



## Experimental evolution with an insect model reveals that male homosexual behaviour occurs due to inaccurate mate choice

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The existence of widespread male same-sex sexual behaviour (SSB) is puzzling: why does evolution allow costly homosexual activity to exist, when reproductive fitness is primarily achieved through heterosexual matings? Here, we used experimental evolution to understand why SSB occurs in the flour beetle *Tribolium castaneum*. By varying the adult operational sex ratio across 82–106 generations, we created divergent evolutionary regimes that selected for or against SSB depending upon its function. Male-biased (90:10 M:F) regimes generated strong selection on males from intrasexual competition, and demanded improved ability to locate and identify female mates. By contrast, Female-biased regimes (10:90 M:F) generated weak male–male competition, and relaxed selection on mate-searching abilities in males. If male SSB functions through sexually selected male–male competition, it should be more evident within Male-biased regimes, where reproductive competition is nine times greater, than in the Female-biased regimes. By contrast, if SSB exists due to inaccurate mate choice, it should be reduced in Male-biased regimes, where males experience stronger selection for improved mate finding and discrimination abilities than in the Female-biased regime, where most potential mating targets are female. Following these divergent evolutionary regimes, we measured male engagement in SSB through choice experiments simultaneously presenting female and male mating targets. Males from both regimes showed similar overall levels of mating activity. However, there were significant differences in levels of SSB between the two regimes: males that evolved through male-biased operational sex ratios located, mounted and mated more frequently with the female targets. By contrast, males from female-biased selection histories mated less frequently with females, exhibiting almost random choice between male and female targets in their first mating attempt. Following experimental evolution, we therefore conclude that SSB does not function through sexually selected male–male competition, but instead occurs because males fail to perfectly discriminate females as mates.

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Male same-sex sexual behaviour (SSB), when males invest homosexual mating effort on males of their own species, has been recorded at significant levels in large numbers of animal taxa (Bagemihl, 1999; Bailey & Zuk, 2009; MacFarlane, Blomberg, & Vasey, 2010; Scharf & Martin, 2013). This widespread SSB presents an evolutionary enigma: why does selection allow males of so many species to invest significantly in SSB when it generates no

direct reproductive benefits, but incurs obvious costs? Investing in any sexual behaviour increases vulnerability to predation, damage and disease (Daly, 2013; Lehtonen, Jennions, & Kokko, 2012); SSB imposes these costs, and potentially more. For example, sexual activity between males in same-sex groups generates significantly increased mortality compared with mixed-sex or female-only groups in waltzing flies, *Prochyliza xanthostoma*, bean weevils, *Callosobruchus maculatus* (Maklakov & Bonduriansky, 2009) and flour beetles, *Tribolium* spp. (Spratt, 1980). Importantly, as well as incurring these direct costs, males engaging in SSB will also reduce their current and future prospects for reproduction with a female (Maklakov & Bonduriansky, 2009; Van Gossum, De Bruyn, & Stoks,

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2005), especially when sperm production is limited (Pitnick, 1993; Wedell, Gage, & Parker, 2002).

There are a number of explanations for the widespread existence of male SSB (reviewed in Bailey & Zuk, 2009; Caballero-Mendieta & Cordero, 2012; Scharf & Martin, 2013), which can be broadly divided into (1) explanations based upon strategies within male–male competition for reproduction versus (2) inaccuracies of mate choice. Explanations for SSB through male–male competition can be further divided into strategies that either (1) enhance the acting male's sexual performance (Carayon, 1974; McRobert & Tompkins, 1988), status (Kotrschal, Hemetsberger, & Weiss, 2006) or attractiveness (Bierbach, Jung, Hornung, Streit, & Plath et al., 2013) or (2) harm the relative fitness of male competitors by injury (Abele & Gilchrist, 1977; Baker, 1983; Bieman & Witter, 1982), distraction (Macias-Garcia & Valero, 2001; Thornhill, 1979) or placation (de Waal, 1987; Peschke, 1985). Both of these explanations are fundamentally based upon the theory that SSB improves a male's reproductive fitness in the face of sexually selected male–male competition or female choice (Fisher & Cox, 2011). By contrast, explanations based around inaccuracies within mate choice are mainly derived from interpretations that males fail to correctly discriminate between the sexes due to physiological or developmental disorders (Roselli, Reddy, & Kaufman, 2011; Zhang & Odenwald, 1995), pleiotropic effects (Berger et al., 2016; Hoskins, Ritchie, & Bailey, 2015; Sanders et al., 2014) or unnatural proximate factors (Bonnet et al., 2016; Dukas, 2010; Lee, Kim, Dunning, & Han, 2008). Although these explanations identify SSB as a fundamentally erroneous tactic, they often theorize that it occurs because its cost is less consequential than that of potentially missed mating opportunities with females when there is greater discrimination over mates, especially in conditions where more discerning mate recognition systems are a challenge to maintain (Bailey & French, 2012; Marco & Lizana, 2002; Scharf & Martin, 2013).

Empirical tests between these divergent explanations have not revealed a consistent reason for the widespread existence of SSB, and there is considerable variation between different taxa in SSB (Scharf & Martin, 2013), even when species are closely related (Serrano, Castro, Toro, & López-Fanjul, 2000). These different study findings could be the consequence of SSB having different functions in different taxa and/or circumstances. Here, we employed experimental evolution within a species to test explicitly whether male–male competition or inaccurate mate discrimination can explain male SSB. We used the red flour beetle, *Tribolium castaneum*, a promiscuous species where SSB is recognized (Levan, Fedina, & Lewis, 2009). In this model, SSB generates measurable costs: when *T. castaneum* males invest in homosexual behaviour they are not engaged in searching for, courting or mating with females and fertilizing their eggs. In addition, there is some indirect evidence that SSB might function in intrasexual competition by reducing rival male life span: average life span of adults in single-sex male groups was under half that of males in isolation, or of females in single-sex groups, and many of the dead males in the group condition exhibited hardened white deposits around the mouth and tip of the abdomen (Spratt, 1980).

We applied divergent experimental evolution regimes that allowed us to test between the two core hypotheses that SSB occurs (1) because it generates sexually selected benefits for males through competition or (2) because males do not perfectly identify females, so they mate indiscriminately with any adult to maximize female mating opportunities. Having maintained replicate independent lines evolved through divergent adult operational sex ratios (Lumley et al., 2015; Michalczyk et al., 2011b), we then conducted tightly controlled mate choice assays to measure how

experimental evolution under different sexual selection regimes had shaped male SSB. Our Male-biased lines were reproduced through adult operational sex ratios containing 90 males and 10 females, while the Female-biased lines reproduced using 10 males and 90 females. Under Male-biased regimes, males must achieve fertilizations in the face of strong levels of sexual selection from male–male competition. In tandem, males in Male-biased conditions face much greater selection to evolve abilities that improve mate location and discrimination, because females are rare in the adult population. Male-biased conditions will therefore promote the evolution of male behaviours that simultaneously improve male–male competition and enhance female location and mate discrimination. By contrast, under Female-biased conditions, male–male competition is weak, and males experience much more relaxed selection to locate and discriminate between potential mates because nine out of 10 adults encountered are female. Our Female-biased regimes therefore relaxed selection on the evolution of male behaviours that are required for reproductive competition, while simultaneously weakening selection on mate finding and discrimination abilities.

Adult population densities ( $N = 100$ ) in every line and both regimes were kept identical throughout to maintain equal adult encounter rates. Since *T. castaneum* is a promiscuous species (Fedina & Lewis, 2008) in which females mate repeatedly with multiple males (Michalczyk et al., 2011a) and males have substantial mating rate and fertilization potential (Lumley et al., 2015), male and female encounter rates were expected to correlate closely with the operational sex ratio. Although there is limited evidence for it, if female *T. castaneum* take 'time out' of mating activity after copulation, this will only exacerbate the differences in selection acting on SSB between our Male-biased and Female-biased regimes: more mating opportunities in the Male-biased lines would increase any female 'time out' in that regime, making females even rarer, and therefore further increasing the selection on males from male–male competition and female mate searching and discrimination.

Previous work with these lines has confirmed that male reproductive competitiveness has evolved to become stronger following selection under male-biased conditions (Godwin et al., 2017). The contrasting regimes therefore provide an ideal opportunity to test between explanations for the evolution of male homosexual behaviour. If SSB functions within male–male competition, male–female signalling, mating practice or some other sexually selected route to indirectly improve male reproductive fitness, then we would predict increased selection for SSB under the Male-biased, strong sexual selection regime. Males that evolved through stronger levels of sexual selection in the Male-biased regime should therefore exhibit a greater level of SSB. On the other hand, if SSB exists because males fail to find and recognize female mates correctly, then we would expect the reverse outcome: males from the Male-biased regime have faced stronger selection to improve their abilities in locating and identifying females as mates, and therefore should evolve lower levels of SSB. Applying this logic in reverse, if male SSB functions within male–male competition, males from Female-biased regimes exposed to relaxed levels of sexual selection should engage less in SSB. If, however, SSB is the result of erroneous female recognition, then the relaxed selection on mate location and discrimination in our Female-biased regimes (where most potential adult mates are female) should result in higher levels of SSB among Female-biased males. Having evolved replicate lines across 82 and 106 generations of these contrasting intensities of selection on SSB depending on its function, we then used experimental mate choice assays to reveal what evolutionary forces influence the existence of male homosexual behaviour.

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