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DOI:

[10.1038/s41559-020-1187-5](https://doi.org/10.1038/s41559-020-1187-5)

*Document Version*

Peer reviewed version

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*Citation for published version (APA):*

Dickins, T. E., & Rahman, Q. (2020). Ancestral primacy of same-sex sexual behaviour does not explain its stable prevalence in modern populations. *Nature Ecology and Evolution*, 4(6), 782-783. <https://doi.org/10.1038/s41559-020-1187-5>

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

3  
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8  
9  
10 **Main:** Monk et al. <sup>1</sup> suggest that same sex behaviour (SSB) was present in  
11 ancestral populations alongside different sex behaviour (DSB). Such  
12 indiscriminate behaviour may not have impaired fitness under certain social and  
13 ecological circumstances, where sufficient levels of DSB enabled reproduction.  
14 The authors see this as a more parsimonious hypothesis compared to a traditional  
15 set, which sees current SSB as either a developmental error or conferring some  
16 indirect fitness benefits.

17  
18 The parsimony claim rests on the idea that SSB is indiscriminate, whereas DSB  
19 relies upon perceivable sexual polymorphisms (e.g., in body shape, size, chemical  
20 signals). Thus the evolutionary transition from indiscriminate sexual behaviour  
21 (ISB) to DSB has need of another round of selection, beyond that establishing  
22 sexual behaviour, in order to install suitable proximate machinery. The  
23 traditional approach is to see DSB as the starting point and then SSB as a  
24 secondary emergence, by accident or design. Given this, both hypotheses in fact  
25 have the same level of antecedent complexity and both also require subsequent  
26 events in order to explain the current SSB:DSB ratios seen in animal populations.  
27 We note that presence of indiscriminate sexual behaviour across a range of taxa  
28 has been proposed before <sup>2</sup>. We are also unconvinced that ISB will be uniform  
29 across taxa. Testing these claims would of course require systematic phylogenetic  
30 analysis within lineages and associated quantitative tests of fitness  
31 functions/mechanisms.

32  
33 As per standard Darwinian accounts, there will quickly have been strong selection  
34 for sex limitation due to the underlying asymmetry at the gamete level  
35 (anisogamy). This will have resulted in a general set of DSBs for the two sexes  
36 (or classical sex roles and other sexual polymorphisms). This may not be uniform  
37 across taxa but, contra Monk et al., anisogamy can generate a stereotypical  
38 asymmetry in the sex roles at the organism level and subsequent variation  
39 thereafter <sup>3</sup>.

40  
41 A better test than parsimony is the generation of novel predictions. Monk et al.  
42 do not deliver on this, but they do suggest changes of perspective for researchers  
43 in the field. As noted, we have no problem with an ancestral SSB before DSB  
44 hypothesis, but we also noted that DSB will rapidly emerge. We do not think that  
45 this leads to the wholesale abandonment of past practices in the field, as we still  
46 have to account for current SSB:DSB ratios.

47  
48 Under a strong selection regime for DSB, hypothesizing that modern SSB is the  
49 outcome of developmental error is legitimate, because SSB is a broad behavioural  
50 phenotype and multiple causes are conceivable. Put another way, modern SSB  
51 may not look precisely like ancestral SSB. Indeed, all that holds these  
52 behaviours together for Monk et al. is that they are interactions between the  
53 same sex. It is also the case that balanced polymorphisms for sexual preferences  
54 and targeting could confer indirect fitness benefits for individuals with a complex  
55 modern SSB phenotype. What Monk et al. have added is the notion that extant  
56 SSB might simply be remnant behaviour from ancestral transitions (cf <sup>2,4</sup>).

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

59  
60 The idea of remnant SSB requires a little inspection. We could predict that the  
61 expression of sexual dimorphisms and preferences are developmentally plastic,  
62 and therefore sensitive to key ecological input for some species. Indeed, the  
63 authors suggest SSB expression is impacted by such factors as sex ratios (a point  
64 not unrelated to the prison effect), encounter rates and other ecological causes.  
65 The developmental costs of building precise targeting machinery are perhaps too  
66 high under circumstances where SSB can be tolerated with minimal impact upon  
67 average lifetime inclusive fitness gains. Within a population with stable SSB:DSB,  
68 this might focus any developmental error hypotheses on specific exposures,  
69 rather than intrinsic error. But this kind of thinking can arise under either  
70 hypothesis set because neither party has any reason to assume a fully sexual  
71 adult is not the outcome of development.

72  
73 A useful line of enquiry for testing Monk et al. is to look at the heritability of SSB  
74 across broad taxa. This is an odd omission for Monk. Selection will, after all, act  
75 only on heritable variation (whether or not the origins of SSB lie in recent  
76 evolutionary events or the earliest forms of sexual behavior phenotypes). This  
77 immediately raises a question about what might be precisely measured here. The  
78 relative frequency of same-sex encounters, preferences, physiological responses  
79 to sexually dimorphic stimuli etc. could all be recruited. Monk et al. take pains to  
80 distance themselves from discussions about sexual orientation, but  
81 fundamentally, that term captures the suite of adaptations they assume must  
82 come into play after the emergence of dimorphisms.

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## 96 97 98 **Author contributions**

99  
100 TED and QR contributed equally to the development of the argument. TED led on  
101 the writing and QR made contributions to the writing. TED produced the final  
102 agreed edited version.

## 103 104 **Competing interests**

105  
106 The authors declare no competing interests.

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