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

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*

increasing residual aggression score (Table 5). There was also a signi cant 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.

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 signi cantly 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 in uenced by positive directional selection, as females in a variety of cricket species often prefer ght 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 suf cient 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. veletiswould 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 misidenti cation 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, pr 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-

the loss of song in the Hawaiian archipelago. Journal of Evolutionary Biology, 27, 2249e2257.
South, S. H., House, C. M., Moore, A. J., Simpson, S. J., & Hunt, J. (2011). Male cockroaches prefer a high carbohydrate diet that makes them more attractive to females: implications for the study of condition dependence. Evolution, 65, 1594e1606.
Stephan, W. (2010). Genetic hitchhiking versus background selection: the controversy and its implications. Philosophical Transactions of the Royal Society B: Biological Sciences, 365, 1245e1253.
Switzer, P. V., Forsythe, P. S., Escajeda, K., & Kruse, K. C. (2004). Effects of environmental and social conditions on homosexual pairing in the Japanese beetle (Popillia japonica Newman). Journal of Insect Behavior, 17, 1e16.
Thomson, I. R., & Bertram, S. M. (2014). Spring eld crickets (Gryllus veletis) use two different pulse types when signaling to attract mates. Journal of Insect Behavior, 27, 217e227.
Tregenza, T., & Wedell, N. (1997). De nitive evidence for cuticular pheromones in a cricket. Animal Behaviour, 54, 979e984.
Vasey, P. L. (2004). Pre-and postcon ict interactions between female Japanese macaques during homosexual consortships. International Journal of Comparative Psychology, 17, 351e359.
Vasey, P. L. (2006). The pursuit of pleasure: an evolutionary history of homosexual behaviour in Japanese macaques. In V. Sommer, & P. L. Vasey (Eds.), Homosexual behaviour in animals. An evolutionary perspective (pp. 107e130). Cambridge, U.K.: Cambridge University Press.
Vasey, P. L., Chapais, B., & Gauthier, C. (1998). Mounting interactions between female Japanese macaques: testing the in uence of dominance and aggression. Ethology, 104, 387e398.
Vasey, P. L., Rains, D., VanderLaan, D. P., Duckworth, N., & Kovacovsky, S. D. (2008). Courtship behaviour in Japanese macaques during heterosexual and homosexual consortships. Behavioural Processes, 78, 401e407.
Vervaecke, H., & Roden, C. (2006). Going with the herd: same-sex interaction and competition in American bison. In V. Sommer, & P. Vasey (Eds.), Homosexual behaviour in animals. An evolutionary perspective (pp. 131e153). Cambridge, U.K.: Cambridge University