping with his or her feet between the mountee's ankles and hips and with his or her hands on the mountee's back.

Improperly oriented mounts and dorso-ventral mounts with at least one of the mounter's foot in contact with the ground (i.e., single or no foot-clasp mounts) were referred to as *incomplete mounts*. Dorso-ventral mounts with the mounter's feet off the ground (i.e., sitting mounts, reclining mounts, and double foot-clasp mounts) as well as ventro-ventral mounts were referred to as *complete mounts*. For each mount, we recorded whether the mounter performed pelvic thrusting (defined as rhythmic movements of the mounter's pelvic girdle toward the mountee's perineum; cf. Vasey et al., 2006) or not.

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).

Within each intermount interval, we recorded whether the two consortship partners were in body contact, in *dorso-ventral*

orientation (i.e., both partners in a sitting position and belly-to-back contact), and engaged in *intermount grasping behavior*. An intermount grasping behavior was defined as one consort partner holding the other while sitting in belly-to-back contact. When adolescent were involved in consortships, ventro-ventral contact and dorso-dorsal contact were very minor body orientations compared to dorso-ventral orientation. Therefore, we discarded these two body orientations from the analyses. Each intermount interval ended with either an *unambiguous mounting initiation* or an *ambiguous mounting initiation*. An unambiguous mounting initiation was defined as a brief behavioral sequence (lasting less than 2 s), during which the future mountee and mounter resumed a quadrupedal stance and positioned themselves dorso-ventrally, with the former performing hindquarter presentation and the latter grabbing its partner's lower back (Vasey et al., 2006, 2008a, b). An ambiguous mounting initiation was defined as a longer behavioral sequence (lasting from 2 to 3 s), during which the two partners faced each other, bounced their heads and torsos from side to side, and alternatively attempted to grab each other's lower backs, as if they were undecided about which individual would be the mounter and which one would the mountee. In a few cases, ambiguous mounting initiations ended without any mounting behavior.

Sexual solicitations performed by females included *heterosexual solicitations* (i.e., directed to males) and *homosexual solicitations* (i.e., directed to females). Sexual mounts performed by females included *heterosexual mounts* (i.e., directed to males) and *homosexual mounts* (i.e., directed to females). Consortships involving females included *heterosexual consortships* (in the case of opposite-sex partners) and *homosexual consortships* (in the case of female partners). The *turnover of solicited targets* was defined as the number of different individuals that each sampled female solicited per hour.

Data Analysis

Absolute behavioral frequencies were defined as the number of behavioral events per hour of observation. To compare the relative frequencies of demonstrative versus non-demonstrative solicitations (Prediction 1c), we used the percentage of demonstrative solicitations. To compare the relative frequencies of solicitations with body contact versus non-contact solicitations (Prediction 1d), we used the percentage of solicitations with body contact.

In all analyses, we reported mean values ± SD and ranges from the minimum to the maximum values, rounded to the nearest non-decimal values (except for behavioral frequencies that were rounded to the nearest first decimal values). Frequencies of solicitations and mounts were weighted by the observation time during which each sampled individual showed typical estrus signs, such as a reddening of the facial and genital skin, vaginal secretion, and genital swelling and odor (Enomoto, 1974; Enomoto et al., 1979). The use of the term "estrus" in adolescent female Japanese macaques was further validated by the occurrence of ovarian cycle phases from 3 years of age, as measured by sex steroid hormonal profiles obtained from fecal sample analyses (Leca, unpublished data).

Because our raw and transformed data violated parametric assumptions, we conducted nonparametric tests. To test age differences between adult females and adolescent females (i.e., pooled data from 3- and 4-year-old females) in the frequency of homosexual solicitations, homosexual mounts, and homosexual consortships, we used Chi square tests for independence. To test age differences between 3-, 4-year-old, and adult females in all the other behavioral variables related to sexual solicitations, sexual mounts, and consortships, we used the Kruskal–Wallis H tests followed, when significant, by multiple paired comparisons based on mean ranks. Juvenile females (aged 1 and 2 years) were not included in the age comparisons because they did not showed any estrus signs and did not perform any sexual behaviors. Statistical analyses were performed using the SPSS 12.0 analytical program and the significance level was set at $\alpha = .05$. 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 1), and in that sense, our analyses were not exploratory (cf. Saville, 1990).

To determine the level of support for each prediction, we used the following conservative procedure: (1) If the overall age difference and all three pairwise age differences were statistically significant, and the age tendency was consistent with the predicted direction, the prediction was fully supported; (2) If the overall age difference but only two pairwise age differences were statistically significant, and were consistent with the predicted direction, the prediction was partly supported; (3) If the overall age difference was not statistically significant, or if the overall age difference and only one pairwise age difference were statistically significant, the prediction was not supported.

Results

Percentage of Homosexual Solicitations, Mounts, and Consortships in Adolescent and Adult Females

Contrary to our expectation, there was no significant difference between adolescent and adult females in the percentage of homosexual solicitations exhibited (61 vs. 53 %, respectively), $\chi^2(1) = 3.61$, $p = .057$ (Table 3). Likewise, there was no significant difference between 3-year-old and adult females in the percentage of homosexual solicitations exhibited (46 vs. 53 %, respectively), $\chi^2(1) = 1.49$. We also found that the percentage of homosexual solicitations was significantly lower in 3-year-old than in 4-year-old females (46 vs. 70 %, respectively), $\chi^2(1) = 16.55$, $p < .001$, which was not consistent with our

Table 3 Number of heterosexual and homosexual solicitations and sexual mounts performed by the sampled females, and consortships involving the sampled females at different ages

	Sexual solicitations performed			Sexual mounts performed			Consortships		
Age	All	Heterosexual	Homosexual	All	Heterosexual	Homosexual	All	Heterosexual	Homosexual
3	111	60	51	35	6	29	19	9	10
4	171	51	120	145	5	140	31	7	24
Adult	290	137	153	197	39	158	20	11	9

prediction that smaller-bodied females would refrain from interacting sexually with potentially dangerous males and rather seek safer homosexual interactions. However, in line with our prediction, the percentage of homosexual solicitations was significantly higher in 4-year-olds than in adult females (70 vs. 53 %, respectively), $\chi^2(1) = 13.51$, $p < .001$.

As expected, the percentage of homosexual mounts was significantly higher in adolescent females than in adult females (94 vs. 80 %, respectively), $\chi^2(1) = 15.31$, $p < .001$. Overall, 4-year-old females exhibited a significantly greater percentage of homosexual mounts than adult females (97 vs. 80 %, respectively), $\chi^2(1) = 19.91$, $p < .001$. In contrast, there was no significant difference between 3-year-olds and adult females in the percentage of homosexual mounts exhibited (83 vs. 80 %, respectively), $\chi^2(1) < 1$. Moreover, 4-year-old females exhibited a significantly greater percentage of homosexual mounts than 3-year-old females (97 vs. 83 %, respectively), $\chi^2(1) = 9.22$, $p = .008$.

Contrary to our expectation, although adolescent females exhibited a higher percentage of homosexual consortships than adult females, the difference was not statistically significant (68 vs. 45 %, respectively), $\chi^2(1) = 3.19$. Likewise, there was no significant difference in the percentage of homosexual consortships exhibited by 3-year-old and adult females (53 vs. 45 %, respectively), $\chi^2(1) < 1$, and no significant difference in the percentage of homosexual consortships exhibited by 3- and 4-year-old females (53 vs. 77 %, respectively), $\chi^2(1) = 3.33$. However, in line with our prediction, the percentage of homosexual consortships was significantly higher in 4-year-olds than in adult females (77 vs. 45 %, respectively), $\chi^2(1) = 5.59$, $p = .018$.

Development of Sexual Solicitations (Hypothesis 1)

Frequency of Solicitations (Prediction 1a)

As predicted, the frequency of heterosexual solicitations tended to increase with age (mean frequency for 3-year-old females: 3.7 ± 2.5 heterosexual solicitations/h, range: 1.4–7.7; 4-year-old females: 4.7 ± 3.0, range: 0.8–7.5; adult females: 6.5 ± 3.3, range: 1.3–10.0). However, this tendency was not statistically significant, Kruskal–Wallis test, $\chi^2(2) = 1.58$. A similar non-significant trend was found in homosexual solicitations (mean frequency for 3-year-old females: 2.4 ± 2.6 homosexual solicitations/h, range: 0–6.2; 4-year-old females: 4.9 ± 6.9, range: 0–15.8; adult females: 7.2 ± 7.7, range: 1.5–16.9), Kruskal–Wallis test, $\chi^2(2) = 1.24$. Therefore, Prediction 1a was not supported for heterosexual and homosexual solicitations.

Range of Solicitation Patterns (Prediction 1b)

We found a significant age difference in the range of heterosexual solicitation patterns, Kruskal–Wallis test, $\chi^2(2) = 8.87$, $p = .012$. Multiple pair comparisons showed that adult females performed a larger range of heterosexual solicitations (mean number of solicitation patterns: 9.4 ± 2.5, range: 5–11) than 3-year-old females (3.2 ± 1.8, range: 1–6; $p < .05$) and 4-year-old females (4.6 ± 1.5, range: 3–7; $p < .05$). Although 4-year-old females performed a larger range of heterosexual solicitation patterns than 3-year-old females, this difference was not statistically significant.

The range of homosexual solicitations also tended to increase with age (mean number of solicitation patterns performed by 3-year-old females: 2.8 ± 2.8, range: 0–6; 4-year-old females: 3.8 ± 4.5, range: 0–10; adult females: 7.6 ± 3.6, range: 4–12). However, this trend was not statistically significant, Kruskal–Wallis test, $\chi^2(2) = 3.58$. Therefore, Prediction 1b was partly supported for heterosexual solicitations but not supported for homosexual solicitations. A number of adult sexual solicitation patterns were not observed in 3- and 4-year-old females in either a heterosexual or homosexual context and these included intense gazing, lip quivering, head bobbing, and pushing.

Percentage of Demonstrative Solicitations (Prediction 1c)

We found a significant age difference in the percentage of demonstrative heterosexual solicitations performed by females, Kruskal–Wallis test, $\chi^2(2) = 7.62$, $p = .022$. Multiple pair comparisons showed that adult females performed significantly more demonstrative heterosexual solicitations (mean percentage: 83.6 ± 8.1 %, range: 72–94 %, $N = 116$ demonstrative heterosexual solicitations) than 3-year-old females (30.7 ± 24.4 %, range: 0–61 %, $N = 22$; $p < .05$) and 4-year-old females (60.1 ± 24.6 %, range: 33–100 %, $N = 27$; $p < .05$). Moreover, 4-year-old females performed significantly more demonstrative heterosexual solicitations than 3-year-old females ($p < .05$).

The percentage of demonstrative homosexual solicitations also tended to increase with age (mean percentage for 3-year-old females: 69.2 ± 10.1 %, range: 60–80 %, $N = 35$ demonstrative homosexual solicitations; 4-year-old females: 85.2 ± 21.2 %, range: 61–100 %, $N = 106$; adult females: 95.8 ± 7.1 %, range: 83 ± 100 %, $N = 149$). However, this tendency was not statistically significant, Kruskal–Wallis test, $\chi^2(2) = 4.94$, $p = .085$. Therefore, Prediction 1c was fully supported for heterosexual solicitations but not supported for homosexual solicitations.

Percentage of Solicitations with Body Contact (Prediction 1d)

We found a significant age difference in the percentage of heterosexual solicitations with body contact performed by females, Kruskal–Wallis test, $\chi^2(2) = 9.87$, $p = .007$. Multiple pair comparisons showed that adult females performed significantly more heterosexual solicitations with body contact (mean percentage: 21.9 ± 7.5 %, range: 16–34 %, $N = 27$ heterosexual solicitations with body contact) than 3-year-old females (0 %, $N = 0$; $p < .05$) and 4-year-old females (6.2 ± 9.1 %, range: 0–0 %, $N = 2$; $p < .05$). Moreover, 4-year-old females performed significantly more demonstrative heterosexual solicitations than 3-year-old females ($p < .05$).

We found no significant age difference in the percentage of homosexual solicitations with body contact performed by females, Kruskal–Wallis test, $\chi^2(2) = 2.08$; mean percentage for 3-year-old females: 15.7 ± 19.5 %, range: 0–37 %, $N = 5$ homosexual solicitations with body contact; 4-year-old females: 10.9 ± 13.2 %, range: 0–26 %, $N = 24$; adult females: 27.3 ± 7.7 %, range: 20 ± 37 %, $N = 36$. Therefore, Prediction 1d was fully supported for heterosexual solicitations but not supported for homosexual solicitations.

Turnover of Solicited Targets (Predictions 1e)

When considering heterosexual solicitations, we found a significant age difference in the turnover of male targets solicited by females, Kruskal–Wallis test, $\chi^2(2) = 8.92$, $p = .012$. Multiple pair comparisons showed that adult females solicited significantly fewer male targets (mean number of targets/h: 0.5 ± 0.1, range: 0–1, $N = 11$ male targets) than 3-year-old females (1.6 ± 0.7, range: 1–3, $N = 26$; $p < .05$) and 4-year-old females (2.2 ± 1.3, range: 1–4, $N = 24$; $p < .05$). There was no statistical difference in the turnover of male targets solicited by 3-year-old and 4-year-old females.

When considering homosexual solicitations, we found no significant age difference in the turnover of female targets solicited by females, Kruskal–Wallis test, $\chi^2(2) < 1$; mean number of targets/h solicited by 3-year-old females: 0.4 ± 0.4, range: 0–1, $N = 7$ female targets; 4-year-old females: 0.3 ± 0.3, range: 0–1, $N = 5$; adult females: 0.3 ± 0.1, range: 0–1, $N = 6$. Therefore, Prediction 1e was partly supported for heterosexual solicitations but not supported for homosexual solicitations.

Development of Sexual Mounts (Hypothesis 2)

Frequency of mounts (Prediction 2a)

We found a significant age difference in the frequency of heterosexual (i.e., female-to-male) mounts performed by females, Kruskal–Wallis test, $\chi^2(2) = 6.74$, $p = .034$. Multiple pair comparisons showed that adult females performed significantly more mounts (mean frequency: 2.3 ± 2.3 mounts/h, range: 0.7–6.3) than 3-year-old females (0.4 ± 0.7, range: 0–1.7; $p < .05$) and 4-year-old females (0.4 ± 0.7, range: 0–1.6; $p < .05$). There was no significant difference in the frequency of mounts performed by 3- and 4-year-old females.

We also found a significant age difference in the frequency of homosexual mounts performed by females, Kruskal–Wallis test, $\chi^2(2) = 6.18$, $p = .046$. Multiple pair comparisons showed that 4-year-old females performed significantly more mounts than 3-year-old females (mean frequency: 7.8 ± 5.6 mounts/h, range: 0–14.6, and 1.8 ± 2.7, range: 0–6.7, respectively; $p < .05$). Moreover, adult females performed significantly more mounts (8.5 ± 1.6, range: 7–10.7) than 3-year-old females ($p < .05$). Although adult females performed more mounts than 4-year-old females, this difference was not statistically significant. Therefore, Prediction 2a was partly supported for heterosexual and homosexual mounts.

Frequency of Complete Mounts (Prediction 2b)

We found a significant age difference in the frequency of complete heterosexual mounts performed by females, Kruskal–Wallis test, $\chi^2(2) = 6.64$, $p = .036$. Multiple pair comparisons showed that adult females performed significantly more complete heterosexual mounts (mean percentage of complete heterosexual mounts: 98.9 ± 2.3 %, range: 95–100 %, $N = 38$ complete heterosexual mounts) than 3-year-old females (10.0 ± 14.1 %, range: 0–20 %, $N = 1$; $p < .05$) and 4-year-old females (12.5 ± 17.7 %, range: 0–25 %, $N = 1$; $p < .05$). Although 4-year-old females performed more complete heterosexual mounts than 3-year-old females, the difference was not statistically significant.

We also found a significant age difference in the frequency of complete homosexual mounts performed by females, Kruskal–Wallis test, $\chi^2(2) = 9.73$, $p = .008$. Multiple pair comparisons showed that 4-year-old females performed significantly more complete homosexual mounts than 3-year-old females (mean percentage of complete homosexual mounts: 89.4 ± 7.5 %, range: 83–100 %, $N = 124$ complete homosexual mounts, and 27.9 ± 19.4 %, range: 0–45 %, $N = 11$, respectively; $p < .05$).

Moreover, adult females performed significantly more complete homosexual mounts (98.7 ± 2.9 %, range: 93–100 %, $N = 156$) than 3-year-old females ($p < .05$). Although adult females performed more complete homosexual mounts than 4-year-old females, the difference was not statistically significant. Therefore, Prediction 2b was partly supported for heterosexual and homosexual mounts.

Pelvic Thrusting (Prediction 2c)

We found a significant age difference in the frequency of heterosexual mounts with pelvic thrusting performed by females, Kruskal–Wallis test, $\chi^2(2) = 6.54$, $p = .038$. Multiple pair comparisons showed that adult females performed significantly more heterosexual mounts with pelvic thrusting (mean percentage: 28.6 ± 8.4 %, range: 20–40 %, $N = 10$ heterosexual mounts with pelvic thrusting) than 3-year-old females (0 ± 0 %; $p < .05$) and 4-year-old females (0 ± 0 %; $p < .05$). There was no statistical difference in the frequency of heterosexual mounts with pelvic thrusting performed by 3- and 4-year-old females.

We also found a significant age difference in the frequency of homosexual mounts with pelvic thrusting performed by females, Kruskal–Wallis test, $\chi^2(2) = 8.70$, $p = .013$. Multiple pair comparisons showed that adult females performed significantly more homosexual mounts with pelvic thrusting (mean percentage: 70.9 ± 6.4 %, range: 61–79 %, $N = 112$ homosexual mounts with pelvic thrusting) than 3-year-old females (17.9 ± 17.9 %, range: 0–33 %, $N = 3$; $p < .05$) and 4-year-old females (21.1 ± 9.0 %, range: 12–33 %, $N = 24$; $p < .05$). Although 4-year-old females performed more homosexual mounts with pelvic thrusting than 3-year-old females, the difference was not statistically significant. Therefore, Prediction 2c was partly supported for heterosexual and homosexual mounts.

Range of Complete Mounting Postures (Prediction 2d)

We found a significant age difference in the range of complete heterosexual mounting postures performed by females, Kruskal–Wallis test, $\chi^2(2) = 10.29$, $p = .006$. Multiple pair comparisons showed that adult females performed a significantly larger range of heterosexual mounting postures (mean number of postures: 2.2 ± 0.8, range: 1–3) than 3-year-old females (0.2 ± 0.4, range: 0–1; $p < .05$) and 4-year-old females (0.2 ± 0.4, range: 0–1; $p < .05$). There was no statistical difference in the range of heterosexual mounting postures performed by 3- and 4-year-old females.

The most frequent heterosexual mounting postures performed by 3-year-old females and 4-year-old females were, respectively, improperly oriented mounts (67 %) and single or no foot-clasp mounts (60 %; Fig. 1). The heterosexual mounting postures not observed in 3- and 4-year-old females included sitting mounts, ventro-ventral mounts, and double foot-clasp mounts. The most frequent heterosexual mounting posture performed by adult females was reclining mounts (62 %). When adult females mounted males, they did not perform improperly oriented mounts and ventro-ventral mounts and very rarely single or no foot-clasp mounts (3 %).

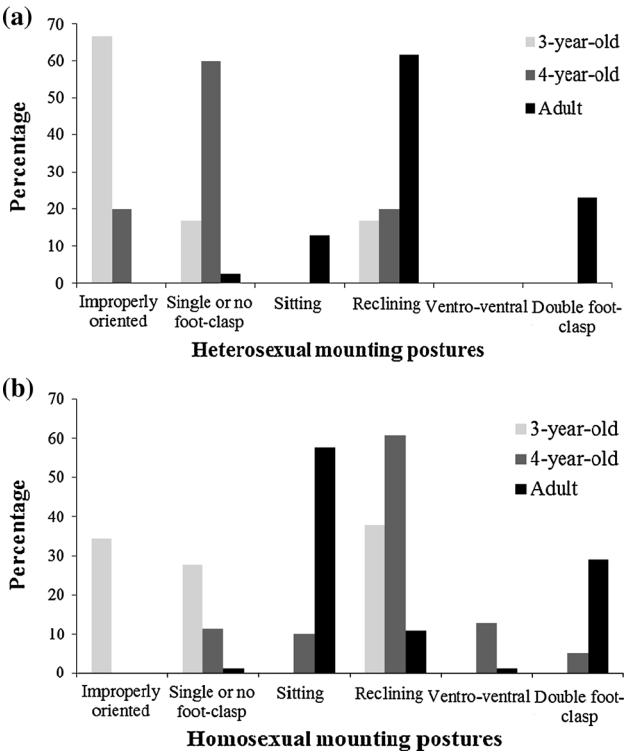

Fig. 1 Percentage of heterosexual (**a**) and homosexual (**b**) mounting postures performed by females of different age classes

We found a significant age difference in the range of complete homosexual mounting postures performed by females, Kruskal–Wallis test, $\chi^2(2) = 8.34$, $p = .015$. Multiple pair comparisons showed that 4-year-old females performed a significantly larger range of homosexual mounting postures than 3-year-old females (mean number of postures: 2.2 ± 1.5, range: 0–4, and 0.6 ± 0.5, range: 0–1, respectively; $p < .05$). Moreover, adult females performed a significantly larger range of homosexual mounting postures (3.2 ± 0.4, range: 3–4) than 3-year-old females ($p < .05$). Although adult females performed a larger range of homosexual mounting postures than 4-year-old females, the difference was not statistically significant. Therefore, Prediction 2d was partly supported for heterosexual and homosexual mounts.

The most frequent homosexual mounting postures performed by 3- and 4-year-old females were reclining mounts (38 and 61 %, respectively). When mounting females, 3-year-old females did not perform sitting mounts, ventro-ventral mounts, and double foot-clasp mounts and 4-year-old females did not perform improperly oriented mounts (Fig. 1). The most frequent homosexual mounting posture performed by adult females was sitting mounts (58 %). As with 4-year-old females, adult females

did not perform improperly oriented mounts when mounting females.

Development of Spatio-Temporal Coordination during Consortships (Hypothesis 3)

Duration of Consortships (Prediction 3a)

We found a significant age difference in the duration of heterosexual consortships, Kruskal–Wallis test, $\chi^2(2) = 14.12$, $p = .001$. Multiple pair comparisons showed that 4-year-old females were engaged in significantly longer heterosexual consortships than 3-year-old females (mean duration: 23.8 ± 13.8 min, range: 9–50, and 8.3 ± 3.5 min, range: 4–14, respectively; $p < .05$). Moreover, adult females were engaged in significantly longer heterosexual consortships (29.2 ± 13.7 min, range: 9–58) than 3-year-old females ($p < .05$). Although adult females engaged in longer heterosexual consortships than 4-year-old females, the difference was not statistically significant.

We also found a significant age difference in the duration of homosexual consortships, Kruskal–Wallis test, $\chi^2(2) = 14.32$, $p = .001$. Multiple pair comparisons showed that 4-year-old females were engaged in significantly longer homosexual consortships than 3-year-old females (mean duration: 28.7 ± 15.6 min, range: 5–63, and 10.3 ± 5.8 min, range: 4–23, respectively; $p < .05$). Moreover, adult females were engaged in significantly longer homosexual consortships (34.0 ± 16.6 min, range: 8–61) than 3-year-old females ($p < .05$). Although adult females engaged in longer homosexual consortships than 4-year-old females, the difference was not statistically significant. Therefore, Prediction 3a was partly supported for heterosexual and homosexual consortships.

Time Spent in Body Contact During Inter-mount Intervals (Prediction 3b)

When considering heterosexual consortships, we found a significant age difference in the time spent by male and female partners in body contact, Kruskal–Wallis test, $\chi^2(2) = 16.93$, $p < .002$. Multiple pair comparisons showed that 4-year-old females spent significantly more time in body contact with their male partners than 3-year-old females (mean percentage of time: 70.5 ± 14.1 %, range: 56–90 %, and 36.0 ± 6.6 %, range: 27–50 %, respectively; $p < .05$). Moreover, adult females spent significantly more time in body contact with their male partners (68.5 ± 10.9 %, range: 44–81 %) than 3-year-old females ($p < .05$). Adult females and 4-year-old females did not differ significantly in the time spent in body contact with their male partners.

The time spent by female partners in body contact during female homosexual consortships tended to increase with age (mean percentage of time for 3-year-old females: 73.8 ± 9.8 %, range: 56–91 %; 4-year-old females: 77.5 ± 12.4 %, range: 43–94 %; adult females: 80.2 ± 12.1 %, range: 50–92 %). However, the difference was not statistically significant, Kruskal–Wallis test, $\chi^2(2) = 3.05$. Therefore, Prediction 3b was partly supported for heterosexual consortships and not supported for homosexual consortships.

Time Spent in Dorso-ventral Orientation During Inter-mount Intervals (Prediction 3c)

When considering heterosexual consortships, we found a significant age difference in the time spent by male and female partners in dorso-ventral orientation, Kruskal–Wallis test, $\chi^2(2) = 20.82$, $p < .001$. Multiple pair comparisons showed that adult females spent significantly more time in dorso-ventral orientation with their male partners (mean percentage of time: 52.9 ± 12.8 %, range: 32–68 %) than 3-year-old females (24.1 ± 7.0 %, range: 14–33 %; $p < .05$) and 4-year-old females (12.9 ± 8.2 %, range: 0–25 %; $p < .05$). There was no significant difference in the time spent by 3- and 4-year-old females in dorso-ventral orientation with their male partners.

When considering homosexual consortships, we found a significant age difference in the time spent by female partners in dorso-ventral orientation, Kruskal–Wallis test, $\chi^2(2) = 16.88$, $p < .001$. Multiple pair comparisons showed that adult females spent significantly more time in dorso-ventral orientation with their female partners (mean percentage of time: 51.6 ± 15.1 %, range: 27–81 %) than 3-year-old females (20.1 ± 12.9 %, range: 0–50 %; $p < .05$) and 4-year-old females (20.6 ± 12.5 %, range: 0–54 %; $p < .05$). There was no significant difference in the time spent by 3- and 4-year-old females in dorso-ventral orientation with their female partners ($p > .05$). Therefore, Prediction 3c was partly supported for heterosexual and homosexual consortships.

Time Spent Performing Intermount Grasping Behavior During Consortships (Prediction 3d)

When considering heterosexual consortships, we found a significant age difference in the time spent by consortship partners in dorso-ventral orientation, Kruskal–Wallis test, $\chi^2(2) = 19.87$, $p < .001$. Multiple pair comparisons showed that adult females spent significantly more time performing intermount grasping behavior with their male partners (mean percentage of time: 33.4 ± 10.5 %, range: 17–47 %) than 3-year-old females (2.9 ± 4.4 %, range: 0–10 %; $p < .05$) and 4-year-old females (3.0 ± 4.9 %, range: 0–13 %; $p < .05$). There was no significant difference in the time spent by 3- and 4-year-old females performing intermount grasping behavior with their male partners.

When considering homosexual consortships, we found no significant age difference in the time spent by consortship partners in dorso-ventral orientation, Kruskal–Wallis test, $\chi^2(2) =$

5.96, $p = .051$; mean percentage of time for 3-year-old females: 14.2 ± 9.9 %, range: 0–33 %; 4-year-old females: 12.6 ± 6.6 %, range: 0–29 %; adult females: 18.3 ± 4.5 %, range: 12–25 %. Therefore, Prediction 3d was partly supported for heterosexual consortships but not supported for homosexual consortships.

Time Spent Moving During Inter-mount Intervals (Prediction 3e)

We found no significant age difference in the time spent moving by consortship partners during heterosexual consortships, Kruskal–Wallis test, $\chi^2(2) = 5.35$, $p = .069$; mean percentage of time for 3-year-old females: 3-year-old females: 20.2 ± 4.0 %, range: 14–25 %; 4–year-old females: 14.9 ± 4.3 %, range: 10–22 %; adult females: 20.4 ± 6.4 %, range: 7–33 %, and homosexual consortships, $\chi^2(2) < 1$; 3-year-old females: 18.0 ± 12.3 %, range: 4–50 %; 4-year-old females: 18.6 ± 7.9 %, range: 6–33 %; adult females: 17.4 ± 8.7 %, range: 8–37 %. Therefore, Prediction 3e was not supported for heterosexual and homosexual consortships.

Frequency of Ambiguous Mounting Initiations (Prediction 3f)

When considering heterosexual consortships, we found a significant age difference in the frequency of ambiguous mounting initiations by female directed to males, Kruskal–Wallis test, $\chi^2(2) = 14.40$, $p = .001$. Multiple pair comparisons showed that 4-year-old females performed significantly fewer ambiguous mounting initiations than 3-year-old females (mean frequency: 0.6 ± 1.1/h of heterosexual consortships, range: 0–2, and 8.3 ± 6.3, range: 0–16, respectively; $p < .05$). Moreover, adult females performed significantly fewer ambiguous mounting initiations (0 ± 0) than 3-year-old females ($p < .05$). Although adult females performed fewer ambiguous mounting initiations than 4-year-old females, the difference was not statistically significant.

When considering homosexual consortships, we found a significant age difference in the frequency of ambiguous mounting initiations between female partners, Kruskal–Wallis test, $\chi^2(2) = 27.50$, $p < .001$. Multiple pair comparisons showed that 4-year-old females performed significantly fewer ambiguous mounting initiations than 3-year-old females (mean frequency: 0.3 ± 0.8/h of heterosexual consortships, range: 0–3, and 11.8 ± 8.3, range: 0–30, respectively; $p < .05$). Moreover, adult females performed significantly fewer ambiguous mounting initiations (0.2 ± 0.6, range: 0–2) than 3-year-old females ($p < .05$). Although adult females performed fewer ambiguous mounting initiations than 4-year-old females, the difference was not statistically significant. Therefore, Prediction 3d was partly supported for heterosexual and homosexual consortships.

Discussion

Percentage of Homosexual Solicitations, Mounts, and Consortships in Adolescent and Adult Females

In the Arashiyama group of Japanese macaques, adult females routinely perform both heterosexual and homosexual behaviors (Vasey, 2006; Vasey & Duckworth, 2006, 2008; Vasey & VanderLaan, 2012; Vasey et al., 2006, 2008a, b). The age of 3 years corresponds to the developmental stage when most Japanese macaque females experience their first estrus (cf. Nigi, 1976). Among 3-year-old females, almost half of all sexual solicitations (46 %) were homosexual and the majority of sexual mounts (83 %) and consortships (53 %) were homosexual as well (Table 3). Among 4-year-old females, the majority of all sexual behavior was homosexual, with 70 % of sexual solicitations, 97 % of mounts, and 77 % of consortships involving same-sex sexual partners (Table 3). These values are considerably higher than those reported for homosexual behavior between adult females in the Arashiyama population (47 % in 1976–1977: Takahata, 1982; 23 % in 1977–1978: Wolfe, 1984; 26 % in 1984–1985: Huffman, personal communication). Our results demonstrated that frequent female homosexual behavior in Arashiyama Japanese macaques has an early developmental onset.

As expected, an omnibus test indicated that the percentage of homosexual mounts was significantly higher in adolescent (i.e., 3- and 4-year-old) females than in adult females. However, closer examination of the data indicated that significant differences between 4-year-old females and adult females were driving this effect. In contrast, 3-year-old females did not differ from adult females in terms of percentage of homosexual mounts. Contrary to our predictions, two additional omnibus tests indicated that the percentage of homosexual solicitations and consortships exhibited were not significantly different between adolescent and adult females. However, once again, closer examination of the data indicated the percentages of homosexual solicitations and consortships performed by 3-year-old females were similar to that of adult females. In contrast, the percentage of homosexual solicitations and consortships was significantly higher significantly among 4-year-old females.

There are at least two complimentary reasons as to why the observed developmental patterns for percentages of homosexual solicitations, mounts, and consortships exist. First, adolescent female Japanese macaques are more likely to receive severe aggressions by adult males and incur more serious injuries when involved in heterosexual interactions compared to homosexual ones (Gunst et al., in press). In macaques, the first and second estrus are risky periods for sexually inexperienced adolescent females who are easy targets of repeated and sometimes severe aggressions by adult males during the mating season (Enomoto, 1981; Perry & Manson, 1995). Therefore, young and vulnerable

female mounters may prefer to engage in safer homosexual interactions in lieu of more risky heterosexual ones. During their first estrus, 3-year-old females often display exaggerated sexual solicitations compared to those displayed by older females (see Anderson & Bielert, 1994). Exaggerated sexual solicitations coupled with the surge of sex steroid hormones females experience during their first estrus may help to account for the adult-like levels of heterosexual interactions exhibited by 3-year-old females. In this hormonal and behavioral context, sexually inexperienced 3-year-old females may attempt to engage in sexual activity with males at a similar frequency to adult females, but males, particularly sub-adult and adult males, would, on average, respond aggressively to such attempts. After being targeted with such aggression, young females may be less inclined to pursue sexual activity with males and, accordingly, female-to-male sexual solicitations, mounting, and consortships would decrease in 4-year-olds relative to female homosexual activity. During their fourth year of life, females may refine their skills at identifying male mates that are less aggressive, more receptive, and more cooperative consortships partners. Once this period of learning takes place, the frequency with which females engage in sexual activity with males may increase once again to adult-like levels.

Second, Vasey and Duckworth (2006) demonstrated that female mounters routinely obtain genital stimulation by rubbing their vulvar region against a female mountee's body during sitting mounts. The vulvar region in female macaques is richly innervated with nerve endings that are specialized for receiving and transmitting erotic sensations (Hill, 1974; Winkelmann, 1959). Consequently, by directing sitting mounts with thrusting to same-sex partners, females have some control over the amount of immediate sexual reward they obtain. The data presented here indicated that 3-year-old females did not engage in sitting mounts whereas 4-year-old females began to exhibit sitting mounts and, in adulthood, sitting mounts became the primary mounting posture exhibited by females. Further, 4-year-old females performed more pelvic thrusting than 3-year-old females although this difference was not significant. Taken together, these data suggest that 3-year-old females had no opportunity to experience immediate sexual reward via genital stimulation during female–female sitting mounts whereas 4-year-old females did. By adulthood, the majority of same-sex mounts that females exhibited were sitting mounts and the vast majority of those were performed with pelvic thrusting against the mountees' backs (see also Vasey & Duckworth, 2006) This might account, in part, for the significant increase female–female mounting observed in 4-year-old females compared to their 3-year-old counterparts.

Testing the Learning Hypothesis in the Development of Heterosexual and Homosexual Behaviors

On the basis of the "learning hypothesis," we predicted that adolescence would serve to provide young female Japanese macaques living at Arashiyama with a period in which to practice, and gradually acquire, three types of adult female-like heterosexual and homosexual behavioral patterns, namely sexual solicitations directed to male or female targets, as well as sexual mounts and spatio-temporal coordination during consortships with male or female mates. When considering both heterosexual and homosexual behavioral patterns, we found significant age differences and tendencies that were fully or partially consistent with 20 of the 30 predictions we generated from the "learning hypothesis" (Table 4). Overall then, adolescent females exhibited immature patterns of heterosexual and homosexual behavior that gradually converged around an adult-like pattern.

However, when considering the comparative development of heterosexual and homosexual behaviors, our analyses revealed marked differences. Of the fully or partially supported predictions, 13 of 15 pertained to heterosexual activity whereas only seven of 15 pertained to homosexual activity (see third column in Table 4).

A comparison of 3-year-old (i.e., first estrus) females with 4-year-old (i.e., second estrus) females and adult females indicated that there were three major categories of sexual behaviors that varied in speed of development. *Fast-developing* behaviors (and *fast-disappearing* behaviors; see below) took on an adult-like pattern by 4 years of age (4 of 13 supported predictions for heterosexual behavior; 6 of 7 supported predictions for homosexual behavior; Table 4). In such instances, 4-year-old females resembled adult females, but differed from 3-year-old females. *Slow-developing behaviors* (and *slow-disappearing* behaviors; see below) did not take on an adult-like pattern until adulthood (7 of 13 supported predictions for heterosexual behavior; 1 of 7 supported predictions for homosexual behavior; Table 4). In such instances, 3- and 4-year-olds resembled each other, but differed from adults. *Intermediate-developing* behaviors where those in which our predictions were fully met (2 of 13 supported predictions for heterosexual behavior; Table 4). In such instances, 3-year-olds differed significantly from 4-year-olds and both differed significantly from adults.

For nine of the 15 behavioral patterns we examined, heterosexual and homosexual behavior differed with respect to patterns of development. Overall, these nine behavioral patterns were slower to develop in a heterosexual context than in a homosexual one although the precise pattern varied in five unique ways (Table 4). First, the frequency of mounts, the frequency of complete mounts, and the range of complete mounting postures were slow-developing in a heterosexual context and fast-developing in a homosexual context. Second, the turnover of solicited partners was a slow-disappearing behavioral pattern in a heterosexual context, but did not differ significantly between age classes in a homosexual context. In other words, within a homosexual context, this behavioral pattern was expressed in an adult-like manner by both 3- and 4-year-old females. Third, the range of solicitation patterns exhibited and the time spent

Table 4 Development of heterosexual and homosexual behaviors in female Japanese macaques: hypotheses, predictions, and results

Predictions	Significant overall age difference	Significant pairwise age differences	Prediction fully/ partly/not supported
Hypothesis 1 (Sexual solicitations)			
1a. Frequency of solicitations should increase with age			
Heterosexual solicitations	No	na	Not
Homosexual solicitations	No	na	Not
1b. Range of solicitation patterns should increase with age			
Heterosexual solicitations	Yes	3y < A, 4y < A	Partly
Homosexual solicitations	No	na	Not
1c. Percentage of demonstrative solicitations should increase with age			
Heterosexual solicitations	Yes	3y < 4y < A	Fully
Homosexual solicitations	No	na	Not
1d. Percentage of solicitations with body contact should increase with age			
Heterosexual solicitations	Yes	3y < 4y < A	Fully
Homosexual solicitations	No	na	Not
1e. Turnover of solicited targets should decrease with age			
Heterosexual solicitations	Yes	3y > A, 4y > A	Partly
Homosexual solicitations	No	na	Not
Hypothesis 2 (Sexual mounts)			
2a. Frequency of mounts should increase with age			
Heterosexual mounts	Yes	3y < A, 4y < A	Partly
Homosexual mounts	Yes	3y < 4y, 3y < A	Partly
2b. Frequency of complete mounts should increase with age			
Heterosexual mounts	Yes	3y < A, 4y < A	Partly
Homosexual mounts	Yes	3y < 4y, 3y < A	Partly
2c. Frequency of mounts with pelvic thrusting should increase with age			
Heterosexual mounts	Yes	3y < 4y, 3y < A	Partly
Homosexual mounts	Yes	3y < 4y, 3y < A	Partly
2d. Range of complete mounting postures should increase with age			
Heterosexual mounts	Yes	3y < A, 4y < A	Partly
Homosexual mounts	Yes	3y < 4y, 3y < A	Partly
Hypothesis 3 (Spatio-temporal coordination in consortships)			
3a. Duration of consortships should increase with age			
Heterosexual consortships	Yes	3y < 4y, 3y < A	Partly
Homosexual consortships	Yes	3y < 4y, 3y < A	Partly
3b. Time spent in body contact should increase with age			
Heterosexual consortships	Yes	3y < 4y, 3y < A	Partly
Homosexual consortships	No	na	Not
3c. Time spent in dorso-ventral orientation should increase with age			
Heterosexual consortships	Yes	3y < A, 4y < A	Partly
Homosexual consortships	Yes	3y < A, 4y < A	Partly
3d. Time spent performing grasping behavior should increase with age			
Heterosexual consortships	Yes	3y < A, 4y < A	Partly
Homosexual consortships	No	na	Not
3e. Time spent moving should decrease with age			
Heterosexual consortships	No	na	Not
Homosexual consortships	No	na	Not
3f. Frequency of ambiguous mounting initiations should decrease with age			
Heterosexual consortships	Yes	3y > 4y, 3y > A	Partly
Homosexual consortships	Yes	3y > 4y, 3y > A	Partly

In pairwise age differences, 3y: 3-year-old, 4y: 4-year-old, and A: adult females; <(versus >): younger females exhibited a significantly smaller (versus larger) frequency, percentage, range or duration than older females (na: not applicable) (see "Results" section for details)

performing grasping behavior were slow-developing in a heterosexual context but, once again, did not differ significantly between age classes in a homosexual context. Fourth, demonstrative solicitations and solicitations with body contact developed at an intermediate-pace within a heterosexual context but, once again, did not differ significantly across age classes in a homosexual context. Consequently, demonstrative solicitations and solicitations with body contact developed neither fast nor slow in a heterosexual context, but rather developed gradually over time. Fifth, time spent in body contact was fast-developing in a heterosexual context, but even faster-developing in a homosexual context where no significant differences between age classes were identified.

We believe that a combination of at least four factors can be invoked to explain why the nine sexual behavioral patterns

outlined above emerged earlier, and developed faster, when directed toward females than when directed toward males. First, the risk of male aggression likely played an important role in the slow development of many heterosexual behaviors. As outlined above, adolescent female Japanese macaques are more likely to receive severe aggressions from adult males and incur more serious injuries when involved in heterosexual interactions compared to homosexual ones (Gunst et al., in press). Performing solicitations within a heterosexual context necessitates attracting the attention of potentially aggressive males toward oneself. Both mounting and grasping behaviors involve close and coordinated interactions with male mates, which would increase the likelihood that adolescent females will be the targets of severe aggression (Enomoto, 1981; Gunst et al., in press; Perry & Manson, 1995). In such circumstances, the relatively slow development of these behaviors furnishes adolescent females with a period of time in which to hone their skills at targeting less aggressive, more cooperative male mates. This is a complex task that requires detailed knowledge about the sexually active males in one's group. Once such knowledge is acquired, females can better identify more desirable male consort partners who are less aggressive and more cooperative. Because females are far less likely to be targeted with aggression by female consortship partners (Vasey, 2004), there is less need for them to be cautious in exhibiting these same behaviors within a homosexual context and, as such, the range of homosexual solicitations expressed, female–female mounting, and grasping behavior during homosexual consortships develop more rapidly (see also the "defense against male harassment hypothesis") (Poiani, 2010).

Second, males, and particularly adult males, are largely disinterested in most adolescent females' sexual solicitations (Gunst et al., in press). Consequently, compared to adult females, adolescent females experience a relatively high rate of failure when soliciting adult males. Not surprisingly then, adolescent females have a greater turnover in solicited male targets compared to adult females (cf. Anderson, 1986; Galdikas, 1995; McDonald, 1985; Perry & Manson, 1995; Scott, 1984; Wolfe, 1978). In addition, overall disinterest on the part of males would restrict adolescent females' opportunities to practice heterosexual activity and this, in turn, would slow the development of the seven heterosexual behavioral patterns outlined above. This may help to explain why females as early as 4 years of age performed the full range of complete homosexual mounting postures (namely, sitting, reclining, ventro-ventral, and double footclasp mounts). In contrast, 4-year-old females performed only one heterosexual mounting posture (i.e., reclining mount; Fig. 1).

Third, in contrast to the overall disinterest shown in adolescent females by adult males, a large majority of partners soliciting adolescent females for sex were adult females (Gunst et al., in press). This was consistent with previous research showing that at any point in time during the mating season, a substantial percentage of adult females are available and willing to mate with other females in the Arashiyama population of Japanese macaques (Vasey, 2002). The presence of motivated same-sex sexual partners would have furnished a social context in which adolescent female Japanese macaques could practice same-sex sexual behavior and, consequently, such behavior would develop more rapidly than heterosexual behavior.

Fourth, the routine occurrence of homosexual consortships between adult females of this group, with conspicuous displays of adult female–female courtship behaviors (including ground smacking, body spams, and loud sexual vocalizations) and a variety of adult female-to-female mounting postures (cf. Vasey et al., 2008a), could attract the interest of sexually motivated adolescent females and promote the early expression of female homosexual behavior, via a social facilitation process. This hypothesis is derived from research on the social transmission of courtship behavior and mating preferences in numerous fish, bird, and mammal taxa, including non-human primates (e.g., Freeberg, 2004; Nishida, 1980; Rees, 2004; Warner, 1990; White, King, & West, 2002).

In six of 15 behavioral patterns (see Table 4), the development of female heterosexual behavior paralleled that of female homosexual behavior although the precise pattern varied in four unique ways. First, we found no significant age differences in the frequency of solicitations and time spent moving during consortships for both heterosexual and homosexual interactions. "Frequency of solicitations" was an umbrella category that we created for the purpose of analysis, which encompassed demonstrative and non-demonstrative solicitations as well as contact and non-contact courtship behaviors. Non-demonstrative and non-contact solicitations are socially unconstrained, in the sense that they do not require intimate physical coordination with potential male or female sexual partners nor do they require complex knowledge pertaining to one's sexual network of potential sexual partners, sexual competitors, and sexually coercive individuals. Such behaviors reflect females' own sexual arousal and mate preferences, but may not necessarily translate into more overt sexual interactions involving contact, such as mounting. As such, non-demonstrative and non-contact solicitations can be directed to both males and females in a relatively indiscriminate manner at relatively little cost to the individual. Because these relatively low-risk courtship behaviors do not necessitate complex social coordination, they may not require learning and therefore, may appear early in development concurrent with the production of sex steroid hormones. This may account for the absence of any significant age differences in the catch-all category "frequency of solicitations." The ability to refrain from moving excessively during consortships appears to be a relatively simple behavioral pattern that is acquired rapidly, which is why adolescent females did not differ from adult females in this regard. Our impression was that once adolescent females were able to attract a male or female consort

partner, they made every effort to maintain body contact with that mate, which would also help explain the absence of movement during consortships across age categories.

Second, a fast-developing pattern was found in both heterosexual and homosexual contexts for mounts with pelvic thrusting and consortship duration. Adolescent females may have rapidly learned to perform mounts with pelvic thrusting because mounting by female Japanese macaques is associated with immediate sexual reward. This occurs either because female mounters push or thrust their genital region against the body of the male or female mountee or because mounters stimulate their genital region with their tails during mounts (Vasey & Duckworth, 2006, 2008; Vasey et al., 2006). Experiencing immediate sexual reward with male or female mates would have facilitated more frequent and diverse mounting patterns, and few failed mounting attempts, in an effort to maximize such reward. More frequent intermount grasping behaviors by females would have ensured that the male or female partner—the source of such reward—remained in the vicinity. Together, these behaviors would have resulted in fast-developing prolonged heterosexual and homosexual consortships.

Third, ambiguous mounting initiations were fast-disappearing behavioral patterns in both heterosexual and homosexual interactions. Ambiguous mounting initiations reflected behavioral indecision and resulted in delayed and sometimes aborted mounts. This would have compromised the experience of sexual reward and potentially precipitated the dissolution of consortship activity due to a lack of coordination between partners. As such, a shift from a sub-optimal behavioral pattern (i.e., failed mounting attempts) to an optimal behavioral pattern occurred early in the sexual development of females.

Fourth, the expression of dorso-ventral orientation during both heterosexual and homosexual consortships was slow-developing. Like mounting, this behavioral pattern involves close contact and coordination with established sexual partners. However, unlike mounting, dorso-ventral orientation did not result in immediate sexual reward via genital stimulation. In the absence of such a powerful proximate motivator, such behavioral pattern may have been slower to develop.

The absence of any significant age class differences for two of the heterosexual behaviors and eight of the homosexual behaviors we examined suggests that learning is not involved in the expression of these activity patterns. Their sudden manifestation, which coincides with a female's first estrus, is likely to reflect physiological triggers, as opposed learning mechanisms. Taken together, however, the results presented here were consistent with the view that the occurrence of behavioral precursors in immature females and their practice over the adolescent period led to the improvement of many adult-like sexual patterns, including the female-to-male and female–female solicitations, mounting, and other consortship behaviors observed in the Arashiyama macaque population (cf. Vasey, 2006). This study showed that, in many instances, the emergence of both conceptive and non-conceptive adult sexual behaviors can be traced back to immature behavioral patterns in adolescent female Japanese macaques, with a major threshold occurring at the age of 4 years. Thus, this study provided further support to the "learning hypothesis" in the development of sexual behaviors in non-human primates. The fact that certain homosexual behavioral patterns emerged earlier and developed faster than their heterosexual equivalents can be explained in terms of risk of aggression, immediate sexual reward, and possibly social influence.

We acknowledge that our study has one limitation that may have affected our results or how we interpreted them. Even though we sampled all the adolescent females present in the group during the study period, our sample size was still relatively small (five individuals per age class). While this is typical of most developmental research based on the observation of sexual behavior in free-ranging primates (e.g., Galdikas, 1995; Hashimoto, 1997; Owens, 1976), caution is required when generalizing such findings to the entire species.

Bearing in mind these limitations, several lines of evidence are consistent with the conclusion that homosexual behavior as expressed by adolescent Japanese macaques is sexual in nature, like heterosexual behavior. First, we found that both homosexual and heterosexual solicitations and mounts appeared at the age of 3 years (Leca et al., 2014b), which corresponds to the period when most Japanese macaque females experience their first estrus signs and begin to exhibit heterosexual behavior (cf. Nigi, 1976). Second, we found similar patterns of development in both heterosexual and homosexual contexts for six of the 15 behavioral patterns we examined. Third, homosexual interactions involving adolescent females closely mirrored adult heterosexual behavior in many aspects of their expression: (1) they were never observed outside of the species' Fall–Winter mating season; (2) they did not occur between close female kin and, as such, they did not reflect generalized patterns of social affiliation; (3) when soliciting their female partners, adolescent females showed behavioral and physiological signs of estrus; and (4) 4-year-old adolescent females performed all of the complete mounting postures and pelvic thrusting exhibited during female-to-male mounting behavior (Gunst et al., in press; Vasey, 2006; Vasey & Duckworth, 2006; Vasey et al., 2006, 2008a). These diverse lines of evidence furnish support for the conclusion that the developing homosexual behaviors exhibited by adolescent females are indeed precursors of adult homosexual behavior, which has itself been shown to be sexually motivated (Vasey & VanderLaan, 2012).

We conclude that the *behaviors* reported here were homosexual *behaviors*, based on the four pieces of evidence previously mentioned. At present, there is no evidence that this homosexual *behavior* reflects homosexual *orientation.* Rather, it likely reflects Japanese macaque females' potential for bisexual behavior, which exists in several other Old World monkeys and in great apes (Dixson, 2012). When considering

how our results may apply to the evolution of human sexuality, one should keep in mind that although reproductive behaviors in humans and Japanese macaques likely share homologous features, non-conceptive sexual behaviors in these two species may be analogous. Exclusive same-sex sexual orientation has not been documented in any free-ranging nonhuman primate species, including Japanese macaques. As such, the study of homosexual *behavior* in nonhuman primates may inform us about the evolution of homosexual *behavior* in humans, but may shed only limited light as to why exclusive male homosexuality evolved.

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