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Title: Ancestral primacy of same-sex behaviour does not explain its stable prevalence in modern populations

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Main: Monk et al. [1] suggest that same sex behaviour (SSB) was present in ancestral populations alongside different sex behaviour (DSB). Such indiscriminate behaviour may not have impaired fitness under certain social and ecological circumstances, where sufficient levels of DSB enabled reproduction. The authors see this as a more parsimonious hypothesis compared to a traditional set, which sees current SSB as either a developmental error or conferring some indirect fitness benefits.

The parsimony claim rests on the idea that SSB is indiscriminate, whereas DSB relies upon perceivable sexual polymorphisms (e.g., in body shape, size, chemical signals). Thus the evolutionary transition from indiscriminate sexual behaviour (ISB) to DSB has need of another round of selection, beyond that establishing sexual behaviour, in order to install suitable proximate machinery. The traditional approach is to see DSB as the starting point and then SSB as a secondary emergence, by accident or design. Given this, both hypotheses in fact have the same level of antecedent complexity and both also require subsequent events in order to explain the current SSB:DSB ratios seen in animal populations. We note that presence of indiscriminate sexual behaviour across a range of taxa has been proposed before [2]. We are also unconvinced that ISB will be uniform across taxa. Testing these claims would of course require systematic phylogenetic analysis within lineages and associated quantitative tests of fitness functions/mechanisms.

As per standard Darwinian accounts, there will quickly have been strong selection for sex limitation due to the underlying asymmetry at the gamete level (anisogamy). This will have resulted in a general set of DSBs for the two sexes (or classical sex roles and other sexual polymorphisms). This may not be uniform across taxa but, contra Monk et al., anisogamy can generate a stereotypical asymmetry in the sex roles at the organism level and subsequent variation thereafter [3].

A better test than parsimony is the generation of novel predictions. Monk et al. do not deliver on this, but they do suggest changes of perspective for researchers in the field. As noted, we have no problem with an ancestral SSB before DSB hypothesis, but we also noted that DSB will rapidly emerge. We do not think that this leads to the wholesale abandonment of past practices in the field, as we still have to account for current SSB:DSB ratios.

Under a strong selection regime for DSB, hypothesizing that modern SSB is the outcome of developmental error is legitimate, because SSB is a broad behavioural phenotype and multiple causes are conceivable. Put another way, modern SSB may not look precisely like ancestral SSB. Indeed, all that holds these behaviours together for Monk et al. is that they are interactions between the same sex. It is also the case that balanced polymorphisms for sexual preferences and targeting could confer indirect fitness benefits for individuals with a complex modern SSB phenotype. What Monk et al. have added is the notion that extant SSB might simply be remnant behaviour from ancestral transitions (cf [2,4]).

Remnant SSB could co-exist with adapted and erroneous SSB within the same population.

The idea of remnant SSB requires a little inspection. We could predict that the expression of sexual dimorphisms and preferences are developmentally plastic, and therefore sensitive to key ecological input for some species. Indeed, the authors suggest SSB expression is impacted by such factors as sex ratios (a point not unrelated to the prison effect), encounter rates and other ecological causes. The developmental costs of building precise targeting machinery are perhaps too high under circumstances where SSB can be tolerated with minimal impact upon average lifetime inclusive fitness gains. Within a population with stable SSB:DSB, this might focus any developmental error hypotheses on specific exposures, rather than intrinsic error. But this kind of thinking can arise under either hypothesis set because neither party has any reason to assume a fully sexual adult is not the outcome of development.

A useful line of enquiry for testing Monk et al. is to look at the heritability of SSB across broad taxa. This is an odd omission for Monk. Selection will, after all, act only on heritable variation (whether or not the origins of SSB lie in recent evolutionary events or the earliest forms of sexual behavior phenotypes). This immediately raises a question about what might be precisely measured here. The relative frequency of same-sex encounters, preferences, physiological responses to sexually dimorphic stimuli etc. could all be recruited. Monk et al. take pains to distance themselves from discussions about sexual orientation, but fundamentally, that term captures the suite of adaptations they assume must come into play after the emergence of dimorphisms.

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Author contributions

TED and QR contributed equally to the development of the argument. TED led on the writing and QR made contributions to the writing. TED produced the final agreed edited version.

Competing interests

The authors declare no competing interests.

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