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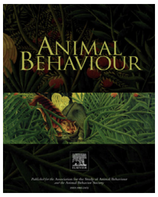

Same-sex sexual behaviour as a by-product of reproductive strategy under male–male scramble competition

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A variety of hypotheses have been suggested to explain the evolution of same-sex sexual behaviour (SSB) in male insects. Males may be poor at discriminating other males from females, inexperienced, or may need to learn how to distinguish females. Alternatively SSB could be a by-product of a plastic reproductive strategy to succeed in scramble competition. Such a strategy could be adaptive if the cost of missing the chance to mate with available females exceeds the cost of mounting single males instead (i.e. SSB). We tested predictions derived from these hypotheses by experimentally varying the sex ratio and thus the intensity of scramble competition in the water strider *Tenagogerris euphrosyne*. We allowed males to experience female-biased or male-biased sex ratio treatments for a week, and then compared their expression of SSB under standard conditions. We also measured daily mating success of males during the treatment and related this to SSB frequency under assay conditions. Males kept in male-biased sex ratio conditions exhibited more SSB, mounting males and females equally often under assay conditions. Males kept under female-biased conditions only mounted males one-quarter as often as they mounted females in the assay. Male mating experience under treatment conditions did not influence the expression of SSB in the assay. In a second experiment we found that males that were more likely to exhibit SSB enjoyed higher initial mating success in a subsequent mating assay in a male-biased sex ratio. Our results indicate that plasticity in reproductive strategy not only increases mating opportunity but also confers a reproductive benefit. Taken together, SSB in *T. euphrosyne* is a highly labile trait responsive to sex ratio that delivers increased mating success under intense scramble competition.

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Mating interactions between members of the same sex (e.g. same-sex courtship or mounting) have been viewed as an evolutionary puzzle. While such same-sex sexual behaviour (SSB) is widespread among animals including humans (Sommer & Vasey, 2006), it is not obvious how such behaviour can deliver fitness benefits that might offset the obvious costs (Bailey & Zuk, 2009; Gavrilets & Rice, 2006). However, a number of recent studies have suggested adaptive or nonadaptive hypotheses concerning the evolution and maintenance of SSB (Bailey & Zuk, 2009; Gavrilets & Rice, 2006).

The majority of insect SSBs appear consistent with two nonadaptive causes: weak sex discrimination and the lack of mating experience (Scharf & Martin, 2013). According to the weak sex discrimination hypothesis, SSB results from perception errors in distinguishing same-sex from opposite-sex individuals. As a result, individuals sometimes mistakenly court and attempt to mate with members of the same sex (Bailey & French, 2012; Burgevin, Friberg, & Maklakov, 2013; Harari, Brockmann, & Landolt, 2000; Serrano, Castro, Toro, & López-Fanjul, 1991, 2000; Switzer, Forsythe, Escajeda, & Kruse, 2004). According to the mating experience hypothesis, deprivation of potential mates might increase mating motivation, which also increases the incidence of SSB (Bailey, Hoskins, Green, & Ritchie, 2013; Field & Waite, 2004; Han & Brooks, 2014; Kim & Ehrman, 1998).

In addition to the two nonadaptive hypotheses, SSB might be a by-product of the need to learn to recognize appropriate mates (social-learning hypothesis). Although individuals might initially attempt to mate with others regardless of their sex, they would learn from unsuccessful mating attempts, such as SSBs, to identify mates of the correct sex (Dukas, 2006). Under this scenario, we can expect that individuals experiencing frequent same-sex sexual interactions would spend less time engaging in SSB than inexperienced ones.

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Last, we argue that SSB could arise as a by-product of male reproductive strategy under strong male–male scramble competition, in which the fitness costs of incorrectly mounting another male are smaller than the costs of mistakenly not mounting an available female. The outlined hypotheses are by no means mutually exclusive, but they do make some differing predictions that allow empirical testing.

SSB is prevalent in water striders (Heteroptera : Gerridae), semiaquatic insects that live on the water surface (Chang & Sih, 2013; Eldakar, Dlugos, Wilcox, & Wilson, 2009; Han & Brooks, 2013a, 2013b, 2014, 2015; Sih & Watters, 2005; Wey, Chang, Fogarty, & Sih, 2015). Water strider mating is characterized by intense male–male scramble competition for females, forced or coerced copulation, long postcopula mate guarding of females by males, and both sexes mating with multiple partners (Arnqvist, 1997). Males of many species will attempt to mount and mate not only with single females, but also with single males, mating pairs (Han & Brooks, 2013b) or even other species.

Water striders rarely show territorial behaviour or aggressive male–male dominance behaviour (but see Hayashi, 1985). Instead, males that quickly find and mount single females tend to get more matings (Han & Brooks, 2013a, 2013b). Under a strong male–male scramble competition and male-biased sex ratio conditions, it is important for males to find single females quickly before other males do (Han & Brooks, 2013a, 2013b). As a result, the best reproductive strategy of males appears to be to increase the rate of mating attempts even if they choose the wrong partners (e.g. the same-sex individual) in mating attempts.

In at least one species of water strider, *Tenagogerris euphrosyne*, studied here, there exists considerable variation among males in SSB, and that variation is underpinned by both genetic and genotype-environment interactions with the social environment during development (Han & Brooks, 2015). Despite the prevalence of SSBs in water striders, research has largely neglected to test the potential explanations for either its presence or the existence of variation in this behaviour.

Here we tested the nonexclusive hypotheses suggested above for the evolution of SSB in male *T. euphrosyne* (Table 1). We first experimentally exposed focal males to either male-biased or female-biased sex ratios for a week, recording each focal male's mating success daily. We then placed each focal male into a standard behavioural assay with two other males and two females (i.e. male:female sex ratio of 3:2), and measured both male mounting (SSB) and female mounting. This approach allowed us to distinguish between the effects of the experimentally applied sex ratios and of individual mating success under these sex ratios as tests of our hypotheses.

Our predictions concerning the effects of mating success and sex ratio environment on SSB are summarized in Table 1. If male *T. euphrosyne* are simply bad at discriminating females from males, then neither factor should have any effect. If SSB is a consequence of inexperience, then successful mating with females should lead to lower SSB. If discrimination is learned by repeatedly mounting males, then SSB should be more pronounced after the female-biased than the male-biased sex ratio treatment in which males would more frequently encounter single males. In contrast, if the level of SSB is higher after the male-biased sex ratio treatment, it would support the hypothesis that SSB is either socially learned from successful matings (higher per male rates of mating in the female-biased treatment), or a by-product of a scramble competition type of reproductive strategy of random mating attempts.

Table 1
Summary of predictions under various hypothetical mechanisms for expression of same-sex sexual behaviours in water strider males

	Factors	
Hypotheses	Mating experience	Sex ratio environments
Weak sex discrimination	No effect	No effect
Mating experience	Low SSB in successful males	No effect
Social learning via mounting males	No effect	High SSB in female-biased sex ratio
Social learning via successfully mating females	Low SSB in successful males	High SSB in male-biased sex ratio
By-product of reproductive strategy	No effect	High SSB in male-biased sex ratio

We also conducted a second experiment to test whether high rates of SSB confer a reproductive advantage under male-biased sex ratios. If water strider males' SSB is a by-product of a reproductive strategy of random mating attempts, we predicted that males' SSB rates under standard conditions would positively predict mating success under male-biased sex ratios.

METHODS

Study Species and Rearing Condition

Tenagogerris euphrosyne is the most common water strider species along the east coast of Australia. The species is found in various freshwater habitats, such as lakes, ponds, slowly running streams, creeks and small rivers (Andersen & Weir, 2004). Individuals often assemble in groups on the water surface, and they encounter microhabitats among which population densities and sex ratios vary. Intersexual and intrasexual encounter rates of individuals vary with the social conditions, and population density and sex ratio environment affect mating behaviour (Han & Brooks, 2013b, 2014, 2015).

Mating in *T. euphrosyne* is initiated when the male forcefully mounts a female. At the initiation of the mating attempt, males try to grasp the female, overcome female resistance and produce courtship signals by vibrating their legs and body. But males sometimes attempt to mount another male, and SSB is very common in *T. euphrosyne* (Han & Brooks, 2013b, 2014, 2015). The initiation of SSB attempts appears to the observer no different from male attempts to mount females. Irrespective of the target's sex, the male approaches an individual, grasps and then mounts it. If he realizes, in attempting to copulate, that he has mounted a male, he dismounts. The majority of male–male mountings are very short ($N = 184$, mean ± SE = 2.8 ± 0.6 s, Han & Brooks, 2013b) and 60% of SSBs take less than 1 s (Han & Brooks, 2013b). The mounted males usually do not respond immediately to other males' SSB trials, but sometimes try to throw off the mounter, especially when the mounting male stays longer than a few seconds (C.S. Han, personal observation).

Adult individuals were collected from the wild population in Platypus Park, Atherton, Queensland, Australia between 17 and 24 August 2012 and brought to our laboratory at the University of New South Wales, Sydney, NSW, Australia. In the laboratory, individuals were kept in groups of 10 males and 10 females in several tanks (60×40 and 40 cm high, water depth 2 cm) under a 14:10 h light:dark cycle at $28 \pm 4\,^{\circ}$C with pieces of floating Styrofoam provided as the resting and oviposition sites. Frozen crickets, *Teleogryllus commodus*, were provided as food every 2 days. All animals were individually marked on the thorax with enamel paint.

Experiment 1: Causes of SSB

To test hypothetical causes of SSB of water strider males, we measured whether variation in the sex ratio environment or

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