Resolving the puzzle of same-sex sexual interactions.

Sexual interactions between members of the same sex are common but the reasons for these behaviours are not always clear. A recent study across mammals suggests increased same-sex behaviour evolved with sociality and may reduce conflict even though male-male sexual interactions are associated with increased adult killing.

Courtship and mating between members of the same sex (same-sex behaviour) is widespread across animals[1] and the incidence of same-sex behaviour can be high: nearly 30% of king penguin pairs in one population consisted of two males for example[2]. Sometimes same-sex behaviour results in the production of young, as seen when hermaphrodites pair and copulate, but typically offspring cannot be produced (because by definition sperm or eggs are missing). Since the fundamental currency of biology is offspring production, and neither male-male nor female-female mating produce offspring, same-sex behaviour is puzzling. This puzzle becomes more acute when considering the costs involved, which at the very least include energy expenditure and possibly gamete wastage. Evolution is an

efficient sieve, selectively removing traits that are costly and generate no net fitness benefit. Given this, how can we explain the prevalence of same-sex behaviour? Writing in *Nature Communications,* Gomez et al.[3] sheds new light on this apparent conundrum, and shows how selection could favour same-sex behaviour in mammals.

Unlike much previous work focusing on single species, Gomez and colleagues[3] explore the evolution of same-sex behaviour across mammals. This approach has caveats – in the underlying data-set the occurrence of same-sex behaviour is incomplete and likely littered with false negatives. However, this broad phylogenetic approach enables the authors to test adaptive explanations for same-sex behaviour on a larger scale than previous studies. This also allows the authors to ask if the last common ancestor of the mammals was likely to engage in same-sex behavior.

Analyses suggest that in mammals, same-sex behaviour probably evolved multiple times. Additionally, clades displaying same-sex behaviour are younger than clades lacking it. The emerging picture then, is that the prevalence of same-sex behaviour has been low for most of mammalian

evolutionary history but began increasing at the origin of Old World monkeys (Catarrhini) and increased further with the origin of apes.

This argues against the idea that same-sex behaviour is an evolutionary hang-over, occurring because the last common ancestor of the mammals engaging in these behaviours. This is interesting given the recent suggestion that indiscriminate mating could be the ancestral state of sexually reproducing organisms[4]. The rationale for this being that the mechanisms needed to discriminate between mates of the same and opposite sex, must have evolved after the evolution of sex itself[4]. The look into our mammalian recent evolutionary past does not preclude indiscriminate mating being the ancestral state of all sexually reproducing organisms. After all, sexual reproduction and the sexes evolved long before the mammals.

The finding that same-sex behaviour has originated independently in many mammalian lineages is suggestive of convergent evolution[3]. Additionally, repeated evolution of same-sex behaviour in similar environments, hints at selection. By testing for associations between same-sex behaviour and

other traits – sociality and the incidence of intrasexual aggression and adulticide – the authors tested two non-mutually exclusive adaptive hypotheses for the evolution of same-sex behaviour[3]. First, the “social glue” hypothesis, which posits that same-sex behaviour promotes social cohesion and facilitates conflict resolution[1]. And second, the “intrasexual conflict” hypothesis, suggesting that same-sex behaviour reduces conflict and aggression, perhaps through establishing dominance hierarchies or by channeling aggressive behavior into courtship activities[1].

Results showed that same-sex behaviour in mammals of both sexes is tightly associated with the evolution of sociality, and the shift from a solitary to a social lifestyle is a key step towards the evolution of same-sex sexual interactions. This suggests that same-sex behaviour could be selectively favoured because it helps establish and strengthen allegiances within social groups.

Same-sex behaviour was also associated with (and its evolution contingent on) adulticide in males, but not in females[3]. Gomez and colleagues interpret this positive association between male same-sex behaviour and

male-male adulticide as evidence that male-male sexual activity dampens male aggression and conflicts. This interpretation feels somewhat counterintuitive. If same-sex behaviour were truly effective in reducing adulticide, how strong and positive should we expect the remaining association to be, and in fact, shouldn't a negative association be seen? Linking same-sex behaviour and the degree of sexual dimorphism in body size (indicative of competition for mates) might offer an additional way to test this idea, but it could be that targeted same-sex behaviour facilitates coalition formation leading to increased attacks on other non-coalition members.

Gomez et al. also suggested that a stronger relationship between same-sex behaviour and sex-specific adulticide in males is further evidence for the intrasexual conflict hypothesis[3]. Their rationale was that conflict between males for access to females is rife, but conflict between females is more often due to protecting progeny and thus, unlikely to be tempered by same-sex behaviour. This prediction assumes that males and females are free to evolve to their sex-specific optimal levels of same-sex behaviour. But a shared genome means that the sexes are frequently not free to evolve to sex-specific optima[5]. That is, in theory, selection on male same-

sex behaviour, could select on females as a correlated response (and vice versa). There is some evidence for this being the case in seed beetles[6]. The current analyses showed that male and female same-sex behaviour are phylogenetically correlated across mammals, meaning that this is a possibility in mammalian systems. More work characterizing intersexual genetic correlations in same-sex behaviour within species may illuminate the capacity for selection in one sex, to influence same-sex behaviour in the other.

Caveats aside, this work[3] demonstrates that same-sex behaviour, sociality, and aggression show correlated evolution in mammals, potentially supporting adaptive explanations for the behaviour across this group. Nonetheless, there is more work to be done. There is widespread same-sex behaviour in solitary insects and arachnids for example and this has been attributed to cases of "mistaken identity"[7]. But is it correct to label weak mate-discrimination as error, especially in light of theory describing how weak mate discrimination could be favored by selection[9]? In any case, work such as this powerful comparative analyses[3], alongside exciting theoretical developments[4,9] and deep dives into same-sex behaviour within species[8] are helping explain why this behaviour is so common. Overall,

there appear to be evolutionary advantages for same-sex behaviour, and this apparent evolutionary puzzle, is becoming far less puzzling.

References

1. Bailey, N. W. & Zuk, M. Same-sex sexual behavior and evolution. *Trends in Ecology & Evolution* **24**, 439–446 (2009).
2. Pincemy, G., Dobson, F. S. & Jouventin, P. Homosexual mating displays in penguins. *Ethology* **116**, 1210–1216 (2010).
3. Gómez, J. M., Gónzalez-Megías, A. & Verdú, M. The evolution of same-sex sexual behaviour in mammals. *Nature Communications* **14**, 5719 (2023).
4. Monk, J. D., Giglio, E., Kamath, A., Lambert, M. R. & McDonough, C. E. An alternative hypothesis for the evolution of same-sex sexual behaviour in animals. *Nature ecology & evolution* **3**, 1622–1631 (2019).
5. Hosken, D. J., Archer, C. R. & Mank, J. E. Sexual conflict. *Current Biology* **29**, R451–R455 (2019).

6. Burgevin, L., Friberg, U. & Maklakov, A. A. Intersexual correlation for same-sex sexual behaviour in an insect. *Animal Behaviour* **85**, 759–762 (2013).
7. Scharf, I. & Martin, O. Y. Same-sex sexual behavior in insects and arachnids: prevalence, causes, and consequences. *Behavioral Ecology and Sociobiology* **67**, 1719–1730 (2013).
8. Richardson, J. & Zuk, M. Rethinking same-sex sexual behaviour: male field crickets have broad mating filters. *Proceedings of the Royal Society of London - B.* **290**, 20230002 (2023).
9. Lerch, B. A. & Servedio, M. R. Same-sex sexual behaviour and selection for indiscriminate mating. *Nature Ecology & Evolution* **5**, 135–141 (2021).

C. Ruth Archer[1*] & David J. Hosken[2]

[1] Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Albert-Einstein Allee 11. D-89069 Ulm

[2] Centre for Ecology and Conservation, University of Exeter, Cornwall, Penryn TR109EZ, UK

*corresponding author: rutharcher0@gmail.com