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**Causes and consequences of same-sex sociosexual
behaviour in male rhesus macaques**

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DECLARATION

This thesis comprises my own work. I have acknowledged collaborative parts of the thesis in the ‘Contributions of authors’ section.

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George was curious –
well, who would not be?

Curious George
MARGRET & H.A. REY

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ABSTRACT

Numerous reports have documented the occurrence of same-sex sociosexual behaviour (SSB) across the natural world. However, distributions of the behaviour within a species are needed to test popular theories describing its evolutionary underpinning, above all, whether the behaviour can be heritable and therefore evolve, and consequently if the behaviour carries fitness costs due to harsh trade-offs with reproductive effort. Chapter 1 provides this intraspecific distribution by using detailed observations collected across three years of the social and mounting behaviour of 236 male semi-wild male rhesus macaques. Results showed that male-male mounting was more common than male-female mounting, and that the likelihood of exclusive SSB orientations (and duly high reproductive costs) were low. Chapter 2 demonstrates that historical theories of social group sex-ratio and dominance (potentially mediating limited-female access) explain SSB only marginally, with increasing age instead weakly influencing both increased dominance rank and decreased SSB. Results therefore opened the possibility of individual identity, and consequently genetic background, influencing the expression of the behaviour. Using a comprehensive pedigree, this chapter provides the first evidence of vertebrate repeatability (19.3%) and heritability (6.4%) of SSB in the natural world. Furthermore, a positive genetic correlation between same-sex mounter and mountee activities indicated a common underpinning to different forms of SSB. In contrast, there was no genetic correlation between male-male and male-female mounting, providing further evidence of a decoupling between SSB and costs to missed mating opportunities. Chapter 3 studies pedigree offspring sired to directly show no evidence of a cost to SSB, but instead that the behaviour predicted coalitionary partnerships associated with likely fitness benefits. Together, the results presented here demonstrate that SSB can be common amongst individuals, can evolve, and is unlikely to be costly, with implications for both animal and human research.

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This research is about same-sex sociosexual behaviour (SSB) in a non-human primate, and not about homosexuality in humans. However, by touching on issues of sexuality and identity, SSB research can have social and political consequences for sexual minority groups (Bailey et al., 2016; Ganna et al., 2019). I hope therefore to clarify my intentions here, in particular concerning conclusions which may or may not be drawn from this research. Firstly, these results do not endorse any form of discrimination based on sexual preference or identity. Instead, it is to be hoped that this research continues to move the broader discussion away from an oversimplistic concept of ‘nature vs nurture’ in influencing sexual preference.

Secondly, while the results presented below challenge the claim that SSB is a rare or deviant behaviour, there is also a caution against the naturalistic fallacy (Sommer and Vasey, 2006; Bailey et al., 2016), by emphasizing here that society’s obligation for sexual inclusiveness should not rely on any observation of phenomena in the natural world. However, it remains that these results may contribute to changing the opinions of those whose prejudice remain regrettably built on the belief that SSB is deviant. By hoping that this work can contribute to a more inclusive society, this thesis does not aim to trivialize the victimization that LGBTQIA+ (lesbian, gay, bisexual, transgender, queer, intersex, asexual, and other+) communities frequently face (Egleston et al., 2010; Hughes, 2018). Indeed, people of LGBTQIA+ backgrounds, including scientists, are still fighting prejudice (Powel et al., 2020).

Thirdly, historical suppression or distortion of SSB research has existed for many decades not only in human and primate studies, but also in the wider field of ecology (Sommer and Vasey, 2006; Bailey et al., 2016; Bailey and Zuk, 2009). Arguably, the persistence of labelling SSB as a ‘paradox’ is itself a legacy of this tension. This issue extends further to the historical preponderance of aggression and dominance in hypotheses of SSB, which has been identified as the by-product of prejudice in associating the behaviour with brutality or a non-sexual underpinning (Sommer and Vasey, 2006; Bailey et al., 2016). While this research did find that SSB predicted conflict coalitions in male rhesus

macaques, it should be emphasised that this proposed function may be species and sex-specific, and does not legitimise the historical overemphasis of social dominance and aggression in SSB research.

Finally, I wish to highlight that these results are broadly sex-specific, and welcome further research into female SSB to redress any imbalance on this topic (see General discussion). The male rhesus was chosen over female here only due to their greater frequency of observable same-sex activity, thereby providing higher volumes of interindividual behaviour data within the timeframe and limitations of study. The few instances of recorded female SSB were not included in this study, since the mechanisms underpinning SSB may differ significantly between sexes (Bailey et al. 1993), making it analytically inappropriate to consider male and female behaviour as interchangeable. This approach is supported by the recent large GWAS of human homosexuality (Ganna et al. 2019), in which results only partially overlapped between men and women and, more importantly, did not allow meaningful prediction of an individual's sexual behaviour.

CONTRIBUTION OF AUTHORS

The work provided in this thesis was submitted as part of a manuscript to *Current Biology* in collaboration with Vincent Savolainen and Ewan Flintham (Clive et al., 2022). I designed the observation protocol, collected all behavioural data on social group R and supervised field assistant data collection of social group V. I designed and performed all analyses and plotting, and wrote the initial manuscript, with comments from Ewan Flintham and edits on drafts by Vincent Savolainen. All research was supervised by Vincent Savolainen. The manuscript in Appendix A was written in collaboration with Vincent Savolainen and William Wisden. The manuscript in Appendix B was written in collaboration with Vincent Savolainen and Ewan Flintham.

GENERAL INTRODUCTION

FIGURE 0.1 WAS PUBLISHED AS PART OF A MANUSCRIPT RESULTING FROM RESEARCH FOR THIS THESIS IN ARCHIVES OF SEXUAL BEHAVIOR (CLIVE ET AL., 2019) SEE APPENDIX A.

FIGURE 0.2 WAS PUBLISHED AS PART OF A MANUSCRIPT RESULTING FROM RESEARCH FOR THIS THESIS IN NATURE ECOLOGY & EVOLUTION (CLIVE ET AL., 2020) SEE APPENDIX B.

Researchers have documented same-sex sociosexual behaviour (SSB, sometimes termed ‘homosexual’ (Sommer and Vasey, 2006; Bailey et al., 2016) or ‘same-sex sexual’ (Bailey and Zuk, 2009; Scharf and Martin, 2013) behaviour, see Section 1.2.1) in wild animals as diverse as insects (Bailey and Zuk, 2009; Scharf and Martin, 2013), squid (Hoving et al., 2012; Hoving et al. 2019), reptiles (Trivers, 1976; Bailey and Zuk, 2009; Bonnet et al., 2016), birds (Bagemihl, 1999; Sommer and Vasey, 2006; Bailey and Zuk, 2009; Macfarlane et al., 2010), felids (Bagemihl, 1999; Bailey and Zuk, 2009), ungulates (Bagemihl, 1999; Bailey and Zuk, 2009), bats (Sugita, 2006; Riccucci, 2011), cetaceans (Sommer and Vasey, 2006; Bailey and Zuk, 2009) and particularly primates (see Fig. 0.1, Fox, 2001; Sommer and Vasey, 2006; Bailey and Zuk, 2009; Jiang et al. 2013; Busia et al. 2018; Sandel and Reddy, 2021). However, such reports of SSB tend to be opportunistic ad-hoc observations of behaviours that are typically described as rare (Sommer and Vasey, 2006; Bailey and Zuk, 2009; Bailey et al., 2016). Due to this general lack of quantitative data, it has been difficult to determine the proximate basis and distribution of SSB, in particular to what degree, if at all, population variation in the behaviour is genetically determined (i.e. heritability). Finding this genetic contribution to SSB matters, since ultimate hypotheses (i.e. concerning the fitness of the behaviour, see below for ultimate-proximate distinction) cannot be valid without heritable variation to the trait (Visser et al., 2008). It is worth clarifying that heritability is not the same as heredity, since heredity does not require natural variation in a population. For example, research has previously suggested that the ancestral pseudogenisation of *TRPC2* was responsible for the high incidence of SSB in old-world primate lineages due to lost olfactory same-sex aversion via the vomeronasal organ (see Fig. 0.1 and Appendix A). While *TRPC2* functioned to influence SSB (i.e. heredity), there was no genetic variation within a species and therefore it was not contributing to heritable variation upon which selection could act. This example also highlights the importance of distinguishing between the evolutionary origins and maintenance of SSB, since selection dynamics underpinning the former may differ significantly from the latter (see Appendix B).

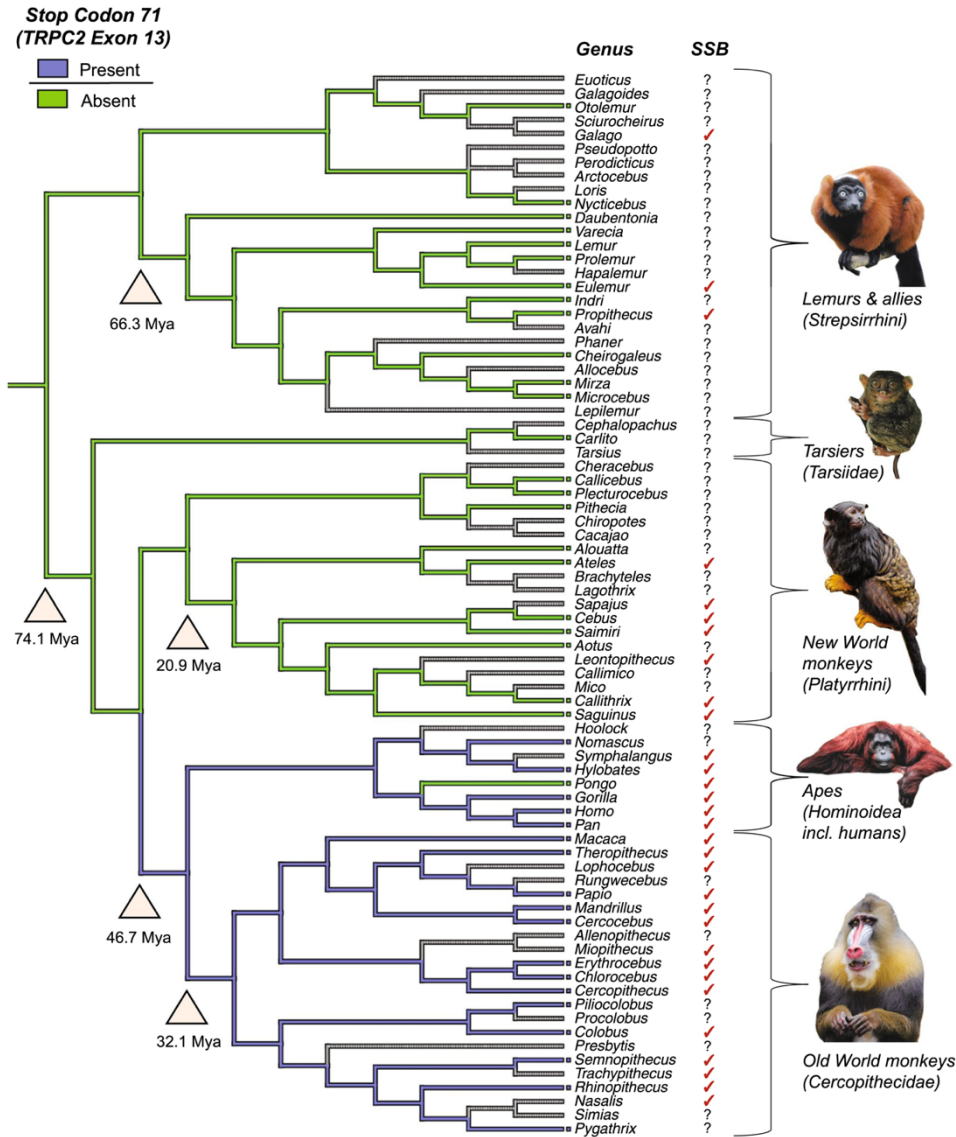


FIGURE 0.1 Distribution of SSB and premature stop codon in exon 13 of *TRPC2* in primates. The presence of SSB in wild primate populations was reported in 31 primate genera, with high incidence in Old World primate lineages that also presented pseudogenisation of *TRPC2*. However, distribution of SSB within species remains uncertain. The earliest stop codon in exon 13 of *TRPC2* to appear in primates was at position 71, along the branch leading to Old World monkeys and apes (blue = stop codon present; green = stop codon absent; grey = unknown). The presence of SSB was determined from behavioural reports, with an uncertain status (indicated by a question mark) applied to genera without confirmed SSB in the wild (Moynihan, 1970; Chandler, 1975; Bagemihl, 1999; Fox, 2001; Carosi and Visalberghi, 2002; Sommer and Vasey, 2006; Poiani, 2010; Huang et al., 2015; Grueter & Stoinski, 2016; Fang et al., 2018; Pfau et al., 2019). Evidence of SSB in *Colobus* is taken from the pers. comm. of Teichroeb in Pfau et al. (2019). The phylogeny was taken from the Open Tree of Life online resource (Hinchliff et al., 2015) and the divergence times from Pozzi et al. (2014). See Appendix A for details.

The ultimate-proximate dichotomy is a useful distinction for sorting the many hypotheses detailing the causes and consequences of SSB. Proximate explanations address the mechanisms by which a behaviour is genetically, neurologically, physiologically or socially underpinned. In contrast, ultimate explanations address why a given distribution of the behaviour would have been favoured by evolutionary processes. In other words, proximate explanations describe how SSB is expressed, whereas ultimate explanations describe the fitness consequences of SSB (Scott-Phillips et al. 2011). Within this framework, there have been numerous proximate and ultimate hypotheses for SSB. Proximate explanations vary from the environmental (e.g. aberrantly skewed social group structures, see Bonnet et al., 2016) neuroendocrinological (Burke et al., 2017), and genetic processes (Ratnu et al., 2017; Pfau et al., 2019). Ultimate explanations frequently assume fitness costs to the behaviour (Sommer and Vasey, 2006; Bailey and Zuk, 2009),

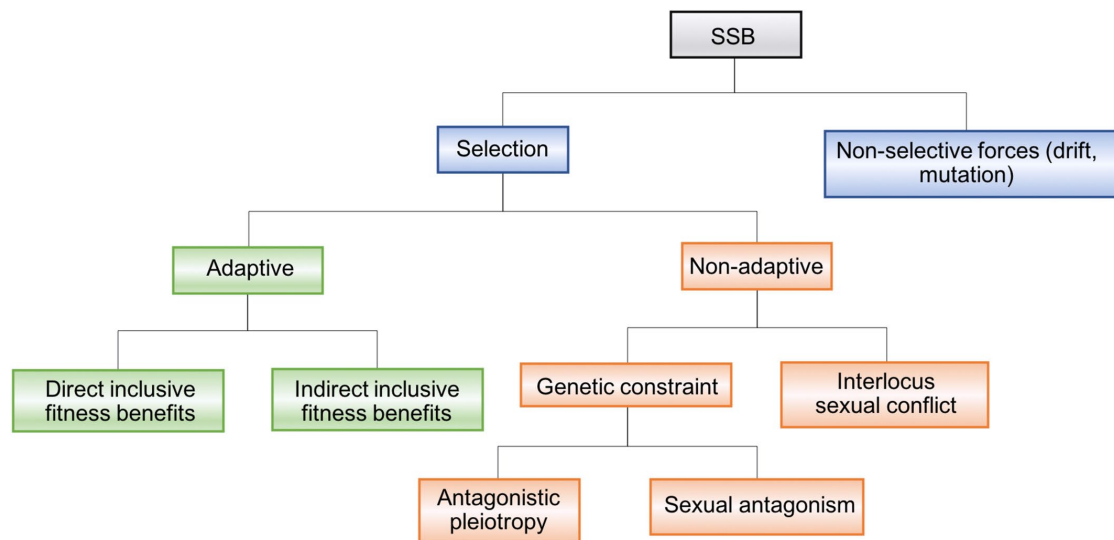


FIGURE 0.2 A behavioural ecology framework for disentangling the evolutionary maintenance of SSB. The trait is maintained in a population owing to either selective forces, or neutral forces such as drift and recurrent mutation. Within selective forces, adaptive explanations for SSB require that the behaviour itself improves fitness through direct or indirect inclusive benefits. Non-adaptive explanations for SSB largely describe scenarios of genetic constraint, in which the alleles underpinning SSB are linked to another adaptive trait expressed either in the same individual or in the opposite sex. Note that neither antagonistic pleiotropy nor sexual antagonism necessarily imply high fitness costs. See Appendix B for details.

and instead seek to describe concurrent fitness benefits that would explain the evolutionary maintenance of the trait in spite of perceived costs. This form of trait maintenance is plausible through a range of selection dynamics (Fig. 0.2). For example balancing selection via overdominance (Gavrilets and Rice, 2006), negative frequency dependence (Pillard and Bailey, 1998) or sexual antagonism (Gavrilets and Rice, 2006). Alternatively a mechanism of stabilising or fluctuating directional selection (Lande, 1975) has been proposed, in which SSB is maintained due to advantages of behavioural bisexuality (Savolainen and Hodgson, 2016).

Many potential fitness benefits have been suggested to explain the evolutionary maintenance of SSB (Sommer and Vasey, 2006; Bailey and Zuk, 2009; Scharf and Martin, 2013). These can typically be divided into those derived from the expression of SSB itself ('adaptive explanations' e.g. where SSB has a social function such as conflict avoidance, or allows individuals to practice for later reproductive encounters, see Sommer and Vasey, 2006), and those arising from other effects of SSB-encoding genes ('non-adaptive explanations', e.g. where SSB genes pleiotropically encode other traits that improve fitness, such as higher sex drive, see Sommer and Vasey, 2006; Scharf and Martin, 2013). Within each of these explanations, fitness benefits beyond the unit of the individual expressing SSB must always be considered (i.e. both direct and indirect components of inclusive fitness, see Scott-Phillips et al., 2011). Indeed, kin-selection has been offered as an explanation of SSB in humans (for example through pleiotropy with increased alloparental care, (Kirkpatrick, 2000; Bobrow and Bailey, 2001), although this hypothesis has been criticised on theoretical and empirical grounds (Sommer and Vasey, 2006; Vasey and VanderLaan, 2012).

In terms of expected costs to SSB, it is of particular interest to understand how SSB covaries with different-sex behaviour (DSB). A degree of dependence and negative covariance between these traits is often assumed, largely due to human behaviour and perceptions of sexual orientation (Bailey et al., 2016). However, it is perhaps more probable that, due to the likely polygenic underpinning of SSB (Hoskins et al., 2015; Ratnu et al., 2017; Ganna et al., 2019), a variety of conflicting pleiotropic effects exist (Swift-Gallant et al., 2019). For example, in contrast with the negative covariance between SSB and DSB anticipated due to the approximate bimodality of intersexual development (Goy et al., 1988; Balthazart, 2016; Burke et al., 2017; Manzouri and Savic,

2018), strong selection on indiscriminate high sex drive (as long as not target-specific) might result in positive covariance between the traits (Sommer and Vasey, 2006; Scharf and Martin, 2013)

In conclusion, SSB appears common across primate species, but variation in individual activity is unclear. This presents a conundrum for researchers – if fitness costs to the behaviour are assumed, then how is the trait maintained? It is therefore essential to clarify if individual variation in SSB activity exists (Chapter 1) and, after accounting for other influences on behavioural activity, whether it can be heritable (Chapter 2). Consequently, any fitness costs or benefits to the behaviour can be explored (Chapter 3), thereby paving the way to comprehensive understanding the causes and consequences of SSB in the natural world.

1.1 INTRODUCTION

1.1.1 How common is SSB within a species?

Across primate species, different behaviours can form the basis of SSB interactions, including types of mounting, oral or manual genital stimulation. In both rhesus and the closely related Japanese macaque species, mounting (Fig. 1.1b) has been described as representative of female (Sommer and Vasey, 2006; Vasey et al., 2014) and male SSB (Altmann, 1962; Leca et al., 2014). SSB in the male rhesus macaques of Cayo Santiago was documented more than 60 years ago, with early field studies indicating that SSB was almost as common as DSB (Carpenter, 1941; Altmann, 1962). However, in the following decades, reports of male rhesus SSB away from the Cayo colony have labelled the behaviour as an ‘aberrant’ or ‘unnatural’ pathology arising from experimental or captive conditions, with no mention of such activity as commonplace (Sommer and Vasey, 2006; Bagemihl, 1999). While subsequent observations of SSB in the wild refute such narratives across numerous species (Bagemihl, 1999; Fox, 2001; Sommer and Vasey, 2006; Bailey and Zuk, 2009; Jiang et al., 2013; Grueter and Stoinski, 2016; Busia et al. 2018; Sandel and Reddy, 2021), including rhesus macaques (Lindburg, 1971), we still lack the detailed distributions of the behaviour needed to evaluate these differing records of male rhesus SSB, namely whether the frequencies of the behaviour could truly be as common as DSB. To test this hypothesis, the thesis revisits the male rhesus macaques of Cayo Santiago.

1.1.2 What about non-mounting types of SSB?

While prior rhesus macaque studies have emphasised mounting behaviour (Altmann, 1962; Lindburg, 1971), it is unclear whether this focus is due to a negligible prevalence of non-mounting SSB, or that specific research interests concerned only behaviours physically analogous to reproductive sex (i.e. mounting). Non-mounting sociosexual behaviours are frequently reported in other macaque species (Ogawa et al., 2019) and apes, for example ventro-ventral genito-genital rubbing between female chimpanzees

(Anestis, 2004), or oral stimulation of genitals between different-sex chimpanzee pairs (Sandel and Reddy, 2021), neither of which would constitute behaviours capable fertilisation via reproductive sex. Therefore, this chapter seeks to answer whether male rhesus SSB largely made up of mounting behaviour, or if other behaviours should be factored into an analysis of inter and intra-individual differences in SSB.

1.1.3 Why the prevalence of arousal and ejaculation matters

Further to characterising types of SSB, the distributions for more or less stimulatory forms of a given behaviour are relatively unknown (Sommer and Vasey, 2006). For example, how many instances of SSB lead to male ejaculation? And how many cases of male-male mounting have both partners displaying penile erections? While these questions are challenging for researchers due to the difficulty of precise observations in the field, such information is critical to understanding the nature of SSB. If the behaviour is frequent, but rarely leads to ejaculation, it is reasonable to suppose a much lower reproductive cost to SSB, since the behaviour would not constitute a direct trade-off in reproductive effort via refractory periods and reduced sperm load. In the second example, the presence of erections in both partners would suggest arousal as a behavioural motivation in both participants, rather than just the mounter, with implications for long-hypothesised socially adaptive functions or proximate mechanisms that could underpin the behaviour.

The question of arousal in SSB also informs on some stricter definitions for SSB itself. If there is no evidence of arousal, it could be argued that the behaviour is not sociosexual at all. For example, should a brief male-male mount with no thrusting and no penile erection in either participant be considered simply gestural? Or should a gestural behaviour be considered not sociosexual? This debate remains controversial, with accusations of politically regressive motives to ‘desexualise’ SSB in nature on one side, and accusations of overly broad definitions artificially inflating prevalence data on the other (Sommer and Vasey, 2006; Bailey et al. 2016). These are semantic and ethical arguments open to discussion, but researchers can at least provide delineated data to inform the debate, in this case by clarifying what proportion of SSB is characterised by varying levels of arousal between participants in male rhesus macaques.

1.1.4 What is the likelihood of exclusive SSB?

Finally, although the occurrence of SSB has been accepted as widespread across old-world primate species, the prevalence of exclusive SSB ‘orientations’ remains unknown. Exclusive SSB is expected to be rare due to the high fitness costs associated with no reproductive sexual activity, and yet in humans (comprising the only comparable data in an old-world primate system), this orientation is consistently reported (e.g. 2% in the UK, see ONS, 2017). Indeed, evolutionary theory can explain even exclusive SSB as a heritable trait, for example, sexually antagonistic selection in which SSB-encoding genes carry fitness benefits when expressed in the male’s female relatives (Gavrilets and Rice, 2006). Therefore, this thesis seeks to characterise the distribution not just of SSB activity, but of behavioural orientations, namely how common exclusive SSB or DSB activity is across individuals.

1.2 METHODS

1.2.1 Defining SSB

Here same-sex mounting (Wickler, 1967; Sommer and Vasey, 2006) was defined as the fundamental mode of ‘same-sex sociosexual behaviour’ (SSB; see Sandel and Reddy, 2021), but as discussed above, the terminology for animal SSB retains some controversy. To circumvent this, the term ‘homosexual behaviour’ is avoided, which has been used interchangeably with ‘SSB’ in some research (Wickler 1967; Vasey, 2002). Furthermore, the term sociosexual is used here, rather than sexual, thereby avoiding the strict definition that a ‘sexual’ behaviour must be directly capable of fertilisation (Paciulli and Emer, 2018). However, this is essentially a semantic distinction, and the term SSB as used here remains effectively synonymous with previous uses of ‘same-sex sexual behaviour’ in the literature.

Crucially, this trait definition of SSB foregoes broader measures of sexual orientation, either in terms of partner-gender predisposition (i.e. preference) or self-identification, with such definitions requiring tests incorporating freedom of choice and, in the latter case, a theoretically unlikely degree of self-recognition in a non-human primate species (Tomasello and Call, 1997; Vasey, 2002). Put simply, SSB is the action, not behavioural orientation, of an individual. Furthermore, while this thesis does use SSB activity over

time to infer such behavioural orientations, these orientations once again do not represent partner-gender predisposition or self-identification. Instead, they are observation-based probabilities of individual activity with regard to a behavioural partner's likely biological sex.

Mounting was defined as a mounter aligning their groin dorsoventrally with the mountee's anogenital region (see Fig. 1.1b, and ethogram in Appendix C, Table 1). Due to the start-stop nature of rhesus consort mounting behaviour (Manson, 1996), repetitive mounting behaviours (occurring within a five-minute interval) between the same participants were collapsed into counts of singular mounting events. This is in convention with previous studies of reproductive behaviour in rhesus macaques (Vasey and Sommer, 2006; Dubuc et al. 2014a), and buffers against the extreme skews arising from this characteristic of rhesus courtship. Non-mounting SSB was defined as one of three possible behaviours: (1) direct genital stimulation by another individual; (2) self-stimulation or (3) erectile displays in which either took place during affiliative contact with another male (for example while being groomed, see Appendix C, Table 1). For each observation of SSB, any observable presence or absence of erections, intromission, and ejaculation were recorded. To test for significant differences in the rate of mounter erections, intromission and ejaculations between same and different-sex mounting, two-sample tests for equality of proportions with continuity correction were used.

1.2.2 Study site

The macaque colony of Cayo Santiago has been maintained for studying primate behaviour under semi-natural conditions since 1938 and is currently managed by the Caribbean Primate Research Centre (CPRC) from the University of Puerto Rico (Widdig et al. 2017). By alleviating the limitations to studying either zoo animals or fully wild primate populations, the Cayo Santiago colony is the best place to conduct this type of research. The population was founded by 409 individuals captured at various locations in India in 1938, and is now maintained at around 1,700 individuals by CPRC (Widdig et al. 2017). The population is dense (~113 animals / ha), but comparable to wild macaques that have been living close to human settlements in India for several thousands of years (Balasubramaniam et al., 2014; Kanthaswamy et al., 2017); for example, about 60% of wild Indian populations are found in rural or urban areas rather than forests (Kumar et al., 2013). The current female-male ratio on Cayo Santiago is ~ 1.1, comparable to that found

wild populations (1.8 \pm 0.8) (Kumar et al., 2013). The monkeys spend at least 50% of their feeding time foraging on the natural vegetation of the island, although CPRC provides additional food as commercial monkey cubes spread across the island (0.23 kg/monkey/day) (Widdig et al., 2016a). This is again comparable to many wild populations that are supplemented with food by monasteries around which they often live. Water is available ad libitum. Although there are no predators on Cayo Santiago, many infants do not survive their first year of life (\sim 15%) (Widdig et al., 2017), mostly due to hurricanes and disease outbreaks. The Cayo colony has also retained a social structure similar to that found in the wild (Balasubramaniam et al., 2014). The high effective number of founders and management practice has had positive effects on the colony's current genetic structure, with evidence of outbreeding via disassortative mating (such that inbreeding is minimal – with less than 7.4% of individuals showing positive inbreeding coefficients) (Widdig et al., 2017) and comparable levels of genetic diversity to wild populations (heterozygosity on Cayo Santiago is \sim 0.7 versus 0.35 \pm 0.27 in India (Kumar et al., 2013; Kanthaswamy et al., 2017).

1.2.3 Observation protocol and sample males

Behavioural data was gathered from two social groups ('R' and 'V') using two observers over 60 days of observations from March-June in 2017 and again in 2019, with a further twelve days of observation in March 2020. Observations were conducted by following the group from 7am to 2pm each day of study, using an ethogram designed to capture all sociosexual behaviours. Data collection for this study was approved by the Institutional Animal Care and Use Committee (protocol no. A500118). A pilot study showed that mounting behaviours were unlikely to be recorded in sufficient detail with focal sampling, therefore continuous all-occurrence sampling observations were collected. This method consists of one observer per group recording the type of behaviour and participant identity for male activity. Observations ranged from the social group centre to the periphery to capture all behaviours in the ethogram, for example different-sex mounting that might only occur when hidden from other monkeys. To support these observations, photographic and video evidence were also recorded. All observers were tested for interobserver agreement (see below).

All-occurrence sampling may lead to unquantified differential observation time between individuals (e.g. if some males tend to hide more than others), or intra-individually

between repeated measures (i.e. counts per 12-day periods of study). Therefore, to assess the potential effect of variation in sampling effort within and between individuals across the eleven 12-day periods of study, traditional scan sampling was used, in which all recognizable males within the line of sight of the observer were recorded at 10-minute intervals throughout data collection. These 25,027 presence-absence counts were totalled per study period to create an index of observer sampling effort per individual in downstream analysis. Furthermore, for an individual's count data per 12-days (i.e. a repeated measure) to be included in analysis, a reliability threshold of ten or more scan samples per individual per 12-day period was set. After filtering for these criteria, count data was available for 236 sample males with a total of 1,076 repeated measures (Appendix C, Table 2). All data logging was semi-automated using smartphone hardware with custom-built interrelated databases to standardize data inputs and minimize errors.

1.2.4 Interobserver agreement

To ensure consistency of behavioural data collection, eight of the eleven 12-day study periods were tested for agreement between observers. Each test used one or two 45-minute inter-observer reliability sessions (depending on behavioural observation rates per session), with agreement evaluated using Cohen's kappa test in the *irr* software package (Gamer et al., 2012). Tests alternated between the two social groups. Due to observer familiarity with individual identities of a single group, sex-age class (e.g. adult male, adult female, juvenile male etc.) rather than individual identity was recorded during test datalogging. Accuracy of individual identification was evaluated orally after each 45-minute session, with the non-group observer selecting random individuals for identification and post-hoc checks of individual identity using the CPRC identity code tattoos located on the inner thigh or chest. No cases of misidentification occurred throughout the study. Agreement for behaviours and sex-age class identification of behavioural participants was high, with all kappa scores exceeding reliability thresholds of 0.95 ($p < 0.005$), with the exception of a single test in which a repeated series of agonistic interactions listed an adult male misclassified as a subadult male by the visiting observer unfamiliar with the social group (observer agreement remained over 90%, Appendix C, Table 3). Observer agreement of mounting behaviour intensity (erections, thrust count etc.) was performed manually, with no cases of disagreement, and only a single case of difference in certainty (in which an erection was observed by one observer but recorded as unknown by the other).

1.2.5 Predicting behavioural orientations

A binomial regression was used to test for a significant effect of mounting interactions observed per individual on whether an individual had been observed mounting with both males and females. Total possible mounting interactions per individual began at two (ranging up to 52), since this was the minimum for which the probability of mounting both males and females was not inherently zero. Using this significant binomial distribution, probabilities for increasing likelihood of having mounted both males and females with increasing number of mounting interactions were calculated (Appendix C, Table 4).

1.3 RESULTS

1.3.1 Male-male mounting was more common than male-female mounting

Same-sex mounting was more frequently observed (1,017 observations) than different-sex mounting (722 observations; Appendix C, Tables 1 and 5). After restricting statistics to those males that could be identified individually and which were seen regularly (i.e. sample males, see Section 1.2.3), male same-sex mounting remained widespread: 72% of sample males engaged in same-sex mounting, in comparison with 46% for different-sex mounting (Fig. 1.1; Appendix C, Tables 5-6). More males were behaviourally bisexual than exclusive behavioural orientations (Fig. 1.1), and these individuals had significantly greater mounting activity levels than either exclusive or different-sex orientations (Fig. 1.2, Tukey HSD; $p < 0.005$).

Mounts were also subdivided based on ‘mounter’ (the animal that performs the mounting) versus ‘mountee’ (the animal being mounted) roles (Sommer and Vasey, 2006; Sandel and Reddy, 2021), and found same-sex mounter counts (531) were equivalent to different-sex mounter counts (530) (Fig. 1.1; Appendix C, Table 5).

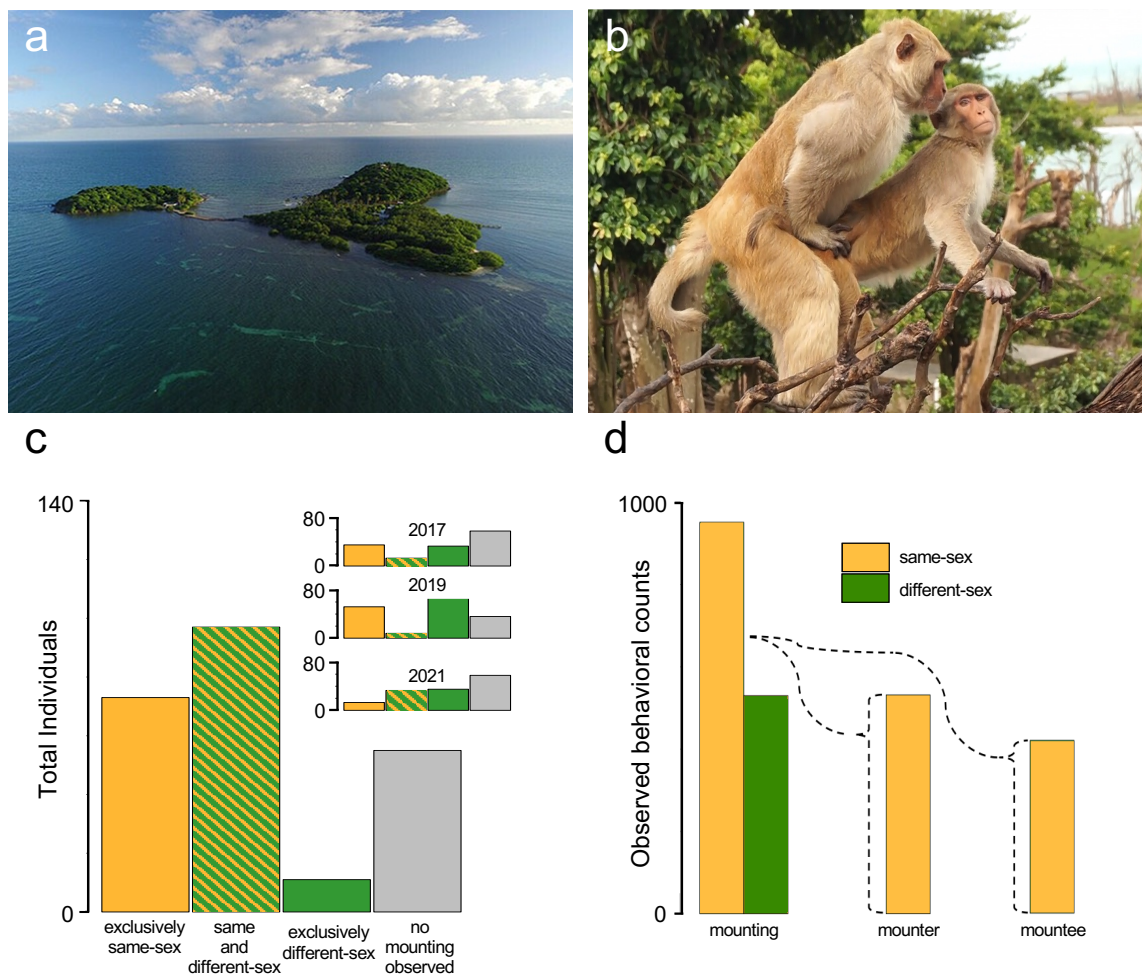


FIGURE 1.1 Prevalence and distributions of mounting behavior. (a) Cayo Santiago island, home to a colony of rhesus macaques (photo credit: CPRC); (b) Two males aged 7.5 (mounter, above) and 4.6 years (mountee, below) engaging in same-sex mounting (photo credit: S. Edwards); (c) Distribution of observed mounting activity for sample males, with totals per study season inset. More individuals were observed engaging exclusively in same-sex mounting than those exclusively in different-sex mounting; (d) Total same-sex mounting counts for sample males (total, mounter, mountee) versus different-sex mounts. Note that mounter and mountee counts are not equal because there were occurrences of a known individual mounting an unknown male.

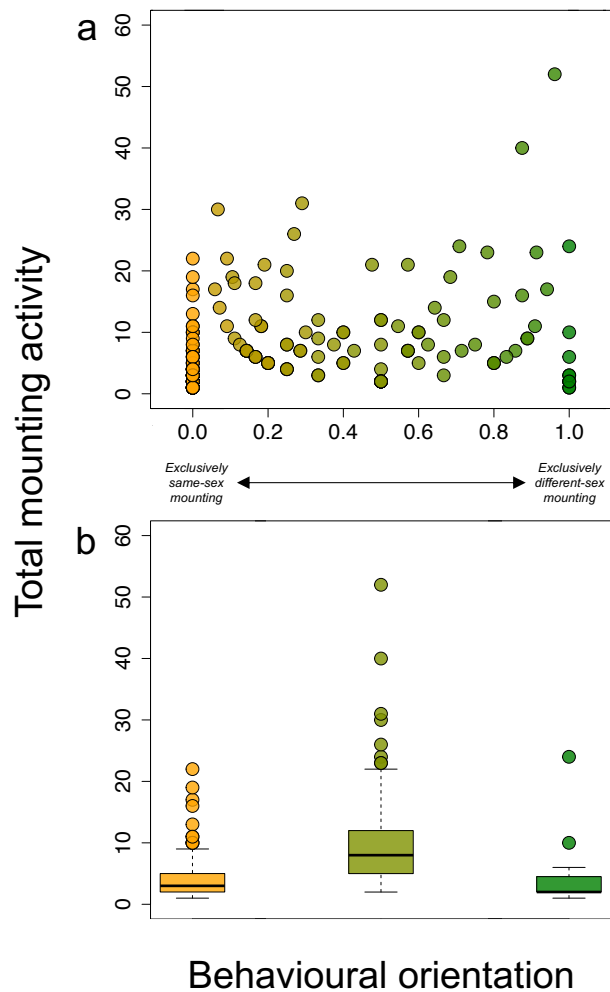


FIGURE 1.2 Total mounting activity across behavioural orientations. (a) The distribution of total mounts per sample male ($n = 236$) across the ratio of same-sex to all mounting behaviour. Mounting activity levels appeared to increase towards the extremes of behavioural orientation, but categorical orientations of mounting behaviour (b) showed that behaviourally bisexual individuals had significantly greater mounting activity levels than either exclusive or different-sex orientations (Tukey HSD; $p < 0.005$).

1.3.2 Mounting was the fundamental mode of SSB

Across the years of study, mounting was by far the most frequently observed type of SSB (Appendix C, Tables 1 and 5). Indeed, mounting interactions made up 99.1% of cases which involved genital contact, with just six observations of oral or manual genital stimulation. Notably, all but one of these six observations involved males under three years of age. Of the non-mounting SSB observed, the vast majority (96.7%) comprised of behaviours with no participant genital stimulation (i.e. were cases of self-stimulation or erectile displays during affiliative physical contact). Results for non-mounting DSB were similar to those of SSB. Once again, genital stimulation was confined to a few observations, in this case partnerships of adult females stimulating younger subadult and juvenile males. Overall, non-mounting behaviours made up a greater proportion of total

behaviour counts (i.e. relative to mounting behaviour; Appendix C, Table 1) for SSB (15.4%) than DSB (5.9%).



FIGURE 1.3: Non-mounting behaviour in male rhesus macaques. (a) A male displaying an erection while being groomed by another male. (b) A male ejaculating from manual self-stimulation while being groomed by another male. (c) Two males resting in affiliative physical contact. Both (a) and (b) were considered as possible forms of SSB (making up 15.4% of general SSB observations). However without direct genital stimulation by the participant individual, status as SSB was considered uncertain and only mounting behaviour was examined in downstream analysis. The behaviour in (c) was not counted as SSB, but was defined as one of many possible contexts that could precede SSB.

1.3.3 Ejaculatory same-sex mounting was rare

The rate of mounter erections was not significantly different between same-sex mounting (0.83) and different-sex mounting (0.88; $X^2 = 3.43$, $p = 0.06$), however rates did significantly decline for intromissive mounting (same-sex = 0.65, different-sex = 0.95; $X^2 = 109.61$, $p < 0.005$) and ejaculatory mounting (same-sex = 0.04, different-sex = 0.68; $X^2 = 70.39$, $p < 0.005$).

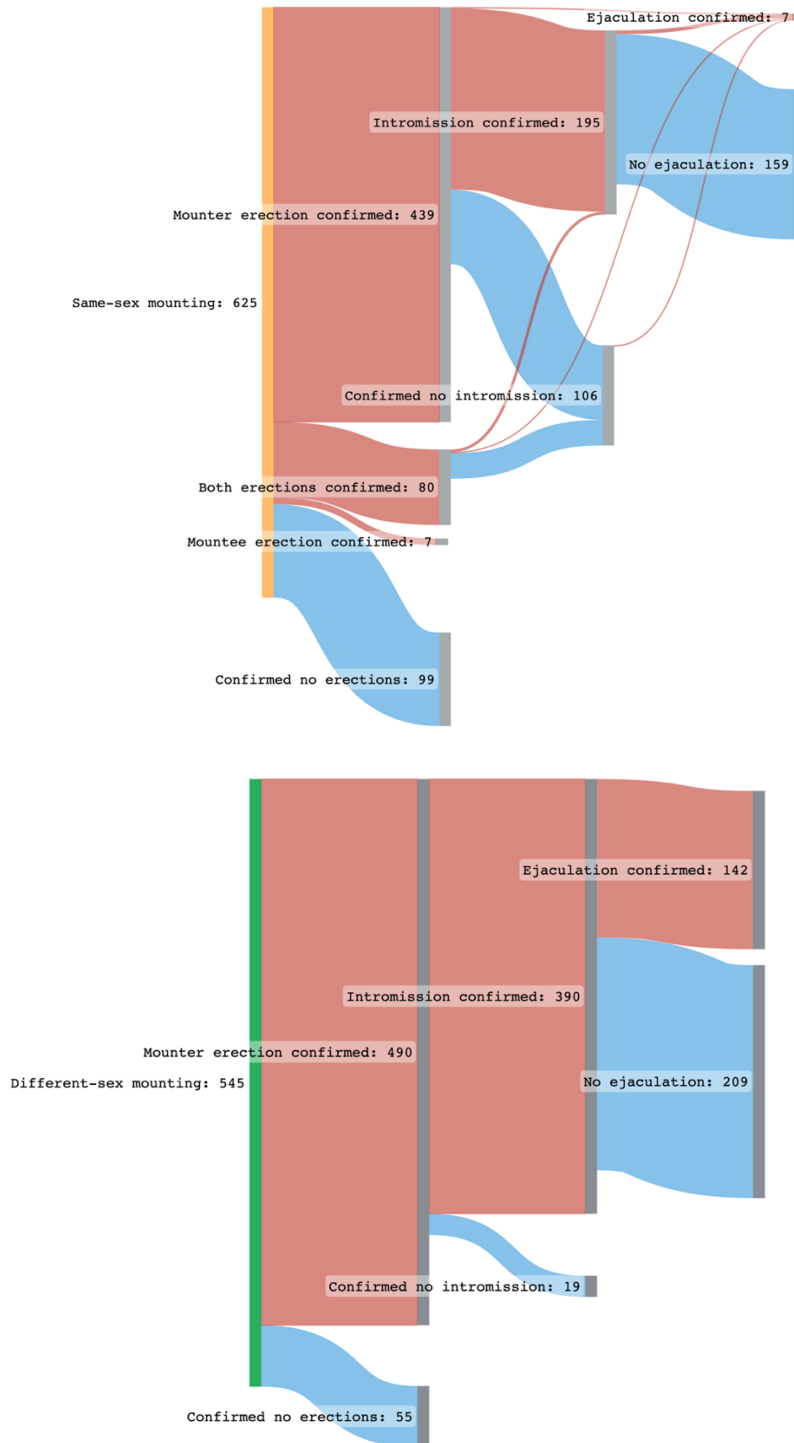


FIGURE 1.4 Distributions of arousal indicators in same-sex and different-sex. Rates of mounter erections were similar between SSB (0.83) and DSB (0.88), but mounting with females showed significantly greater rates of intromissive ($\chi^2 = 109.61, p < 0.005$) and ejaculatory ($\chi^2 = 70.39, p < 0.005$) mounting. Proportions are made up of observations in which the presence or absence of a characteristic was confirmed, therefore total mounting counts are lower than total observations reported in main text due to the exclusion of observations for which a given characteristic was uncertain.

In particular, mounting with ejaculation was rarely observed for males mounting males ($n = 7$) relative to mounting females ($n = 142$; see Fig. 1.4). When males mount females and ejaculate, a sperm plug is formed that presumably increases the likelihood of fertilization by keeping the sperm inside the female's reproductive tract. These anal sperm plugs were also visible on several males during the study, further demonstrating that, although rare, ejaculation can occur during male-male mounting (Fig. 1.5 and Appendix C, Table 1).

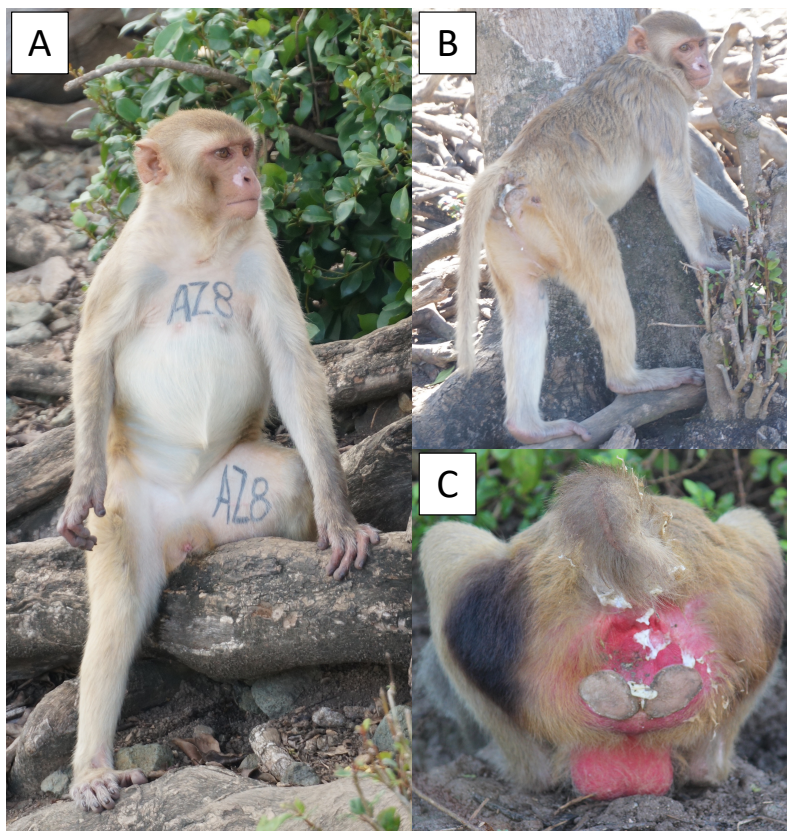


FIGURE 1.5 Evidence of ejaculate in male rhesus anogenital regions. (a) A young male (identity code: AZ8) displaying male genitalia and CPRC identity tattoos. (b) The same male (see facial birth mark on right cheek) with ejaculate in anogenital region. (c) An older male with developed testes and ejaculate in anogenital region. Video evidence of ejaculatory same-sex mounting was also recorded.

1.3.4 Most males will mount with both males and females

With every mounting event observed, the likelihood of an individual mounting only males decreased (slope $\beta = -0.192$, $p < 0.005$). The model predicted that after observing an individual perform 21 mounts, the likelihood of it being categorized as exclusively same-sex was less than 5% (Fig. 1.6; Appendix C, Table 6).

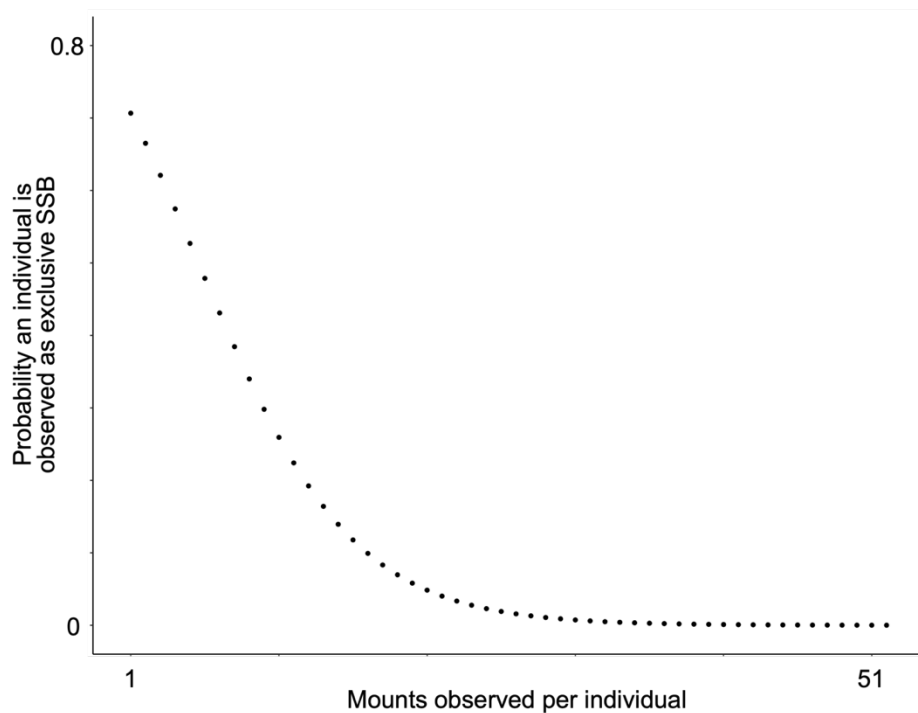


FIGURE 1.6 Probabilities of a sample male being categorized as exclusively same-sex in mounting activity based on number of mounts observed. Probabilities were calculated based on a significant binomial regression of the number of mounts observed per individual against their exclusive same-sex mount status.

1.4 DISCUSSION

Results here show that male primate SSB can be more frequent than DSB, but highlight the need for clarity when defining behaviours. In particular, partitioning mounter and mountee behaviours resulted in a drastic reduction, from double that of DSB, to roughly equivalent frequencies. However, even after this split same-sex mounting still marginally

exceeded different-sex mounting, thereby vindicating and surpassing the early 1962 observations from Cayo Santiago, which concluded that a male ‘monkey’s sexual behaviour was not appreciably more likely to be heterosexual than homosexual’ (Altmann, 1962). Expectations that SSB would be much rarer than DSB may have arisen because of an assumed high fitness cost to the behaviour, but there are other explanations for this belief. Firstly, many theorists of the previous century characterised the behaviour as an aberrant pathology, arising purely from captive or extreme environmental conditions (Sommer and Vasey, 2006). This view may have been partly based on the heteronormative cultural stigma of the day (Bailey et al., 2016), but also from an overreliance on observations of captive individuals (Sommer and Vasey, 2006). For example, it is reasonable to suppose that captive conditions, which can impose extreme stress or access to only conspecifics of the same-sex, could be the cause of unusually high frequencies of SSB (Jankowiak et al., 2018). Indeed, the same observation has been made in human societies about prison systems (Bailey et al., 2016). However, it does not follow that high frequencies must therefore not exist in mixed-sex systems. This ‘prisoner-effect’ hypothesis has occasionally entered ecological theory (McGraw and Hill, 1993; Bonnet et al., 2016), but conflation should be avoided between data that suggests limited DSB access could increase an existing level of SSB, and a conclusion that SSB only exists purely because of limited DSB access.

A second reason for the assumed rarity of SSB relative to DSB is early primate field observations did not report much of the behaviour (Lindburg, 1971). Once again, this may have been a historical reporting bias due to cultural stigma on the topic, but it has also been suggested that some low SSB frequency estimates in wild habitats (i.e. with low visibility) may have been deflated by assumptions that an observed sociosexual behaviour inherently denoted male and female participants (Sommer and Vasey, 2006; Bailey and Zuk, 2009). Either way, more recent studies of macaques have suggested these estimations were low, although never yet to the degree that frequencies of SSB could exceed DSB. For example, a recent study showed that wild male Tibetan macaques (Jiang et al., 2013) did not exhibit SSB as frequently as DSB (except in juveniles aged 2-3 years), with DSB greatly exceeding SSB for younger adult males and then becoming near equivalent again in older individuals (+15 years). While valuable to SSB research, such group-level assessments of SSB versus DSB can fail to discern whether the behaviour is confined entirely to certain individuals within a group, for example males that cannot

access to females due to peripheral social network status or low dominance ranks. Here, the distributions of behaviour within an individual showed that more males engaged in SSB than DSB, with 31% of males engaged exclusively in SSB. This result could point to limited female access contributing to the high frequencies of SSB observed. However, most males engaged in both SSB and DSB to at least some degree (41%), showing that even males with access to females are likely to perform SSB to some degree.

This prevalence of behavioural bisexuality, in which males mount both males and females throughout their lifetimes, has been predicted by the ‘bisexual advantage model’ (Savolainen and Hodgson, 2016). This concept is based on the idea of stabilizing or fluctuating directional selection mediating the trait of behavioural bisexuality, and predicts that some degree of bisexual behaviour is more common than exclusive SSB or DSB (Fig. 1.6). In support of this concept, bisexual mounting was the most common category for sample males, even within only three years of study. Additionally, sexual activity was significantly greater in behaviourally bisexual individuals, lending support to ultimate hypotheses of SSB that rely on fitness benefits to high sex drive (Sommer and Vasey, 2006). Male rhesus lifespans can exceed 20 years, and the binomial regression of mounting partners showed that the probability of mounting both males and females increased to statistically significant levels ($p < 0.05$) within just 21 mounts. This is an extraordinarily small number of behavioural events for a male’s lifespan, and suggests that the 31% of males observed exclusively engaging in SSB would be revealed as behaviourally bisexual within just a few more seasons of study. Indeed, only a single male was statistically likely to be an exclusively same-sex individual (by having exclusively mounted males on more than 21 occasions). However, even this case was somewhat unresolved, since the individual was noted as a young and low-ranking male that only just exceeded the significance threshold with 22 observed mounting interactions recorded. Therefore, with further sampling for a young individual that might have improved access to females in later life, even this case could support the idea that all rhesus males are behaviourally bisexual across their lifespan.

Results showed that mounting was the fundamental mode of SSB in male rhesus macaques, in contrast with a recent comparison of Assamese and Tibetan macaques which suggested that other genital-contact behaviours could still play a role in SSB interactions (Ogawa et al., 2019). Non-mounting genital-contact behaviours in the sample males were

extremely rare and characterised by the participation of at least one juvenile individual. Potentially these behaviours reflect an extension of play and induced social learning, but were far too rare to be examined here in detail. The behaviours without partner stimulation of genitals were more common, but arguably represent less clearcut instances of SSB. Indeed, any instance affiliative same-sex contact could plausibly be circumstantial to the individual's expression of arousal through erections and self-stimulation. Subsequent analysis would benefit from assessing these behaviours in parallel with mounting activity, thereby capturing any possible correlations between the behaviours without assuming a common basis. It is unclear why macaque SSB appears more mount-centric than in other primates. Perhaps there are differences in morphology that result in varying strengths of pleasure-feedback mechanisms between such behaviours, resulting in differing behavioural motivations between species (Sommer and Vasey, 2006; Macfarlane and Vasey, 2016).

Here, not all same-sex mounts involved mounter erections with plausible genital stimulation. While this opens up the possibility of a proportion of same-sex mounting being more gestural (and even not sociosexual under some stricter definitions for the trait), the proportion size was not significantly different from different-sex mounting without erections. Therefore any restriction on SSB based on this definition would also have a proportional restriction on DSB, leaving overall relative frequencies unaffected. However, the differences in arousal mediating same-sex versus different-sex mounting behaviour did become more apparent for intromissive and ejaculatory mounting. In particular, the low incidence of ejaculatory mounting fits with the expectation that this form of SSB would be rarer due to fitness costs via trade-offs with reproductive effort. Firstly, frequent same-sex ejaculations might lower sperm load for reproductive opportunities taking place soon after SSB (and even if SSB was not underpinned by a sexual preference). However, males were frequently seen performing self-stimulation until ejaculation, suggesting that the act itself does not carry a significant fitness cost. Alternatively, a heightened strength of motivation for same-sex interactions mediated by pleasurable ejaculation might lead to more extreme trade-offs in activity budget allocation between SSB and DSB. Once again, the question of reproductive cost comes down to the degree of trade-off with DSB, rather than the type and amount of SSB.

In both SSB and DSB, the majority of mounting showed some degree of genital stimulation. Notably, 16.2% of male mountees displayed erections during same-sex mounts (Fig. 1.4). The presence of these cases suggest that males can be aroused by the act of SSB beyond the potentially indiscriminate tactile stimulation of their genitals. While individuals might also be feeling arousal in unobservable ways, it is critical to show that same-sex mounting can be mutually stimulating for participants, with the inference that (1) coercion is not fundamental to the behaviour; and (2) that sexual arousal reinforcement mechanisms may be doubly mediating behavioural frequencies. These two inferences may prove essential to disentangling proposed social functions to SSB, for example cases of dominance expression (in which mountee, or even mounter arousal might be less likely) or alliance formation (with stronger social bonds for interactions with mutually aroused participants).

1.5 CONCLUSION

These results lay the foundations for further investigation into male SSB. Male mounting was confirmed as fundamental mode of SSB, legitimising a focus on this form of the behaviour over the rarer forms of genital contact or less clearcut instances of sociosexual interaction. However, questions remain over the different subtypes revealed within male mounting that could dramatically influence downstream analyses, in particular between mounter and mountee activities, and also mounting with evidence of arousal. In summary, results showed that male SSB was widespread, with most individuals engaging in same-sex mounting, and all males likely to be behaviourally bisexual. This is a critical finding, since it suggests that fitness costs to SSB should not be inferred by solely from the incidence of SSB, but rather how SSB trades-off with DSB within behavioural bisexuality. The role of limited female-access in mediating SSB was also highlighted as a possible influence on the more even distribution across males of SSB than DSB, as was the influence of age in general. Through investigating these individual profiles of SSB, it is now possible to explore effects on intraindividual and interindividual differences in behavioural activity, thereby assessing the potential repeatability and heritability of the behaviour.

2.1 INTRODUCTION

2.1.1 SSB evolution requires heritability

Evolution cannot occur unless there is variation in the trait (i.e. repeatable differences between individuals) and a mechanism for its inheritance (i.e. heritability). To validate investigations of SSB evolution, it is therefore essential to show that variation in SSB can indeed be heritable (Visccher et al., 2008). In insects, SSB is observed in certain genotypes (Hoskins et al., 2015). However, it appears this form of SSB stems from indiscriminate sex recognition (Scharf and Martin, 2013), and it is unclear whether such observations are relevant for SSB in other animals, in which the behaviour instead appears underpinned by definite sex recognition and even same-sex attraction (Bailey and Zuk, 2009; Hoskins et al., 2015). Meanwhile in vertebrates, heritability of SSB has only been shown in humans (Burri et al., 2015; Ganna et al., 2019; Hu et al. 2021). For example, a recent genome wide association study (GWAS) of UKBiobank/23andMe data for nearly 500,000 men and women showed that genetic variants accounted for 8 to 25% of variation in SSB. However, such results are complicated with human subjects since they rely on self-reporting of sexual orientation, which can be heavily biased (Xue et al., 2021). For example, as reported in the GWAS above, there was a strong relationship between birth year and the reporting of same sex intercourse, with older people reporting much less homosexuality (Ganna et al., 2019). To circumvent these problems, the behavioural profiles constructed in Chapter 1 of rhesus macaques, our closest model species in medical research (Xue et al., 2016), were used to test the hypothesis that vertebrate SSB is heritable in nature and therefore capable of evolving.

2.1.2 Labile effects must be accounted for

As an alternative to evolutionary theories, SSB has at times been described as a by-product of environmental conditions (Bonnet et al., 2016; Jankowiak et al., 2018), with the inference that it is without repeatable differences between individuals. These

conditions include periods of social instability (Sommer and Vasey, 2006) or unusual social group structure, for example skewed male-female sex ratios (Vasey and Gauthier, 2000), in which populations skewed towards a particular sex are expected to exhibit greater SSB activity in that sex. Evidence for SSB due to this DSB ‘deprivation hypothesis’ (Vasey and Gauthier, 2000) has occasionally been supported (Goy and Wallen, 1979; Bonnet et al., 2016; Jankowiak et al., 2018), but also questioned, at least in macaques (Vasey et al., 2014). This hypothesis was tested using seasonal social group demographic data to predict variation in repeated measures of SSB across 236 sample males.

For social mammals, particularly primates, social dominance is also frequently proposed explanation for SSB, and can be traced back to 1936 with Maslow’s belief that primate sexual behaviour is either motivated by sex drive or by dominance drive (Altmann, 1962). In fact, social dominance hypotheses centre largely around two entirely separate theories. One suggests that SSB could function as an expression of relative dominance between individuals (i.e. mounters proving their dominance over mountees), potentially comprising an adaptive function by improved social cohesion. Support for this hypothesis has been shown in some mammal species (Sommer and Vasey, 2006; Bailey and Zuk, 2009, but has also been discredited in primate research on both theoretical (Sommer and Vasey, 2006) and empirical grounds (Reinhardt et al., 1986; Jiang et al., 2013; Grueter and Stoinski, 2016; Rufo et al., 2020; Sandel and Reddy, 2021). Alternatively, a second social dominance concept relates again to the DSB ‘deprivation hypothesis’, whereby SSB is a by-product of a low-rankers failure to access the opposite sex (Vasey et al., 2014). Both of these dominance-related hypotheses were here tested using seasonal dominance ranks calculated independently from mounting with 3508 agonistic winner-loser interactions observed throughout the study (Appendix C, Table 1) Unlike the deprivation hypothesis, the dominance expression hypothesis does not rest on predicting varying intra- and interindividual SSB activity, but rather the distribution of relative rank between mounters and mountees per mounting event.

Age has also been suggested as influencing the expression of SSB, although the manner of this effect is unresolved (Carpenter, 1941; Sommer and Vasey, 2006). If age effects are due to changing levels of sex-drive affecting all sociosexual motivation, then higher rates of SSB are to be expected in males at their young and middle-ages of peak libido.

Alternatively, if SSB functions adaptively as juvenile practice for later heterosexual opportunities, then heightened expression might be expected during adolescence (with behavioural expression under age-related pleiotropy due to assumed costs of expression in later-life). If age associates with access to females, then a further mechanism for the aforementioned ‘deprivation hypothesis’ may also apply. The effect of differing age was therefore tested here for effects on varying SSB activity both across and within individuals.

If variation in SSB is entirely due to these types of transient environmental effects (individual age, social group structure etc.), then there cannot be heritable variation in the trait. However, if they explain only a proportion of behavioural variance, accentuating trends rather than being their sole cause, then repeatable and heritable variation of SSB remains possible.

Repeated measures of individual activity (in this case, absolute counts of same-sex mounting per sample male per 12-day period) allow calculations of the proportion of phenotypic variance attributable to a given individual, that is, ‘repeatability’ (Visscher et al., 2008; Wilson, 2018). Although repeatability can include both genetic and non-genetic factors (Visscher et al., 2008), it is sometimes taken as an upper estimate of the heritability of a given trait (Wilson, 2018). It is therefore important to partition repeatable variance between these non-genetic and genetic sources (see Section 2.2.5), in addition to accounting for other more labile factors (e.g. individual age, social group structure etc.), to avoid inflated estimates for heritability (Wilson, 2018).

2.1.3 How does SSB trade-off with DSB?

Lastly, this chapter explores potential phenotypic and genetic correlations between types of SSB and DSB. While the question of fitness costs to SSB can only apply if the trait is heritable, it also rests on how the behaviour trades-off with different-sex mounting (i.e. reproductive sexual effort). Differences within subtypes of SSB are also explored, for example should we consider all types of SSB as underpinned by a common genetic basis (e.g. genes coding for same-sex attraction)? Or are different forms of SSB genetically unrelated, or even inversely related (e.g. genes coding for the orthodox male behaviour of mounter versus the orthodox female mountee behaviour)?

2.2 METHODS

2.2.1 Repeated measures of behaviour

To investigate effects on inter and intraindividual variation in same-sex mounting, repeated measures were constructed by dividing sampling effort into equal length observation periods (for full observation protocol methods, see Section 1.2.1). A period of 12 days was chosen as the longest interval available while maximizing available count data (due to curtailed observation season in 2020). Therefore, for each individual, up to 11 repeated measures of counted mounts per 12-day period were possible. For downstream analyses, the final sample size was 1,076 repeated measures across 236 males (mean individual age = 9.7 years, SD = 4.3; Appendix C, Table 2). To support the results obtained with 12-day interval repeated measures, corroborating intercept-only results have also been provided for six-day and thirty-day interval periods (see Appendix C, Table 2 for corresponding sample sizes and Table 7 for results). Furthermore, results from analysis of un-collapsed mounting counts (see Section 1.2.1 for rationale) are also listed in Appendix C, Table 7.

2.2.2 Mounting with evidence of arousal

Same-sex mounting was chosen as a discrete and common form of SSB (see Section 1.3.2). In additional support of a heritability result for SSB, results were also reanalysed using repeated measures constructed only for mounting with evidence of arousal. This added constraint served to provide results for a stricter criterion of SSB (see Section 1.4). Mounting with evidence of arousal was categorised as an interaction in which the mounter displayed an erection or, in cases where erectile status could not be observed, made >3 thrusting motions. This was due to the challenge of confirming erection presence/absence during mounting observations, whereas thrusting motions were easily observed and significantly predicted mounter erections in cases where both traits were confirmed (binomial regression, $p < 0.05$; Appendix C, Table 8). This method was applied for the latter six of eleven study periods (i.e. undertaken in 2019 and 2020). Mounting with at least four thrusting motions gave an 84% probability of the mounter also having an erection (greater thrust count thresholds were too limiting to data availability for analysis). Mountee erections were less frequent and were not predicted by thrust count, therefore only mounter arousal counts were investigated.

2.2.3 Accounting for labile effects

Since possible effects and interactions have not been well established for SSB, all combinations of candidate labile effects same-sex and different-different-sex mounting were permuted to test for optimal goodness of fit. For downstream analyses, effects were considered significant when they were retained in the permutation of effect structure with the lowest deviance information criterion in which all fixed effects were statistically significant ($pMCMC < 0.05$; Appendix C, Tables 9-10; for model parametrization see below). All modelling was performed in R using the *MCMCglmm* package (Hadfield, 2010). Group sex ratio, group ratio of older to younger males, and social group size were taken from annual census surveys, and fit as fixed effects in Bayesian Monte Carlo Markov Chain Poisson generalized linear mixed-models (MCMC GLMMs) of same-sex mount repeated measures. Sex ratio calculations were performed using the rhesus age-class categories adult male (5+ years) and subadult male (3.5-5 years) against adult female (3+ years) and juvenile female (2-3 years). Individual age was calculated based on colony census records using the start date of each new repeated measure. Other permutations of group sex ratio calculations (e.g. based on exclusively adult male and females, or no juvenile females etc.) did not perform as strongly during preliminary analyses. Mating season effects, with reference to the female-access deprivation hypothesis (see main text), were also tested using group and multi-group level counts of different-sex mounting behaviour per 12-day observation period, but did not predict SSB (Appendix C, Table 10). Given the proximity of the two social groups under investigation, population level ratios and sizes were investigated and discarded due to clear non-significance during preliminary analysis. Birth season effects, in which a binary score was assigned to observation periods based on dating from the second census births in a given season, were also discarded due to non-significance.

Dominance ranks were calculated for each study season (since the 12-day repeated measure periods were considered too short to reliably infer dominance rank fluctuations), using agonistic interactions with a clear winner and loser recorded for all identifiable males throughout the study. Both Elo and David's scores were calculated (David, 1987; Neumann et al., 2011). Although Elo stability may be a genuine reflection of transience in a given social group, it was used here as a function of rank estimate reliability. Ranks were calculated for individuals with a minimum of three agonistic observations per

season, which retained Elo stability of >0.9 , but did not significantly reduce the sample size of available phenotype data for analysis (individuals = 220, repeated measures 963; Appendix C, Table 2). Where winners of agonistic interactions were unclear, the sample was considered a draw and not scored, since rank assessments here aimed to capture relative group rank rather than agonistic activity. In spite of the uncertain evidence for the dominance expression hypothesis, some studies have by default used same-sex mounting role as a scored input to assess relative dominance rank between individuals. Given the aim here was to investigate the dominance expression hypothesis, this component of scoring was not used here. Rank scores per group were normally distributed. In keeping with previous research (Balasubramaniam et al., 2013), differences between Elo and David's scores were minimal (Appendix C, Table 11). David's scores were therefore used for analysis due to the relative brevity of the study period. All dominance rank analysis was performed using the *EloRating* package in R (Neumann et al., 2011). Previous research has suggested that rather than possessing a genetic basis, male dominance rank is determined by queuing (i.e. group residency length), rather of male-male competition or heritable morphometric features linked to competitive advantage (Dubuc et al., 2014b; Kimock et al., 2019). Therefore, variance significantly explained by dominance rank was not expected to artificially deflate genetic effect estimations in cases of covariance between rank and mounting activity.

Finally, as expected, increased sampling effort between repeated measures resulted in increased same-sex mounting (posterior mean coefficient = 0.014, $p_{\text{MCMC}} < 0.01$). Therefore the artificial variance in same-sex mounting explained by this effect was therefore accounted for by including sampling effort in the finalized bivariate model (Appendix C, Tables 9-10).

2.2.4 Count data availability

In addition to the primary bivariate model (i) of same-sex and different-sex mounting, labile environment effect structures were also assessed to account for non-permanent effects in (ii) same-sex mounter versus same-sex mountee trait models, and (iii) for same-sex mounter with evidence of arousal versus different-sex mounter with evidence of arousal trait models. Finalized effect structures are included in Appendix C, Table 9, with effect structure permutation results for the latter two provided in tables Appendix C, Tables 12-13. For the primary bivariate model of same-sex mounting versus different-sex

mounting (giving the main heritability and repeatability results), the significance of social dominance positively predicting DSB meant that available count data was restricted to 220 individuals across 963 repeated measures (table S4). In contrast, social dominance was not needed for the same-sex mounter versus same-sex mountee model. Here, the only limitation to useable count data was available measures of sampling effort, which reduced the number of repeated measures from 1,076 to 1,051, but did not reduce the total number of sample males ($n = 236$). For the same-sex mounting with arousal versus different-sex mounting with arousal models, social dominance no longer significantly predicted DSB. Since sampling effort was also not significant in this case, all available count data was useable (individuals = 236, repeated measures = 1,076).

2.2.5 Estimating repeatability and heritability

Variance component analysis for SSB was performed by fitting individual identity as a random effect into existing MCMC GLMMs across 220 males (note that previous sample size of 236 males is here reduced for heritability analysis because the dominance rank of 16 animals was unknown, see above). For this study, heritability was defined as the proportion of phenotypic variance attributable to relatedness; see Visscher et al., (2008) for comprehensive definitions of heritability. The matrix of relatedness was constructed using a pedigree derived from the colony records. Phenotypic variation in SSB is expected to result from some combination of genetic and environmental effects. Total phenotypic variance can be divided into interindividual and intraindividual variance. The intraindividual component represents residual variance derived from the non-repeatable proportion of phenotypic variance, including measurement error, unmeasured variables and short term micro-environmental effects on phenotypic variance (Roche et al., 2016). The interindividual variance can be further decomposed into additive and non-additive genetic components, along with permanent environmental effects (i.e. the remaining interindividual variance). Therefore, repeatability gives a standardized index of phenotypic consistency across time or contexts, and should be greater than narrow-sense heritability (i.e. variance contribution from additive genetic effects; Dochtermann et al., 2014). However, non-additive genetic effects were not investigated due to prohibitive model runtimes experienced when fitting allelic dominance effects using an epistatic matrix calculated with the *Nadiv* R package (Wolak, 2012). Therefore, the genetic effect analysed here is not referred to as additive, but rather as the effect of relatedness between individuals.

Individual identity and pedigree-defined relatedness were simultaneously fit as random effects in the optimized fixed effect MCMC Poisson GLMMs of behavioural data. This method has been advocated for assessing repeatability and heritability of behavioural count data in rhesus macaques (Blomquist and Brent, 2014). The Poisson distribution describes a rate of event incidence where the probability of an event is low but the number of opportunities for an event to occur is high, thereby capturing the relative rarity and unpredictability of mounting behaviour measured as count data. A log-link function was used to scale and predict the expected value of the phenotype based on the linear sum of effects in a given model.

The genetic coefficient of variation (Cheung, 2020) for SSB was calculated using variance attributable to relatedness to represent additive genetic variance (V_A) and the phenotypic mean of repeated measure counts (\bar{X}) (see Equation 1 below).

$$\text{genetic coefficient of variation} = \frac{\sqrt{V_A}}{\bar{X}} \times 100 \quad (\text{Eq. 1})$$

Posterior modes for variance attributable to relatedness at the observed-scale were 0.117 for SSB and 0.137 for DSB (for latent scales see Appendix C, Table 7). Phenotypic means of mounting were calculated by taking the mean across of individuals of the means of repeated measure counts per individual (SSB = 0.883; DSB = 0.492).

Variance estimates were used to build a variance-covariance matrix and derive the phenotypic and genetic correlations (de Villemereuil, 2012) between behaviours in each bivariate model (Appendix C, Table 7). A genetic correlation and heritability of respective traits will underpin a phenotypic correlation. Expected phenotypic correlations were calculated by taking the product of the square roots of each trait heritability and their genetic correlation (Kruuk et al., 2008). This was then taken as a proportion of the observed phenotypic correlation to give the subset of observed phenotypic correlation explained by genetic effect (Reynolds, 2013). By assessing for correlations in this way, the trade-off between SSB and DSB was explored without assuming a definite link between the two behaviours. This approach, by allowing the possibility of SSB and DSB

being independent, was therefore chosen over modelling a single behavioural trait defined by the ratio of SSB to DSB.

Maternal identity, which is a common source of non-genetic permanent environment effect (Wilson, 2018), was not investigated due to the high ratio of mothers to sample males in the dataset (sample males = 236, mothers = 185), which caused maternal identity to overly resemble individual identity in variance partitioning. Instead, matriline were investigated to represent a degree of shared environment effects. Matrilines, i.e. lines of descent traced through the maternal side of a family, are often seen as strong non-genetic determinants of rhesus macaque group structure and behaviour, because females remain in their natal group for life and form dominance hierarchies along matrilineal lines (Kulik et al., 2012; Watson et al., 2015). While males normally leave during puberty and move between subsequent groups roughly every four years, those that reside or were raised in a high-ranking matriline may have significant lifetime advantages or differences over other males (Watson et al., 2015).

2.2.6 Model parametrization

Posterior distributions of variance estimates were generated from 1.2×10^4 chain samples (all model posterior distributions are provided in table S9). To accelerate runtime for MCMC GLMMs, each model run was parallelized into an array of twenty separate chains using code adapted from Wolak et al. (2017). Each chain was run for 5.2×10^6 iterations with the initial 4×10^6 discarded to allow for convergence of estimates. Gelman's diagnostic was used for ensuring convergence between parallel runs for chain stitching (Hadfield, 2010). Heidelberger and Welch tests were used to assess the probability that Markov chains had been sampled from a stationary distribution, which in effect gives an estimation of model convergence (Wolak and Reid, 2017). Chains were sampled at intervals of 2×10^3 to reduce autocorrelation between sample estimates, with satisfactorily low autocorrelation between components being considered < 0.05 . Only mounter activity with evidence of arousal, when fitted with fixed effects, required a greater discard (6×10^6) for convergence, with the necessary adjustments to chain length to keep the full chain length of 1.2×10^4 samples. Fixed effect optimization required shorter chains and was performed using models with posterior distributions of 600 samples generated with thinning per 800 samples after a discard of 8×10^4 iterations (Appendix C, Tables 9-10 and 12-13). Inverse Wishart prior distribution matrices were set for all MCMC GLMMs,

based on parametrizations listed in de Villemereuil (2012) as relatively uniform and uninformative. Results were robust to more informative prior parametrization (Appendix C, Table 7), with inverse Gamma (0.5, 0.5) and Beta (0.5, 0.5) distributions for variances and correlation. Estimating variance components is challenging for log-linked Poisson GLMMs with normal random effects, since a simple ratio of interindividual to total phenotypic variance assumes a normally distributed phenotype (Nakagawa and Schielzeth, 2010). This issue also extends to estimates of heritability. In effect, there are three scales at play within the GLMM: the latent (linear effect), the expected, and the observed scales. Here, the package *QGglmm* provided a precise method (de Villemereuil et al., 2016; Nakagawa et al., 2017) to impute repeatability and heritability onto the observed scale from the latent model components. Critically, this method accounts for fixed effects (i.e. age, social dominance etc.) on the latent distribution in a given model by averaging over their marginal predicted values, giving repeatability and heritability as proportions of phenotypic variance on the observed scale (de Villemereuil et al., 2016). All variance estimates are given at all scales in Appendix C, Table 7.

2.2.7 Intercept-only models

Given the risk of inflating genetic contributions to phenotypic variance through the fitting of fixed effects (by soaking up residual error), intercept-only results have also been provided, but did not markedly influence estimates for same-sex mounting (Appendix C, Table 7). However, repeatability estimates were significantly reduced by fitting of fixed effects. Various methods have been proposed for allowing phenotypic variance explained by fixed effects to be carried into estimations of phenotypic variance (de Villemereuil et al., 2018), but a standard approach has not been determined (Wilson, 2018). Therefore both fitted and intercept-only estimates have been provided here to allow interpretation of results.

2.2.8 Permutation tests

The use of proper priors inherently causes variance estimates to be constrained to >0 (Hadfield, 2010). Since heritability estimates gave highest posterior density intervals (i.e. error estimates) close to zero, post-hoc permutation tests were used to test for significant differences in estimates from 25 models with count data randomly reassigned across repeated measures (sensu Good, 2000; Kasper et al., 2017; Araya-Ajoy and Dingemanse, 2017). Only intercept-only models were tested, due to the anticipated confounding effect

of decoupled fixed effects from count data scores on variance estimates. The distribution of posterior mode null distributions for heritability of intercept-only same-sex mounting ($\mu = 3.6\%$) was significantly different from the observed value (heritability = 6.68%, $t = -31.8$, $p < 0.005$), and for different-sex mounting (heritability = 2.97%, $t = -89.1$, $p < 0.005$). Full posterior distributions of permutation tests are in listed Appendix C, Table 7 and complete test results in Table 14.

2.3 RESULTS

2.3.1 Group structure and age marginally explain SSB

There was no effect of group sex ratio on same-sex mounting (Fig. 2.1; Appendix C, Tables 9-10), whereas increasing group size had a small negative effect (posterior mean coefficient = -0.002, $p\text{MCMC} = 0.017$). Additionally, greater same-sex mounting was significantly predicted by a reduced group ratio of older to younger males within a social group (i.e. more younger males relative to older ones, posterior mean coefficient = -0.139, $p\text{MCMC} < 0.002$). Increasing age for an individual was a significant negative predictor of same-sex mounting (posterior mean coefficient = -0.082, $p\text{MCMC} < 0.002$). Social dominance rank was multicollinear with age, which outperformed rank in the optimized fitting for same-sex mounting. When assessing each mounting interaction for signs of dominance expression, mounters were the relatively lower ranked individual of a mounting pair in 42.7% of same-sex mounts, but this value was reduced to 29% for mounting interactions that took place within five seconds of aggression between participants (Appendix C, Table 15).

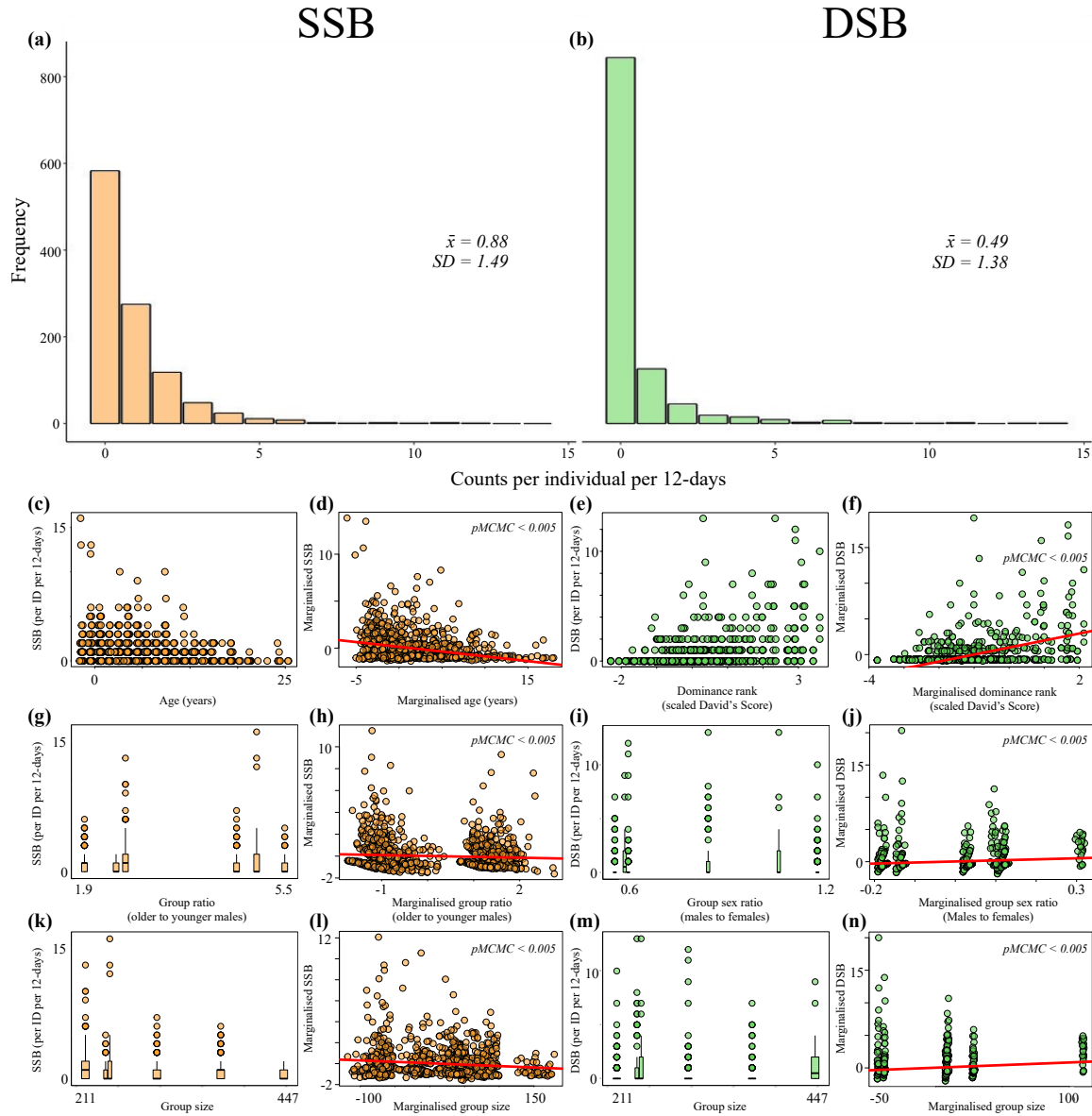


FIGURE 2.1 Labile effects on same-sex and different mounting. Distributions of (a) same-sex and (b) different-sex mounting repeated measures (counts per individual per 12-days). Age, seasonal group ratio of older to younger males (+5yr to 3.5-5 years) and group size all negatively predicted same-sex mounting, whereas seasonal dominance rank, group sex ratio, and group size positively predicted different-sex mounting. Observed-scale distributions are shown for same-sex (c, g, k) and different-sex (e, i, m). All effects were fit using MCMC Poisson GLMMs with significance at $pMCMC < 0.005$. Trend lines are shown using partial regression plots with marginalised variables to demonstrate effect sizes given interactions with other significant effects for same-sex (d, h, l) and different-sex mounting (f, j, n). Marginalisation takes the regression residuals of mounting behaviour on all other effects, and the designated effect on all other effects respectively (Fox and Weisberg, 2018). Results demonstrate clear differences in underpinning between SSB and DSB, and open the door to investigations of heritability by accounting for environmental variance within the traditional animal model.

2.3.2 SSB is both repeatable and heritable

The repeatability of same-sex mounting in males was 19.3% and heritability was 6.4 % (modes of posterior kernel density; Fig. 2.2). This heritability estimate was robust to quality control checks (Appendix C, Tables 7 and 14) including permutation testing (Good, 2000), intercept-only effect structures (Blomquist and Brent, 2014) and varying prior parametrization (de Villemereuil, 2012). The genetic coefficient of variance was 35.06 for SSB and 75.04 for DSB. The proportion of phenotypic variance in same-sex mounting attributable to matriline was 5%, but did not dramatically reduce the estimate of SSB heritability (down to 5.1%; Appendix C, Table 7). After accounting for other effects (Appendix C, Tables 9 and 13), mounting activity with evidence of arousal was, again, both repeatable (19%) and heritable (4.5%) (Appendix C, Table 7).

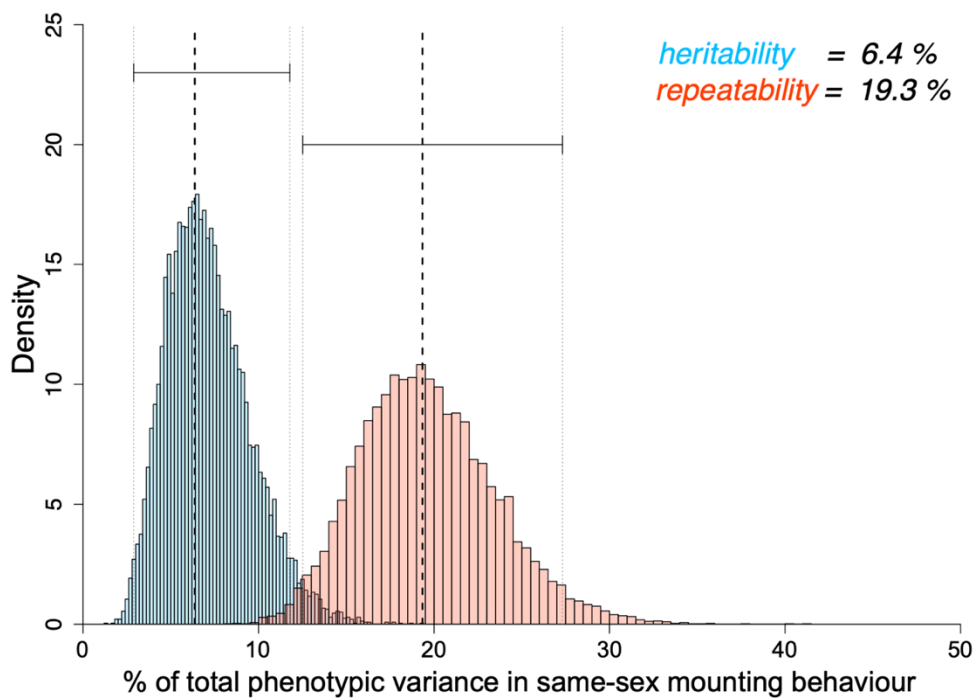


Figure 2.2 Repeatability and heritability of same-sex mounting behavior. Observed-scale estimate distributions for repeatability and heritability of SSB in male rhesus macaques (MCMC samples = 12,000, individuals = 220; repeated measures = 963). Values describe the proportions of phenotypic variance attributable to individual identity (repeatability = 19.3%) and relatedness (heritability = 6.4%). Values are given as modes of posterior kernel density with error defined by highest posterior density intervals (12.5-27.3% for repeatability and 2.9-11.8% for heritability). Relatedness and individual identity effects were fitted simultaneously to prevent inflation of heritability estimates. Estimates were derived after accounting for effects of social group structure and individual age.

2.3.3 Mounter and mountee activities are genetically correlated

After accounting for other effects (Appendix C, Tables 9 and 12), same-sex mounter and mountee activities were found to be phenotypically correlated ($r_p = 0.279$; sensu Kruuk et al., 2008), meaning that an individual mounter was also more likely to be a mountee, and vice versa, relative to other individuals (Fig. 2.3). Both mounter and mountee same-sex activities were heritable (mounter heritability = 4.5%; mountee heritability = 5.7%, see table S9) and genetically correlated ($r_g = 0.499$, Fig. 2.3).

2.3.4 No genetic correlation between SSB and DSB

As with SSB, DSB explained by other effects was first accounted for (Appendix C, Tables 9-10). Social dominance rank was a strong positive predictor of different-sex mounting (posterior mean coefficient = 0.814, pMCMC < 0.002), as was increasing the group ratio of males to females (posterior mean coefficient = 2.723, pMCMC < 0.002). Increasing total group size also had a small positive effect on different-sex mounting (posterior mean coefficient = 0.011, pMCMC < 0.002). DSB repeatability was 4.1% and heritability 1% (Appendix C, Table 7). Phenotypic correlation between same and different-sex mounting was marginally negative ($r_p = -0.02$, Fig. 2.3). However, there was no genetic correlation between SSB and DSB, with posterior distributions extremely diffuse around zero.

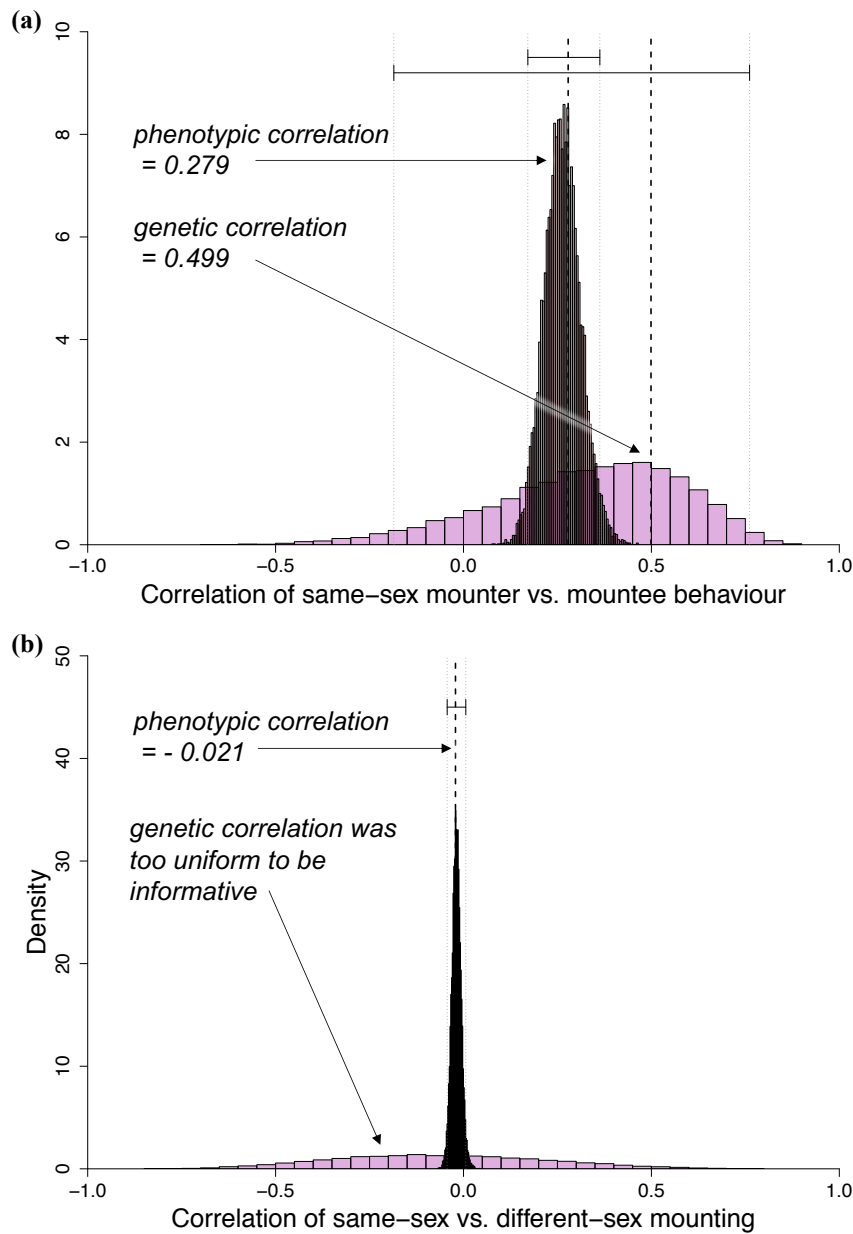


FIGURE 2.3 Correlations of mounting behaviors. (a) Correlations between variance estimates for same-sex mounter (heritability = 4.5%) and same-sex mountee (heritability = 5.7%) activities. Full posterior distributions of variance for each behavior are provided in table S9 (MCMC samples = 12,000, individuals = 236; repeated measures = 1,051). Phenotypic (0.279) and genetic (0.499) correlations were positive, indicating a common genetic basis to the expression of same-sex activity across different behaviors. (b) Correlations between variance estimates for SSB (heritability = 6.4%) and DSB (heritability = 1%). Phenotypic correlation was small and negative (-0.02). Estimation of genetic correlation was unresolved with a near uniform distribution. Values are given as modes of posterior kernel density with error defined by highest posterior density intervals (MCMC samples = 12,000, individuals = 220; repeated measures = 963).

2.4 DISCUSSION

In contradiction with the dominance expression hypothesis, mounters were the lower ranked individual of a mounting pair in nearly half of all cases, indicating that mounting role is not a reliable expression of relative dominance rank (202 of 473 interactions; Appendix C, Table 15). However, this value was reduced to 29% for mounting interactions that took place within five seconds of aggression between participants, which may indicate a behavioural function of dominance expression depending on specific contexts of tension regulation and conflict avoidance (Sommer and Vasey, 2006; Bailey and Zuk, 2009).

No support was found for the DSB deprivation hypothesis, since neither mating season activity (i.e. group-level DSB per 12-days, see Section 2.2.3), nor group or population level sex ratios predicted changes in SSB. While lower dominance rank positively covaried with SSB in support of the deprivation hypothesis, it was also multicollinear with greater SSB in younger males (Appendix C, Table 10). Research has previously suggested that it was not increasing dominance rank that caused decreased SSB per se, but rather increased individual age that influenced both increased dominance rank and decreased SSB (Sommer and Vasey, 2006; Jiang et al., 2013). This case of ‘correlation not causation’ was again observed here, with increasing age outperforming social dominance rank in predicting SSB (and rendering social dominance rank not significant). This effect, in any case, only explained a small proportion of variance, as older dominant males also frequently performed SSB. In all permutations, individual age was the strongest labile predictor of variation in same-sex mounting. This small decline in overall SSB activity with age is consistent with the hypothesis that the behaviour could partially function as ‘practice’ for future reproductive activity (Carpenter, 1941; Sommer and Vasey, 2006), although it somewhat assumes selection against the expression of SSB after critical adolescent stages of sociosexual learning. Group structure and dominance rank were better predictors of DSB than SSB, with inverse covariances often apparent between the two behaviours and a given candidate effect. For example, SSB and DSB responded oppositely (albeit weakly) to changing social group density. The increasing group ratio of older to younger males predicted reduced SSB for an individual (even after individual age had itself been fit within the model), further highlighting the importance of age in

mediating male rhesus SSB. Conversely, neither age-group structure, nor age itself, predicted DSB. Increasing dominance rank was a very strong predictor of greater DSB (in contrast with previous work on Cayo macaques that did not support a high mating-skew based on rank, see Dubuc 2014b), but negatively covaried and did not significantly predict greater SSB. These results cement the obvious distinction between SSB and DSB, and lay to rest any question of indiscriminate, imperfect, or entire lack of sex-recognition that has been reported as the basis of SSB in invertebrate systems. In general, results here suggest that changes in social environment may accentuate trends in SSB, perhaps with possible gene-social environment interactions (Han and Brooks, 2015), but are unlikely to be the key factor in explaining the behaviour.

Since age and social group effects only explained a small proportion of the variance in same-sex mounting, it was plausible that individual identity, and thereby genetics could play a role in the expression of the behaviour. The estimation of a genetic contribution to male same-sex mounting in a population of rhesus macaques reported here represents the first reported heritability value for SSB in vertebrates, with the exception of human beings (Ganna et al., 2019; Hu et al., 2021). There are various hypotheses for the evolution of SSB, including kin altruism selection (Kirkpatrick, 2000), overdominance selection (Gavrilets and Rice, 2006), sexually antagonistic selection (Rice et al., 2016), bisexual advantage (Savolainen and Hodgson, 2016), and paternal and maternal effects (e.g. epigenetic factors; see Rice et al., 2016). Apart from the latter case, all these hypotheses require that SSB is heritable to a degree, as was found here. This rhesus heritability estimate (6.4%) falls within the range of reported values for SSB activity in human GWAS and twin studies (between 1-40%: Bailey et al., 2016; Burri et al., 2015; Ganna et al., 2019), but it is important to note that any heritability estimate is population specific (Visscher et al., 2008). Therefore the exact degree of male SSB heritability is only an indicator of the predictive quality of the genotype on the phenotype in the Cayo Santiago population of macaques. While the exact degree of heritability estimated in any study system is inherently population-specific (Visscher et al., 2008), there is no reason to think heritable variation on Cayo Santiago is not representative of other rhesus macaque populations. Specifically, the Cayo population has only been isolated for 80 years from wild Indian populations (in which SSB has also been repeatedly observed), making the existence of novel genetic variation unlikely. Furthermore, as the population has retained

similar social ecology to wild populations, with low levels of inbreeding, the chance of novel environmental or non-additive genetic effects is also minimised.

A low heritability does not guarantee weak fitness consequences of a trait, (see Visscher et al. (2008) for many examples), indeed in past decades it has been taken as indicative of a strong influence on fitness (Hansen et al., 2011). A more appropriate measure of evolvability is the genetic coefficient of variation (CVA), which standardises the additive genetic variance of a trait by the phenotypic mean (Cheung, 2020). This approach captures the importance of a large degree of additive genetic variance in determining strong fitness consequences of a given trait (Kruuk et al., 2000). For example, while heritability was lower in DSB than SSB, the CVA of DSB was more than twice that of SSB. This is to be expected, since a trait relating so directly to reproductive effort is likely capable of extreme fitness consequences. Nevertheless, the CVA of SSB was still significant and demonstrates the plausibility of evolutionary consequences to variation in the behaviour.

Social group matrilineal lines were shown to influence 5% of phenotypic variation in SSB. Interestingly, the inclusion of matrilineal lines only reduced the estimate of SSB repeatability by 2.9%, suggesting that the basis of the matrilineal effect was not much related to an individual's permanent environment. Furthermore, matrilineal lines are also based on relatedness and consequently some or all of a matrilineal effect could still be genetic and legitimately contribute to heritability in a population. It is therefore also unclear to what degree the small reduction in SSB heritability estimate (-1.3%) due to matrilineal effect is a true reflection of a non-genetic effect. Consequently, these matrilineal results have been presented alongside the original heritability estimate of 6.4%, with an acknowledgement that some degree of matrilineal effects are contributing to differences in SSB.

The positive correlations between mounter and mountee activities demonstrate a common basis to different forms of SSB, with the inference that same-sex targeting of sociosexual behaviour, rather than mounting indiscriminately, underpins same-sex activity. Notably, proximate hypotheses of same-sex activity mediated by varying intersexual development (e.g. natal androgen exposure; Rice et al., 2006; Ratnu et al., 2017) would indicate an inverse relationship between the mounter (masculinized individual) and mountee

(feminized individual) roles, yet results here displayed a shared genetic basis to these different components of SSB (Fig. 2.3).

It is often assumed that there is a ‘trade-off’ between SSB and DSB, leading SSB to have a fitness cost because those who engage in SSB miss reproductive DSB opportunities. In support of the trade-off concept, there was a negative, although small, phenotypic correlation between same and different-sex mounting. However, there was no genetic correlation between SSB and DSB, indicating that selection on one behaviour would not affect the other (Lande, 1984). In this instance, the results for mounting with evidence of arousal were arguably superior in informing upon reproductive costs via trade-offs DSB, since a higher proportion of the different-sex mounts were likely to have led to ejaculation and therefore a chance of insemination. However, once again the negative phenotypic correlation was small and narrowly distributed around zero ($r_p = -0.03$; Appendix C, Table 7), and the posterior distribution for a genetic correlation was too diffuse around zero to infer a link between the two traits. Notably, a recent GWAS of 358,426 individuals found evidence of antagonistic pleiotropy in human SSB, suggesting fitness costs to SSB genes were offset by also causing a greater number of sexual partners in exclusively different-sex orientated individuals (Zietsch et al., 2021). Since male rhesus have been shown to be behaviourally bisexual in Chapter 1, and the genetic effects on variation SSB and DSB appeared independent, this evolutionary mechanism is unlikely in rhesus macaques.

2.5 CONCLUSION

The idea of a ‘Darwinian paradox’ to SSB requires both a heritable component and a fitness cost. In this chapter, a genetic influence on variation in vertebrate SSB activity has been shown for the first time in natural world, both corroborating findings in human beings and legitimising the many competing and complementary theories describing the evolutionary underpinning of the trait. Further to the behavioural bisexuality evident in Chapter 1, results here suggest that reproductive costs due to trade-offs with DSB should not be assumed. However, evidence of fitness consequences to variation in SSB activity can still be investigated more directly in this study system by using the colony pedigree to examine siring rates between individuals. Meanwhile, the support of a dominance

expression hypothesis in a specific social context highlights both the possibility of adaptive behavioural functions to SSB and the importance of social context in future efforts to determine possible functions of the behaviour.

CHAPTER 3

SAME-SEX BEHAVIOUR MEDIATES CONFLICT COALITIONS NOT FITNESS COSTS

3.1 INTRODUCTION

3.1.1 Expected fitness costs of SSB

Fitness costs to SSB via trade-offs with different-sex mounting (and different-sex mounting with arousal) were found to be unlikely given the lack of genetic link between the two traits in Chapter 2. However, fitness costs may still occur due to SSB if variation in DSB is not a good signal of reproductive success. Furthermore, SSB could still carry fitness costs in spite of independence from DSB, for example if genes for high SSB activity were pleiotropic with poor sperm quality (Sommer and Vasey, 2006), or if the behaviour had social consequences that restricted the reproductive success of close genetic relatives (thereby minimising the indirect component of Hamilton's inclusive fitness, Scott-Phillips et al., 2011). In the case of poor sperm quality and other post-copulatory selection pressures, few hypotheses have been proposed for SSB. The sexually antagonistic selection hypothesis of male SSB posits that genes for SSB persist, in spite of fitness costs in males, because of strong fitness benefits when the same genes are expressed in females (Gavrilets and Rice, 2006). This theory of intralocus sexual conflict is often based on the idea that same-sex attraction in males is more specifically due to genes for attraction to males, which in females might improve reproductive success. If not due to sexual activity itself, then costs are anticipated by other hypomasculinised traits in males, which could include poor sperm quality, resulting in corresponding adaptive hyperfeminine traits in females. Evidence for sexual antagonistic selection in natural variation of SSB has been found in fruit flies (Hoskins et al., 2015) and seed beetles (Berger et al., 2016), but the evolutionary dynamics of indiscriminate SSB in invertebrates are likely to be different from the behaviour in primates (Bailey and Zuk, 2009). In humans, some evidence has been provided for male SSB underpinned by

sexually antagonistic selection (Lemmola and Camperio-Ciani, 2009; Semenyina et al., 2017; Gavrillets et al., 2018). However, three independent studies recently reported no evidence of this effect (Ablaza et al., 2022; Blanchard and Lippa, 2022; Raymond et al., 2022), instead finding support for the fraternal birth order effect (although some controversy surrounds the debate between the two theories, see Section 3.1.2 below).

This chapter will therefore test the hypothesis that reproductive success (i.e. offspring sired based on pedigree records) is negatively affected by increased same-sex behaviour in sample males. The role of different-sex behaviour in predicting siring will also be explored, to further assess the importance of finding no genetic correlation between SSB and DSB in Chapter 2. To investigate sexual antagonistic selection, this chapter will also test the hypothesis that female reproductive success will be greater in the near relatives of males expressing higher levels of SSB.

3.1.2 Can birth order explain male SSB?

Theories of birth order effect on male SSB derive from the frequent observations of increased SSB (or non-heterosexual orientations) in human males with a greater number of older male siblings (Blanchard and Skorska, 2022). A common explanation for this effect is an acquired maternal immunity to Y-linked antigens (namely *NLGN4Y* and *PCDH11Y*; see Blanchard, 2004; Bogaert et al., 2018) arising from repeated male fetus exposure, consequently suppressing sex-differentiation via anti-male antibodies in subsequent male fetuses (i.e. developmentally ‘feminising’ subsequent sons leading to increased likelihood of SSB; Blanchard and Skorska, 2021). Researchers have disputed both the empirical (Vilsmeier et al., 2021) and theoretical (Gavrillets et al., 2018) evidence for this effect, but generally agree that it is only ever capable of explaining a proportion of male SSB, since many males without older brothers are frequently observed performing SSB in a range of taxa (Blanchard and Skorska, 2022). Frequently, disagreements land on choosing between the birth order effect and mechanisms of sexual antagonism discussed above (i.e. female advantage) (see Gavrillets et al., 2018 and response from Blanchard, 2018). This is a strange distinction, since birth order is a proximate hypothesis for SSB while sexual antagonism is an ultimate hypothesis (Scott-Phillips et al., 2011), and neither would preclude the other. Furthermore, the two mechanisms are inherently related, since both rely on more maternal births associating with SSB (for mathematical proof see Khovanova, 2020). Another criticism of the birth

order hypothesis is that the effect has been exclusively reported in human beings, and in particular in western populations (Gavrilets et al., 2018). Indeed, a study of male sexual orientation in a Chinese population did not find support of a birth order effect, although this was potentially due to the small number of sibships in the study population (Xu and Zheng, 2017). It is therefore critical to establish tests for birth order effects outside of human beings, since the maternal immunity effect should also be true in (at the very least) old-world primates. Since SSB was found to be 19.3% repeatable in Chapter 2, it is possible that some of this variance is attributable to the number of older male siblings per sample male. This chapter will therefore test the hypothesis that SSB predicts fraternal sibling birth order. Total birth order (i.e. all older siblings) will also be investigated, since this has been frequently offered as a useful proxy for likelihood of maternal exposure to male antigens by reflecting the effect of miscarried male fetuses (Blanchard and Lippa, 2021).

3.1.3 Can SSB increase the likelihood of adaptive coalitionary behaviour?

Coalitions in ecology are defined as two (or sometimes more) individuals showing aggression towards a third party (Harcourt and de Waal, 1992). They describe single mutually exclusive events of co-operation (Mesterton-Gibbons et al., 2011), and have been frequently reported across primate species (reviewed in Bissonnette et al., 2015) and other mammalian taxa (Feh, 1999; Wahaj et al., 2004). Critically, coalitions are considered distinct from social alliances, which can be defined as longer-term relationships in which coalitions are likely to occur (Mesterton-Gibbons et al., 2011). Fitness benefits to coalition formation in male macaques have been predicted by theoretical models (van Schaik et al., 2004; van Schaik et al., 2006), and recently shown empirically in male crested macaques (Neumann et al., 2022). In the Cayo macaques, studies 12 years apart in the same social group offered conflicting reports of male-male coalitionary behaviour (confining the behaviour to mid-rankers in Higham and Maestripieri, 2010; and high-rankers in Kulik et al., 2012), with the conclusion that advantages to the behaviour may depend on shifts in group social system (e.g. rank steepness, male dispersal; Kulik et al., 2012).

A connection between primate SSB and coalitionary behaviour has frequently been proposed, in which the behaviour functions to strengthen social bonds between pairs through establishing trust and emotional attachment (Sommer and Vasey, 2006;

Macfarlane and Vasey, 2016). However, evidence of this connection has largely focussed on females, with mixed reports in bonobos (Sommer and Vasey, 2006), negative findings in langurs (Sommer et al., 2006) and Japanese macaques (Sommer and Vasey, 2006; Vasey et al., 2008), but some evidence the female rhesus, at least at the broader level of social alliances. Indeed, research has indicated that female rhesus macaques use SSB to effectively accelerate alliance formations upon migration into new social groups, but only under unusual conditions of group disruption (Sommer and Vasey, 2006). Rhesus macaques are generally male-biased dispersers (Widdig et al., 2016b), but the female-new group effect has been shown in free-ranging as well as experimental conditions (Fairbanks et al., 1977). In males, the connection between SSB and coalitionary behaviour remains uncertain, although observations in wild olive baboons (Smuts and Watanabe, 1990) have suggested male mounting might be a ritualised and ‘calming’ precursor to coalitionary behaviour (i.e. co-ordinating an attack on another individual). This observation presents an interesting question – perhaps the function of SSB in relation to coalitionary behaviour could be more than just increased likelihood via strengthening social bonds. Firstly, it could function as a literal precursor to coalitionary behaviour, as posited anecdotally in the baboons, but secondly the SSB could itself function as part of an aggressive display. There have been some anecdotal reports of SSB as a threat display in blue-bellied rollers and langurs, but only within intergroup conflicts (Moynihan 1990; Sommer et al., 2006). This chapter will therefore test the hypothesis that males who mount together are also more likely to engage in coalitionary behaviour together, but it will also examine whether the behaviour itself could function as a display, either as an act of coalitionary aggression (i.e. threat) itself, or alternatively as an honest signal of coalition likelihood for the pair.

3.2 METHODS

3.2.1 Offspring data

To evaluate reproductive costs to SSB, the colony pedigree was used to total the offspring sired per sample male with census data available up to 2022. Since SSB was found to be repeatable, an evaluation of any hypothetical effect on siring was expected to derive from this consistent proportion of the behaviour. To account for the effect of varying total

sampling effort on SSB per individual, totalled same-sex mounts per individual (i.e. summed across all repeated measures) were divided by the \log_{10} of total scan samples per individual. This approach thereby accounted for the diminishing effect of varying sampling effort on SSB that occurred as sampling effort increased (which was previously described by the generalisation in the log-linked MCMC GLMMs predicting SSB in Chapter 2). Using a quasi-Poisson generalized linear model, this adjusted measure of individual SSB was used alongside individual age (taken as the mean of an individual's age across their repeated measures throughout the study) to predict total siring counts per individual. Since SSB and DSB were shown to be weakly related in Chapter 2, the model was also fit individual mean dominance rank (across repeated measures) and sampling-adjusted different-sex arousal mounting (see Section 2.2.2) to assess the effect of reproductive sexual opportunities. The quasi-Poisson distribution was chosen to account for the count-based offspring data, in which overdispersion was high (dispersion parameter = 5.83). Results were also retested for siring data only up to the behavioural observation range of 2020, rather than the entire available span up to 2022, as were seasonal behavioural counts on seasonal siring success. An alternative approach with estimation of genetic correlation between repeated measures of SSB (with fitted significant fixed effects as in upstream analysis) and total offspring sired (fit with individual age) was also explored using a bivariate Bayesian approach. However, results were unavailable due to a range of attempted model parametrizations failing to converge on an estimate for the effect on siring due to relatedness (e.g. even after a discard of 1.25×10^7), making an estimation of genetic correlations unsuitable. Reproductive success in female relatives was tested by first scoring the product of total offspring per female with their coefficient of relatedness (r) to a given sample male. Relatedness was calculated using an additive relationship matrix for diploids with the *AGHmatrix* software package in R (Amadeu et al., 2016). For each sample male, the mean of these scores was taken to give a combined measure of reproductive success in their female relatives that adjusted for the genetic closeness between individuals (Eq. 2 below). These scores were normally distributed ($\bar{x} = 0.07$, $SD = 0.014$), and fit as a response variable in a generalised linear regression with sampling-adjusted SSB per individual as the predictive variable.

$$\text{reproductive score of female relatives} = \frac{1}{n} \sum_{i=1}^n (r_i \times \text{offspring}_i) \quad (\text{Eq.2})$$

3.2.2 Predicting coalitionary partnerships

Coalitions were defined as male pairs that fought together against a common enemy during agonistic interactions between more than two individuals (Mesterston-Gibbons et al., 2012). Counts per pair were tallied across all observation periods, with zero counts assigned only to sample male pairs that were scan sampled in the same social group within the same 12-day period. Pearson correlations between pairwise coalition counts and subtypes of same-sex mounting (i.e. varying arousal status and context) were then calculated. Mounting with absence of arousal was defined as an interaction with a confirmed absence of erection in either participant or (in cases where erectile status was unobservable) less than three thrusting motions by the mounter (for the converse definition of mounting with evidence of arousal see Section 2.2.2). Context was defined as the most recent behavioural state within the previous five seconds of a mounting interaction. Mounting in a co-aggressive context described the two individuals collectively showing aggressive behaviour to another individual or individuals, which is itself a form of coalitionary behaviour. However, these were not counted towards coalitionary events per pair to avoid replication between correlates. An affiliative context was defined as non-aggressive physical contact between the mounting pair (e.g. grooming), whereas an aggressive context described interactions preceded by aggressive behaviour between the mounting pair. Quasi-Poisson generalized linear model of pairwise counts was also used to test for the effect of SSB partnerships on coalitionary partnerships, and significance testing with Pearson correlations were used to assess the strength of association between subtypes of mounting and coalitionary partnerships. Apart from same-sex mounting events between pairs, the regression model was also fit with mean age between pairs, mean dominance rank between pairs, and relatedness between individuals. Coefficients of relatedness between pairs were again calculated using an additive relationship matrix with *AGHmatrix* (Amadeu et al., 2016). The difference in age between a pair, the difference in dominance rank, and mean sampling effort between pairings were discarded from model fittings due to non-significance (Appendix C, Table 16). To assess the possibility of a broader display function to co-aggressive mounts, counts of individuals within a 10-metre radius of a mounting event were recorded. The means of these proximity counts were then compared between pairs that had at least one coalitionary interaction against pairs that were not observed to ever have been in a coalition. For assessing coalitionary partnerships, behavioural data was supplemented by an additional 99 mounting observations and 198 agonistic interactions

across 1649 scan samples. These were collected in 2021 across a 16-day period from March-April, with observations confined to just one of the two social groups in the existing dataset. This additional data strengthened the significance of (but did not change overall results for) analyses performed with the 2017-2020 dataset.

3.2.3 Birth order effects

The fraternal birth order and sibling birth orders per sample male was counted from pedigree data. The significance of birth order effects on SSB were tested by fitting either elder maternal brother counts, or elder maternal sibling counts in quasi-Poisson GLMs of repeated measures of same-sex mounting, with existing effect structure defined by results from MCMC GLMMs in Chapter 2 (i.e. with age, sampling effort, and group structure effects; see Appendix C, Tables 9 and 16). Birth order effects were also tested against total counts per sample male across repeated measures, with mean age and total sampling effort per sample male fit as covariates.

3.3 RESULTS

3.3.1 No sign of fitness consequences to SSB

While age was a significant predictor of offspring sired (slope $\beta = 0.147$, $p < 0.005$; Appendix C, Table 16: Models A-C), sampling-adjusted SSB was not significant, although a positive trend was evident (Fig. 3.1). Dominance rank (slope $\beta = 0.14$, $p < 0.005$) and sampling-adjusted different-sex mounting with arousal (slope $\beta = 0.138$, $p < 0.005$) were both significant positive predictors of siring. Effect significance and slopes were equivalent for tests of siring data limited up to 2020, except that dominance rank also failed to predict siring. Conversely, for seasonal behavioural data and corresponding seasonal siring success, only dominance rank significantly predicted siring (slope $\beta = 0.47$, $p < 0.005$). Sampling-adjusted SSB also did not predict the reproductive success of a sample male's female relatives (Appendix C, Table 16: Model D).

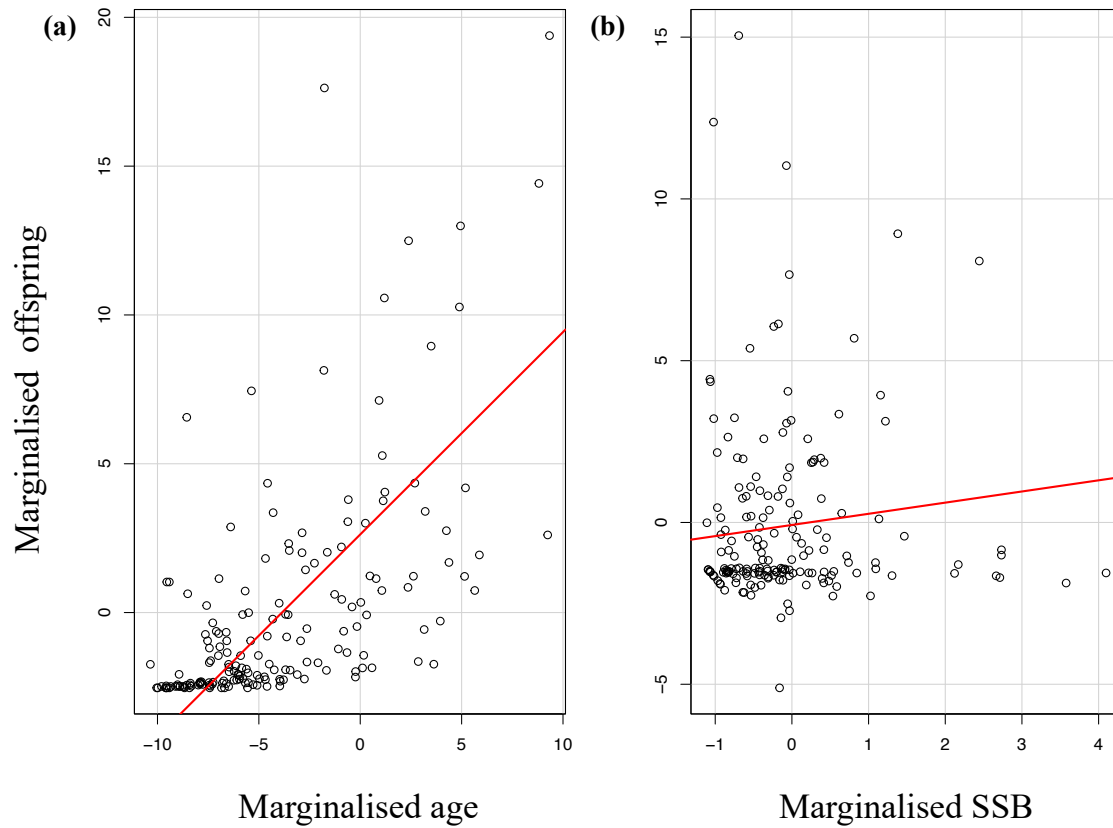


FIGURE 3.1 Partial regression plots of effect on siring. (a) Age was a strong significant predictor of total offspring sired per sample male (slope $\beta = 0.147$, $p < 0.005$) (b) A non-significant positive trend between standardized SSB and standardized total offspring (slope $\beta = 0.073$, $p = 0.37$). Axes are standardized for the effect of age, which had a significant effect on both SSB and total offspring per individual. Standardization was performed by taking the regression residuals of offspring on age, and SSB on age respectively (Fox and Weisberg, 2018). Results in both (a) and (b) are also standardised for the significant positive effects of dominance rank and different-sex mounting with evidence of arousal (Appendix C, Table 16).

3.3.2 SSB partnerships predicted coalitionary partnerships

With the addition of new 2021 behavioural data, a total of 3682 agonistic interactions were recorded involving a sample male ($n = 262$). Of these interactions, 110 cases contained a coalition between sample males. Across the total 1051 same-sex mounts

observed, 11.4% took place in a behavioural context of co-aggression (i.e. were themselves coalitionary events). This proportion was similar for different-sex mounting (10.1% of 778 observations). The proportions of mounts in an affiliative context were also similar between SSB (17.7%) and DSB (18.4%). For an aggressive context (i.e. aggression between the mounting pair), cases were rarer for both SSB (6.8%) and DSB (3.3%). For cases of mounting between sample males (total = 736), proportions were slightly altered for behavioural context (co-aggression = 15.6%; affiliation = 17.4%; aggression = 8.6%) and arousal status (with arousal = 68.2%; without arousal = 17.9%; unconfirmed status = 13.9%).

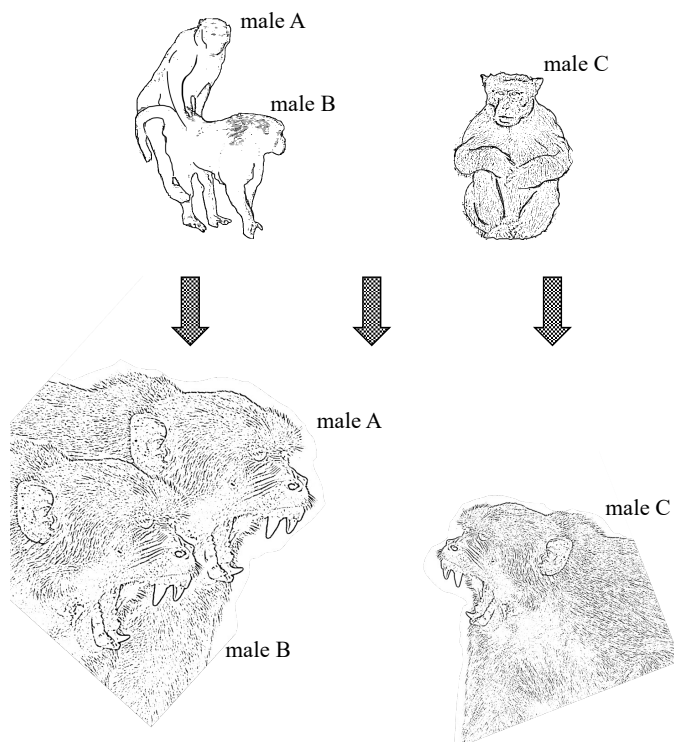


FIGURE 3.2 SSB mediates coalitions. Monkeys A and B engage in same-sex mounting, and are therefore more likely to support each other during antagonistic interactions with other individuals (slope $\beta = 0.424$, $p < 0.005$). In over 15% of cases, same-sex mounting in sample males itself functioned as part of coalitionary threat behaviour toward a third-party.

Using the quasi-Poisson generalized linear models of pairwise counts, same-sex mount partnership frequency significantly predicted coalitionary partnership frequency (slope $\beta = 0.42$, $p < 0.005$; Appendix C, Table 16: Model E). Alongside this, mean rank between pairs positively predicted coalitionary partnerships (slope $\beta = 0.76$, $p < 0.005$) while mean age between pairs negatively predicted partnerships (slope $\beta = -0.14$, $p < 0.005$). Although increasing relatedness between pairs was not a statistically significant predictor of coalitionary pairing frequency, it was retained in the model because the effect was on

the cusp of significance criteria (slope $\beta = 1.2$, $p = 0.06$) and preliminary analysis of data from 2017-2020 had previously given statistical significance. Same-sex mounting in contexts of aggression appeared to negatively covary with coalition pairs, but was not statistically significant (Appendix C, Tables 16 and 17), unlike the effects of mean dominance rank (slope $\beta = 0.68$, $p < 0.005$) and mean age (slope $\beta = -1.6$, $p < 0.05$) which remained significant. Pearson correlations of coalitionary pairing frequencies with subtypes of mounting by behavioural context or arousal state all gave significant positive correlations, with the exception of mounting in an aggressive context (Fig 3.3; Appendix C, Table 17). Mounting with evidence of arousal (15.7%, $p < 0.005$) was more than twice as correlated with coalitionary pairing than mounting with evidence of low arousal (7.6%, $p < 0.005$). The strongest association with coalitionary pairings was for same-sex mounting in the context of co-aggression (24%, $p < 0.005$).

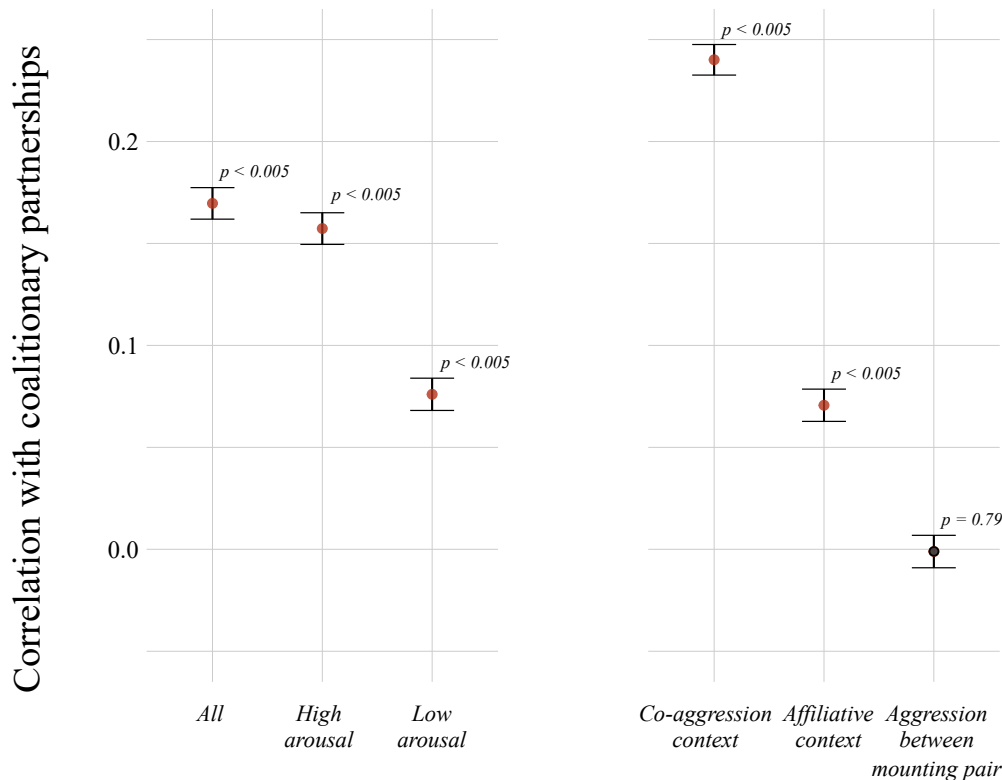


FIGURE 3.3 Strength of correlations between coalitionary pairings and pairings by subtypes of same-sex mounting. Mounting with evidence of arousal was more strongly associated with coalitionary pairings than mounting with evidence of low arousal. Overall, SSB still gave a higher correlation than either arousal or non-arousal due to the proportion of uncertain arousal status cases which also correlated well with coalitionary pairings. Same-sex mounting that was itself a coalitionary event was the strongest correlate with coalitionary partnerships (24%, CI = 23.2-24.8).

Same-sex mounting between coalitionary pairs took place in more socially dense areas (Fig. 3.4; $\bar{x}_{\text{individuals in 10m radius}} = 7.29$) than mounting pairs that had not been in coalition ($\bar{x}_{\text{individuals in 10m radius}} = 5.11$; $t = 3.17$, d.f. = 819, $p < 0.005$). However, this significant effect disappeared when mean age (rank (slope $\beta = 0.02$, $p < 0.05$) and dominance rank (slope $\beta = 0.08$, $p < 0.05$) per pair were fit as covariates in a regression model (Appendix C, Table 16, Model L). Since same-sex mounting in an aggressive context appeared to reflect a different behavioural function (see Section 2.3.1), results were re-analysed with these interactions discarded to give a final correlation statistic for same-sex mounting pairs with coalitionary pairs of 17.5% ($p < 0.005$; Appendix C. Table 17).

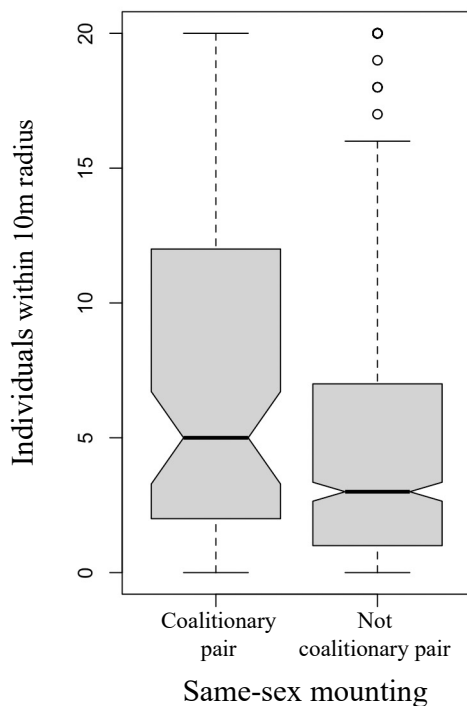


FIGURE 3.4 Mean proximity counts around mounting behaviours by coalition pair status. Coalitionary pairs mounted with a significantly greater number of individuals in a 10m radius ($t = 3.17$, d.f. = 819, $p < 0.005$), suggesting a possible display function to the behaviour. However, greater dominance rank influenced both coalitionary pair likelihood and increased group-centrality, thereby increasing the probability of SSB occurring in higher social densities.

3.3.3 Birth order did not predict SSB

Neither maternal elder brothers nor elder siblings significantly predicted either repeated measures of SSB or totalled SSB per sample male (Appendix C, Table 16: models H-K).

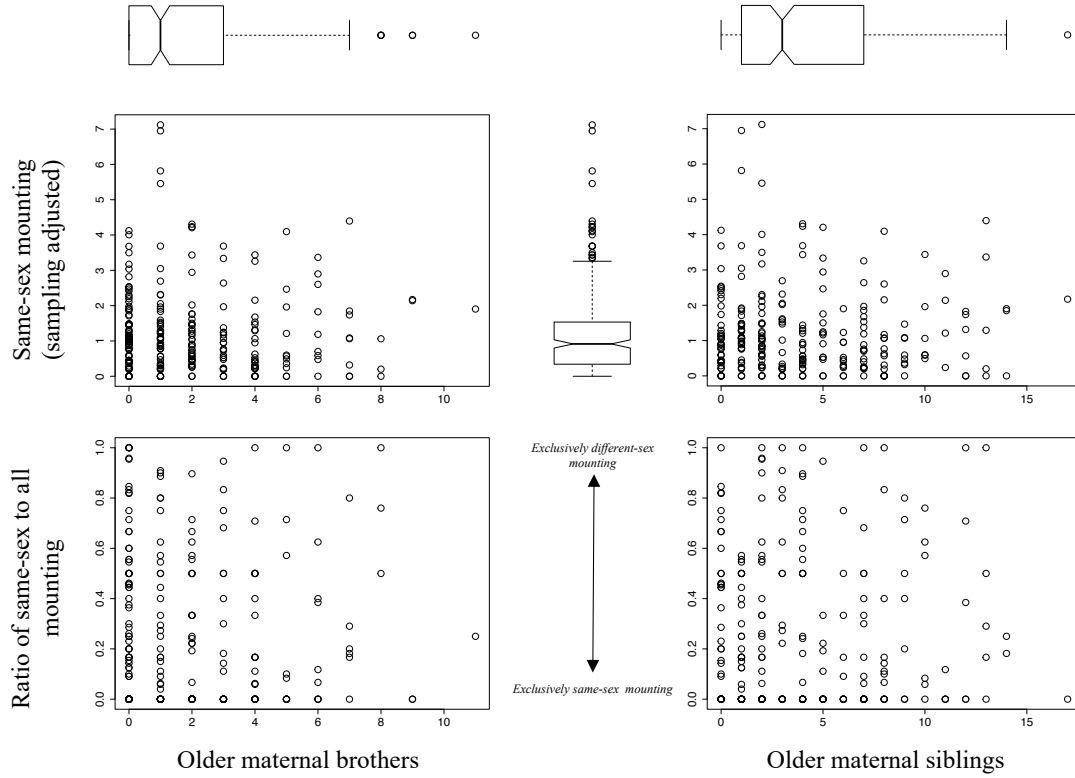


FIGURE 3.5 Distributions of birth order and SSB. There was no evidence of birth order effects on SSB or the ratio of SSB to all-mounting. Models to predict SSB were defined by non-repeatable effect structures taken from Chapter 2, including individual age, relative sampling effort and group structure.

3.4 DISCUSSION

In general, fitness costs to SSB were not evident. While it is possible that SSB is simply a neutral trait that evolves by drift, the lack of a result here may also reflect the need for larger sample sizes across broader a timespan. In particular, the inability to test for effects on the isolated repeatable and heritable components of SSB (due to failed MCMC convergence, see Section 3.2.1) meant that a large degree of noise from remaining

behavioural variance may have obscured significant relationships between siring and SSB. It was notable however, that there was a positive trend (albeit non-significant) between offspring sired and SSB counts (Fig. 3.1), further highlighting the unlikelihood of fitness costs to the behaviour.

In support of an adaptive function, males that mounted each other were more likely to also support each other during conflicts with other individuals (i.e. as part of coalitions). In line with this, a recent study in crested macaques (*M. nigra*) showed that forming coalitions had a positive effect on male fitness (Neumann et al., 2022); and indeed, given the positive trend between offspring sired and SSB counts found here, results suggest that social benefits of SSB can at least partly explain its evolutionary maintenance in macaques.

The importance of behavioural context to SSB became apparent through predicting coalitionary pairings. Firstly, the context of aggression between a mounting pair rarely took place and did not predict coalitions, unlike affiliative and co-aggressive same-sex mounting. This fits with the evidence from Chapter 2 that mounting in this context may instead function as a tension-regulating expression of relative dominance that avoids riskier acts of aggression (Sommer and Vasey, 2006). Crucially, by showing that a subtype of SSB did not predict coalitionary pairing, and by accounting for the effect of relatedness between individuals, results establish that the positive relationship between coalitionary and same-sex mounting partnerships is not merely an artefact of spatial distribution or group structure, in which all pairwise counts of behaviours are inherently correlated due to increased spatial proximity. In theory, a positive relationship between pair relatedness and coalitionary frequencies is to be expected if there are fitness benefits attached, as effect size is compounded by the indirect component of inclusive fitness. However, a previous study of male coalitionary behaviour in the Cayo macaques found no evidence of a relatedness effect, although this may have been due to low number of natal males in the group at the time (Kulik et al., 2012). Here the role of pair relatedness was somewhat unresolved in predicting a positive effect on coalitionary frequencies, and further investigations may benefit from differentiating between parent-offspring vs other kin relatedness, since rhesus males are thought to have poor recognition of self-paternity (Widdig, 2007).

It is unsurprising that co-aggressive same-sex mounting was the strongest predictor of coalitionary partnerships, since in this context the mounting behaviour itself seems to become an act of coalition, in which the pair mount and continue to threaten (and often subsequently physically attack) other individuals. Overall, more than one in ten cases of same-sex mounting took place in this context, but it remains unclear why the behaviour itself occasionally becomes part of a threat display. Perhaps it is simply that the act of mounting is reassuring to individuals during nerve-wracking aggressive exchanges with their opponent(s), as was suggested in baboons (Smuts and Watanabe, 1990). However, another explanation is that the behaviour also adds to the severity of a threat display. Not only might the behaviour emphasise the strength of coalition between the mounting pair (and therefore the legitimate threat of cost to conflict with either member of the pair), but the act of mounting itself can also be visually impressive and dynamic. The physical fitness (and therefore legitimate threat) of the pair is signalled by the mounter raised off the ground in a towering posture, and by the mountee displaying the strength to support their partner, all while both continue to threaten their opponent(s). In addition to an honest signal of their vigour, the behaviour is also eye-catching due to the evolutionary legacy of attention paid to different-sex mounting behavioural activity. Strong selection on mate-access and mate-guarding means that when mounting happens, individuals around pay close attention. Notably, data revealed that co-aggressive mounting contexts were as common for SSB and DSB, suggesting that this threat display function may exist indiscriminately across all mounting behaviours.

It was unclear whether same-sex mounting in general, beyond a threat display in co-aggression contexts, can function as display of coalition towards the broader social group (i.e. an honest signal of coalition likelihood). While coalitionary partners mounted when surrounded by more individuals than non-coalitionary partners, this effect disappeared when age and dominance rank were taken into account. Yet results also showed that higher ranking males were more likely to be in coalitionary partnerships, and it is therefore uncertain whether this dominance rank effect means that broader group-level mounting displays of higher-ranking individuals are a privilege of, or circumstantial to, their more group-central spatial distribution. Given the positive relationship between age and dominance rank evident in Chapter 2, it was interesting to note their inverse effect on

coalitionary partnerships. Since younger (and more dominant) individuals were more active in coalitions, the higher rates of SSB in younger males evident in Chapter 2 may be partly explained by coalition mediation.

Contrary to expectations, the more gestural (i.e. non-arousal) mounting was less than half as correlated with coalitions than the mounting with evidence of arousal. Instead of the behaviour becoming ‘less sexual’ and ‘more social’ in sociosexual function, it seems that sexual excitement and perhaps pleasure motivation appear to underpin the behavioural function of coalitionary mediation. In short, the better and more sincere the sex is, the stronger the ally will be. This finding is supported by the aforementioned study of male baboon coalitions, which suggested that male pairs engaging in ‘reciprocated’ SSB associated more strongly with coalition activity than male pairs engaging in non-reciprocal SSB (Smuts and Watanabe, 1990).

Together, these results describe the first direct evidence of SSB mediating coalitionary partnerships. This newly tested theory might fittingly be termed the ‘Sacred Band Hypothesis’ after the celebrated Sacred Band of Thebes of antiquity (4th century BC), in which 150 pairs of male lovers formed a lethal military unit that were famed, due to the unique motivation of their lover’s presence, for their ferocity and bravery on the battlefield (Shrimpton, 1971).

In support of recent research in humans (Blanchard and Skorska, 2022), evidence for fitness consequences to male SSB in close female relatives was not found here. Once again, more behavioural data is required to estimate covariance directly with partitioned repeatable and heritable variances, but the concept of SSB mediating a hypermasculine versus hyperfeminine phenotype (i.e. the suggested basis of sexual antagonistic selection in humans) was also challenged by the positive genetic correlation between same-sex mounter and mountees shown in Chapter 2.

Finally, there was no evidence for a birth order effect in male rhesus, which has been proposed as explaining one in eight of ‘SSB cases’ in male humans. This result is surprising, given the apparent volume of evidence in humans for this effect (Blanchard and Skorska, 2022), and the shared role of *NLGN4Y* in sex-differentiation for rhesus

macaques and humans (Bellot et al., 2014). Beyond subtle species-specific differences in immunology, the complexity of human cultural stigma in self-regulating and self-reporting biases (and its interaction with self-identified sexual orientation) may once again be obscuring commonalities with other primate systems (Bailey et al., 2016).

3.5 CONCLUSION

The Darwinian paradox of SSB assumes large fitness costs, which have been reported in human studies (Ganna et al., 2019). However, results here showed that expressing SSB is unlikely to carry fitness costs in macaques and may even confer fitness benefits by mediating coalition formation. Further research is essential to clarify this theory, in particular the fitness consequences of the heritable component of SSB (and coalitionary behaviour), but for now this work has finally put to rest the so-called Darwinian paradox of SSB in one of our close genetic relatives, thereby challenging the claim that SSB is a rare or deviant behaviour, a belief that sadly still leads to prosecutions and even death sentences in many countries.

GENERAL DISCUSSION

This work in this thesis has provided the first evidence of a genetic contribution to vertebrate SSB in the natural world. This both complements the recent findings of heritability in human beings and legitimises the broader evolutionary discussions surrounding the behaviour. Results should provide a basis on which to explore the proximate and ultimate foundations to the behaviour, although there is always the need for more study subjects and longer timeframes of observation to comprehensively assess life histories. In particular, finding a genetic effect should encourage further effort to understand the undoubted polygenicity of SSB. For instance, the use of GWAS and candidate gene studies would be the logical next step in our understanding of the link between genotype and phenotype for the behaviour. This could also be complemented by further assimilation of ongoing research into hormonal mediation of SSB, which has thus far remained a somewhat isolated field of study (e.g. see the decades of work in rams, most recently detailing the role of kisspeptin-GnRH: Roselli et al., 1998; Roselli 2018).

It is also hoped that this work provides a foundation on which the quantitative genetics of female SSB can be explored. Prior to this thesis, macaque SSB research was largely confined to females, although without long-term inter and intra-individual distributions of behaviour (see Fairbanks et al., 1977; Jiang et al., 2013; Leca et al., 2018). While the underpinning of SSB is expected to be different between males and females, careful comparisons may yet reveal new insights into the ecology of the behaviour. For example, the distribution of SSB between males and females appears inverted between rhesus and Japanese macaques (Leca et al., 2014). The two species are closely related and have similar social systems, so where does this pattern, if true, come from?

Although clarity is needed on defining homosexuality and bisexuality in current debates about homologies between SSB in non-human animals versus humans (Sommer and Vasey, 2006; Bailey et al., 2016; Savulescu et al., 2021), it is reasonable to speculate, given that rhesus macaques are used as our closest model species in medical research (sharing a common ancestor with humans approximately 25 million years ago; Xue et al.,

2016) that there may be some common genetic basis to sexual behaviour. Therefore, what can we learn from them about our own sexual orientations?

For example, bisexuality is widespread in humans, as was found here in rhesus macaques, with reports ranging from 37% (Bailey et al., 2016) to 49% (YouGov plc, 2015). However, a small proportion of the human population remains exclusively homosexual, for example 2% in the UK (ONS, 2017). From the data, it is still unclear how this latter figure in humans compares with exclusive SSB in macaques, although once such animal out of 236 was identified. It may also be that exclusive homosexuality is a product of human-specific biological or social factors. Nonetheless there are clearly differences in the reproductive biology of macaques and humans, for instance, ejaculation appeared to be rare in macaque SSB.

Moreover, large fitness costs of homosexuality and bisexuality are reported in human studies (Ganna et al., 2019). Given results here show that expressing SSB is not costly in macaques (and potentially confers fitness benefits by mediating coalition formation), it is possible that such large costs are a consequence of human social factors. Therefore, negative fitness effects of SSB may have been absent in our evolutionary pasts where some degree of SSB expression may have in fact been beneficial. In modern humans, homosexuality and bisexuality may thus be maintained either because of antagonistic pleiotropy (Zietsch et al., 2021), stabilising selection on same-sex behaviour (i.e. bisexual advantage; Savolainen and Hodgson, 2016), or because strict homosexuality emerges purely due to social conditions that are independent of genetics.

In conclusion, this thesis has detailed the causes and consequences of a widespread and fascinating behaviour in male rhesus macaques. Both genetic and non-genetic influences on SSB been shown, while our understanding of the fitness consequences to the trait have also been refined: firstly in that fitness consequences are possible through the heritable component of the behaviour; secondly that the behaviour is unlikely to carry previously assumed fitness costs; and thirdly that social functions may even result in fitness benefits to the behaviour.

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consistent with antagonistic pleiotropy may help explain the evolutionary maintenance of same-sex sexual behaviour in humans. *Nature human behaviour*, 5(9):1251-1258.

APPENDIX A

Archives of Sexual Behavior
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COMMENTARY



The De-Scent of Sexuality: Should We Smell a Rat?

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In their Target Article, Pfau, Jordan, and Breedlove (2019) proposed a connection between the transient receptor potential cation channel 2 gene (*TRPC2*) and same-sex sexual behavior (SSSB) in primates. This novel theory is an attractive prospect for researchers investigating sexuality in the natural world. The proposal relies on evidence from proximate mechanism studies of *TRPC2* knockout (KO) experiments in mice, in which non-functional *TRPC2* alters the development of an olfactory sensory structure called the vomeronasal organ (VNO), resulting in an increase in SSSB in both males and females (Axel et al., 2002; Kimchi, Xu, & Dulac, 2007). In combination with an examination of *TRPC2* sequence data and evolutionary relationships across primates, Pfau et al. proposed some hypotheses for the fitness consequences of SSSB in primates. Pfau et al. speculated that primates with multi-male/multi-female societies may have evolved via improved social cohesion facilitated by an increase in SSSB, mediated by non-functional *TRPC2*, and/or pleiotropy between increased SSSB and reduced same-sex aggression. Here, although we support some of these ideas by providing a more complete examination of *TRPC2* in primates, we also advocate greater caution when interpreting available data on SSSB.

Multiple Genes Underpin Same-Sex Sexual Behavior

Before discussing the evidence for a potential link between the *TRPC2* gene and SSSB in primates, and indeed all mammals, it is essential to clarify that any such link ought not to be interpreted as promoting a single “gay gene” theory of homosexuality (i.e., same-sex sexual partner preferences) and SSSB. Firstly, there is already a growing body of evidence for an epigenetic and polygenic underpinning of homosexuality and SSSB (Ratnu, Emami, & Bredy, 2017; Rice, Friberg, & Gavrilets, 2016; Sanders et al., 2017). Secondly, since it is the absence of functional *TRPC2* that appears to facilitate heightened SSSB, it seems that the gene is not itself driving SSSB, but instead that it is perhaps underpinning same-sex *aversion*, which is inversely related but not inherently antithetical to SSSB. Finally, it is evident from the presence of SSSB in animals with functioning *TRPC2* and VNO (for example, in rodents, spider monkeys, and bison; see Bagemihl, 1999; Busia, Denice, Aureli, & Schaffner, 2018; Sommer & Vasey, 2006) that the effect of *TRPC2* pseudogenization (i.e., loss of function due to a premature stop codon) cannot completely explain the expression of the behavioral phenotype for SSSB.

Further support for the polygenic nature of SSSB derives from comparisons of *TRPC2* with another gene, tryptophan hydroxylase 2 (*TPH2*). Initial work suggested that *TPH2*, which facilitates 5-HT neurotransmitter synthesis and is critical for serotonergic neuron function, had a strong role in the modulation of SSSB (Liu et al., 2011; Zhang, Liu, & Rao, 2013). These researchers reported that *TPH2* KO males showed no significant preference for either males or females, in addition to showing significant increases in SSSB. This result was contrasted with *TRPC2* KO males that, by comparison, exhibited only a reduced preference for females relative to males (Axel et al., 2002; Liu et al., 2011). However, subsequent attempts to replicate the effects of *TPH2* KO have questioned the connection between functional *TPH2* and sexual partner preference (as a different type of sexual preference behavior experiment showed that both *TPH2* KO and wild-type males preferred females), although SSSB

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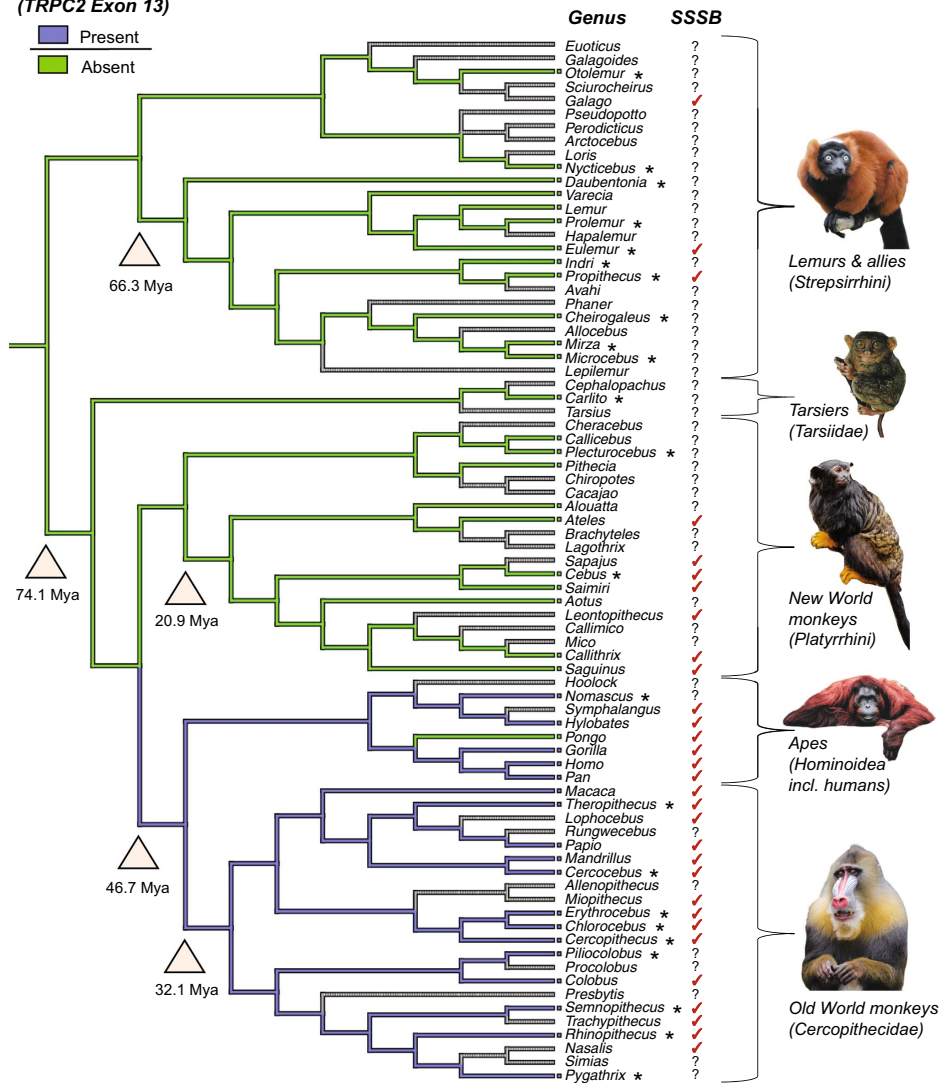
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**Stop Codon 71
(TRPC2 Exon 13)**

Present
Absent



nevertheless increased in *TPH2* KO males (Angoa-Pérez et al., 2015). Importantly, this contention brings into question the assumption of a direct inverse relationship, or degree of non-independence, between opposite-sex sexual behavior

and SSSB. Attraction or propensity for SSSB might plausibly be independent of opposite-sex attraction and behavior, whereas a sexual preference for one sex versus the other must inherently be directly and inversely dependent.

Fig. 1 Distribution of a premature stop codon in exon 13 of *TRPC2* and SSSB across the phylogeny of primates. We found that the earliest stop codon in exon 13 of *TRPC2* to appear in primates was at position 71, along the branch leading to Old World monkeys and apes (blue=stop codon present; green=stop codon absent; gray=unknown). The presence of SSSB was determined from behavioral reports, with an uncertain status (indicated by a question mark) applied to genera without confirmed SSSB in the wild (Bagemihl, 1999; Carosi & Visalberghi, 2002; Chandler, 1975; Fang, Dixon, Qi, & Li, 2018; Fox, 2001; Grueter & Stoinski, 2016; Huang, Zhou, Li, Huang, & Wei, 2015; Moynihan, 1970; Poiani, 2010; Sommer & Vasey, 2006). Evidence of SSSB in *Colobus* is taken from a pers. comm. of Teichroeb in Pfau et al. (2019). The phylogeny was taken from the Open Tree of Life online resource (Hinchliff et al., 2015) and the divergence times from Pozzi et al. (2014). Stars indicate sequences that have been provided here in addition to those reported in Pfau et al. (Photo credits: Flickr and David Gonzales, Pexels; Christine Wehrmeier, Unsplash) (Color figure online)

TRPC2 in the VNO, and Same-Sex Sexual Behavior Across Primates

The experimental evidence of *TRPC2* KO mice, combined with the loss of *TRPC2* in frequently SSSB-exhibiting cetaceans (Harvey, Dudzinski, & Kuczaj, 2017; Sommer & Vasey, 2006; Yu et al., 2010) and bats (Ricucci, 2011; Sugita, 2016; Yohe et al., 2017), provides a reasonable basis for supposing a homologous effect in Old World monkeys and apes (*Catarrhini*) as argued by Pfau et al. However, the evidence for such a connection is at present limited primarily by taxon sampling. Previous reconstructions establishing the ancestral pseudogenization of *TRPC2* only assessed up to 15 species as representatives of the respective 77 extant primate genera (Liman & Innan, 2003; Zhang & Webb, 2003). After mining GenBank to retrieve all possible sequences of *TRPC2*, we performed an updated reconstruction using 42 species of separate primate genera (Fig. 1 and supplementary information). We focused on a stop codon at position 71 in exon 13 of *TRPC2*, which was postulated by Pfau et al. to represent the ancestral loss of *TRPC2* function and hypothetical increase in SSSB in Old World monkeys. Using this larger sampling, and examining the distribution of this stop codon, we found that indeed the likely point of pseudogenization was after the split between the New World monkeys (*Platyrrhini*) versus Old World monkeys and apes (Fig. 1), as postulated by Pfau et al. We estimated this stop codon to have appeared between 46.7 and 32.1 million years ago (Mya; Fig. 1), slightly earlier than what was reported in Pfau et al. (i.e., 25 Mya). Other stop codons are found in exon 13 (supplementary information), although their distribution in fewer lineages would indicate that they appeared more recently than the premature stop at position 71. Ancestral state reconstructions for all stop codons indicated in the supplementary information were conducted using parsimony in Mesquite 3.6 (Maddison & Maddison, 2018). However, the pattern of SSSB and lost *TRPC2* function in primates does not map so easily.

SSSB has only been observed in three genera within *Strepsirrhini*, the lesser bushbabies (*Galago*), brown lemurs (*Eulemur*), and sifaka (*Propithecus*) (Bagemihl, 1999; Chandler, 1975), but in New World monkeys, at least 7 out of 19 genera are reported as exhibiting SSSB (Bagemihl, 1999; Carosi & Visalberghi, 2002; Dixon, 2012; Moynihan, 1970). Furthermore, the functionality of *TRPC2* in New World monkeys is still unclear. For example, spider monkeys (*Ateles*) appear to possess functioning *TRPC2* and yet also exhibit SSSB (Busia et al., 2018). Squirrel monkeys (*Saimiri*) and Atlantic forest marmosets (*Callithrix*) also perform SSSB, but they have an incomplete VNO with a reduced vomeronasal epithelium (VNE), through which *TRPC2* might not be able to express the phenotype for increased same-sex aversion (Pfau et al., 2019). Similarly, a reduced VNE has been reported in capuchins (*Cebus*), and interrupted or interspersed VNE in tamarins (*Saguinus*) and lion tamarins (*Leontopithecus*) (Smith et al., 2011), with all three species exhibiting SSSB (Bagemihl, 1999; Carosi & Visalberghi, 2002; Moynihan, 1970). Conversely, owl monkeys (*Aotus*) are reported to have a complex VNO (Pfau et al., 2019) and do not seem to exhibit SSSB (Hunter & Dixon, 1983), although the VNO of owl monkeys has also been described as small and unlikely to play a role in communication (Hunter, Fleming, & Dixon, 1984). Similarly, Smith et al. (2011) showed that SSSB-expressing lion tamarins possess a thicker VNE than owl monkeys (and described the owl monkey VNE as being poorly developed), thereby undermining the notion of VNE layers mediating *TRPC2* functionality and consequently SSSB. Both of the aforementioned VNO studies emphasize that the owl monkey VNO is similar in microanatomy to that of tamarins, an SSSB-exhibiting genus, and suggest that spider monkeys, which also exhibit SSSB, have the most similar VNO to the lemurs, which rarely, if ever, exhibit SSSB (Hunter et al., 1984; Smith et al., 2011). The pattern of SSSB expression in New World monkeys, therefore, cannot comfortably be coupled with variation in overall VNO structure.

Absence of Evidence for Same-Sex Sexual Behavior is not Evidence of Absence

As mentioned above, SSSB is reported among New World monkeys in 7 out of 19 genera (Bagemihl, 1999; Carosi & Visalberghi, 2002; Dixon, 2012; Moynihan, 1970), but is believed to be substantially less frequent and less intense than in Old World monkeys and apes (Dixon, 2012). Although likely to be broadly true, caution should be taken when making such comparative statements, since studies are often non-equivalent, with different objectives, sampling effort, and variables; an analysis of mounting behavior alone might assess only a subset of mount frequency, latency, copulatory duration, intromission, and ejaculation. Functionality of *TRPC2* might better predict variation in frequency of SSSB, rather than presence-absence,

but comparative studies of frequency and intensity of SSSB between primate genera are limited.

Generally, behavioral field studies of SSSB have only recently been substantially conducted, with early reports often taking the form of opportunistic anecdotes (Sommer & Vasey, 2006). For example, a recent study of spider monkeys reported the opportunistic observation of three homosexual couplings of one male with three different male partners as “low levels” of SSSB (Busia et al., 2018; Pfau et al., 2019), whereas the evidence for SSSB in wild Sumatran orangutans (*Pongo*) is comprised of opportunistic anecdotes involving mere two copulatory mounts (Fox, 2001). Furthermore, the relatively low frequencies of SSSB in primates other than Old World monkeys and apes do not explain the indisputably high frequencies observed in other mammals with functioning *TRPC2* and VNO, such as bison and red deer (Sommer & Vasey, 2006). We further argue that one cannot rely on behavioral studies unless they have been explicitly designed to assess SSSB, since without a mandate to observe SSSB, studies that report low frequencies or even absences may potentially be suffering from long-standing homophobic biases, or even the simple mistake of sexing individuals by presuming heterosexuality when any sexual coupling between individuals is observed (Bailey et al., 2016; Sommer & Vasey, 2006).

Can a Premature Stop Codon in *TRPC2* be Compensated for?

TRPC2 is considered non-functional because of a premature stop codon, but newly discovered mechanisms have shown that the function(s) of one gene with premature stop codons are frequently compensated for by the upregulation of orthologues from the same gene family (Peng, 2019). This discovery initially hinged on the fact that deleterious mutations with premature stop codons often only give a reduction in the relevant phenotype compared with the effects of acute knockdowns (reduced expression) of the same genes (Rossi et al., 2015). It now turns out that RNA transcripts with premature stop codons are preferentially degraded and gene family orthologues upregulated (El-Brolosy et al., 2019; Ma et al., 2019). This compensatory mechanism requires transcription of the mutant gene (RNA capping), and also the COMPASS complex, which catalyzes the methylation of histones at the transcriptional start site of upregulated gene orthologue family members. If there is no transcription of the mutant gene (for example, it is deleted entirely), there is no genetic compensation. Thus, a still unaddressed but critical issue is: could other *TRPC* gene orthologues be partially rescuing, perhaps

tissue specifically, the phenotype of the *TRPC2* gene KOs with premature stop codons?

Conclusion

To fully understand any behavior (here SSSB), it is important to distinguish between proximate hypotheses (“how it works”) from ultimate hypotheses (the “why” question). We note that Pfau et al. refer to the link between non-functional *TRPC2* and SSSB, and its loss in primate lineages, as an *ultimate* explanation; however, these are instead proximate hypotheses. Ultimate explanations require the expected fitness consequences of trait variation to be defined (Scott-Phillips, Dickins, & West, 2011). Since the proximate link between *TRPC2* and SSSB in primates remains unclear, we believe its clarification should be a priority for investigators in this field. This is not to say that the proposed explanation of group cohesion through socially adaptive functions facilitated by SSSB (which is an ultimate hypothesis) and/or pleiotropy with reduced aggression is unappealing, but we also note that a preliminary question, for example, would be to ask why *TRPC2* loss has not then been documented in the multi-male multi-female group-living diurnal lemurs, squirrel monkeys, and capuchins (Sussman, 1999).

Given recent progress on genome editing in primates (e.g., CRISPR; Zhou et al., 2019), researchers might consider the possibility of *TRPC2* KO in New World monkeys or lemurs, although by deleting the gene entirely and not by introducing premature stop codons. If Pfau et al.’s theory is true, then those KO mutants should exhibit increased SSSB. One might even attempt to rescue the function of *TRPC2* in an Old World monkey or ape and thereby expect suppression of SSSB, given that the true redundancy of their VNO has been contended (D’Aniello, Semin, Scandurra, & Pinelli, 2017). These investigations would need effective ethical oversight, not only because of animal welfare, but also because under no circumstances should *TRPC2* be advocated as a way to “cure” homosexuality. SSSB is likely under the control of multiple genes (Ratnu et al., 2017; Rice et al., 2016; Sanders et al., 2017), but linking *TRPC2*, VNO, and SSSB represents an exciting hypothesis by which genes can fine-tune the development of complex behaviors.

Compliance with Ethical Standards

Conflict of interest All authors declare that they have no conflict of interest.

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Understanding same-sex sexual behaviour requires thorough testing rather than reinvention of theory

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ARISING FROM J. D. Monk et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-019-1019-7> (2019)

Monk et al.¹ argue that they have outlined an alternative hypothesis for same-sex sexual behaviour (SSB), whereby an ancestral condition of indiscriminate sexual behaviour would have led to the evolution of SSB in various lineages. They justify the novelty of their claim by suggesting that previous research has implicitly assumed that SSB carries high fitness costs and derives from an ancestral state of different-sex sexual behaviour (DSB). We argue that their views arise from a misreading of current theory, and a conflation of the evolutionary origins and maintenance of the trait. Instead, we propose that rather than reinventing theory, a thorough testing of existing hypotheses is needed.

Monk et al.¹ assert that current adaptive hypotheses for SSB describe “indirect fitness benefits” to the trait. It is unclear what “indirect fitness benefits” here refers to. If Monk et al.¹ are describing the indirect component of Hamilton’s inclusive fitness², their statement is untrue since a number of adaptive hypotheses describe direct fitness benefits of SSB. These include the behaviour mediating social alliance formation or mate attraction, or facilitating juvenile practice for heterosexual behaviour (reviewed in Sommer and Vasey³).

Monk et al.¹ also argue that previous non-adaptive and maladaptive theories have considered SSB a “fundamentally erroneous tactic”. Non-adaptive and maladaptive theories are not equivalent, since neutral traits are non-adaptive but not maladaptive. By redefining existing non-adaptive hypotheses as presuming SSB to be erroneous and costly, Monk et al.¹ have reinvented the idea that SSB could be cost-free (Fig. 1). However, non-adaptive hypotheses based on genetic constraint specify that the costs of SSB could be non-existent or negligible, thereby explaining why selection has not decoupled the expression of SSB with a beneficial covarying trait. This is a well-established concept in SSB research, with theoretical and empirical examples in a range of species. For example, in invertebrates, low-cost SSB may be coupled with an overall propensity to engage in mating with the opposite sex^{4–7}.

Monk et al.¹ further assert that the costs of SSB have previously been considered obvious and high. However, within the models listed in their paper, fitness costs are not referred to as obvious, and instead have often been rigorously quantified both empirically and theoretically^{4,8,9}. For example, Gavrillets and Rice⁸ consider the evolution of homosexuality across a range of costs, from 0 (absent) to 1 (strong). Indeed, the majority of research does not suggest that the costs are high and benefits low when discussing SSB^{4,10,11}. Moreover, where high costs of SSB are discussed, it is generally within the specific context of SSB being underpinned by same-sex attraction that

is inversely proportionate to opposite-sex attraction (rather than SSB and DSB as relatively independent traits), as in sociological models of bimodal male sexual orientation¹².

Furthermore, Monk et al.¹ claim that contemporary hypotheses for SSB necessarily derive from the premise of an ancestral state population with exclusive DSB. This is untrue, since no published research, as far as we know, has asserted an ancestral state of exclusive DSB. Importantly, adaptive and non-adaptive explanations for the maintenance of a behaviour are largely independent of its evolutionary origins. It is true that, to infer the putative function of some traits, it may be useful to consider the evolutionary history of individuals bearing the trait, since closely related organisms may share phenotypes from a common ancestry rather than due to being under the same selection pressures. However, Monk et al.¹ are proposing a much deeper homology of SSB across the tree of life—even though it is unclear whether sexual reproduction arose only once. We argue that if SSB were mapped onto the phylogeny of animals and optimized to determine the ancestral state, it would probably be unresolved. This is because, rather than appearing to be homologous, SSB takes different forms across the tree of life¹³. For example, while it appears that SSB in some invertebrates is due to imperfect recognition of sexes, in some primates it may be underpinned by actual same-sex attraction. Sexual reproduction indeed takes multiple forms, with imperfect but not indiscriminate recognition¹⁴.

Finally, Monk et al.¹ suggest that researchers have followed Parker’s model¹⁴ to explain the origin of SSB. In short, those researchers believe that after the evolution of anisogamy from isogamous organisms, female targeting evolved (that is, DSB), and that subsequently SSB arose independently in the different branches of the tree of life. Monk et al.¹ argue that they have proposed an alternative model, whereby female targeting would not evolve after anisogamy, but instead an indiscriminate sex recognition would have taken place, which then facilitated both DSB and SSB. This was also their explanation for why SSB would then be homologous across the tree of life. However, a careful reading of the work of Parker¹⁴ reveals the possibility of an imperfect degree of sex recognition, rather than exclusive DSB. Indeed, Parker’s model acknowledges that the level of female targeting that males would evolve is sensitive to ecological conditions and will not always need to be complete.

The evolutionary basis for SSB in humans and other animals is a controversial topic that has generated a vast number of complementary and competing hypotheses. Monk et al.¹ do not provide us with an alternative theory but may rather have confounded existing ones.

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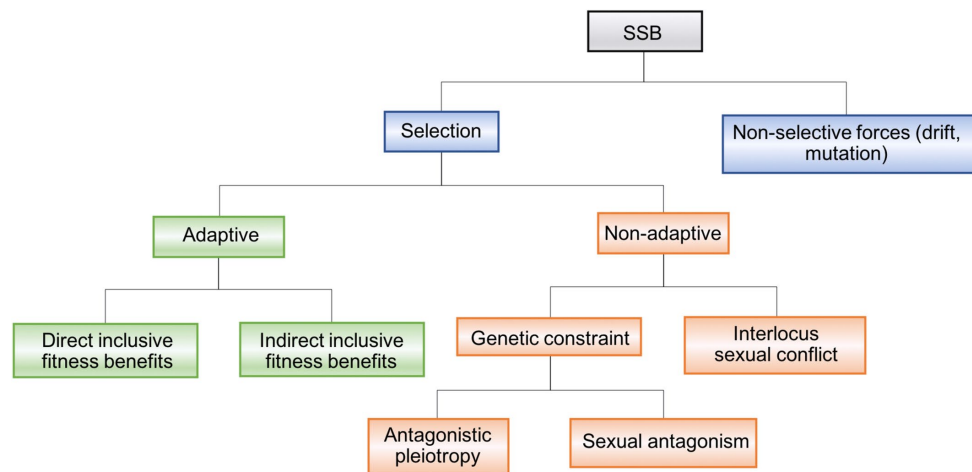


Fig. 1 | A behavioural ecology framework for disentangling the evolution of SSB. The trait is maintained in a population owing to either selective forces, or neutral forces such as drift and recurrent mutation. Within selective forces, adaptive explanations for SSB require that the behaviour itself improves fitness through direct or indirect inclusive benefits. Non-adaptive explanations for SSB largely describe scenarios of genetic constraint, in which the alleles underpinning SSB are linked to another adaptive trait expressed either in the same individual or in the opposite sex. Note that neither antagonistic pleiotropy nor sexual antagonism implies high costs (for example, refs. 4–7). In this framework, the well-studied hypothesis revisited by Monk et al.¹ is a non-adaptive ultimate explanation, whereby the behaviour occurs owing to poor sex recognition (a proximate mechanism) and is maintained because the evolution of improved opposite-sex targeting incurs trade-offs with fitness (that is, genetic constraint).

Instead, we call for thorough investigation of the ultimate evolutionary causes, and proximate genetic and epigenetic underpinning, of SSB and sexuality in nature (Fig. 1).

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Author contributions

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Competing interests

The authors declare no competing interests.

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APPENDIX C

Table 1: Ethogram

Description: Ethogram of all behaviours logged throughout the study. Total counts for each type of observation for SSB and DSB are provided (note that these are often greater than total counts for sample males).

Observation	Description	Total Counts	SSB	DSB
Mount	Mounter aligns their groin with the mountee's and made repeated pelvic thrusts. Incidence of erection, intromission and ejaculation and thrust number (up to 7) were recorded. Counts were collapsed where participants repeated the interaction within 5 minutes (see Methods). Most recent behavioural context of the preceding 5 seconds was recorded where observed (feeding, aggression between pair, aggression towards a third party, grooming etc.).	1739	1017	722
Copulatory plug	A copulatory (sperm) plug visible in a male's anus.	3	3	-
Genital stimulation	Non-mounting stimulation of genital area between an actor and recipient. Incidence of erection and/or ejaculation were also recorded. Totals are greater than the sum of SSB and DSB since in some cases individuals couldn't be identified.	11	6	3
Self-stimulation	Rapid manual manipulations of the erect penis. A minimum of 3 successive manipulations, while not exhibiting any other behaviour listed in the ethogram. Where the behaviour was displayed while in affiliative contact (e.g. resting/grooming/embracing), the partner ID(s) was recorded. These were then added as non-mounting SSB or DSB counts depending on the partner sex. Totals are greater than the sum of SSB and DSB since in some cases since the behaviour could be solitary.	335	82	16
Erection	Animal displayed an erection while not exhibiting any other behaviour listed in the ethogram. Where the behaviour was displayed while in affiliative contact (e.g. resting/grooming/embracing), the partner ID(s) was recorded. These were then added as non-mounting SSB or DSB counts depending on the partner sex. Totals are greater than the sum of SSB and DSB since in some cases since the behaviour could be solitary.	185	97	27
Sampling effort	At 10 min scan-intervals, a record of all identifiable males within line of sight of the observer was recorded. Presence-absence data was fitted as a fixed effect in variance component models to reflect the effect of any difference in sampling effort between individuals (see main text).	25016	-	-
Aggression	Any male agonistic behaviour directed at another male, including vocal, gestural and physical violence (e.g. biting another individual). Whether the recipient ignores or refuses the aggression will also be recorded and the interaction scored as a tie. The actor was scored as a winner and recipient as loser in dominance rank calculations.	1557	-	-
Submission	Any male submissive behaviour directed at another male, in which the actor deferred to the recipient. This included fear grins, avoidance and being displaced, and could be an active response to a passive recipient. The actor was scored as a the loser and recipient as winner in dominance rank calculations.	1951	-	-
Context	Most recent behaviour within preceding 5 seconds is recorded for any logged sociosexual activity. Fields are feeding, resting, travelling, aggression between pair, pair aggressing observer, pair aggressing third party, grooming, affiliative physical contact, play, and reciprocal (i.e. reciprocating a behaviour just logged e.g. mounting the individual that just mounted it)	-	-	-
Unknown ID Codes	Where individuals are not recognised, generic codes are used: MUN = unknown adult male (>5 years), FUN = unknown adult female (>3 years), SAMUN = unknown subadult male (3.5-5 years), JUVUN = unknown juvenile, JUVJUN = unknown juvenile male (1-3.5 years), JUVFUN = unknown juvenile female (1-3 years), INFANT = infant (<1 year), MOTHER = unknown female with infant.	-	-	-

Table 2: Data availability for repeated measures

Description: Data availability for repeated measures of sample males. Repeated measures are counts per 12-days of observation. Limited data availability of individual dominance rank and observer sampling effort per individual per 12-days meant that bivariate models requiring these fitted fixed effects were necessarily reduced in total sample size. While reductions due to data availability were small and did not markedly affect the results of analysis, we chose to always use the maximum available data for a given model, rather than restrict our sample sizes.

<i>Repeated measure interval</i>	<i>Data availability filter</i>	<i>Individuals</i>	<i>Repeated measure samples</i>	<i>Mean repeated measure sample age in years (sd)</i>	<i>Model usage</i>
12 Day	Dominance & sampling effort	220	963	9.6 (4.2)	SSB Mounting vs DSB mounting
12 Day	Sampling effort (scan samples)	236	1051	9.7 (4.3)	Mounter SSB vs mountee SSB
12 Day	Dominance	220	987	9.6 (4.2)	-
12 Day	None	236	1076	9.7 (4.3)	Mounter with evidence of arousal SSB vs Mounter with evidence of arousal DSB

Table 3: Interobserver test results

Description: Results of the eight tests of observer agreement conducted throughout the study. Results are discussed in Methods.

<i>Method</i>	<i>Subjects</i>	<i>Raters</i>	<i>Study phase</i>	<i>Percentage agreement</i>	<i>Date</i>	<i>Observation sessions used</i>	<i>kappa value</i>	<i>stat.name</i>	<i>statistic</i>	<i>p.value</i>
Cohen's Kappa for 2 Raters (Weights: unweighted)	42	2	B	100	Apr-17	2	1	z	12.42871232	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	144	2	D	99.30555556	May-17	2	0.987908305	z	17.04255004	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	36	2	E	100	Jun-17	1	1	z	7.637258554	2.22E-14
Cohen's Kappa for 2 Raters (Weights: unweighted)	39	2	G	92.30769231	Mar-19	2	0.886297376	z	9.660253149	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	60	2	H	96.66666667	Apr-19	2	0.957983193	z	16.09033213	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	36	2	I	100	May-19	1	1	z	10.57730032	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	24	2	J	95.83333333	May-19	1	0.951903808	z	12.38457543	0
Cohen's Kappa for 2 Raters (Weights: unweighted)	42	2	K	100	Mar-20	1	1	z	13.26880616	0

Table 4: Predicting behavioural orientations

Description: Probabilities of a sample male being categorized as exclusively same-sex in mounting activity based on number of mounts observed. Probabilities were calculated based on a significant binomial regression of the number of mounts observed per individual against their exclusive same-sex mount status. The model used only statuses for individuals with at least one mount (see Section 1.2.5). All the predictions are calculated from the single regression model, intercept, coefficient and p-value also provided. The model predicts that after observing an individual perform 21 mounts, the likelihood of it being categorized as exclusive same-sex was less than 5%. Of 236 sample males, of which 73 were observed only mounting with other males, just one individual (ID: '8V2') fit this description.

<i>Probability of Exclusive Same-sex mounting</i>	<i>Mounts observed</i>	<i>Model Intercept</i>	<i>Model Coefficient</i>	<i>Model Pvalue</i>	<i>Individuals meeting 0.05 Criteria</i>
0.706675879	1	1.072134824	-0.19284092	6.29647E-07	1
0.665177411	2	1.072134824	-0.19284092	6.29647E-07	1
0.620956972	3	1.072134824	-0.19284092	6.29647E-07	1
0.574631018	4	1.072134824	-0.19284092	6.29647E-07	1
0.526956393	5	1.072134824	-0.19284092	6.29647E-07	1
0.478785071	6	1.072134824	-0.19284092	6.29647E-07	1
0.431005083	7	1.072134824	-0.19284092	6.29647E-07	1
0.384476008	8	1.072134824	-0.19284092	6.29647E-07	1
0.339968755	9	1.072134824	-0.19284092	6.29647E-07	1
0.298118322	10	1.072134824	-0.19284092	6.29647E-07	1
0.259395024	11	1.072134824	-0.19284092	6.29647E-07	1
0.224095661	12	1.072134824	-0.19284092	6.29647E-07	1
0.192352335	13	1.072134824	-0.19284092	6.29647E-07	1
0.164154181	14	1.072134824	-0.19284092	6.29647E-07	1
0.139376409	15	1.072134824	-0.19284092	6.29647E-07	1
0.117811496	16	1.072134824	-0.19284092	6.29647E-07	1
0.099198608	17	1.072134824	-0.19284092	6.29647E-07	1
0.083248851	18	1.072134824	-0.19284092	6.29647E-07	1
0.069665262	19	1.072134824	-0.19284092	6.29647E-07	1
0.05815748	20	1.072134824	-0.19284092	6.29647E-07	1
0.048451632	21	1.072134824	-0.19284092	6.29647E-07	1
0.040296281	22	1.072134824	-0.19284092	6.29647E-07	1
0.033465358	23	1.072134824	-0.19284092	6.29647E-07	1
0.027758901	24	1.072134824	-0.19284092	6.29647E-07	1
0.023002343	25	1.072134824	-0.19284092	6.29647E-07	1
0.019044867	26	1.072134824	-0.19284092	6.29647E-07	1
0.015757281	27	1.072134824	-0.19284092	6.29647E-07	1
0.01302967	28	1.072134824	-0.19284092	6.29647E-07	1
0.010769047	29	1.072134824	-0.19284092	6.29647E-07	1
0.008897102	30	1.072134824	-0.19284092	6.29647E-07	1
0.007348133	31	1.072134824	-0.19284092	6.29647E-07	1
0.006067187	32	1.072134824	-0.19284092	6.29647E-07	1
0.005008411	33	1.072134824	-0.19284092	6.29647E-07	1
0.004133633	34	1.072134824	-0.19284092	6.29647E-07	1
0.003411121	35	1.072134824	-0.19284092	6.29647E-07	1
0.002814539	36	1.072134824	-0.19284092	6.29647E-07	1
0.002322052	37	1.072134824	-0.19284092	6.29647E-07	1
0.001915575	38	1.072134824	-0.19284092	6.29647E-07	1
0.001580139	39	1.072134824	-0.19284092	6.29647E-07	1
0.001303365	40	1.072134824	-0.19284092	6.29647E-07	1
0.001075017	41	1.072134824	-0.19284092	6.29647E-07	1
0.000886641	42	1.072134824	-0.19284092	6.29647E-07	1
0.000731249	43	1.072134824	-0.19284092	6.29647E-07	1
0.000603075	44	1.072134824	-0.19284092	6.29647E-07	1
0.000497356	45	1.072134824	-0.19284092	6.29647E-07	1
0.000410162	46	1.072134824	-0.19284092	6.29647E-07	1
0.00033825	47	1.072134824	-0.19284092	6.29647E-07	1
0.000278942	48	1.072134824	-0.19284092	6.29647E-07	1
0.00023003	49	1.072134824	-0.19284092	6.29647E-07	1
0.000189694	50	1.072134824	-0.19284092	6.29647E-07	1
0.000156429	51	1.072134824	-0.19284092	6.29647E-07	1
0.000128997	52	1.072134824	-0.19284092	6.29647E-07	1

Table 5: Totalled count data

Description: Totalled count data for sample males across DSB and SSB. Counts are subdivided by mounting, which is the sum of mounter and mountee counts. All sample male counts are totalled from repeated measure count data (Table 2). The vast majority of observed SSB was mounting (i.e. 951 of 1071 observations). For description of non-mounting SSB, see ethogram in Table 1 and panel in Fig. 1.3. Note that ‘all mounting’ counts, which are also displayed in Fig. 1.1d, are totalled counts for sample males, hence there were often two counts per observed mounting event (i.e. where both males were identifiable sample males). This is not equivalent to counts of mounting events, which are provided here as counts including those observed for unidentified non-sample males (Tables 1 & 5).

Type	Behaviour	Counts
Same-sex	All mounting	951
Same-sex	Mounter	531
Same-sex	Mountee	420
Same-sex	Mounter with evidence of arousal	356
Same-sex	Non-mounting	120
Same-sex	All sociosexual	1071
Same-sex	Mounting events (including counts from non-sample males)	1017
Different-sex	All mounting	530
Different-sex	Mounter	530
Different-sex	Mountee	0
Different-sex	Mounter with evidence of arousal	409
Different-sex	Non-mounting	34
Different-sex	All sociosexual	564
Different-sex	Mounting events (including counts from non-sample males)	722

Table 6: Distributions of behavioural orientation

Description: Ordinal mounting categories of sample males ($n = 236$). These values are also displayed in Fig. 1.1c.

<i>Trait</i>	<i>Individuals</i>	<i>Percentage</i>
Exclusive same-sex mounting behaviour	73	0.31
Same & different sex mounting behaviour	97	0.41
Exclusive different-sex mounting behaviour	11	0.05
No mounting behaviour observed	55	0.23

Table 7: Posterior modes of variance

Description: Modes of posterior distributions of variance components for all bivariate MCMC GLMMs with error estimates defined by highest posterior density intervals (HPD). Results from all models are provided here, including intercept-only and randomized count data models, models with matrilineal effect, models using count data totalled for six and thirty-day periods, and models with raw un-collapsed mounts of rhesus' characteristic start-stop mounting behaviour. Distributions are given at the latent and observed scales (marginalized for potential fixed effects). Distributions for effect of individual identity, relatedness, and matriline are taken as proportions of total phenotypic variance at the corresponding scale, for example the first row gives the posterior modes for repeatability (19.3%) and heritability (6.4%) to same-sex mounting in columns six and ten, which are also displayed in Fig. 2.2.

Table 8: Predicting mounter erectile state from thrust counts

Description: Results from two binomial models predicting the confirmed presence of an erection using number of thrusting motions during a mount. The first model significantly predicted a mounter's erection, while the second did not significantly predict a mountee's erection (see Methods).

Participant	Probability of erection	Thrust Number	Coefficient	P value <
mounter	0.459	0	0.45825	2.29E-16
mounter	0.573	1	0.45825	2.29E-16
mounter	0.679	2	0.45825	2.29E-16
mounter	0.770	3	0.45825	2.29E-16
mounter	0.841	4	0.45825	2.29E-16
mounter	0.893	5	0.45825	2.29E-16
mounter	0.930	6	0.45825	2.29E-16
mounter	0.954	7	0.45825	2.29E-16
mountee	0.190	0	-0.0492	0.325
mountee	0.183	1	-0.0492	0.325
mountee	0.175	2	-0.0492	0.325
mountee	0.168	3	-0.0492	0.325
mountee	0.162	4	-0.0492	0.325
mountee	0.155	5	-0.0492	0.325
mountee	0.149	6	-0.0492	0.325
mountee	0.143	7	-0.0492	0.325

Table 9: Optimised fixed effect structures

Description: Results for the optimal permutation for each of the three bivariate models presented in the main text: SSB mounting vs. DSB mounting; SSB mounter vs. SSB mountee; SSB mounting with arousal vs. DSB mounting with arousal. Permutations were performed using Bayesian Monte Carlo Markov Chain Poisson generalized linear mixed-models (MCMC GLMMs) by taking the lowest deviance information criterion (DIC) in which all fitted effects were statistically significant ($p_{\text{MCMC}} < 0.05$). The posterior means describe the slope of effect within a given model structure. Data availability per model and the stored model data file names are also provided. Some effects were discarded (e.g. birth season, colony population level structure) or refined (e.g. scan sampling and age always not significant for DSB) during preliminary analysis. Note that group level mating activity was not fit for DSB since it was derived from DSB totals per 12-days.

Phenotypes	DIC	Trait intercept				Scan samples				Age				Seasonal dominance rank (David's score)				Group ratio (males (4-5yr): males (3.5-5yr))				Group ratio (males (4-5yr): females (4-5yr))				Dataset filters	Individuals	Samples
		Trait1	Posterior mean	pMCMC	Posterior mean	Trait2	Posterior mean	pMCMC	Posterior mean	Trait1	Posterior mean	pMCMC	Posterior mean	Trait2	Posterior mean	pMCMC	Posterior mean	Trait1	Posterior mean	pMCMC	Posterior mean	Trait2	Posterior mean	pMCMC	Posterior mean			
Mounting same-sex	3609.152	1.010	0.007	-7.562	0.002	0.014	0.007	-0.082	0.002	0.002	0.002	-0.139	0.002	0.002	0.002							2.723	0.002	0.017	0.002	Dominance & scan sample	220	963
Mounter same-sex; mountee different-sex																												
Mounter same-sex; mountee same-sex	3344.648	0.135	0.713	0.688	0.133	0.019	0.020	-0.081	0.002	-0.118	0.002	-0.113	0.010	-0.167	0.003							-0.002	0.020	-0.003	0.003	Scan sample	236	1051
Mounter with evidence of arousal same-sex; mounter without evidence of arousal same-sex	2380.975	-0.779	0.002	-3.589	0.002			-0.106	0.002							0.858	0.002					1.010	0.007			Dominance	220	987

Table 10: Mounting fixed effect permutations

Description: Table contains all permutations for candidate fixed effects predicting same-sex and different-sex mounting. In some cases, the same effect structures were permuted with differing data availability due to the potential non-significance of social dominance rank and/or sampling effort (i.e., scan samples). The ‘X’ denotes the optimal permutation (DIC = 3609.152), which is consequently listed above in table S7, whereas ‘X*’ denotes an optimal permutation at an invalidated level of data availability (in which relative sampling effort was dropped).

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Table 11: Seasonal dominance ranks

Description: David's and Elo scores per year of study for sample males.

<i>Animal ID</i>	<i>Study season</i>	<i>Seasonal David's score</i>	<i>Seasonal Elo</i>
04I	2017	0.066076742	0.814225267
76Z	2017	-0.811347958	-0.400289517
9EE6	2017	-0.03997336	0.163754802
6L8	2017	-0.229501391	0.072779912
46N	2017	0.342073274	0.277473415
5D1	2017	0.66519695	1.173576084
4L9	2017	2.718802367	1.842241527
6M0	2017	0.314760839	0.040938701
2N1	2017	-2.065180714	-2.351700912
30L	2017	-0.570134794	-0.236534715
9J3	2017	0.773104138	1.25090474
5B2	2017	-1.612091982	-1.751266636
3B9	2017	-0.55045198	-0.327509605
7D2	2017	-0.280185392	-0.09097489
9K7	2017	0.706548125	0.418484495
8D6	2017	1.319087893	1.460146988
0G8	2017	0.052427967	-0.359350816
6EE6	2017	0.838698633	0.741445355
8K9	2017	0.816926083	0.982528814
8A7	2017	-1.155070397	-1.464695732
49L	2017	0.51441445	0.432130728
6F0	2017	-1.326166341	-1.692132958
5EE1	2017	0.195238511	0.022743723
0H8	2017	0.37392034	-0.186498525
4I8	2017	-1.048461566	-0.482166918
8C3	2017	1.990449862	1.501085688
84EE	2017	1.079863252	1.983252606
3EE1	2017	-0.744410453	-0.564044319
5G2	2017	1.246822316	1.078052449
7H9	2017	0.340566997	0.450325707
0J1	2017	-0.70728638	-1.037113748
1M1	2017	1.519577535	2.529101948
4H2	2017	-0.782231105	-0.827871501
3I2	2017	2.225083769	2.269823511
8B5	2017	-0.233017487	0.195596014
0J8	2017	1.229860327	1.155381106
31S	2017	0.073655299	0.627726742
25L	2017	1.048342035	1.478341966
3K6	2017	-0.3865144	0.545849341
4D3	2017	-0.744345421	-0.905200158
7B2	2017	-1.045460004	-0.868810201
9D7	2017	-0.074766115	-0.045487445
1B1	2017	0.094164782	0.009097489
3Z2	2017	0.162504294	-0.004548745
2K0	2017	-0.093190243	-0.100072379
61R	2017	3.129730369	1.846790271
2K6	2017	2.29686541	1.464695732
7M8	2017	-0.856984787	-1.141734872
0J4	2017	0.317943183	0.386643283
3M2	2017	-0.522596267	-0.127364846
77I	2017	0.747471024	0.723250377
19T	2017	0.407478907	0.227437226
0M8	2017	-0.548543354	-0.354802072
5K8	2017	-1.335848639	-0.495813152
51A	2017	3.070527156	2.338054678
2N8	2017	0.073090387	0.150108569
4J2	2017	-0.78853054	-1.282745952
7G9	2017	-1.630726493	-1.128088639
6H9	2017	-0.657579237	-0.46397194
2N2	2017	-0.783293834	-1.505634433
6M4	2017	0.242591437	0.163754802
1EE5	2017	0.031997968	0.932492625
9K2	2017	0.684209977	0.87790769
8D8	2017	-0.229799532	-0.482166918
7K4	2017	-0.435218809	-1.005272537
5L2	2017	2.898521278	2.256177277
1M3	2017	1.231577959	1.551121878
5P8	2017	1.65545206	2.128812431
3M9	2017	1.282211354	1.755815381
0L0	2017	-0.848245334	-0.764189078
88T	2017	1.068165218	0.791481545
8D2	2017	0.200763511	0.509459385
6I1	2017	-1.482453462	-1.369172098
96Z	2017	-0.764366678	-0.682311677
97V	2017	-0.146073152	0.341155838
2J9	2017	-0.738096592	-0.423033239
3I3	2017	2.912049835	3.425204616
5I0	2017	0.354945096	0.200144758
3I6	2017	-0.235716498	0.227437226

2K3	2017	1.695331525	1.360074609
7O4	2017	0.31221777	0.759640333
0L4	2017	0.233889238	0.341155838
3I5	2017	0.21025668	-0.059133679
8J3	2017	-0.608477471	-0.468520685
0G1	2017	0.070775858	-0.045487445
2K5	2017	1.822143347	1.237258507
3K1	2017	0.292361548	0.727799122
12O	2017	1.01814909	0.573141808
5N9	2017	-0.673332633	-1.096247427
1Q9	2017	-0.315264382	-0.527654363
93R	2017	0.024778693	0.040938701
6M2	2017	-0.844038612	-1.037113748
8M1	2017	0.725239654	0.668665443
3L7	2017	-0.401273992	-0.950687603
4M1	2017	-0.21860962	-0.432130728
22R	2017	0.218046999	0.655019209
9C8	2017	-0.906891903	-0.518556874
4N3	2017	-0.7594762	-1.200868551
3K4	2017	-1.361404019	-1.81494906
7J0	2017	-0.959028141	-1.44195201
8R6	2017	-0.560359633	-0.191047269
6P9	2017	-0.438542322	-0.250180948
81O	2017	1.169811643	0.636824231
4G8	2017	-0.677547887	-0.32296086
7F5	2017	-1.211107712	-1.305489674
7G1	2017	-1.654035457	-0.545849341
3M8	2017	0.176614991	0.568593064
5I5	2017	-0.310316887	-0.732347866
3I9	2017	-0.200998564	-0.222888481
0C7	2017	-1.847115896	-1.44195201
3J7	2017	0.253989095	0.359350816
1F2	2017	-0.012425366	0.154657313
0M1	2017	2.006696574	1.646645513
4EE2	2017	-0.144353514	-0.186498525
9I9	2017	-0.374588233	0.145559824
60EE	2017	-0.542087037	-0.650470465
5B0	2017	-0.433669629	-0.236534715
18I	2017	1.39834092	1.10989366
33T	2017	1.077474121	1.055308726
5N5	2017	0.569739566	0.577690553
6M3	2017	-0.20607418	-0.46397194
2F8	2017	-0.365573752	-0.213790992
8K1	2017	0.087343012	0.218339736
73S	2017	-0.970274887	-0.577690553
5EE6	2017	1.200509606	0.946138858
7A2	2017	-0.564623239	-0.714152888
4G6	2017	-0.988547483	-1.264550974
9EE3	2017	-0.006699952	0.527654363
4K7	2017	0.220732969	0.313863371
25R	2017	0.14678986	0.236534715
1D5	2017	-1.792907192	-1.405562054
36V	2017	-0.976731204	-1.087149938
5K5	2019	-0.146168807	-0.038589669
88T	2019	1.055631068	1.500709342
7D2	2019	1.11492412	1.62076609
3M9	2019	1.977594792	2.088129856
4D3	2019	-0.752737283	-1.170553287
9C8	2019	0.175752581	0.848972714
3I3	2019	2.891840101	3.670306277
3K4	2019	-0.622967495	-0.385896688
5G2	2019	1.73135153	1.380652595
5P8	2019	2.877693158	2.757017449
7G9	2019	-0.034011231	0.540255363
5D1	2019	1.526426544	1.697945427
5B2	2019	-0.917083064	-1.230581661
2Q9	2019	2.148940835	2.289653682
1T4	2019	-0.081995095	0.634585665
8D6	2019	1.02994485	1.089086208
4I8	2019	-0.314021691	-0.313005091
4L9	2019	1.135729678	1.625053831
2N1	2019	-0.484112706	-0.274415423
30Z	2019	-1.049007315	-0.861835937
1EE5	2019	1.480924104	1.144826841
9R6	2019	-0.242804541	-0.162934157
8A7	2019	-0.578095121	-0.43734958
12O	2019	2.68324262	1.925195699
25L	2019	0.862315082	1.264883589
7A2	2019	-0.978174987	-0.463076026
76Z	2019	0.8730107	0.780368858

4P8	2019	-0.678718582	-0.724628225
7Q8	2019	2.358725564	2.14815823
7H9	2019	0.818926011	1.149114582
4N3	2019	-0.564622686	-0.604571478
5EE1	2019	-1.687739343	-0.999043648
96Z	2019	0.339345346	0.475939249
5R1	2019	-0.441692795	-0.96474172
4O5	2019	-1.875742382	-1.517860306
3L7	2019	-0.158231011	-0.188660603
7J0	2019	-1.032894163	-0.608859219
6J3	2019	0.209910232	0.270127682
9N9	2019	-0.545964618	-0.287278646
2J6	2019	-1.204839829	-1.350638408
1G9	2019	-0.557524811	-0.861835937
2M3	2019	-0.536231187	-0.192948344
6H9	2019	0.335489624	0.810383045
1M1	2019	1.985508435	2.945678052
97V	2019	0.365847332	0.214387049
5L1	2019	-1.403001614	-0.866123678
5K8	2019	1.63560299	0.707477261
0C7	2019	0.806212053	0.617434701
33T	2019	0.549178891	0.711765002
2D0	2019	1.384536668	1.033345576
3M2	2019	-0.841783607	-0.364457983
0P9	2019	-1.031345564	-0.540255363
0M1	2019	3.417164096	2.259639495
2N0	2019	0.149400526	0.801807563
07D	2019	-2.296086419	-1.800851211
0H8	2019	0.419744334	0.57026955
2K6	2019	-0.857618686	-0.291566387
8I0	2019	3.172982592	2.06240341
2N2	2019	-0.954924097	-1.663643499
19T	2019	1.348735621	1.427817746
7K4	2019	0.790606468	0.630297924
8J3	2019	0.614584651	0.784656599
61R	2019	3.602595164	2.714140039
36V	2019	0.25863962	0.553118586
3P3	2019	0.141368239	-0.278703164
5B0	2019	1.020559351	1.149114582
04T	2019	-0.447513095	-0.107193524
0J4	2019	0.955842073	1.342062926
7G1	2019	0.102354277	1.00761913
8N5	2019	-0.500985173	-0.034301928
8R6	2019	0.051636126	-0.167221898
77I	2019	0.956530554	0.801807563
6EE6	2019	1.207826369	0.222962531
8O5	2019	-0.591635261	-0.291566387
4EE2	2019	-0.657958997	-0.578845032
9K9	2019	-0.473904893	-0.094330302
1B1	2019	1.363882218	0.977604943
6R3	2019	-0.737363885	-0.827534009
2N8	2019	-0.069766144	0.540255363
0G8	2019	0.408958121	0.518816658
8K1	2019	0.222609078	0.278703164
6B8	2019	0.736904897	0.827534009
32Z	2019	-0.019736475	0.120056747
9O9	2019	-0.811507407	-1.213430697
6Q1	2019	-0.774756034	-1.350638408
8S8	2019	-0.552783598	-0.61314696
6P3	2019	-1.100254249	-1.659355758
3R8	2019	-0.757715557	-1.432105487
4U2	2019	0.060457438	-0.025726446
6V1	2019	0.001952264	0.115769006
4S4	2019	-1.041602656	-1.290610034
3L1	2019	-0.731626537	-1.011906871
7S9	2019	-1.21080979	-1.676506722
4U9	2019	-0.269196339	-0.240113495
5P4	2019	-0.317849045	-0.445925062
93R	2019	-0.380271384	-0.30871735
4K7	2019	0.012851658	0.13291997
4U6	2019	-0.520951142	-0.78894434
8C3	2019	0.36351833	1.016194612
6I9	2019	-0.710742593	-0.823246268
1F2	2019	2.291037554	1.367789372
8V2	2019	-0.858077673	-0.939015274
6K5	2019	-0.006655323	0.801807563
0I9	2019	-0.881027063	-0.450212803
5W6	2019	-0.622616937	-0.454500544
6P9	2019	-0.950104725	-0.557406327
3I6	2019	0.470691979	0.017150964

5U1	2019	-0.571210305	-0.051452892
4U0	2019	-0.495706813	-0.287278646
1R8	2019	-1.010691114	-0.638873406
3U6	2019	-0.466561089	-0.43734958
9F9	2019	1.418960753	1.063359763
8V9	2019	-0.302931941	-0.171509639
8K9	2019	-0.425252187	-0.210099308
3U3	2019	-0.273097735	0.201523826
9EE3	2019	-0.727266153	-0.39447217
4G8	2019	-0.760313274	-0.055740633
5Q4	2019	-0.320415356	-0.343019278
4T5	2019	0.022060585	0.338731537
7U9	2019	0.248725427	0.986180425
8R0	2019	-0.515495353	-1.149114582
1Q0	2019	-0.490464537	-1.384940336
5S5	2019	-0.378934474	-0.540255363
7M8	2019	-0.688940673	-0.604571478
5U6	2019	-0.469315015	-0.574557291
3U7	2019	-0.152154452	0.068603856
8V5	2019	-0.246705937	-0.403047652
8M1	2019	-1.374209443	-1.616478349
7V9	2019	-0.400925835	-0.158646416
3U1	2019	-0.38945114	-0.231538013
1S4	2019	-0.455545382	-0.252976718
9V0	2019	-0.562489537	-0.65602437
7P0	2019	-0.280212046	-0.540255363
1U7	2019	-0.157203318	-0.145783193
4R8	2019	-0.240050614	-0.381608947
5J7	2019	-0.469315015	-0.724628225
8V7	2019	-0.213429322	-0.518816658
6W3	2019	-0.247164925	-0.488802471
5U3	2019	-0.421121297	-0.514528917
6W0	2019	0.058520943	0.343019278
3M8	2019	-0.134483422	-0.265839941
8V3	2019	-0.443382205	-0.553118586
3P6	2019	-0.566849921	-0.343019278
8V6	2019	-0.417678889	-0.510241176
8U5	2019	-0.480330722	-0.158646416
6W7	2019	-0.253590754	-0.523104399
4V6	2019	-0.249541194	-0.83182175
4T8	2019	-0.108838727	-0.338731537
7S3	2019	0.030448349	0.467363767
9R5	2019	-0.45296712	-1.149114582
9M5	2019	-0.82548954	-0.848972714
1U9	2019	-0.496854283	-0.83182175
7U9	2020	1.816359544	1.722874772
2J6	2020	-0.542113464	-0.574291591
76Z	2020	0.760076609	0.954565752
96Z	2020	0.547702262	1.28827573
3K4	2020	-0.346505513	-0.457881133
7H9	2020	1.089815726	1.28827573
73V	2020	-0.122953569	-0.093128366
4N3	2020	0.301795124	0.760548323
3L7	2020	-0.363271909	-0.442359739
0H3	2020	-0.631534241	-0.923522963
9N9	2020	-0.480636679	-0.527727408
1T4	2020	2.280229827	2.025541962
9C8	2020	1.51456442	1.28827573
3M9	2020	3.085016825	2.832654468
5EE1	2020	-0.055887986	-0.395795556
7J0	2020	0.122953569	0.551009499
1G9	2020	-0.776843005	-0.46564183
2N1	2020	-1.682228377	-2.087627539
30Z	2020	-0.312972721	-0.65965926
97V	2020	0.430337492	0.908001569
6V1	2020	-0.732132616	-0.939044358
6Q1	2020	-0.603590248	-1.451250371
5J5	2020	-0.849497387	-1.086497604
5U1	2020	1.146746219	0.830394597
5B0	2020	0.049858531	0.395795556
0M1	2020	1.670260797	0.884719478
3P6	2020	-0.872524297	-0.535488105
8C3	2020	-1.141760366	-0.884719478
3M2	2020	-0.852580884	-0.706223443
5K8	2020	1.071958422	1.102018998
6P9	2020	0.822665766	0.426838344
1F2	2020	-0.049858531	-0.605334379
7A2	2020	-0.872524297	-1.117540393
9S8	2020	-1.346180344	-1.039933421
8K9	2020	0.149575594	0.388034859
8V3	2020	-0.792750647	-0.667419957
8J3	2020	-0.244306803	-0.884719478
3M8	2020	-0.299151187	-0.085367669
61R	2020	2.343350969	1.89361011
6EE6	2020	0.653146759	0.434599042
8Q5	2020	-0.199434125	0.457881133
0H8	2020	1.146746219	1.218429456
810	2020	1.605444706	1.420207582
1B1	2020	0.473656047	0.504445316
6W0	2020	-0.448726781	-0.388034859
0J4	2020	-1.002156478	0.139692549
2N0	2020	-0.623231641	-1.063215512

Table 12: Mounter mountee fixed effect permutations

Description: Table contains all permutations for candidate fixed effects predicting same-sex mounter and same-sex mountee repeated measures. In some cases, the same effect structures were permuted with differing data availability due to the potential non-significance of social dominance rank and/or sampling effort (i.e., scan samples). The ‘X’ denotes the optimal permutation (DIC = 3344.648), which is consequently listed above in Table 9.

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Table 13: Arousal mounter fixed effect permutations

Description: Table contains all permutations for candidate fixed effects predicting repeated measures for same-sex and different-sex mounter with evidence of arousal. In some cases, the same effect structures were permuted with differing data availability due to the potential non-significance of social dominance rank and/or sampling effort (i.e., scan samples). The 'X' denotes the optimal permutation (DIC = 2380.98), which is consequently listed above in Table 9.

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Table 14: Randomised count data test results

Description: Results from permutation tests of whether heritability and repeatability of same-sex and different-sex mounting were significantly different from null distributions. Null distributions were created by i.e. randomly reassigning count data values across repeated measures, and running intercept-only models (i.e. with no fixed effect structure) under the same parametrization as our observed values (also derived from an intercept-only structure, hence not those reported in main text, but provided as quality control for assessing the influence of inflating estimates due to reduced residual variance within fixed-effect models). One sample t-tests were used to test for significant differences.

<i>Trait</i>	<i>Variance Type</i>	Heritability, observed scale marginalised (posterior mode)	Mean of 25 permuted posterior modes	<i>t-value</i>	<i>p value <</i>	Heritability of equivalent model with fixed effects, observed scale marginalised (posterior mode)
Same-sex mounting (intercept-only)	heritability	0.066888175	0.036333374	-31.77199949	4.01E-21	0.063663782
Different-sex mounting (intercept-only)	heritability	0.029756805	0.0045397	-89.14810413	8.95E-32	0.009679664

Table 15: Dominance expression data

Description: Data table of 473 same-sex mounting interactions with known rank difference between participants defined by seasonal David's score. These observations tally to give 202 interactions (42.7%) in which the mounter was beneath the mountee in rank (i.e., a negative rank difference). The context of a mounting interaction (see ethogram in Table 1), shows that aggression between participants ('between pair') greatly reduces the proportion of interactions with a lower-ranked mounter versus mountee.

Action	Dominance rank difference (mouter rank minus moutee rank)	Mouter rank (seasonal David's score)	Moutee rank (seasonal David's score)	Context (preceding 5 seconds)	Erectile status	Thrust Number	Mouter age	Moutee age
Mount	-3.762	-1.403	2.359	Aggression between pair	Absence of erection was confirmed	0	8.54	5.58
Mount	-3.735	-0.562	3.173	NA	Erectile status unconfirmed	5	3.62	18.38
Mount	-2.950	0.223	3.173	Travelling	Mounter erection confirmed	7	8.50	18.38
Mount	-2.857	-0.560	2.297	NA	Erectile status unconfirmed	NA	3.58	6.40
Mount	-2.464	-0.239	2.225	Resting	Mounter erection confirmed	NA	3.69	7.48
Mount	-2.443	-0.152	2.291	Reciprocal	Mounter erection confirmed	7	4.55	11.35
Mount	-2.231	-0.082	2.149	Playing	Erectile status unconfirmed	0	4.54	5.62
Mount	-2.157	-0.521	1.636	Aggression between pair	Erectile status unconfirmed	4	4.55	8.49
Mount	-2.068	-0.082	1.986	Playing	Mounter erection confirmed	3	4.51	7.49
Mount	-1.976	-0.744	1.232	Feeding	Erectile status unconfirmed	NA	10.56	5.57
Mount	-1.973	-1.631	0.342	Pair aggressing third party	Mounter erection confirmed	NA	8.61	17.55
Mount	-1.915	-0.093	1.822	Travelling	Mounter erection confirmed	NA	6.55	6.46
Mount	-1.883	0.342	2.225	Resting	Erectile status unconfirmed	NA	17.53	7.56
Mount	-1.676	0.615	2.291	Travelling	Erectile status unconfirmed	7	9.54	11.37
Mount	-1.654	-1.336	0.318	Travelling	Mounter erection confirmed	NA	6.49	7.59
Mount	-1.649	-0.858	0.791	Travelling	Erectile status unconfirmed	7	3.68	8.44
Mount	-1.618	-0.387	1.232	Resting	Erectile status unconfirmed	NA	6.57	5.61
Mount	-1.433	-1.374	0.059	Aggression between pair	Erectile status unconfirmed	0	7.65	3.73
Mount	-1.392	1.520	2.912	Pair aggressing third party	Erectile status unconfirmed	NA	5.63	7.57
Mount	-1.392	1.520	2.912	Resting	Erectile status unconfirmed	NA	5.66	7.60
Mount	-1.392	1.520	2.912	Pair aggressing third party	Mounter erection confirmed	NA	5.74	7.68
Mount	-1.392	-2.065	-0.673	Resting	Mounter erection confirmed	NA	5.67	5.79
Mount	-1.381	-1.042	0.339	Travelling	Mounter erection confirmed	7	5.52	14.31
Mount	-1.287	-0.040	1.247	Resting	Mounter erection confirmed	NA	9.52	8.53
Mount	-1.235	-0.570	0.665	Grooming	Mounter erection confirmed	NA	17.25	10.53
Mount	-1.227	0.409	1.636	NA	Erectile status unconfirmed	2	11.58	8.51
Mount	-1.156	0.052	1.208	Travelling	Mounter erection confirmed	5	5.54	11.35
Mount	-1.156	0.052	1.208	Travelling	Mounter erection confirmed	5	5.69	11.50
Mount	-1.147	-1.346	-0.199	NA	Erectile status unconfirmed	NA	5.57	6.46
Mount	-1.122	-0.050	1.072	Feeding	Erectile status unconfirmed	NA	12.31	9.37
Mount	-1.112	-0.387	0.725	Resting	Mounter erection confirmed	NA	6.63	5.76
Mount	-1.112	-0.387	0.725	Resting	Mounter erection confirmed	NA	6.65	5.79
Mount	-1.100	-1.336	-0.236	Feeding	Mounter erection confirmed	NA	6.44	7.50
Mount	-1.072	0.409	1.481	Pair aggressing observer	Mounter erection confirmed	3	11.67	12.59
Mount	-1.067	-0.658	0.409	Aggression between pair	Absence of erection was confirmed	0	11.43	11.47
Mount	-1.063	-1.033	0.030	Pair aggressing third party	Mounter erection confirmed	4	9.46	4.60
Mount	-1.050	-0.977	0.073	Affiliative physical contact	Mounter erection confirmed	NA	13.49	5.48
Mount	-1.036	-0.421	0.615	Travelling	Erectile status unconfirmed	5	4.67	9.58
Mount	-0.992	-0.219	0.773	Resting	Mounter erection confirmed	NA	5.56	7.45
Mount	-0.985	0.223	1.208	NA	Erectile status unconfirmed	6	8.46	11.39
Mount	-0.955	-0.230	0.725	Feeding	Mounter erection confirmed	NA	6.62	5.68
Mount	-0.943	1.282	2.225	Resting	Mounter erection confirmed	NA	5.52	7.48
Mount	-0.922	-2.296	-1.374	Pair aggressing observer	Both mouter and moutee displayed an erection	7	24.23	7.61
Mount	-0.915	0.315	1.230	Pair aggressing third party	Absence of erection was confirmed	NA	5.77	7.73
Mount	-0.914	0.471	1.385	Pair aggressing third party	Erectile status unconfirmed	7	9.50	12.44
Mount	-0.905	-1.374	-0.469	Travelling	Mounter erection confirmed	3	7.55	4.50
Mount	-0.905	0.342	1.247	Feeding	Mounter erection confirmed	NA	17.51	8.60
Mount	-0.902	-0.536	0.366	Aggression between pair	Absence of erection was confirmed	0	7.58	15.45
Mount	-0.895	-0.230	0.665	Pair aggressing third party	Both mouter and moutee displayed an erection	NA	6.57	10.51
Mount	-0.888	-0.273	0.615	NA	Erectile status unconfirmed	0	4.63	9.56
Mount	-0.878	-0.560	0.318	Pair aggressing third party	Mounter erection confirmed	NA	3.78	7.71
Mount	-0.869	0.862	1.731	Pair aggressing third party	Mounter erection confirmed	7	19.34	10.59
Mount	-0.867	-1.403	-0.536	Pair aggressing third party	Mounter erection confirmed	5	8.50	7.48
Mount	-0.867	-1.403	-0.536	Affiliative physical contact	Erectile status unconfirmed	4	8.54	7.52
Mount	-0.860	-0.070	0.791	Travelling	Mounter erection confirmed	7	7.51	8.34
Mount	-0.858	0.873	1.731	Pair aggressing third party	Erectile status unconfirmed	2	14.46	10.56
Mount	-0.838	-1.403	-0.565	Aggression between pair	Mounter erection confirmed	6	8.55	7.61
Mount	-0.833	2.297	3.130	Resting	Erectile status unconfirmed	NA	6.59	15.46
Mount	-0.832	1.526	2.359	Aggression between pair	Mounter erection confirmed	7	12.62	5.65
Mount	-0.813	-0.565	0.249	Pair aggressing third party	Mounter erection confirmed	7	7.61	4.43
Mount	-0.781	0.249	1.030	Pair aggressing third party	Mounter erection confirmed	3	4.38	12.43
Mount	-0.775	-1.482	-0.707	Resting	Mounter erection confirmed	NA	7.56	7.72
Mount	-0.737	-0.950	-0.213	Pair aggressing third party	Absence of erection was confirmed	1	6.63	3.39
Mount	-0.733	0.223	0.956	Pair aggressing third party	Mounter erection confirmed	6	8.46	9.50
Mount	-0.731	-0.439	0.292	Pair aggressing third party	Mounter erection confirmed	NA	4.81	6.67
Mount	-0.730	-1.211	-0.480	Playing	Mounter erection confirmed	7	4.64	4.66
Mount	-0.723	-0.303	0.420	Grooming	Erectile status unconfirmed	6	3.67	10.18
Mount	-0.718	-0.379	0.339	Pair aggressing third party	Mounter erection confirmed	NA	4.41	14.28
Mount	-0.718	-0.379	0.339	Playing	Both mouter and moutee displayed an erection	7	4.49	14.36
Mount	-0.706	1.520	2.225	Resting	Mounter erection confirmed	NA	5.53	7.43
Mount	-0.680	0.956	1.636	NA	Erectile status unconfirmed	NA	9.52	8.41
Mount	-0.673	0.474	1.147	Resting	Erectile status unconfirmed	2	15.33	11.10
Mount	-0.672	-0.439	0.234	Affiliative physical contact	Mounter erection confirmed	NA	4.59	6.46
Mount	-0.653	-0.623	0.030	Pair aggressing third party	Absence of erection was confirmed	3	8.52	4.66
Mount	-0.636	-0.549	0.087	Resting	Mounter erection confirmed	NA	5.71	6.59
Mount	-0.630	-0.578	0.052	NA	Erectile status unconfirmed	NA	14.42	5.64
Mount	-0.630	-0.578	0.052	Pair aggressing observer	Both mouter and moutee displayed an erection	3	14.42	5.64
Mount	-0.617	-0.442	0.176	Travelling	Erectile status unconfirmed	2	5.52	12.41
Mount	-0.611	-0.858	-0.247	Pair aggressing observer	Mounter erection confirmed	7	3.66	3.78
Mount	-0.611	-0.858	-0.247	Pair aggressing observer	Mounter erection confirmed	5	3.56	3.69
Mount	-0.611	-0.858	-0.247	Pair aggressing third party	Both mouter and moutee displayed an erection	7	3.56	3.69
Mount	-0.611	-0.858	-0.247	Pair aggressing observer	Mounter erection confirmed	7	3.56	3.69
Mount	-0.611	-0.858	-0.247	Pair aggressing third party	Mounter erection confirmed	7	3.58	3.71
Mount	-0.611	-0.858	-0.247	Affiliative physical contact	Mounter erection confirmed	7	3.61	3.73
Mount	-0.611	-0.858	-0.247	Travelling	Erectile status unconfirmed	7	3.64	3.76
Mount	-0.602	1.695	2.297	Pair aggressing third party	Both mouter and moutee displayed an erection	NA	6.72	6.64
Mount	-0.596	-0.523	0.073	Grooming	Both mouter and moutee displayed an erection	NA	5.62	5.48
Mount	-0.596	-0.523	0.073	NA	Only moutee displayed erection	NA	5.61	5.48
Mount	-0.589	-0.379	0.210	NA	Both mouter and moutee displayed an erection	4	4.51	9.48
Mount	-0.569	-0.842	-0.273	Pair aggressing third party	Both mouter and moutee displayed an erection	7	7.70	4.67
Mount	-0.555	-0.379	0.176	Grooming	Mounter erection confirmed	2	4.63	12.53
Mount	-0.554	-0.689	-0.134	Pair aggressing observer	Mounter erection confirmed	NA	7.38	7.49
Mount	-0.552	-0.259	0.292	Travelling	Erectile status unconfirmed	NA	5.69	6.53
Mount	-0.547	0.684	1.232	Resting	Mounter erection confirmed	NA	6.50	5.55
Mount	-0.536	-0.978	-0.442	Aggression between pair	Absence of erection was confirmed	0	14.43	5.45
Mount	-0.531	0.243	0.773	Pair aggressing third party	Absence of erection was confirmed	NA	5.59	7.46
Mount	-0.525	-0.775	-0.250	Travelling	Erectile status unconfirmed	1	5.63	3.82
Mount	-0.502	-0.443	0.059	Pair aggressing observer	Erectile status unconfirmed	4	3.76	3.81
Mount	-0.499	-0.448	0.052	Pair aggressing third party	Erectile status unconfirmed	3	16.39	5.59

Table 16: Results for coalition, birth order and female advantage models

Description: Test statistics for a range of models assessing coalition, birth order and female advantage models. Each model is indexed by a letter with a row given to each effect within the model.

Model ID	Model response	Model structure	Coefficient	Coefficient estimate	Std. Error	t-value	p value <
A	Siring per sample male (all paternity data)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	(Intercept)	0.003205	0.21303	0.015	0.988
A	Siring per sample male (all paternity data)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Mean age per sample male	0.147108	0.013401	10.978	<2e-16
A	Siring per sample male (all paternity data)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Sampling-adjusted different-sex mounting with arousal per sample male	0.138261	0.053877	2.566	0.011
A	Siring per sample male (all paternity data)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Mean dominance rank per sample male	0.140327	0.069348	2.024	0.0443
A	Siring per sample male (all paternity data)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Sampling-adjusted same-sex mounting per sample male	0.072649	0.080809	0.898	0.3702
B	Siring per sample male (paternity data up to 2020)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	(Intercept)	-0.34404	0.23702	-1.452	0.1481
B	Siring per sample male (paternity data up to 2020)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Mean age per sample male	0.16505	0.01437	11.487	<2e-16
B	Siring per sample male (paternity data up to 2020)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Sampling-adjusted different-sex mounting with arousal per sample male	0.14211	0.05731	2.48	0.0139
B	Siring per sample male (paternity data up to 2020)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Mean dominance rank per sample male	0.1237	0.07242	1.708	0.089
B	Siring per sample male (paternity data up to 2020)	Mean age per sample male + sampling-adjusted same-sex mounting per sample male + sampling-adjusted different-sex mounting with arousal per sample male + mean dominance rank per sample male	Sampling-adjusted same-sex mounting per sample male	0.08962	0.08875	1.01	0.3137
C	Seasonal siring per sample male (paternity data 2017, 2019, 2020)	Seasonal mean age per sample male + seasonal sampling-adjusted same-sex mounting per sample male + seasonal sampling-adjusted different-sex mounting with arousal per sample male + seasonal dominance rank per sample male	(Intercept)	-0.51656	0.43647	-1.183	0.23748
C	Seasonal siring per sample male (paternity data 2017, 2019, 2020)	Seasonal mean age per sample male + seasonal sampling-adjusted same-sex mounting per sample male + seasonal sampling-adjusted different-sex mounting with arousal per sample male + seasonal dominance rank per sample male	Seasonal mean age per sample male	-0.02725	0.03785	-0.72	0.47197
C	Seasonal siring per sample male (paternity data 2017, 2019, 2020)	Seasonal mean age per sample male + seasonal sampling-adjusted same-sex mounting per sample male + seasonal sampling-adjusted different-sex mounting with arousal per sample male + seasonal dominance rank per sample male	Sampling-adjusted different-sex mounting with arousal per sample male	0.04121	0.19812	0.208	0.83536
C	Seasonal siring per sample male (paternity data 2017, 2019, 2020)	Seasonal mean age per sample male + seasonal sampling-adjusted same-sex mounting per sample male + seasonal sampling-adjusted different-sex mounting with arousal per sample male + seasonal dominance rank per sample male	Seasonal dominance rank per sample male	0.4727	0.15012	3.149	0.00179
C	Seasonal siring per sample male (paternity data 2017, 2019, 2020)	Seasonal mean age per sample male + seasonal sampling-adjusted same-sex mounting per sample male + seasonal sampling-adjusted different-sex mounting with arousal per sample male + seasonal dominance rank per sample male	Sampling-adjusted same-sex mounting per sample male	-0.29742	0.2709	-1.098	0.27307
D	Reproductive score of female relatives per sample male	Sampling-adjusted same-sex mounting per sample male	(Intercept)	0.0703513	0.0011931	58.965	<2e-16
D	Reproductive score of female relatives per sample male	Sampling-adjusted same-sex mounting per sample male	Sampling-adjusted same-sex mounting per sample male	0.0004031	0.000901	0.447	0.655
E	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair	(Intercept)	-4.69532	3.47E-01	-13.542	<2.00E-16
E	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair	Same-sex mounting per pair	0.4243	3.09E-02	13.748	<2.00E-16
E	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair	Relatedness between pair	1.20395	0.65148	1.848	0.064611
E	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair	Mean rank between pair	0.76178	1.48E-01	5.132	2.89E-07
E	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair	Mean age between pair	-0.14544	4.24E-02	-3.431	0.000602
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	(Intercept)	-4.691829	3.49E-01	-13.457	2.00E-16
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Same-sex mounting per pair	0.424556	3.10E-02	13.689	2.00E-16
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Relatedness between pair	1.201383	0.652433	1.841	0.065574
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Mean rank between pair	0.762374	1.49E-01	5.102	3.37E-07
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Mean age between pair	-0.145647	4.25E-02	-3.427	0.000611
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Age difference between pair	0.001946	2.17E-02	0.09	0.928653
F	Coalitional events per pair	Same-sex mounting per pair + pair relatedness + mean dominance rank between pair + mean age between pair + age difference + rank difference	Rank difference between pair	0.004741	7.85E-02	0.06	0.951864
G	Coalitional events per pair	Same-sex mounting counts after aggression between pair + pair relatedness + mean dominance rank between pair + mean age between pair	(Intercept)	-4.5125	0.35946	-12.553	2.00E-16
G	Coalitional events per pair	Same-sex mounting counts after aggression between pair + pair relatedness + mean dominance rank between pair + mean age between pair	Same-sex mounting counts after aggression between pair	-11.29668	521.65231	-0.022	0.982723
G	Coalitional events per pair	Same-sex mounting counts after aggression between pair + pair relatedness + mean dominance rank between pair + mean age between pair	Relatedness between pair	1.14933	0.68627	1.675	0.093996
G	Coalitional events per pair	Same-sex mounting counts after aggression between pair + pair relatedness + mean dominance rank between pair + mean age between pair	Mean dominance rank of pair	0.68531	0.15632	4.38E+00	1.17E-05
G	Coalitional events per pair	Same-sex mounting counts after aggression between pair + pair relatedness + mean dominance rank between pair + mean age between pair	Mean age between pair	-0.15771	0.04456	#####	0.000402
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	(Intercept)	1.394164	0.297592	4.685	3.16E-06
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Mean age per repeated measure	-0.099695	0.013213	-7.545	9.62E-14
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Scan samples per repeated measure	0.023875	0.005352	4.461	9.02E-06
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Seasonal group ratio of older to younger males per repeated measure	-0.107311	0.039406	-2.723	6.57E-03
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Seasonal group size	-0.002805	0.000711	-3.945	8.50E-05
H	Same-sex mounting per repeated measure	Number of older male siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Number of older male siblings per repeated measure	0.017649	0.021349	0.827	0.40859
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	(Intercept)	1.4385135	0.2987269	4.815	1.68E-06
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Mean age per repeated measure	-0.098779	0.0132201	-7.472	1.64E-13
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Scan samples per repeated measure	0.0236486	0.0053536	4.417	1.10E-05
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Seasonal group ratio of older to younger males per repeated measure	-0.1103522	0.0392896	-2.809	5.06E-03
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Seasonal group size	-0.0028411	0.0007122	-3.989	7.07E-05
I	Same-sex mounting per repeated measure	Number of older siblings per repeated measure + mean age per repeated measure + scan samples per repeated measure + seasonal group ratio of older to younger males per repeated measure + seasonal group size	Number of older siblings per repeated measure	0.0016589	0.0126293	0.131	8.96E-01
J	Same-sex mounting per sample male	Number of older male siblings per sample male + mean age per sample male + scan samples per sample male	(Intercept)	1.3702634	0.1682693	8.143	2.36E-14
J	Same-sex mounting per sample male	Number of older male siblings per sample male + mean age per sample male + scan samples per sample male	Mean age per sample male	-0.1044173	0.0206368	-5.06	8.54E-07
J	Same-sex mounting per sample male	Number of older male siblings per sample male + mean age per sample male + scan samples per sample male	Scan samples per sample male	0.0079145	0.0008719	9.078	<2.00E-16
J	Same-sex mounting per sample male	Number of older male siblings per sample male + mean age per sample male + scan samples per sample male	Older maternal brothers per sample male	0.0238333	0.029469	0.809	0.419
K	Same-sex mounting per sample male	Number of older siblings per sample male + mean age per sample male + scan samples per sample male	(Intercept)	1.387347	0.1714379	8.092	3.28E-14
K	Same-sex mounting per sample male	Number of older siblings per sample male + mean age per sample male + scan samples per sample male	Mean age per sample male	-0.1029754	0.0206741	-4.981	1.24E-06
K	Same-sex mounting per sample male	Number of older siblings per sample male + mean age per sample male + scan samples per sample male	Scan samples per sample male	0.0078395	0.0008688	9.023	<2.00E-16
K	Same-sex mounting per sample male	Number of older siblings per sample male + mean age per sample male + scan samples per sample male	Older maternal siblings per sample male	0.006523	0.017449	0.374	0.709
L	Individual proximity counts per mount interaction (10m)	Mean rank dominance per pair + mean age per pair + mounting pair status (coalitionaly vs. not coalitionaly)	(Intercept)	1.487222	0.184266	8.071	9.10E-15
L	Individual proximity counts per mount interaction (10m)	Mean rank dominance per pair + mean age per pair + mounting pair status (coalitionaly vs. not coalitionaly)	Mean dominance rank per pair	0.083801	0.035107	2.387	0.0175
L	Individual proximity counts per mount interaction (10m)	Mean rank dominance per pair + mean age per pair + mounting pair status (coalitionaly vs. not coalitionaly)	Mean age per pair	0.02285	0.009216	2.48	0.0136
L	Individual proximity counts per mount interaction (10m)	Mean rank dominance per pair + mean age per pair + mounting pair status (coalitionaly vs. not coalitionaly)	Coalitionaly mounting pair status (vs. not coalitionaly)	-0.210812	0.14281	-1.476	0.1407

Table 17: Correlations with coalitionary behaviour

Description: Correlations between different subtypes of same-sex mounting by pairwise frequency with coalitionary pair frequencies.

Trait 1	Trait 2	Pearson.correlation	CI_1	CI_2	p.value <	Sig
Coalitionary events per pair	Same-sex mounting per pair	0.169662338	0.161924	0.17738	1.53E-71	Sig
Coalitionary events per pair	Same-sex mounting with high arousal per pair	0.157308472	0.149539	0.165059	3.59E-68	Sig
Coalitionary events per pair	Same-sex mounting with low arousal per pair	0.076017835	0.068102	0.083924	1.85E-78	Sig
Coalitionary events per pair	Same-sex mounting in co-aggressive context	0.240089352	0.232577	0.247573	8.22E-151	Sig
Coalitionary events per pair	Same-sex mounting in an affiliative context	0.070651488	0.06273	0.078564	5.32E-68	Sig
Coalitionary events per pair	Same-sex mounting in an aggressive context	-0.001102026	-0.009059	0.006855	7.86E-01	Not sig
Coalitionary events per pair	Same-sex mounting per pair (with aggressive contexts cases removed)	0.174999806	0.167276	0.182702	1.03E-76	Sig