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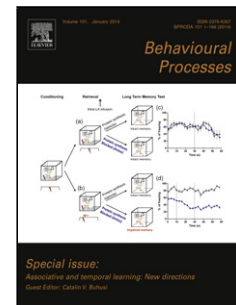
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Promiscuous primates engage in same-sex genital interactions

Short title: same-sex genital interactions in primates

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Highlights

- We hypothesised that in more promiscuous primate species, where mating effort and sexual motivation is higher, SSGIs would also occur at greater frequencies
- Through comparative analyses, both male and female SSGIs were greater in multimale systems
- Both male and female SSGIs were also positively correlated with the degree of promiscuity (relative testes mass)
- We controlled for availability of members of the same sex and results were largely congruent.
- SSGIs may be a neutral by-product of selection for increases in promiscuous sexual activity, and these interactions may be co-opted for adaptive social functions

Abstract

Same-sex genital interactions (SSGIs) occur across the order Primates, yet explaining their maintenance in evolutionary terms appears problematic; as such interactions seem to counteract reproductive goals. We hypothesised that in more promiscuous species, where sexual motivation, mating effort, and non-conceptive heterosexual behaviour are greater, SSGIs may also occur at greater frequencies without necessarily impeding reproduction. We found that the expression of both male and female SSGIs were greater in multimale systems than in unimale ones. Both male and female SSGIs were positively correlated with the degree of promiscuity (relative testes mass). As mating system confers biases in the sex ratio that may influence the expression of SSGIs, we controlled for availability of members of the same-sex. When employing this control, results were largely congruent. For males, SSGIs were expressed more frequently in multimale systems. For both sexes, SSGIs were expressed more frequently with greater relative testes mass. We suggest SSGIs in primates may be a neutral by-product of selection for increases in promiscuous sexual activity, and that in certain instances these interactions may be co-opted to facilitate adaptive social functions.

Keywords: homosexual behaviour; mating system; primates; promiscuity; same-sex genital interactions.

1. Introduction

Same-sex genital interactions (hereafter, SSGIs) among adults are phylogenetically widespread in non-human primates (e.g., Vasey, 1995; Bagemihl, 1999). These interactions most frequently take the form of ventro-dorsal mounting (e.g. mounting with thrusting and penile erection between male vervets, *Chlorocebus aethiops*, Struhsaker, 1967, and male Japanese macaques, *Macaca fuscata*, Leca et al., 2014) and less commonly ventro-ventral mounting (e.g. genito-genital rubbing between female bonobos, *Pan paniscus*, Hashimoto 1997). Oral-genital contact (e.g. male-male fellatio in Tibetan macaques, *M. thibetana*, Ogawa, 2006) and mutual genital manipulation (e.g. ‘diddling’ between male Guinea baboons, *Papio papio*, Whitham and Maestripieri, 2003) also occur among individuals of the same sex.

SSGIs have been observed in primate species that are principally socially monogamous (e.g. siamang, *Hylobates syndactylus*, Fox, 1977) through to those that exhibit extreme promiscuity in both sexes (e.g. bonobo, *P. paniscus*, Hashimoto, 1997). However, the frequency with which SSGIs are expressed varies greatly from one primate species to the next. Some species rarely exhibit SSGIs (e.g. isolated instances of female-female mounting observed in wild moor macaques, *M. maura*, Matsumura and Okamoto, 1998), while others engage in SSGIs on a routine basis (e.g. mounting between female Hanuman langurs, *Semnopithecus entellus*, Sommer et al., 2006). Typically, one sex engages in SSGIs more often than the other, but the direction and magnitude of the sex difference varies across species (e.g., F > M, rhesus macaque, *M. mulatta*, Akers and Conaway, 1979; M > F, *M. radiata*, bonnet macaque, Makwana, 1980).

The reasons for the expression and maintenance of SSGIs remain poorly understood (for reviews, see Vasey, 1995; Vasey and Sommer, 2006; Bailey and Zuk, 2009; Poiani, 2010). The prevailing proximate hypothesis holds that individuals engage in SSGIs when they are unable to access opposite-sex mates (Poiani, 2010), yet such individuals are often present during SSGIs and their sexual solicitations can be rebuffed (e.g., *M. fuscata*, Vasey, 1998). Prevailing adaptive hypotheses propose SSGIs may be deployed to facilitate functional social goals such as dominance demonstration, alliance formation, social bonding, tension regulation, or conflict resolution (Vasey and Sommer, 2006), yet some species appear to engage in SSGIs that are devoid of any functional social value (e.g., *M. fuscata*, Vasey, 2006). In sum, no one theory has proved satisfactory in terms of explaining patterns and frequency of occurrence across multiple taxa. Here we quantitatively investigate whether the propensity towards promiscuous sexual behaviour has any bearing on the frequency of SSGIs in non-human primates, and how expression may vary between the sexes.

Humans (*Homo sapiens*) and domestic rams (*Ovis aries*) are the only species for which exclusive SSGIs have been conclusively documented (Bell & Weinburg, 1978; Perkins & Fitzgerald, 1997). As such, all non-human primate individuals that engage in SSGIs do not do so in isolation, rather, they do so in conjunction with reproductive ones (Vasey, 1995; Bagemihl, 1999). This pattern of co-occurrence suggests that both reproductive and SSGIs are evolutionarily linked. Indeed, evidence from other taxa suggests sexual polygamy plays a role in the expression of SSGIs. In birds, lower relative contribution to parental care, and thus increased potential opportunity to engage in polygamous sexual behaviour, translates to increased expression of SSGIs for both males and females (MacFarlane et al., 2010). One potential explanation for this pattern is that polygamous males and females have experienced strong selection for increased sexual motivation and performance and SSGIs occur as a by-

product of this selection because they furnish an alternative outlet when sexual motivation is high. It is likely that similar patterns occur in other clades such as primates.

In primates, unimale mating systems (monogamous and polygynous species) are characterised by males, and especially females, engaging exclusively with one, or a limited number of sexual partners. Sexual behaviour occurs infrequently and relationships are bonded and relatively enduring. Conversely, multimale mating systems are characterised by both sexes engaging in multiple, brief, and non-bonded sexual encounters with numerous partners (i.e., promiscuous sexual interactions). The number of male sexual partners multimale females engage with during a single ovarian cycle can range from 2 to 11, with up to 19 during a single mating season (Dixon, 1997). Female promiscuity drives post-copulatory intrasexual selection on males, translating to increased investment in testes mass as female promiscuity increases (Harcourt et al., 1995). In line with these findings, multimale males exhibit greater sexual arousal and performance, and show greater copulation frequencies (0.13 ejaculations/hour in unimale species versus 0.88 in multimale species, Dixon, 1997).

Non-conceptive heterosexual behaviour is also frequent in more promiscuous non-human primate species. Unlike females from unimale mating systems, which restrict their copulations to periods when they are fertile, multimale females regularly mate at stages of their cycle when conception is not possible, exhibit extended proceptivity, and their number of copulations per birth far exceed that required to achieve reproductive success (e.g. 25 copulations per birth for unimale gorillas, versus 1110 for multimale baboons and 1267 for multimale bonobos; Wrangham, 1993). Female-male mounting also occurs on a routine basis in some multimale non-human primate species (*M. fuscata*, Vasey & Duckworth, 2008). Taken together, multimale non-human primate species exhibit greater sexual motivation and engage in both

reproductive and non-conceptive heterosexual interactions more often. SSGIs are, by their nature, another form of non-conceptive sex and, as such, we reasoned that they are also likely to be expressed more frequently in more promiscuous species.

Our working hypothesis is that in more promiscuous primates, there is intense selection on both males and females for increased reproductive motivation and performance. We hypothesise that SSGIs occur as a by-product of this selection and act as an alternative route for sexual gratification when motivation is high. Thus we predict that both male and female SSGIs would be expressed at higher frequencies in multimale species, as well as those species with a greater degree of inferred promiscuity (i.e. greater relative testes mass).

2. Methods

A survey of the literature was conducted, initially sourcing references from published surveys (Dagg, 1984; Tyler, 1984; Nadler, 1990; Vasey, 1995; Bagemihl, 1999; Ren et al., 2002; Dixson, 2010), along with database searches and personal communications. This yielded a database of over 250 records of SSGIs in primates, of which 95 met the inclusion criteria detailed below.

Our definition of SSGIs included mounting (ventro-dorsal and ventro-ventral) with and without pelvic thrusting, oral-genital contact, and manual genital manipulation (Vasey, 1995). We also scored the frequency of same-sex mounting behaviour alone and assessed these patterns separately. Only interactions involving reproductively competent adults were included to assess partitioning between SSGIs and potentially reproductive interactions. Adult status was assigned when the author(s) stated in their methods that the individuals sampled were adult or mature individuals.

We chose to separately code data observed under: (a) all living conditions (which included captive, semi-free-ranging [enclosures > 0.5 ha], and wild [free-ranging] conditions) and (b) semi-free-ranging and/or wild conditions (hereafter wild). Semi-free ranging and wild studies were grouped as “wild” as semi-free ranging conditions usually comprised of sufficient individuals to form natural social groups and grouping was necessary as there was insufficient N to analyse them separately.

We limited our analyses of SSGIs to groups where access to opposite sex individuals was possible. We did, however, run separate analyses including frequencies of male SSGIs in all-male groups with frequencies in mixed-sex groups; inclusion did not alter interpretation of findings with the same significance patterns observed. No studies with experimentally manipulated individuals were included.

Each species was scored for the proportion of adult male-male and female-female genital interactions in which they engaged. The proportion was calculated as the percentage of adult-adult sexual interactions involving males that were same-sex, and the same was done for females. Frequencies reported are the maximum observed among studies (68 references cited in Appendix 1). References to SSGIs that were anecdotal in nature were assumed to be rare events and thus were arbitrarily scored as 1%. For a number of species, overall frequency of male-male and/or female-female genital interactions were documented without details of age-class, thus the frequency of adult-adult SSGIs was not able to be reliably ascertained. These data points were noted but excluded from analyses. For each species, no evidence of SSGIs and/or same-sex mounting for a particular sex was scored as a non-occurrence (0%). As absence may reflect insufficient sampling effort, we analysed data including non-occurrences

(all data) and excluding them (reduced). Species for which no studies were available under wild conditions were excluded from wild analyses. Duration of the data collection, number of groups observed and methods of data collection varied among studies, though expressing data as percentages standardised these differences among studies. The final dataset included 34 species where adult SSGIs have been observed under captive and/or wild conditions (Appendix 1).

We employed two measures of variability in promiscuity in testing our hypotheses. First, we categorised the dominant mating system using a two-category classification, unimale (monogamous and polygynous) or multimale (multimale-multifemale, promiscuous). Secondly, we employed testes residuals of the least-squares linear regression between \log_{10} male body mass and \log_{10} combined testes mass as a relative testes size index and thus a continuous proxy for the degree of promiscuity (Appendix 1).

Primates vary in the relative proportions of males and females co-resident in social groups, with sex ratios in most species female-biased. One of the issues with interpretation of the data is that expression of SSGIs may not be due to mating system/promiscuity per se, but rather just the availability of same-sex partners which may covary with mating system and/or degree of promiscuity. For example, in monogamous species there are few potential adults of the same-sex available to engage with in sexual interactions, so SSGIs may be expected to be rare. Similarly, for some polygynous species, there may be few males to engage with sexually, relative to females, so the proportion of male SSGIs may be expected to be minimal. From a female perspective, in some polygynous and multimale species there may be many females and a small number of males, so frequency of female SSGIs, may be elevated.

To control for the potential confounding effect of availability of same-sex partners, the proportion (%) of same-sex dyads was calculated from the number of males and females present in typical primate groups. The proportion was calculated as the percentage of dyads in the group involving males that were same-sex and the same for females.

The average number of adult males and adult females in social groups were obtained from the literature, based on the synthesis of numerous studies (Appendix 1). These values were used over group numbers in the studies where SSGIs were evidenced as many of these studies did not contain information on group size/composition. For those polygynous species which exhibit higher-order group structures, numbers at the clan/troop level were employed rather than the reproductive unit. We decided to only analyse availability patterns for semi free-ranging/wild studies as populations in many captive studies did not comprise sex ratios typical of their wild counterparts.

We conducted a phylogenetically informed analysis, employing generalised least-squares regression models (GLS) assuming a Brownian motion model of evolution. The phylogeny utilised was the most recent molecular consensus tree for primates (Arnold et al., 2010). Initially, male and female SSGIs were $\log_{10}(x + 1)$ transformed and regressed against the explanatory variables mating system (unimale vs. multimale) and residual testes mass. Then an analysis of covariance (ANCOVA) model was employed, assessing the effect of mating system controlling for availability of same-sex partners. A model was run with an interaction term, allowing the relationship between SSGIs (all data) and availability (% same-sex dyads, $\log_{10}(x+1)$ transformed) for each mating system category to vary thereby enabling assessment of homogeneity of slopes. If the interaction term was non-significant, the ANCOVA model was reduced to a parallel regression lines main effects model, providing a test for differences

in frequency of expression of SSGIs between mating systems controlling for availability of members of the same-sex under wild conditions. Finally, a multiple regression model was employed, assessing variation in SSGIs (all data) in relation to relative testes mass controlling for availability of members of the same-sex (% same-sex dyads, $\log_{10}(x+1)$ transformed) under wild conditions. Analyses were performed using R version 2.13.0. with the ape and nlme packages.

3. Results

3.1 Expression of SSGIs with mating system and degree of promiscuity

The proportions of male SSGIs and male-male mounting were greater in multimale than unimale systems, both under all living conditions and wild conditions alone. Significant patterns were similar when non-occurrences were removed, excepting male-male mounting in the wild, which was not significant (Table 1, Figure 1a). Similarly, both male SSGIs and male-male mounting were positively associated with inferred promiscuity (relative testes mass) under all living conditions and in the wild. The same patterns of significance were observed when non-occurrences were removed (Table 2, Figure 2a).

Female SSGIs were predominantly expressed in multimale systems for all living conditions and in the wild. Similar patterns were observed when non-occurrences were removed. Female-female mounting was greater in multimale groups once non-occurrences were excluded for both all living conditions and the wild (Table 1, Figure 1b). Equally, female SSGIs and female-female mounting covaried positively with relative promiscuity (testes mass residuals) under all living conditions (for both all data and reduced data). However, only the proportion of female SSGIs was greater at higher degrees of promiscuity (residual testes mass) under wild conditions with non-occurrences included (Table 2, Figure 2b).

3.2 Controlling for availability

The slopes of male SSGIs with male availability were similar between unimale and multimale groups with a non-significant interaction term ($\beta = -0.09$, $t = -0.19$, $p > 0.05$). Thus, we examined results for the reduced model, assuming homogenous slopes. There was no relationship between male availability and male SSGIs. After controlling for male availability, male SSGIs were expressed more frequently in multimale systems (Table 3).

For females, the interaction term was significant ($\beta = -4.83$, $t = -2.44$, $p < 0.05$). A significant interaction indicated heterogeneous slopes, implying the relationship between relative female availability and frequency of female SSGIs differed between mating systems. Through an examination of the slopes, female SSGIs increased with increasing female availability in unimale systems while female SSGIs were consistently high in multimale systems across a range of female availabilities. As a consequence, differences between mating systems decreased with increasing female availability.

After controlling for male availability, a positive relationship between male SSGIs and relative testes mass was still observed. After adjusting for relative testes mass, however, increases in male availability did not translate to increased expression of male SSGIs (Table 3).

When female availability was held constant, female SSGIs increased with increases in relative testes mass. Female availability was not a significant predictor of expression of female SSGIs, after controlling for relative testes mass (Table 3).

4. Discussion

For both sexes, SSGIs were expressed more frequently in multimale systems. Similarly, as the degree of promiscuity increased, so too did the proportion of total sexual activity both males and females partitioned to SSGIs. For the most part, these patterns held under all living conditions as well as under wild conditions alone, suggesting that the observed patterns of expression were not mere artefacts of captivity.

Mating system and the sex ratio of the social unit are somewhat linked. For males, some unimale mating systems have a paucity of males compared with multimale systems. For females, some unimale (polygynous) and a number of multimale species, exhibit great female-bias. Thus, differences in the frequency of SSGIs observed may reflect availability of members of the same-sex, rather than a propensity for promiscuous sexual behaviour, especially for males. Although there was some indication that expression of female SSGIs in both unimale and multimale mating systems approached parity when female availability was high; most analyses indicated little influence of availability. Importantly, when controlling for availability of members of the same sex in the model, the frequency of expression of male SSGIs was greater in multimale species thus corroborating results for comparisons between mating systems alone. Equally, the positive relationship between SSGIs and residual testes mass was maintained for both sexes after controlling for availability of members of the same-sex. Overall, it can be said that availability of same-sex partners has limited influence on the frequency of expression of SSGIs, suggesting that a propensity for promiscuity is the factor with greater explanatory power.

It appears that in unimale species where individuals engage exclusively with one, or limited, bonded heterosexual partners, and copulatory activity occurs infrequently, both sexes are less

motivated to engage in SSGIs. Instead, genital interactions are largely constrained to heterosexual activity presumably because the reproductive costs associated with SSGIs are too high. In more promiscuous taxa, however, there is strong selection pressure for greater sexual arousal, motivation and elevated sexual activity in both sexes (Dixon, 1997). SSGIs may be more frequently enacted in such species primarily because it serves as an alternative route for sexual gratification when sexual motivation is high.

Indeed, in many instances, SSGIs can be accurately described as “homosexual” because they frequently involve genital arousal, stimulation and orgasm. For example, males sometimes exhibit erections during these interactions, anal intromission has been documented, and ejaculation occurs occasionally (e.g., *Gorilla beringei*, Yamagiwa, 2006). Similarly, female-female mounts are sometimes accompanied by vulvar/perineal stimulation (e.g., *M. fuscata*, Vasey & Duckworth, 2006; *P. paniscus*, Hohmann & Fruth, 2000). Thus, SSGIs may be a neutral by-product of selection for increased reproductive performance in promiscuous species. SSGIs may not be selected against as the absolute heterosexual budget in promiscuous species is greater and, as such, SSGIs do not impact reproductive fitness in a negative manner.

However, not all SSGIs appear to be solely sexually motivated. Indeed, many SSGIs are, at least in part, *sociosexual* in character; that is, sexual in terms of their outward form, but enacted to facilitate some sort of adaptive social goal(s). In some instances, SSGIs may be altogether devoid of sexual arousal and entirely enacted to facilitate sociosexual goals (e.g., agonistic dominance mounts in pigtail macaques, *M. nemestrina*, Oi, 1991). For the most part, however, SSGIs appear to be characterized by some mixture of both sexual and sociosexual motivation (Vasey, 1995, Bagemihl, 1999). For example, in bonobos (*P.*

paniscus), genito-genital rubbing is accompanied by vocalizations and facial expressions that are indicative of sexual reward, but it also appears to reduce social tension associated with food sharing (Hohmann & Fruth, 2000).

Why would SSGIs be co-opted in this manner when non-genital social interactions could presumably achieve the same fitness-enhancing endpoint? Researchers have suggested that SSGIs represent an optimal means for communicating social messages of conformity, coordination, co-operation and trust (Smuts & Watanabe, 1990; Wrangham, 1993). For example, asymmetrical agonistic mounting among pigtail macaques may actually embody the social message of both the physical domination of the mounter over the mountee and the mountee's acceptance of a subordinate status. Similarly, bi-directional SSGIs among bonobos may embody the message of coordination and cooperation because such interactions require that partners accommodate each other to begin, sustain and complete the behavioural exchange. Partners demonstrate vulnerability to each other by exposing their genitalia and in doing so, signal mutual trust.

SSGIs that facilitate sociosexual roles might be best characterized as *exaptations*, that is, nonaptive by-product of an adaptation, which has subsequently been co-opted to fulfil a social goal (Gould & Vrba, 1982). Sociosexual SSGIs may have serendipitous, fitness-enhancing "effects" (Williams, 1966) even though they were not originally built by selection to serve such a purpose. If exapted SSGIs resulted in markedly elevated fitness advantages due to the sociosexual roles they facilitated, then this could form a unique basis on which selection might act. If so, then the *secondary* adaptive modification of the exapted SSGIs may have occurred. Indeed this suggestion is consistent with numerous studies, which demonstrate that sociosexual SSGIs exhibit elements of adaptive design (e.g., economy, efficiency,

precision) in that they are enacted in a very context-specific manner that is consistent with the realization of a particular social goal (Vasey, 1995; Bagemihl, 1999). For example, male baboons (*P. cynocephalus*) that frequently engage in bi-directional SSGIs form the most cohesive and successful alliances against other third-party males. These bi-directional SSGIs often occur just before challenging a rival male at which time reaffirming alliance bonds would be of optimal functional consequence (Smuts & Watanabe, 1990).

It is conceivable that in some primate species secondary adaptive modification of sociosexual SSGIs may have selected against the occurrence of any sexual motivation during these interactions. In some instances, we might reasonably expect that this could facilitate the most functional expression of these interactions. As noted previously, however, the vast majority of SSGIs that have been documented in the primatological literature appear to be characterized by both sexual and sociosexual motivation. This suggests that in most instances, sexual motivation during sociosexual SSGIs does not detract from their functionality.

In sum, our findings demonstrate that in promiscuous primates both males and females allocate a greater proportion of their sexual budgets to SSGIs. The sexual and/or social circumstances conferred by elevated promiscuity may be a necessary prerequisite for SSGIs to be routinely expressed and maintained. The potential exapted benefits of engaging in such interactions and, as such, the context in which they occur, vary greatly among extant primate taxa.

Conflict of interest

The authors have declared that no competing interests exist. The work was unfunded.

References

- Akers JS, Conaway CH (1979) Female homosexual behaviour in *Macaca mulatta*. Arch Sex Behav 8: 63-80
- Arnold C, Matthews LJ, Nunn CL (2010) The 10kTrees website: a new online resource for primate phylogeny. Evol Anthropol 19: 114-118
- Bagemihl B (1999) Biological exuberance. Animal homosexuality and natural diversity. Profile Books Ltd, London
- Bailey NW, Zuk M (2009) Same-sex sexual behavior and evolution. Trends Ecol Evol 24: 439-446
- Bell AP, Weinberg MS (1978) Homosexualities: A study of diversity among men and women. Simon and Schuster, New York
- Dagg AI (1984) Homosexual behaviour and female-male mounting in mammals-a first survey. Mammal Rev 14: 155-185
- Dixon AF (1997) Evolutionary perspectives on primate mating systems and behavior. Ann NY Acad Sci 807: 42-61
- Dixon AF (2010) Homosexual behaviour in primates. In: Poiani A (ed) Animal homosexuality: a biosocial perspective. Cambridge University Press, Cambridge, pp 381-400

Fox GJ (1977) Social dynamics in siamang. Ph.D. thesis. University of Wisconsin, Milwaukee, Wisconsin, USA

Gould SJ, Vrba ES (1982) Exaptation-a missing term in the science of form. *Paleobiol* 8: 4-15

Harcourt AH, Purvis A, Liles L (1995) Sperm competition: mating system, not breeding season, affects testes size of primates. *Funct Ecol* 9: 468-476

Hashimoto C (1997) Context and development of sexual behaviour of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *Int J Primatol* 18: 1-21

Hohmann G, Fruth B (2000) Use and function of genital contacts among female bonobos. *Anim Behav* 60: 107-120

Leca J-B, Gunst N, Vasey PL (2014) Male homosexual behavior in an all-male group of Japanese macaques at Minoo, Japan. *Arch Sex Behav* 43: 853-861

MacFarlane GR, Blomberg SP, Vasey PL (2010) Homosexual behaviour in birds: frequency of expression is related to parental care disparity between the sexes. *Anim Behav* 80: 375-390

Makwana SC (1980) Observations on population and behaviour of the bonnet monkey. *Macaca radiata*. *Comp Physiol Ecol* 5: 9-12

Matsumura S, Okamoto K (1998) Frequent harassment of mounting after a takeover of a group of moor macaques (*Macaca maurus*). *Primates* 39: 225-230

Nadler RD (1990) Homosexual behavior in nonhuman primates. In McWhirter DP, Sanders SA, Reinisch JM (eds) *Homosexuality/heterosexuality: concepts of sexual orientation*. Oxford University Press, New York, pp 138-170

Ogawa H (2006) *Wily monkeys: social intelligence of Tibetan macaques*. Trans Pacific Press, Melbourne

Oi T (1991) Non-copulatory mounting of wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra, Indonesia. In: Ehara A, Kimura T, Takenaka O, Iwamoto M (eds) *Primate today*. Elsevier Science Publishers, Amsterdam, pp 147-150

Perkins A, Fitzgerald JA (1997) Sexual orientation in domestic rams: Some biological and social correlates. In: Ellis L, Ebertz L (eds) *Sexual orientation: Toward biological understanding*. Praeger, Westport, CT, pp 107-128

Poiani A (2010) *Animal homosexuality: a biosocial perspective*. Cambridge University Press, Cambridge

Ren BP, Xia SZ, Li QF, Liang B, Lu MQ, Zhang SY (2002) Homosexual mounting behavior in non-human primates. *Chinese Journal of Zoology* 37: 95-101

Smuts BB, Watanabe JM (1990) Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *Int J Primatol* 11: 147-172

Sommer V, Schauer P, Kyriazis D (2006) A wild mixture of motivations: same-sex mounting in Indian langur monkeys. In: Sommer V, Vasey PL (eds) *Homosexual behaviour in animals: an evolutionary perspective*. Cambridge University Press, Cambridge, pp 238-272

Struhsaker TT (1967) Behavior of vervet monkeys (*Cercopithecus aethiops*). University of California Publications in Zoology 82: 1-74

Tyler PA (1984) Homosexual behaviour in animals. In: Howells K (ed) *The psychology of sexual diversity*. Blackwell Scientific, Oxford, pp 42-62

Vasey PL (1995) Homosexual behavior in primates: a review of evidence and theory. *Int J Primatol* 16: 173-204

Vasey PL (1998) Female choice and inter-sexual competition for female sexual partners in Japanese macaques. *Behaviour* 135: 579-597

Vasey PL (2006) The pursuit of pleasure: Homosexual behaviour, sexual reward and evolutionary history in Japanese macaques. In: Sommer V, Vasey PL (eds) *Homosexual behaviour in animals: an evolutionary perspective*. Cambridge University Press, Cambridge, pp 191-219

Vasey PL, Duckworth N (2006) Sexual reward via vulvar, perineal, and anal stimulation: a proximate mechanism for female homosexual mounting in Japanese macaques. *Arch Sex Behav* 35: 523-532

Vasey PL, Duckworth N (2008) Female-male mounting in Japanese macaques: The proximate role of sexual reward. *Behav Processes* 77: 405-407

Vasey PL, Sommer V (2006) Homosexual behaviour in animals: topics, hypotheses and research trajectories. In: Sommer V, Vasey PL (eds) *Homosexual behaviour in animals: an evolutionary perspective*. Cambridge University Press, Cambridge, pp 3-42

Whitham JC, Maestripieri D (2003) Primate rituals: the function of greetings between male Guinea baboons. *Ethology* 109: 847-859

Williams GC (1966) *Adaptation and natural selection*. Princeton University Press, Princeton, NJ.

Wrangham RW (1993) The evolution of sexuality in chimpanzees and bonobos. *Hum Nature* 4: 47-79

Yamagiwa J (2006) Playful encounters: the development of homosexual behaviour in male mountain gorillas. In: Sommer V, Vasey PL (eds) *Homosexual behaviour in animals: an evolutionary perspective*. Cambridge University Press, Cambridge, pp 273-293

Figure legends

Figure 1: Average species level $\log_{10}(x+1)$ (\pm SE) a. male SSGIs and b. female SSGIs in unimale and multimale groups under all living conditions.

Figure 2: Relationships between $\log_{10}(x+1)$ a. male SSGIs, b. female SSGIs and relative testes mass (residuals) under all living conditions. Species level data (● = all data, ● = reduced data) with phylogenetic regression lines.

FIGURE 1

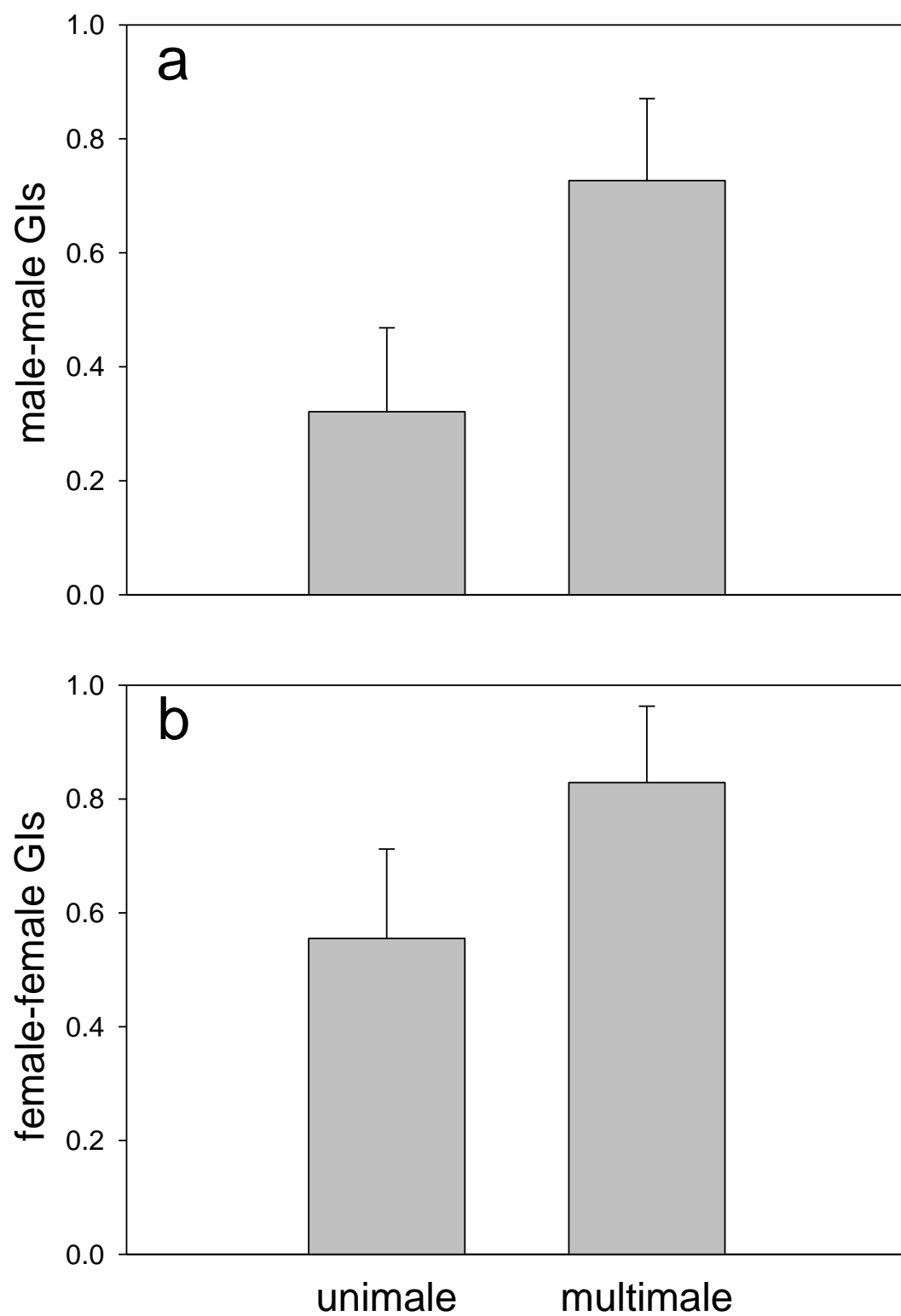


FIGURE 2

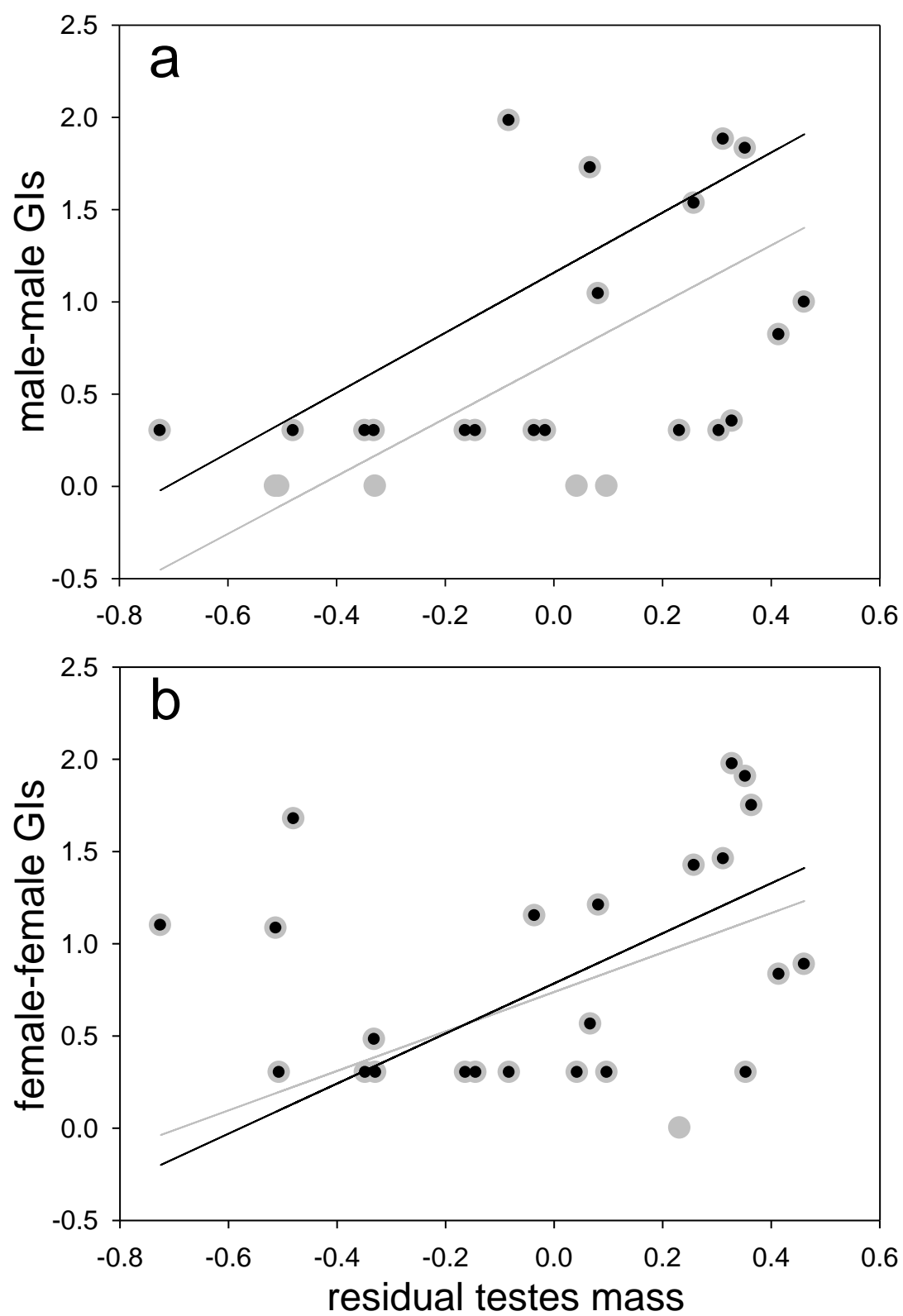


Table 1: Generalised least squares regression models comparing SSGIs between unimale (intercept) and multimale groups. MMAA= adult male SSGIs, MMAAm= adult male-male mounting. FFAA= adult female SSGIs, FFAAm= adult female-female mounting ($p < 0.05$ highlighted).

		β	se	t	p
male-male					
All living conditions					
all data	MMAA	0.927	0.188	4.927	0.000
reduced	MMAA	0.882	0.239	3.695	0.001
all data	MMAAm	0.732	0.215	3.402	0.002
reduced	MMAAm	0.842	0.239	3.528	0.002
Semi-free-ranging and wild					
all data	MMAA	1.196	0.151	7.911	0.000
reduced	MMAA	1.190	0.194	6.123	0.000
all data	MMAAm	1.156	0.201	5.744	0.000
reduced	MMAAm	0.757	0.470	1.611	0.125
female-female					
All living conditions					
all data	FFAA	0.640	0.236	2.711	0.011
reduced	FFAA	0.787	0.181	4.341	0.000
all data	FFAAm	0.330	0.196	1.688	0.102
reduced	FFAAm	0.376	0.175	2.147	0.042
Semi-free-ranging and wild					
all data	FFAA	0.981	0.209	4.693	0.000
reduced	FFAA	0.702	0.197	3.571	0.002
all data	FFAAm	0.331	0.211	1.570	0.128
reduced	FFAAm	0.535	0.223	2.398	0.028

Table 2: Generalised least squares regression models of relationships between SSGIs and relative testes mass (residuals). MMAA= adult male SSGIs, MMAAm= adult male-male mounting. FFAA= adult female SSGIs, FFAAm= adult female-female mounting (p<0.05 highlighted).

		β	se	t	p
male-male					
All living conditions					
all data	MMAA	1.563	0.378	4.132	0.000
reduced	MMAA	1.628	0.442	3.686	0.002
all data	MMAAm	1.433	0.402	3.567	0.002
reduced	MMAAm	1.780	0.364	4.889	0.000
Semi-free-ranging and wild					
all data	MMAA	1.854	0.314	5.895	0.000
reduced	MMAA	1.871	0.342	5.470	0.000
all data	MMAAm	1.939	0.388	5.002	0.000
reduced	MMAAm	1.450	0.418	3.472	0.004
female-female					
All living conditions					
all data	FFAA	1.070	0.429	2.492	0.021
reduced	FFAA	1.358	0.328	4.139	0.001
all data	FFAAm	0.624	0.290	2.148	0.043
reduced	FFAAm	0.777	0.276	2.815	0.011
Semi-free-ranging and wild					
all data	FFAA	1.502	0.381	3.943	0.001
reduced	FFAA	0.642	0.344	1.868	0.081
all data	FFAAm	0.489	0.314	1.556	0.136
reduced	FFAAm	0.387	0.405	0.957	0.357

Table 3: Generalised least squares regression models including an ANCOVA model assessing differences in male SSGIs between mating systems controlling for male availability and multiple regression models between SSGIs and residual testes mass controlling for availability. MMAA= adult male SSGIs, FFAA= adult female SSGIs (p<0.05 highlighted).

	β	se	t	p
MMAA				
unimale:multimale	1.224	0.173	7.063	0.000
male-male dyads	-0.068	0.198	-0.345	0.734
MMAA				
residual testes mass	1.875	0.318	5.893	0.000
male-male dyads	-0.328	0.391	-0.841	0.413
FFAA				
residual testes mass	1.557	0.387	4.023	0.001
female-female dyads	0.740	0.801	0.924	0.368