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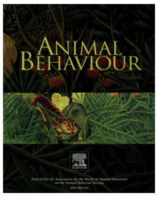

Same-sex sexual behaviour as a dominance display

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Same-sex sexual behaviour (SSB) is widespread across taxa. One adaptive hypothesis to explain the occurrence and maintenance of SSB is that it acts to intensify or diminish aggression by providing males with a means to reinforce or resolve dominance. However, evidence for this hypothesis is very limited across taxa and the possibility that SSB acts as an extension of intrasexual competition remains contentious. We investigated the role of SSB in intensifying or diminishing aggression in the broad-horned flour beetle, *Gnatocerus cornutus*. We tested the hypothesis that SSB is an extension of male–male competition by observing how the occurrence of SSB and the stability of SSB courtship roles (i.e. whether males switched between mounting and being mounted) influenced levels of aggression within pairs. We found that, typically, males rapidly establish fixed SSB roles and moreover that the occurrence of SSB and the stability of SSB roles had a highly significant effect on levels of aggression observed within pairs. Pairs in which one male consistently mounted the other showed significantly lower levels of aggression than pairs in which neither male exhibited SSB or in which males continuously switched SSB roles and attempted to mount each other. Furthermore, males that were consistently on the receiving end of SSB demonstrated lower propensity to court females and had a lower mating success than active males. This pattern was analogous to that found in loser males as a result of fighting. Males that lost fights also courted less and had lower mating success than males that won fights. Our findings provide the first empirical support for the hypothesis that SSB is an extension of male–male competition. Furthermore, our results suggest that SSB may act as a display, allowing males to resolve dominance hierarchies without escalating into an injurious fight.

Same-sex sexual behaviour (SSB) is a widespread phenomenon seen across a huge variety of taxa (see Bailey & Zuk, 2009 for a review). SSB ranges from courtship to mounting to even long-term pairing in some species (e.g. Laysan albatross, *Phoebastria immutabilis*: Young, Zaun, & VanderWerf, 2008). There are many different hypotheses for the existence and maintenance of SSB, both adaptive and nonadaptive (reviewed in Bailey & Zuk, 2009). Examples of adaptive hypotheses include social bonding (e.g. bottlenose dolphins, *Tursiops* spp.: Mann, 2006; Japanese macaques, *Macaca fuscata*: Vasey, Chapais, & Gauthier, 1998), practice for future mating (*Drosophila* spp.: McRobert & Tompkins, 1988) and even increasing attractiveness to potential mates (Atlantic mollies, *Poecilia mexicana*: Bierbach, Jung, Hornung, Streit, & Plath, 2013). Mistaken identity, in which individuals fail to distinguish between the sexes and thus to recognize potential mates, constitutes the major nonadaptive hypothesis for the occurrence of SSB and has been invoked to explain the majority of SSB cases observed in insects (SSB occurs in over 100 species of insects; see supplementary material of Sharf & Martin, 2013 for details).

One adaptive hypothesis for the occurrence of SSB is that it provides a way for males to reinforce or resolve dominance hierarchies (Bailey & Zuk, 2009). Furthermore, by carrying out SSB, dominant individuals may increase their reproductive success relative to that of their competitors (Bailey & Zuk, 2009). However, while these hypotheses have been investigated in a range of species, evidence for SSB as an extension of intrasexual competition remains contentious. When testing for a link between dominance, aggression and SSB in female Japanese macaques, Vasey et al. (1998) found that SSB was not carried out more often by dominant females, nor were levels of aggression affected by the occurrence of SSB. In the male American bison, *Bison bison*, SSB is commonplace and, although there is some link between SSB and dominance, it appears to be more clearly linked to age than social rank and it remains unclear whether this behaviour is an attempt to vie for dominance or simply an act of play between immature bulls

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(McHugh, 1958; Reinhardt, 1985; reviewed in Vervaecke & Roden, 2006). In insects the evidence is similarly lacking. Many studies have investigated the dominance/aggression hypothesis but, as in the Japanese macaques, found no evidence to support it (e.g. the flour beetle, *Tribolium castaneum*: Levan, Fedina, & Lewis, 2009; the parasitoid wasp *Psyttalia concolor*: Benelli & Canale, 2012). Although some insect studies have linked SSB to a reduction in aggression (Peschke, 1985, 1987; Ruther & Steiner, 2008; Steiner, Stiedle, & Ruther, 2005), the evidence is indirect. These studies show that when males deliberately mimic a female's chemical profile they are treated as females (i.e. courted and not fought with) but they do not directly show that SSB causes a reduction in aggression. Although this pattern is interesting, it seems more likely that SSB is driven by mistaken identity than that it is used to establish dominance. Finally, other studies have found anecdotal evidence to support a direct link between SSB and decreased aggression but this evidence has yet to be backed up empirically (Iguchi, 1996; Preston-Mafham, 2006).

Although the occurrence of SSB is undisputed, it remains unclear who benefits from it, the male performing SSB (referred to hereafter as the active male) or the male receiving SSB (referred to hereafter as the passive male; sensu Sharf & Martin, 2013). In the dung fly *Hydromyza livens* males are thought to mount other males in order to deny them mating opportunities, increasing their own mating success by eliminating competition (Preston-Mafham, 2006); however, this hypothesis has again yet to be tested empirically. In contrast, many studies of SSB have found that male–male courtship has a positive effect on the subsequent mating behaviour of the males that received SSB. For example *Drosophila melanogaster* and *P. concolor* males that received courtship from other males while still young subsequently exhibited significantly higher levels of courtship with females as well as shorter copulation latency, in comparison with control males that had never received SSB (Benelli & Canale, 2012; Dukas, 2010; McRobert & Tompkins, 1988). However, this behaviour did not translate into increased mating success for passive males. Thus whether or not SSB serves to increase or decrease aggression by reinforcing dominance and who might benefit from its occurrence remains unclear.

Males of the broad-horned flour beetle, *Gnatocerus cornutus*, are armed with enlarged mandibles which they use to push, bite and flip each other over during fights. Males fight to guard both territories and mates and males that lose fights disperse to new territories, where they actively avoid engaging in further contests for 4 days after the fight, investing instead in increased sperm production (Okada, Yamane, & Miyatake, 2010; Yamane, Okada, Nakayama, & Miyatake, 2010). Female mate choice in *G. cornutus* is not based on traits associated with fighting ability (i.e. mandible size) but rather on male courtship effort, traits that are neither phenotypically nor genetically correlated (Okada, Katsuki, Sharma, House, & Hosken, 2014). However, as more aggressive (winner) males are better able to secure access to females, they attain a significant mating advantage under competitive scenarios (Harano, Okada, Nakayama, Miyatake, & Hosken, 2010; Yamane et al., 2010). Alongside this fighting behaviour, males also exhibit SSB that is clearly distinguishable from aggression and is characterized by a male mounting another male and drumming his tibia along the other male's elytra, closely mimicking male–female courtship behaviour. Fighting has been extensively studied in *G. cornutus* (Demuth, Naidu, & Mydlarz, 2012; Okada et al., 2014; Okada, Miyanoshita, & Miyatake, 2006; Okada & Miyatake, 2009, 2010; Okada et al., 2010; Yamane et al., 2010), but the role of SSB is yet to be examined. Furthermore, cuticular hydrocarbons are highly sexually dimorphic in this species (Lane et al., 2015), which suggests that mistaken identity is less likely to be driving SSB in *G. cornutus*.

Here, we investigated whether SSB is an extension of male–male competition in *G. cornutus* by testing three main hypotheses. First, we investigated whether SSB is the result of mistaken identity: If males are unable to identify mates we would expect that males would direct similar levels of courtship behaviour towards females and other males; we would also expect a positive intramale correlation between levels of same-sex and heterosexual courtship, reflecting the activity levels of individual males. Second, we investigated whether SSB diminishes aggression by providing a noninjurious way for males to establish dominance. If this is the case, we would predict that levels of aggression would be significantly reduced in male–male pairs where a single male consistently mounts the other (i.e. SSB roles are fixed), as we expect SSB role stability to reflect whether males have been able to resolve dominance using SSB alone. Finally, we investigated whether experiencing SSB (i.e. being the passive male within a pair) has negative consequences on subsequent male mating success. If SSB is an extension of male–male competition, we would expect the consequences of SSB and male–male fighting to be similar. Thus, we compared the effects of these two interaction types on the subsequent mating success of passive and loser males, respectively.

METHODS

Stock Populations and Rearing Protocols

Gnatocerus cornutus is a stored-product pest that feeds on a variety of grains, flours, yeasts and dry animal products (Linsley, 1944; Zakladnoi & Ratanova, 1987). Beetles used in this study were taken from stock populations of *G. cornutus* derived from the Japanese National Food Research Institute (NFRI; see Okada et al., 2006 for details) and reared in our laboratory in the U.K. following the protocol outlined in Lane et al. (2015). For this experiment, 120 final-instar larvae were collected from stock pots daily and monitored daily for eclosion. On eclosion, adults were moved into individual wells in a 24-well plate (one larva per well), provided ad libitum with wholemeal wheat flour and maintained at 27 °C with 60% humidity on a 14:10 h light:dark lighting cycle (Lane et al., 2015; Okada et al., 2006).

Experiment 1: Male–Male Courtship, Aggression and Mating Behaviour

Behavioural trials took place 11–15 days after eclosion. On the morning of the trials we randomly assigned males of the same age to the categories ‘focal’ or ‘nonfocal’ and marked the tip of their elytra accordingly with either a green or pink gel pen (Pentel Hybrid Gel Grip DX Metallic). The colour of the focal male was alternated between trials to control for any potentially confounding effects of marking. After marking we returned males to individual petri dishes with ad libitum flour until the afternoon. To observe male–male behaviour, focal and nonfocal males were paired in arenas and observed for 20 min. We recorded the number of courtship attempts observed within the 20 min and noted whether they were made by the focal or nonfocal male. We also recorded the number of aggressive acts that occurred between the males. At the end of the 20 min we removed the nonfocal males and allowed our focal males to rest for 5 min before introducing a single female (of the same age) to each of them. We then observed these opposite-sex pairs for a further 20 min recording the number of courtship attempts (courtship effort) along with copulation latency if a successful mating occurred. A male will continue to court with the same female even after he has mated with her and thus we recorded courtship effort throughout the trial regardless of whether or not a pair had mated. All individuals used in trials were