



## Same-sex sexual behaviour in crickets: understanding the paradox



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Same-sex sexual behaviour (SSSB) occurs in animals ranging from insects to mammals, yet its evolutionary origins remain enigmatic. Is it adaptive, or has it evolved as a by-product of selection for other traits? Using data from two experiments on male spring field crickets, *Gryllus veletis*, we tested whether SSSB is socially adaptive, sexually adaptive, correlated with other sexual behaviours and/or a result of sex misidentification. By identifying how sexual experience, audience composition, mate attraction signalling time, body size/mass, food composition and aggression levels correlated with levels of SSSB, we found support for the misidentification and phenotypic correlation hypotheses. More aggressive males were more likely to court other males, and males who spent the most time signalling to attract mates tended to spend the most time courting other males, suggesting that aggression, mate signalling effort and same-sex courtship may all be phenotypically correlated. However, the positive relationship between mate attraction signalling effort and probability of expressing same-sex courtship only occurred in males on a high-carbohydrate, low-protein food, suggesting that the expression of such a phenotypic correlation may be constrained by dietary carbohydrate availability. Finally, males were more likely to be courted if they were less aggressive and spent little time signalling for mates, but, for the latter, only if they were on high-carbohydrate foods, suggesting that together, diet, which may alter chemical cues involved in sex identification, and behavioural cues may lead to sex misidentification. Thus, SSSB in male *G. veletis* does not appear to be adaptive, probably evolving instead as a by-product of selection for other sexually selected traits. By investigating both proximate and ultimate factors contributing to the evolutionary enigma of SSSB, we may gain important insights into the selective forces shaping aggression, social interactions and reproductive strategies in social animals.

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Same-sex sexual behaviour (SSSB), in which individuals of the same sex court or attempt to mate with each other, is ubiquitous across the animal kingdom, observed in animals as phylogenetically distant as mammals (Vasey, Rains, VanderLaan, Duckworth, & Kovacovsky, 2008) and insects (Scharf & Martin, 2013). In fact, same-sex mounting can account for up to 11% of mounting behaviour in bearded vultures, *Gypaetus barbatus* (Bertran & Margalida, 2003), 50% in seed beetles, *Callosobruchus maculatus* (Burgevin, Friberg, & Maklakov, 2013), and 46% in Japanese

macaques, *Macaca fuscata* (Vasey et al., 2008). However, explaining the persistence of SSSB presents an evolutionary paradox, as SSSB cannot result in offspring and thus offers no direct fitness advantage (Bailey & Zuk, 2009). Nevertheless, the persistence of SSSB suggests that it may be an evolutionarily maintained characteristic rather than a chance occurrence (e.g. Bertran & Margalida, 2003; MacFarlane, Blomberg, Kaplan, & Rogers, 2006; Mann, 2006; Vasey, 2006; Vasey et al., 2008; Vervaecke & Roden, 2006).

Four nonmutually exclusive hypotheses have been proposed to explain how SSSB may be maintained in animal populations, suggesting that SSSB may be (1) socially adaptive, (2) sexually adaptive, (3) due to phenotypic correlations or (4) the result of sex misidentification (Bailey & French, 2012; Bailey & Zuk, 2009; Harari, Brockmann, & Landolt, 2000; Hoskins, Ritchie, & Bailey, 2015; Levan, Fedina, & Lewis, 2009; Table 1). The socially adaptive hypothesis focuses on the role of SSSB in shaping social interactions, both aggressive and peaceful (Harari et al., 2000; Levan et al., 2009). For example, SSSB may mitigate future aggression by

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**Table 1**  
Four nonmutually exclusive hypotheses proposed to explain how same-sex sexual behaviours (SSSB) may be maintained in animal populations, with the associated predictions tested in the present study

Hypothesis	Description	Predictions	Tested in
Socially adaptive	SSSB may reduce intrasexual conflict by diffusing aggressive interactions (Vasey et al., 1998) and help establish or maintain social bonds and dominance hierarchies (Vervaecke & Roden, 2006)	<ul style="list-style-type: none"> <li>• Less aggressive males court more than aggressive males</li> </ul>	<ul style="list-style-type: none"> <li>• Experiments 1, 2</li> </ul>
Sexually adaptive	SSSB may increase mating and reproductive success by providing a way to display sexual prowess to an audience, practise for heterosexual interactions (McRobert & Tompkins, 1988), or be an indirect means of sperm transfer (Levan et al., 2009)	<ul style="list-style-type: none"> <li>• Males court more in the presence of a female audience than when in the presence of a male or no audience</li> </ul>	<ul style="list-style-type: none"> <li>• Experiment 1</li> </ul>
Phenotypic correlations	SSSB may be correlated with other sexually selected traits and may result from positive selection for increased sexual activity in general (Burgevin et al., 2013)	<ul style="list-style-type: none"> <li>• Males with high mate attraction signalling effort court more than low-effort signalers</li> <li>• More aggressive males court more than less aggressive males</li> </ul>	<ul style="list-style-type: none"> <li>• Experiments 1, 2</li> <li>• Experiments 1, 2</li> </ul>
Sex misidentification	SSSB may result from misidentifying the sex of a conspecific and might occur because the receiver of SSSB resembles the opposite sex in behaviour or appearance, or the performer cannot discern sex due to a lack of sexual experience (Harari et al., 2000)	<ul style="list-style-type: none"> <li>• Less aggressive males get courted by others more than aggressive males</li> <li>• Larger males get courted by others more than smaller males</li> <li>• Laboratory-reared males court others more than wild-caught males</li> <li>• Males consuming low carbohydrate foods get courted by others more than males consuming other foods</li> </ul>	<ul style="list-style-type: none"> <li>• Experiments 1, 2</li> <li>• Experiments 1, 2</li> <li>• Experiment 1</li> <li>• Experiment 2</li> </ul>

reducing aggressive tension, resulting in less frequent, less intense or shorter intrasexual conflicts (Vasey, 2006). Reduced aggression should lower fitness costs of fighting by minimizing body damage and energy expenditure during same-sex conflicts. SSSB may also be a mechanism through which dominance hierarchies are established, with dominant males mounting subordinates as a means of intimidation (e.g. American bison, *Bison bison*; Vervaecke & Roden, 2006), or may help establish and maintain social bonds, typically resulting in increased offspring care (e.g. bottlenose dolphins, *Tursiops* spp.; MacFarlane et al., 2006; Mann, 2006).

The sexually adaptive hypothesis suggests that SSSB may increase mating and reproductive success. SSSB may provide practise for future heterosexual encounters, serve as an indirect means of sperm transfer among males or provide a social platform to display sexual prowess (Harari et al., 2000; Judge & Bonanno, 2008; Levan et al., 2009; McRobert & Tompkins, 1988). There are also indications that SSSB may be maintained by both social and sexual interactions, increasing individual fitness under different social and developmental circumstances. For example, in a phylogenetic review of mating systems and hatching development in birds, MacFarlane et al. (2006) found that female birds are more likely to perform SSSB when their young hatch precociously, potentially increasing parental care for precocious young from other females. Conversely, male birds appear to be more likely to perform SSSB in species with polygamous mating systems (MacFarlane et al., 2006). It seems that, in polygamous mating systems, male birds are more motivated to court other individuals regardless of sex, increasing their probability of finding a female by reducing missed mating opportunities.

The phenotypic correlation hypothesis suggests that SSSB may covary with selection for other sexually selected traits. For example, increased levels of same-sex mounting could result from positive selection for increased activity levels in general (Harari et al., 2000), especially if the costs of SSSB are low. Supporting this hypothesis, Maklakov and Bonduriansky (2009) found that the fitness cost of SSSB is relatively low in male carrion flies (*Prochyliza xanthostoma*), suggesting that there may not be strong selection against SSSB. SSSB may also covary with other sexually selected traits, such as aggression. For example, winners of aggressive encounters tend to

be more aggressive and more likely to win in subsequent fights (winner effect), and females tend to prefer winners over losers (Judge & Bonanno, 2008; Kortet & Hedrick, 2005; Loranger & Bertram, 2016, in this issue; Rook, Fitzsimmons, & Bertram, 2010), suggesting that selection should favour aggressive behaviours (Rillich & Stevenson, 2011). If males that are both more aggressive and more sexual (i.e. perform more courtship, and possibly SSSB) mate more, these two behaviours may show a phenotypic correlation. Alternatively, SSSB might be maintained in an animal population if it offers some heterozygote advantage, in which individuals heterozygous for SSSB genes show greater fitness than those who are homozygous. Supporting this hypothesis, Hoskins et al. (2015) suggested that SSSB is a heritable trait in male *Drosophila melanogaster*, with males heterozygous for SSSB genes having offspring with greater fecundity than those who are homozygous. This study also provides limited support for a genetic hypothesis for why SSSB may be maintained in animal populations: the sexual antagonism hypothesis; if genes underlying SSSB offer a fitness advantage in one sex, they may be maintained at the population level despite their possible fitness costs in the opposite sex (Hoskins et al., 2015).

The misidentification hypothesis suggests that SSSB may be the result of misidentifying the sex of conspecifics. This proximate hypothesis implies that both the social and physical environment could influence SSSB (Bailey, Hoskins, Green, & Ritchie, 2013; Field & Waite, 2004). For example, a male-biased sex ratio tends to increase the frequency of male–male mounting in beetles (Switzer, Forsythe, Escajeda, & Kruse, 2004), and male crickets deprived of heterosexual interactions are more likely to display SSSB than those with heterosexual experience (Bailey & French, 2012). Moreover, male beetles are more likely to attempt to mate with a larger conspecific regardless of gender, suggesting that some insects may have poor sex discrimination (Harari et al., 2000). The ability of male insects to achieve large adult size depends on the acquisition of appropriate nutrient ratios during development (Hunt et al., 2004), indicating a potential mechanism through which diet may affect SSSB. Nutrient consumption may also alter chemical cues important in mate choice, potentially obscuring sex discrimination.

Female Nile tilapia, *Oreochromis niloticus*, for example, select males based on chemical cues that vary as a function of diet (Giaquinto, Silva Berbert, & Delicio, 2010). Similarly, South, House, Moore, Simpson, and Hunt (2011) found that high-carbohydrate foods increase male sex pheromone production in cockroaches (*Nauphoeta cinerea*).

Together these four hypotheses highlight the polarized views regarding the adaptive value of SSSB (cf. adaptive: MacFarlane et al., 2006; nonadaptive: Bailey & French, 2012). Here we sought to test the socially adaptive, sexually adaptive, phenotypic correlation and misidentification hypotheses for SSSB by (1) investigating how body mass/size at adulthood, audience composition, rearing environment, food composition, aggression and mate attraction signalling relate to the performance of same-sex courtship, and (2) determining how these factors relate to a male's tendency to be courted by same-sex conspecifics (Table 1). The four hypotheses were addressed by collecting data on SSSB and by reanalysing video recordings from two previous experiments on field cricket aggression. One of our experiments (experiment 1) was originally designed to examine how aggressive interactions (fights) between male *Gryllus veletis* were influenced by audience composition (male, female, or no audience) and rearing environment (laboratory or wild) (Fitzsimmons & Bertram, 2013). The other experiment (experiment 2) was originally designed to examine the relationship between aggression and food composition (carbohydrate, protein, and phosphorus) in laboratory-reared male *G. veletis* (Harrison et al., n.d.). The fairly frequent occurrence of SSSB in both experiments allowed us to explore whether there was correlative support for the social, sexual, phenotypic correlation and misidentification hypotheses (Table 1).

Male field crickets (Gryllidae) fight for access to territories. Once a territory has been established, the male rubs his forewings together to produce long-distance acoustic mate attraction signals (Alexander, 1961). Once a female approaches a male, the male switches to short-range acoustic courtship signals. During courtship the male courter backs up towards the head of the female. Females control mating and mount their preferred mate (Alexander, 1961). Females select mates using male body size, dominance status, mate attraction signals, courtship signals and cuticular hydrocarbons (Bertram & Rook, 2012; Kortet & Hedrick, 2005; Nandi & Balakrishnan, 2013; Simmons, 1986a). Male crickets can use cuticular hydrocarbons (CHCs) to discriminate between male and female conspecifics (Tregenza & Wedell, 1997).

We explored the four alternative hypotheses for the maintenance of SSSB (Table 1), defining SSSB as occurring when a male produced a courtship signal or performed 'backing up' courtship behaviour. We only included behaviours that a male would typically use towards a female, but that he instead used towards a male. Therefore, we did not include male–male mounting behaviour in our definition of SSSB because in field crickets, females are the mounting sex. We predicted that if SSSB is socially adaptive and functions to reduce aggressive tension, less aggressive males should perform more SSSB than more aggressive males (Bailey & Zuk, 2009). Alternatively, we predicted that if SSSB is sexually adaptive, serving as a medium for male sexual displays, males should perform more same-sex courtship in the presence of a female audience than in the presence of a male audience or no audience. We make this prediction because males have already been shown to modify their behaviour by fighting more aggressively when a female audience is present (Fitzsimmons & Bertram, 2013); SSSB may help to communicate sexual prowess. If SSSB results from phenotypic correlation for more sexual activity in general, we predicted that males expressing more SSSB should signal for mates more often or be more aggressive. Finally, we predicted that if SSSB results from sex misidentification, then (1) males with

no sexual experience at adulthood (laboratory-reared virgins) should display more SSSB than males that presumably have mating experience (wild-caught), (2) larger males should be courted more often than smaller males since female crickets tend to be larger than males (Judge & Bonanno, 2008), (3) less aggressive males should be courted by others more than aggressive males since females are typically less aggressive than males and/or (4) males consuming low-carbohydrate foods should be courted more often than males consuming higher-carbohydrate foods since carbohydrates are important in the production of chemical cues (sensu South et al., 2011), which may be involved in sex identification.

## EXPERIMENT 1

### Methods

Fitzsimmons and Bertram (2013) quantified the aggressive behaviour of 32 laboratory-reared and 44 wild-caught *G. veletis* males under three different audience treatments (detailed in Fitzsimmons and Bertram (2013) and briefly reviewed here). Wild-reared crickets were captured in greenspaces around Ottawa, Ontario, Canada (45°15'40"N, 76°09'00"W and 45°24'34.6"N, 75°32'52.4"W) in spring 2008. Laboratory-reared crickets were first-generation offspring that were housed in communal plastic bins on a 14:10 h light:dark cycle at  $28 \pm 2^\circ\text{C}$  with ad libitum standard colony food (Teklad Rodent Diet 8604M: Harlan Laboratories, Indianapolis, IN, U.S.A.). Newly eclosed adult males were then housed individually. All laboratory-reared males were virgins at the time of the trials, whereas wild-captured males had an unknown mating status.

At 7 days post imaginal moult for laboratory reared males and the day following capture for wild-captured males, male mean daily time spent producing acoustic mate attraction signals was quantified using an Electronic Acoustic Recording System (EARS II) (Cambridge Electronic Design, Cambridge, U.K.). Male mate attraction signalling was monitored over 6 days, continuously for the first 3 days, and then for 18 h per day (1600–1000 hours) over the subsequent 3 days. However, only the first 3 days (prefight) of signal recording was used in the analyses to ensure that fight outcome did not affect our signalling measure. During the non-recording times, each male participated in a fight (one fight per day) for a total of three fights over 3 days.

Each fight consisted of pair of males interacting in the presence of a female audience, a male audience, or no audience. Fights were conducted on sand in a two-chamber arena constructed of Plexiglas between 1000 and 1200 hours; the fight took place in one chamber (14 × 14 and 21 cm high) and the audience cricket (if applicable) was placed in the adjacent chamber (7.5 × 14 and 21 cm high). The clear Plexiglas that separated the two adjacent chambers had small holes to allow transmission of chemical, auditory and visual cues. Each fight was run until a clear winner was established (see Fitzsimmons & Bertram, 2013, for details). If no clear winner was established, the trial continued for a maximum of 30 min. Each male participated in three fights (one of each audience type; order randomized); males were never fought twice against the same opponent. In total, 44 wild-caught males were paired in 66 trials and 32 laboratory-reared males were paired in 48 trials.

Opponents were weight matched to ensure they were within 20% of each other. To facilitate weight matching, wild-caught males were weighed on the morning after capture, and laboratory-reared males were weighed on their 9th day of adulthood using a Denver Instruments analytical balance (Pinnacle Series model PI-114; precision  $\pm 0.1$  mg, Denver Instruments, Bohemia, NY, U.S.A.). Following weighing, males were marked with paint to allow

identification during fights. Each fight was recorded from above using a colour video camera (Canon Vixia HG10).

Fitzsimmons and Bertram (2013) used videos to score the duration and intensity of aggressive behaviours using the following codes: 1 = antennal fencing; 2 = kick; 3 = chase, mandible spread, bite; 4 = mandible engagement, grapple. They determined the aggression levels for each male by calculating the male's aggression intensity score (sensu Bertram & Rook, 2012):

Aggression intensity score

$$= \frac{\sum \text{Score of behaviour} \times \text{time(s) spent performing behaviour}}{\text{Total time engaged in behaviours}} \quad (1)$$

We then calculated how aggressive each male was compared to his opponent by saving the residuals of a regression of focal male aggression intensity score on opponent aggression intensity score. Focal male residual aggression intensity score was then used in all statistical analyses.

To quantify same-sex sexual behaviour, we re-examined the videos using VLC Media Player (available from <http://www.videolan.org/vlc/index.html>) and determined when SSSB (same-sex courtship signalling and/or 'backing up' towards another male as if to be mounted) occurred. For each fight containing SSSB ( $N = 40$ ), we recorded the courting male's identity and the duration of the courtship event for every occurrence of male–male courtship. We categorized a male as being the recipient of same-sex courtship if he was within one body length of a male performing courtship signalling or courtship behaviours. We quantified total fight time as the time from initial contact to the end of the fight. Only fights that contained SSSB were included in subsequent statistical analyses.

All statistical analyses were carried out using R v.3.2.2 (R Foundation for Statistical Computing, Vienna, Austria; <https://www.r-project.org/>). We first investigated how body mass, audience, rearing environment, aggression and mate attraction signalling time affected same-sex courtship behaviour. Because these data contained a large proportion of zeros (32 out of 80 individuals did not perform same-sex courtship behaviour), we used a two-part logit-linear model to investigate (1) the probability of performing courtship behaviour, and, (2) for those males that showed courtship behaviour, what factors affected the amount of time they spent courting. For the former, we performed a mixed-effects logistic regression (R package 'glmmADMB') to test how each factor affected a male's probability of performing courtship behaviour towards another male. For those males that courted other males, the second part of the model used a linear mixed model (R package 'nlme') to investigate the influence of those same independent variables on the amount of time that males spent courting others. For both parts of the model, the independent variables included in the initial models were: focal male body mass (g), audience composition (male, female, or no audience), rearing environment (laboratory or wild), focal male residual aggression intensity score, mean daily time spent producing mate attraction signals by the focal male (min), and the interactions between audience and mate attraction signalling, audience and focal male residual aggression, rearing environment and mate attraction signalling, and rearing environment and residual aggression. Interaction terms that were not found to be significant in either part of the model were removed. If an interaction term was found to be significant in only one part of the model, it was retained in both. As such, only the interaction between rearing environment and mate attraction signalling was retained in both parts of the final model. Since some males were used in multiple trials, the ID of the focal male was included as a random effect in both parts of the model.

Because of a large proportion of zeros (32 out of 80 individuals were not recipients of courtship behaviour), we then created a similar two-part logit-linear model to determine (1) which factors affected whether or not a male was courted by other males, and, (2) for those males that were courtship recipients, which variables influenced the amount of time for which they were courted. For the first part of the model, a mixed-effects logistic regression was performed to investigate the effect of the independent variables on the probability of a male being courted by other males. For those males that were courted by others, a linear mixed model was created as the second part of the model to examine the influence of the same variables on the amount of time for which males were courted. The independent variables in the initial models were: focal male body mass (g), audience composition (male, female, or no audience), rearing environment (laboratory or wild), focal male residual aggression intensity score, focal male mean daily time spent producing mate attraction signals (min), and the interactions between audience and mate attraction signalling, audience and focal male residual aggression, rearing environment and mate attraction signalling, and rearing environment and residual aggression. None of the interaction terms were found to be significant in either part of the model; thus, none were retained in the final model. Focal male ID was again included as a random effect in both parts of the model, since some males were used in multiple trials.

For all analyses, residuals were visually examined using diagnostic plots (residuals versus fitted values and Q–Q plots). Residuals were relatively uniformly distributed around a mean of zero. As such, the model assumptions of homoscedasticity were met; therefore, data were not transformed.

## Results

SSSB occurred in 35% of the aggressive trials (40 of 114), with a similar probability of being performed by wild-caught (20 of 66 = 30%) and laboratory-reared (20 of 48 = 42%) animals. In trials where SSSB occurred, focal male body mass, audience composition, rearing environment, focal male residual aggression intensity score, focal male mate attraction signalling time, and the interaction between rearing environment and mate attraction signalling time did not significantly influence the probability of a male being a courter (Table 2). Time spent courting was influenced by a significant interaction between rearing environment and mate attraction signalling effort (Table 2). Wild-caught males of unknown mating status spent less time courting other males the more time they spent signalling for potential mates. Conversely, males reared in the laboratory showed no relationship between time spent courting other males and time spent signalling for potential mates.

The probability of a male being a courtship recipient was not significantly influenced by focal male body mass, the composition of the audience, rearing environment, focal male residual aggression intensity score, or focal male mate attraction signalling time (Table 3). Similarly, the time spent being courted by other males was not significantly influenced by any of the aforementioned variables (Table 3).

## EXPERIMENT 2

### Methods

Harrison et al. (n.d.) quantified the aggressive behaviour of male *G. veletis* that were fed foods that differed in their carbohydrate, protein and phosphorus composition. All laboratory-reared crickets were third- generation to fifth-generation descendants of wild *G. veletis* individuals captured in spring 2010 from greenspaces

**Table 2**

Results of a two-part logit-linear model for experiment 1 examining factors influencing the probability of a male being a courter (mixed-effects logistic regression) and the amount of time males spent courting others (linear mixed model)

Model	Model parameter	Estimate±SD	df	t	Z	P
Mixed-effects logistic regression	Intercept	-0.145±2.604			-0.06	0.956
	Body mass	0.003±0.007			0.45	0.652
	Audience(Female)	0.212±0.731			0.29	0.772
	Audience(Male)	-0.814±0.867			-0.94	0.348
	Environment(Lab)	-0.441±1.043			-0.42	0.672
	Residual aggression intensity score	-4.610±2.463			-1.87	0.061
	Mate attraction signalling	-0.016±0.016			-1.01	0.313
	Environment (Lab)*mate attraction signalling	0.020±0.017			1.17	0.240
Linear mixed model	<b>Intercept</b>	<b>393.406±135.474</b>	<b>28</b>	<b>2.904</b>		<b>0.007</b>
	Body mass	-0.380±0.333	28	-1.139		0.264
	Audience(Female)	-5.164±34.400	12	-0.150		0.883
	Audience(Male)	48.857±41.864	12	1.167		0.266
	<b>Environment(Lab)</b>	<b>-137.194±51.484</b>	<b>28</b>	<b>-2.665</b>		<b>0.013</b>
	Residual aggression intensity score	13.191±97.555	12	0.135		0.895
	<b>Mate attraction signalling</b>	<b>-2.748±1.264</b>	<b>28</b>	<b>-2.173</b>		<b>0.038</b>
	<b>Environment(Lab)*mate attraction signalling</b>	<b>2.857±1.266</b>	<b>28</b>	<b>2.257</b>		<b>0.032</b>

Both parts of the model included male ID as a random effect, and this random effect explained 24.842% of the total variance in the linear mixed model. Significant model effects are shown in bold.

around Ottawa, Ontario, Canada (45°15'53"N, 76°08'43"W; 45°24'33"N, 75°32'51"W). Laboratory-reared crickets were housed in communal plastic bins on a LD 14:10 h regime at 28 ± 2 °C with ad libitum standard colony food until they reached adulthood. Newly eclosed adult males were housed individually and fed their assigned food. All males were virgins at the time of the trials.

Harrison et al. (n.d.) quantified how food composition influenced each male's aggressive behaviour by running 42 aggression trials with six males in each trial ( $N = 252$  males in total). Beginning the day they reached adulthood, each of the six males per trial was fed a different food that contained one of three protein:carbohydrate ratios (3:1, 1:1 or 1:3) and one of two phosphorous levels (0.45% or 1.45%). Foods were created following Harrison, Raubenheimer, Simpson, Godin, and Bertram (2014).

The six males per aggression trial (group) differed in weight by no more than 25%, and differed in age by no more than 7 days. Weights were obtained using a Denver Instruments analytical balance (Pinnacle Series model PI-114; precision ± 0.1 mg) on the first day of adulthood. Aggression trials were performed on the 11th day of adulthood of the youngest male in a group. Thus, males were fed their respective foods for a minimum of 11 days and a maximum of 18 days prior to aggression trials.

Males were placed in the EARS II on the 7th day of adulthood of the youngest male in a group and had their mate attraction signals recorded for 4 days before being fought in an aggression trial. The first day in the EARS II was used as an acclimatization period, and only signalling data from 3 days prior to the aggression trial were included in analyses.

For each aggression trial, the six males in a group were placed into a clear Plexiglas arena (cylinder with 20.3 cm diameter and 25.4 cm height) with a sand-covered bottom. Prior to beginning a trial, males were isolated by an opaque Plexiglas divider that divided the arena into six equal sectors. After a 10 min acclimatization period, the divider was carefully removed and aggressive behaviours were quantified for 15 min. All aggression trials were run between 0900 and 1400 hours in a silent room and were recorded from above using a colour video camera (Canon Vixia HG10). The sand substrate was raked between trials and replaced every three trials. In addition, the walls of the arena and divider were wiped down with 99% ethyl alcohol prior to every trial to minimize the possibility of pheromones affecting future interactions.

Following aggression trials males were euthanized by freezing and then photographed dorsal side up beside a ruler using a Sony

**Table 3**

Results of a two-part logit-linear model for experiment 1 examining factors influencing the probability of a male being courted by others (mixed-effects logistic regression) and the amount of time males spent being courted by others (linear mixed model)

Model	Model parameter	Estimate±SD	df	t	Z	P
Mixed-effects logistic regression	Intercept	2.624±2.251			1.17	0.244
	Body mass	-0.006±0.006			-1.03	0.302
	Audience(Female)	0.046±0.651			0.07	0.943
	Audience(Male)	-0.508±0.742			-0.68	0.494
	Environment(Lab)	0.127±0.665			0.19	0.848
	Residual aggression intensity score	2.933±1.770			1.66	0.098
	Mate attraction signalling	0.004±0.005			0.76	0.445
	Linear mixed model	<b>Intercept</b>	<b>249.583±96.929</b>	<b>42</b>	<b>2.575</b>	
Body mass		-0.436±0.264	42	-1.653		0.106
Audience(Female)		14.380±30.420	31	0.473		0.640
Audience(Male)		25.379±35.232	31	0.720		0.477
Environment(Lab)		-14.424±30.344	42	-0.475		0.637
Residual aggression intensity score		80.692±66.960	31	1.205		0.237
Mate attraction signalling		-0.163±0.192	42	-0.848		0.401

Both parts of the model included male ID as a random effect, and this random effect explained 10.189% of the total variance in the linear mixed model. Significant model effects are shown in bold.

Nex 7 camera (30 mm, F3.5 macro lens). ImageJ software (<http://imagej.nih.gov/ij/>) was used to obtain three measures of body size, as measured when viewing crickets' dorsal side: maximum pronotum height (length along the anterior–posterior axis), maximum pronotum width and maximum distance between eyes. Size was quantified using the first principal component from a principal component analysis of pronotum height, pronotum width, between-eye distance and body mass (eigenvalue = 3.36; body size PC1 explained 84% of the variation).

To score aggressive behaviours Harrison et al. (n.d.) used JWatcher v.1.0 (<http://www.jwatcher.ucla.edu/registerjwatcher.html>). Aggressive behaviour was scored on a scale from 0 to 5 as follows: 0 = no aggression/withdrawal; 1 = unilateral or bilateral antennal fencing; 2 = back leg kick or victory display (body judder or judder combined with an aggressive call); 3 = unilateral mandible spread, chasing, aggressive call and/or biting; 4 = bilateral mandible spread, chasing, aggressive call and/or biting; 5 = bilateral grapple: two males lock mandibles and pull or wrestle (adapted from: Bertram & Rook, 2012; Jang, Gerhardt, & Choe, 2008). We modified the aggressive behaviour scoring system from experiment 1 because it did not distinguish between unilateral and bilateral aggressive behaviours and intentionally analysed victory displays separately. Mean aggression intensity scores were calculated using equation (1), above. We then calculated how aggressive each male was compared to his opponents by saving the residuals of a regression of focal male aggression intensity score on the average aggression intensity score of his five opponents. Focal male residual aggression intensity score was then used in all statistical analyses.

To quantify same-sex sexual behaviour, we re-examined the videos using VLC Media Player (experiment 1; <http://www.videolan.org/vlc/index.html>) or Media Player Classic-Home Cinema v.1.7.1 (experiment 2; <http://mpc-hc.org/>) and determined when SSSB occurred ( $N = 18$  aggression trials). For every occurrence of male–male courtship we recorded the courting male's identity and the duration of the courtship event. Given there were multiple potential recipients of the SSSB in this experiment, we also quantified the identity of the courtship recipient and the duration of time that the recipient was courted. A male was categorized as the recipient of same-sex courtship if he was the clear target of courtship behaviours or signalling, as determined by a proximity of within one body length of the courting male. Males sometimes performed courtship behaviours and signals not directed towards the other male in the arena; these were still classified as part of the focal male's SSSBs because they are still considered sexual behaviours, even if not directed towards a specific recipient.

We investigated how body size, food, aggression and mate attraction signalling time affected same-sex courtship behaviour. Because our data contained a large proportion of zeros (78 out of 108 males did not show same-sex courtship behaviour), we created a two-part logit-linear model to investigate (1) the probability of performing courtship behaviour, and, (2) for those males that showed courtship behaviour, what factors affected the amount of time they spent courting. The first part consisted of a mixed-effects logistic regression that investigated the effect of each predictor on a male's probability of performing courtship behaviour. For those males that courted other males, the second part of the model used a linear mixed model to examine the influence of those same independent variables on the amount of time that males spent courting other males. While our original models examined all six food types used, phosphorous was observed to have no significant effects (the observed interaction of food type and mate attraction signalling was clearly linked to the protein:carbohydrate ratios); therefore, phosphorous was not included in our final models. Instead, food type was quantified as the ratio of protein to carbohydrates. As

such, the independent variables included in both parts of the model were focal male body size PC1, focal male food type (ratio of protein to carbohydrate), focal male residual aggression intensity score, focal male mean daily time spent producing mate attraction signals (min), and the interactions between food type and mate attraction signalling, and food type and residual aggression. The latter interaction term, between food type and residual aggression, was not significant in either part of the model, and was thus removed from both parts. Each fight consisted of six males and male behaviour was influenced by opponent behaviour; thus, trial ID was included as a random effect in both parts of the model. Visual examination of residuals using diagnostic plots (residuals versus fitted values and Q–Q plots) revealed a relatively uniform distribution around a mean of zero. As such, the model assumptions of homoscedasticity were met; therefore, data were not transformed.

Because of a large proportion of zeros (58 out of 108 males were not recipients of same-sex courtship behaviour), we created a similar two-part logit-lognormal model to determine (1) which factors affected whether or not a male was courted by other males, and, (2) for those males that were courtship recipients, which variables influenced the amount of time for which they were courted. A mixed-effects logistic regression was performed to investigate the effect of the independent variables on the probability of a male being courted by other males. For those males that were courted by others, a linear mixed model was created to examine the influence of the same variables on the amount of time for which males were courted. In this two-part model, the initial independent variables were focal male body size PC1, focal male food type (ratio of protein to carbohydrate), focal male residual aggression intensity score, focal male mean daily time spent producing mate attraction signals (min), and the interactions between food type and mate attraction signalling, and food type and residual aggression. The latter interaction term, between food type and residual aggression, was, again, not significant in either part of the model, and was thus removed from both parts of the model. Trial ID was included as a random effect in both parts of the model. For the linear mixed model of time spent being courted, a visual inspection of the diagnostic plots of residuals versus fitted values, and a Q–Q plot of residuals indicated some heteroscedasticity (scatter increased with increasing fitted values). The dependent variable (time spent being courted) was log transformed, and the same diagnostic plots showed residuals distributed fairly evenly around a mean of zero, indicating that the assumption of homoscedasticity was met.

## Results

SSSB occurred in 43% of the aggression trials (18 of 42). For trials with SSSB, a male's probability of performing same-sex courtship increased with increasing residual aggression intensity score (Table 4). There was also a significant interaction between food type and mate attraction signalling (Table 4). The probability for males to engage in same-sex courtship increased with increasing mate signalling effort, provided they were fed a high-carbohydrate food. For males on high-protein foods, the probability of courting others decreased with increasing mate signalling effort, while males on the food with equivalent amounts of protein and carbohydrates showed no relationship between mate signalling effort and the probability of courting others. Time spent engaged in same-sex courtship was not significantly influenced by any of the independent variables, although there was a trend for increased time spent engaged in same-sex courtship with increased time spent engaged in mate attraction signalling (Table 4).

In terms of being courted by other males, the probability for males to be the recipient of same-sex courtship decreased with

**Table 4**

Results of a two-part logit-linear model for experiment 2 examining factors influencing the probability of a male being a courter (mixed-effects logistic regression) and the amount of time males spent courting others (linear mixed model)

Model	Model parameter	Estimate±SD	df	t	Z	P
Mixed-effects logistic regression	<b>Intercept</b>	<b>−2.071±0.617</b>			<b>−3.36</b>	<b>0.001</b>
	Body size PC1	−0.197±0.137			−1.44	0.150
	<b>Food(P:C)</b>	<b>0.691±0.341</b>			<b>2.02</b>	<b>0.043</b>
	<b>Residual aggression intensity score</b>	<b>1.173±0.404</b>			<b>2.90</b>	<b>0.004</b>
	<b>Mate attraction signalling</b>	<b>0.005±0.002</b>			<b>2.19</b>	<b>0.028</b>
	<b>Food(P:C)*mate attraction signalling</b>	<b>−0.005±0.002</b>			<b>−2.31</b>	<b>0.021</b>
Linear mixed model	Intercept	31.157±20.521	17	1.518		0.147
	Body size PC1	3.933±4.869	7	0.808		0.446
	Food(P:C)	2.174±12.286	7	0.177		0.865
	Residual aggression intensity score	15.261±12.783	7	1.194		0.271
	Mate attraction signalling	0.170±0.074	7	2.297		0.055
	Food(P:C)*mate attraction signalling	−0.079±0.079	7	−0.996		0.353

P:C: protein:carbohydrate ratio. Both parts of the model included trial ID as a random effect, and this random effect explained 0.004% of the total variance in the linear mixed model. Significant model effects are shown in bold.

increasing residual aggression score (Table 5). There was also a significant interaction between food type and the focal male's mate attraction signalling effort (Table 5). The probability for males to be the recipient of same-sex courtship decreased with increasing mate signalling effort, provided they were fed a high-carbohydrate food. For males on high-protein foods, the probability of being the recipient of same-sex courtship increased with increasing mate signalling effort. Males on the food with equivalent amounts of protein and carbohydrates showed no relationship between mate signalling effort and the probability of being the recipient of same-sex courtship. Time spent being courted by other males was negatively influenced by mate attraction signalling times, as males were courted significantly less often when they showed high mate attraction signalling times (Table 5).

## DISCUSSION

Adaptive and nonadaptive hypotheses for the persistence of SSSB are not mutually exclusive, yet only a handful of studies have simultaneously tested both types of hypotheses (e.g. Bailey & French, 2012; Harari et al., 2000; Levan et al., 2009), potentially underestimating the complex array of factors contributing to the expression of SSSB. We used the results of two separate experiments on aggression to simultaneously test the hypotheses that, in male spring field crickets, *G. veletis*, SSSB may be socially adaptive, sexually adaptive, the result of a phenotypic correlation with other

sexually selected traits or due to sex misidentification. Overall, we found support for nonadaptive hypotheses explaining SSSB.

We predicted that if SSSB were socially adaptive in *G. veletis*, less aggressive males would court more aggressive males to distract or calm aggressive interactions. However, we found no significant negative correlation between an individual's residual aggression intensity score and his time spent courting members of the same sex in experiments 1 or 2 (Tables 2, 4). Thus, same-sex courtship in male crickets is unlikely to function in reducing the aggression of conspecifics. Our results are in accordance with previous findings suggesting that SSSB does not reduce aggression in male insects (Bailey & French, 2012; Harari et al., 2000; Levan et al., 2009). Similarly, Vasey (2004) found that SSSB does not help to re-establish social bonds following conflict in female Japanese macaques, further suggesting that same-sex courtship is unlikely to be socially adaptive in the context of same-sex aggression.

We also found a lack of support for the sexually adaptive hypothesis. We predicted that if SSSB were sexually adaptive in *G. veletis*, more same-sex courtship would occur in the presence of a female audience to demonstrate sexual prowess (Doutrelant & McGregor, 2000). However, we found no significant relationship between same-sex courtship time and audience composition in experiment 1 (Table 2). It is unlikely that this result is due to a methodological flaw in which audience treatments were ineffective, as our previous work clearly showed that audience composition had a significant impact on male aggression levels (Fitzsimmons & Bertram, 2013). Other sexually adaptive

**Table 5**

Results of a two-part logit-lognormal model for experiment 2 examining factors influencing the probability of a male being courted by others (mixed-effects logistic regression) and the amount of time males spent being courted by others (linear mixed model with dependent variable log transformed)

Model	Model parameter	Estimate±SD	df	t	Z	P
Mixed-effects logistic regression	Intercept	0.092±0.506			0.18	0.855
	Body size PC1	0.011±0.125			0.09	0.929
	Food(P:C)	−0.367±0.293			−1.25	0.210
	<b>Residual aggression intensity score</b>	<b>−0.590±0.293</b>			<b>−2.02</b>	<b>0.044</b>
	Mate attraction signalling	−0.003±0.002			−1.42	0.156
	<b>Food(P:C)*mate attraction signalling</b>	<b>0.004±0.002</b>			<b>2.24</b>	<b>0.025</b>
Linear mixed model	<b>Intercept</b>	<b>3.645±0.355</b>	<b>27</b>	<b>10.256</b>		<b>&lt;0.001</b>
	Body size PC1	0.079±0.086	27	0.915		0.369
	Food(P:C)	−0.329±0.194	27	−1.698		0.101
	Residual aggression intensity score	0.087±0.170	27	0.510		0.614
	<b>Mate attraction signalling</b>	<b>−0.004±0.002</b>	<b>27</b>	<b>−2.176</b>		<b>0.038</b>
	Food(P:C)*mate attraction signalling	0.001±0.001	27	1.206		0.238

P:C: protein:carbohydrate ratio. Both parts of the model included trial ID as a random effect, and this random effect explained 26.814% of the total variance in the linear mixed model. Significant model effects are shown in bold.

hypotheses for SSSB, such as those suggesting that same-sex courtship may provide a means of indirect sperm transfer or provide practise for future heterosexual interactions, have also not been supported in the literature (Levan et al., 2009).

Our data support the hypothesis that SSSB may not be inherently adaptive in *G. veletis*. Contrary to what would be predicted by the socially adaptive hypothesis, relatively more aggressive males were significantly more likely to engage in same-sex courtship in experiment 2 (Table 4). The positive correlation between aggression and the probability of engaging in same-sex courtship suggests the potential for a phenotypic correlation, where levels of SSSB covary with levels of other sexually selected traits. If the correlation between same-sex courtship and aggression is driven by underlying genetics, hormones (Moretz, Martins, & Robison, 2007) or environmental factors, selection or environmental factors favouring high aggression levels could maintain SSSB in *G. veletis*, provided the cost of SSSB is relatively low (Przeworski, Coop, & Wall, 2005; Stephan, 2010). There is the potential for aggression to be influenced by positive directional selection, as females in a variety of cricket species often prefer fight winners over losers (Judge & Bonanno, 2008; Kortet & Hedrick, 2005; Loranger & Bertram, 2016, in this issue; Rook et al., 2010). A similar correlation was observed by Fujioka and Yamagishi (1981), who found that more aggressive males were more likely to perform SSSB than less aggressive males in the cattle egret *Bubulcus ibis*.

The potential also exists for a behavioural syndrome characterized by high levels of sexual activity in general, as males with high mate attraction signalling effort were also more likely to engage in same-sex courtship in experiment 2, but only when they were fed high-carbohydrate food (Table 4). Males may require sufficient carbohydrate-derived energy to fuel these activities (Thomson & Bertram, 2014). In support of this, we found that when males were fed a low-carbohydrate food, males with high mate attraction signalling effort were less likely to engage in same-sex courtship (Table 4), suggesting that they did not have enough energy to maintain both behaviours (i.e. a trade-off occurred). Given that our results suggest a potential phenotypic correlation involving same-sex courtship, aggression and mate attraction signalling, a quantitative genetics study estimating genetic variances and covariances for SSSB, aggression and mate attraction signalling time in *G. veletis* could provide further insight into the genetic underpinnings of such behaviours. For example, Hoskins et al. (2015) recently showed that there are repeatable differences in SSSB among different lines of *D. melanogaster*, suggesting that these behaviours are indeed heritable and independently genetically determined. A similar study conducted in *G. veletis* would provide a useful starting point for understanding the relative contributions of genetics and environment in determining the expression of SSSB.

We also found support for the misidentification hypothesis in experiment 2, further suggesting that SSSB is not adaptive in *G. veletis*. Males had a higher probability of being courted by other males if they were relatively less aggressive in experiment 2 (Table 5). Given that females are rarely aggressive, the behaviour of less aggressive males may be more female-like (Alexander, 1961). There was also a significant interaction between food type and mate attraction signalling effort in the same model; males on the high-carbohydrate food were more likely to be courted the less time they spent engaged in mate attraction signalling, while males on the high-protein food were more likely to be courted the more time they spent engaged in mate attraction signalling (there was no effect of mate attraction signalling time on the probability of being courted for males on the food with equal levels of protein and carbohydrates). These results suggest that a combination of behavioural cues and diet may be important for sex identification in *G. veletis* (Table 5). The availability of carbohydrates in the diet may alter the

composition or amount of sex-specific chemical cues produced by male insects, potentially resulting in some males being more attractive to conspecifics as a result of their diet (Bailey et al., 2013; Peschke, 1987; South et al., 2011; Tregenza & Wedell, 1997). Harrison et al. (2014) showed that, when given a choice of foods, male *G. veletis* preferentially consume high-carbohydrate, low-protein foods. The selective pressures favouring such a food preference may be two-fold. First, carbohydrate metabolism appears to fuel the energetics of mate attraction signalling (Bertram, Thomson, Auguste, Dawson, & Darveau, 2011; Thomson & Bertram, 2014), and female mate selection in crickets tends to be based on the energetically demanding features of male mate attraction signalling such as loudness and time spent signalling (Cade & Cade, 1992; Crnokrak & Roff, 1995; Holzer, Jacot, & Brinkhof, 2003; Hunt et al., 2004; Judge, Ting, & Gwynne, 2008; Judge, Ting, & Gwynne, 2014; Pacheco & Bertram, 2014; Simmons, 1986b). Second, cuticular hydrocarbon (CHC) production appears to be critical in female field cricket mate choice (Simmons, Thomas, Gray, & Zuk, 2014), suggesting that selection favouring diet preferences that maximize CHC production should be strong. Supporting this hypothesis, South et al. (2011) found that when male cockroaches (*N. cinerea*) are given a choice of foods, they prefer high-carbohydrate foods that increase their production of sex pheromones, and males that consume high-carbohydrate foods are also more attractive to females. Together these results hint that male *G. veletis* fed higher-carbohydrate foods may have higher fitness because higher-carbohydrate foods fuel mate attraction signalling and increase the production of sexually attractive chemical compounds. Members of both sexes may find these chemical compounds attractive, resulting in SSSB. Future studies should characterize and quantify the effect of relative nutrient ratios in the diet on the composition of cuticular hydrocarbons in both male and female crickets.

The lack of support for the phenotypic correlation and misidentification hypotheses observed in experiment 1 could be due to dietary effects. In experiment 1, laboratory-reared males were all fed the same standard colony food with an intermediate protein:carbohydrate ratio (1:2). Given our finding of no relationship between mate attraction signalling and courtship behaviour for males in experiment 2 that consumed a diet equal in protein and carbohydrates (1:1; Table 4), it is possible that laboratory-reared males also may not have had sufficient carbohydrates to produce significant amounts of pheromones or to express a correlation between mate attraction signalling time and time engaged in same-sex courtship. Conversely, the consistent diet may have not provided enough variation in male pheromone production or mate attraction signalling to provide support for the phenotypic correlation or misidentification hypotheses.

SSSB is generally assumed to be more common in laboratory-reared insects than in wild-captured insects (reviewed in Scharf & Martin, 2013). However, we found that wild crickets were as likely to engage in SSSB as first-generation laboratory-reared crickets (experiment 1; Table 2). The fact that males with very little experience with laboratory conditions were just as likely to show SSSB as those reared in the laboratory provides a strong counterpoint to the common claim that the laboratory favours expression of SSSB. It is possible that the discrepancy between our findings and other studies could be an artefact of our isolating individuals from conspecifics for 3 days prior to conducting aggression trials. Conversely, the (assumed) sexual experience of wild-captured *G. veletis* males may not influence engagement in same-sex courtship behaviour.

Interestingly, there was a significant interaction between rearing environment and mate signalling time on the amount of time spent courting. Males that were captured as adults in the wild (mating status unknown) spent decreasing amounts of time

courting other males the more time they spent signalling to attract a potential mate. Conversely, males that were laboratory reared (virgins) did not show a significant relationship between courtship time and mate attraction signalling time. This finding suggests that the wild males may not have had enough access to carbohydrates in their diet to be able to afford the energetic demands required to signal for mates and show same-sex courtship behaviour, resulting in a trade-off similar to that expressed by males reared on the high-protein (low-carbohydrate) food in experiment 2. Alternatively, wild-captured males that have high mate attraction signalling times may be a lot more discerning in who they court. Future studies should seek to quantify SSSB in the wild to further elucidate the correlations between mate attraction signalling effort, male–male aggression and the expression of SSSB.

Overall, we examined four hypotheses for the prevalence of SSSB in the spring field cricket, *G. veletis*. Our results suggest that nonadaptive hypotheses may best explain the persistence of SSSB in male *G. veletis*, with same-sex courtship potentially persisting as a result of both misidentification and phenotypic correlations with aggression and sexual activity. These results align nicely with those of recent reviews on SSSB in arthropods (e.g. Scharf & Martin, 2013), which suggest that SSSB is largely a by-product of high levels of sexual activity in general. The interactions between food type, aggression and mate attraction signalling time, and their relationship with SSSB in our study hint at the complex underpinnings of these behaviours, with both proximate and evolutionary factors probably contributing to the selective forces shaping reproductive and social behaviours in animals.

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