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**Divergence is not speciation, or why we need females: a comment on
Tinghitella et al.**

Emily R. Burdfield-Steel^{1,2} and David M. Shuker^{3*}

1. Centre of Excellence in Biological Interactions, Department of Biological and
Environmental Science, University of Jyväskylä, Finland

2. Department of Biological Sciences, Macquarie University, Australia

3. School of Biology, University of St Andrews, UK.

*author for correspondence:

Dr David M. Shuker

School of Biology

Harold Mitchell Building

University of St Andrews

St Andrews

KY16 9TH, UK.

Tel: +44 1334 34 3376

Email:david.shuker@st-andrews.ac.uk

25 Tinghitella et al (2018) provide a wonderful review of the role of male-male
26 competition in the divergence of traits across populations. Using a range of examples,
27 the authors show how male traits associated with intra-sexual competition for mates
28 can diverge. They also show that, in a few examples, male-male competition can interact
29 with other processes – such as mate choice or natural selection on ecologically relevant
30 traits – to influence how reproductive isolation (RI) may come about. In this comment,
31 we wish to build on that latter aspect, and emphasise that divergence itself is not
32 enough for speciation. We note from the outset that the authors caution this, but we
33 wish to add further emphasis, as it has important ramifications for the role of males and
34 females in speciation.

35

36 Divergence is not speciation. Something else is needed to close the loop, so that
37 diverging populations become separate species. Under common definitions of species,
38 that something else is one or more forms of RI (Coyne and Orr 2004). In other words,
39 among-population variation in phenotypes and genotypes is not speciation until
40 something about those phenotypes or genotypes limits gene flow absolutely, or at least
41 to negligible levels. Typically, we envisage pre- or post-zygotic RI, with pre-zygotic
42 isolation occurring as either pre-copulatory or post-copulatory mechanisms of isolation.
43 The question therefore is not whether male-male competition traits diverge (they do),
44 but rather how they influence RI.

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46 As briefly mentioned by Tinghitella et al (2018), the simplest situation is when changes
47 in male-male competitive phenotypes involve genetic changes that lead to post-zygotic
48 genetic incompatibilities, such that individuals from divergent populations mate and
49 produce unfit or inviable hybrids. This loss of fitness may be due to the production of
50 sons that are unable to compete effectively (a form of extrinsic incompatibility).
51 Alternatively, the loss of fitness may involve mutations not obviously associated
52 phenotypically with male-male competition, in the extreme case being lethal in hybrid
53 genetic backgrounds (a form of intrinsic incompatibility). Of course, any evolutionary
54 change can lead to such incompatibilities, and so in this sense male-male competition
55 joins all forms of selection as a source of RI and therefore a “process” of speciation.

56 However, we feel that the emphasis of Tinghitella et al (2018) is more specific, focusing
57 on sexual selection and pre-zygotic isolation.

58

59 With pre-zygotic isolation, we need the divergence in male traits to either lead to
60 isolation independently of females, or via female-male interactions. Our discussion will
61 be quite general, although we note that perhaps the most likely venue for such effects is
62 in the post-copulatory sphere (see Simmons 2018). Tinghitella et al (2018) discuss how
63 male-male competition might lead to reproductive isolation without females, although
64 perhaps their most convincing examples also include male mate choice (Heathcote et al.
65 2016; Martin and Mendelson 2016). But let's take a step back and consider the situation
66 more from a mating systems perspective than a speciation one (see also Parker and
67 Partridge 1998).

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69 Let us assume that females mate indiscriminately, accepting as mates males successful
70 in male-male competition, in whatever form. In this case, it is not immediately clear why
71 the nature (or extent) of that male-male competition should influence reproductive
72 isolation. Even if populations diverge in male-male competition traits, on secondary
73 contact indiscriminate females from either population should mate with successful
74 males, breaking down population barriers. On the other hand, if females have
75 preferences for male traits also involved in male-male competition, then these
76 preferences may well limit the scope for divergence in those traits. Whilst Tinghitella et
77 al (2018) mention how male-male competition will likely interact with mate choice (and
78 natural selection) if it is to influence RI, we suggest that considering the role of male-
79 male competition in pre-zygotic isolation will *only* be relevant in terms of the context of
80 male-female interactions, because of the need to bias which females mate with which
81 males for RI to occur.

82

83 In summary, in terms of post-zygotic incompatibilities, male-male competition may, like
84 all aspects of selection, generate genetic incompatibilities among diverging populations
85 yielding RI. In this context, male-male competition should neither be ignored nor be
86 considered a particularly special part of speciation. In terms of pre-zygotic

87 incompatibilities, sex and gene flow means that females will nearly always play an
88 integral role in influencing how male-male competition influences reproductive
89 isolation, and so females will typically have the last word on how males influence
90 speciation.

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