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Conflict over resources generates conflict over mate choice: Reply to Smaldino & Newson

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1 Conflict over resources generates conflict over mate choice:
2 reply to Smaldino & Newson

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24 Evolutionary computer simulations are an important part of the theoretical biologist's toolkit (Peck, 2004;
25 DeAngelis & Mooij, 2005; Kokko, 2007), offering insights into a range of fundamental evolutionary
26 processes, not least sexual selection (e.g. van Doorn & Weissing 2004, 2006; Fawcett *et al.*, 2007, 2011;
27 van Doorn *et al.*, 2009; reviewed in Kuijper *et al.*, 2012). Like all theoretical tools, they must be used with
28 care (Hamblin, 2012). Smaldino & Newson (2013, henceforth S&N) have challenged our recent work on
29 parent–offspring conflict over mate choice (Van den Berg *et al.*, 2013), arguing that our simulations rely
30 on unrealistic assumptions and that our conclusions are not supported. But all four points of criticism they
31 present are misguided. (1) The accusation that the handicap principle cannot work in our model is wrong;
32 Fig. 1a in Van den Berg *et al.* (2013) clearly demonstrates that a costly preference for a signal of male
33 quality does evolve. (2) The assertion that mutation bias drove male quality close to zero in our model is
34 wrong; in fact, male quality reached very high, stable levels in our simulations. (3) The assertion that
35 overcompensation was responsible for our results is wrong; parent and offspring preferences also diverge
36 in the absence of overcompensation. (4) The alternative explanation offered for our results is wrong,
37 because it predicts the opposite pattern to that we actually observed in our simulations. Below we address
38 each of these misunderstandings and consider two alternative hypotheses suggested by S&N.

39

40 **1. Relation between male signaling and mate quality**

41 S&N claim that, in our model, males of higher quality pay a higher cost of exhibiting the trait. This is not
42 true. In our model there is no direct relation between male quality (i.e. provisioning ability) and survival
43 cost; instead, a male's survival depends solely on his expression of the indicator trait (t_e). But it is true
44 that for the same genetic value of trait expression (t), we assumed that higher-quality males signal at
45 higher intensity and hence pay higher survival costs. Based on this, S&N conclude that we have ignored
46 the “well accepted common sense rule of costly signaling” that “signaling quality must incur a cost which
47 only quality individuals can afford.” However, standard theory on sexual selection shows that costly
48 preferences can evolve if higher-quality males produce stronger signals for the same genetic value of trait

49 expression (Iwasa *et al.*, 1991; Fawcett *et al.*, 2007). This is the form of costly signaling we implemented
50 in our model. That the handicap principle works in this case is evident from the results in Step 1 of our
51 model, which is a standard sexual selection model without parental involvement: Fig. 1a in Van den Berg
52 *et al.* (2013) shows stable exaggeration of a costly female preference for a costly indicator of male
53 quality. More importantly, our findings are robust to the specific assumptions of our model; if we assume,
54 as S&N recommend, that low-quality males pay higher costs of trait expression, we still predict the
55 emergence of parent–offspring conflict over mate choice (Fig. 1).

56 **2. The evolution of male provisioning ability**

57 S&N criticize our assumption of a negative mutation bias on male quality. However, this is a common
58 assumption in models of sexual selection with heritable male quality (Pomiankowski *et al.*, 1991; Iwasa *et al.*,
59 1991), including the one S&N refer to (Iwasa & Pomiankowski, 1999). It is a standard way of
60 resolving the so-called ‘lek paradox’ (Kotiaho *et al.*, 2008); without such a mechanism, male quality
61 rapidly tends to fixation at the highest possible value, negating the benefits of female choosiness, which
62 disappears as a result.

63 It is not surprising that male provisioning ability rapidly declines to zero if a negative mutation bias is the
64 only force affecting its evolution (as in S&N’s Fig. 1), but in our model this mutation bias is opposed by
65 two selection pressures. First, males of higher quality have more resources to invest in their offspring, and
66 therefore on average obtain higher reproductive success. Second, evolved female preferences for males
67 with a larger indicator trait also favor higher-quality males. As a result, male parenting ability is
68 maintained at high levels in our simulations (averages \pm s.e.m. over the last generation of all replicates:
69 0.940 ± 0.001 [step 1]; 0.937 ± 0.001 [step 2]; 0.899 ± 0.001 [step 3]; 0.895 ± 0.001 [step 4]) —far from a
70 “negligible” contribution to child-rearing. This incorrect assertion appears to be at the root of most of the
71 issues raised by S&N. Nonetheless, to address concerns about our assumptions, we have investigated a

72 modified version of our model without biased mutations (Fig. 2); here, too, we predict the emergence of
73 parent–offspring conflict over mate choice.

74 **3. Parental allocation strategies**

75 S&N suggest that parent–offspring conflict emerges in our model because the parents’ compensatory
76 resource-allocation strategy “overcompensates (or *overaugments*) for disparities in mate-provided
77 resources.” This is not the case; in Fig. 3 in Van den Berg *et al.* (2013), where allocation strategies are
78 free to evolve, the onset of parent–offspring conflict already occurs before parents overcompensate (i.e.,
79 while the evolved value of α is still smaller than -1). This is confirmed by one of the modified
80 versions of our model presented here (Fig. 1), in which *undercompensation* evolves but the conflict over
81 mate choice is still strong.

82 S&N speculate why evolution drives the sum of female and parental preferences ($p + q$) to “consistent
83 values.” Their explanation rests on the presumption that in our model it is in the parents’ interest to avoid
84 having daughters with very low fecundity. This is not true: parents maximize their fitness by maximizing
85 the total fecundity of all of their daughters, regardless of how that fecundity is distributed over individual
86 daughters. In our model, there is a persistent selection pressure on daughters to be less choosy than their
87 sisters, resulting in a weakening of the female preference. Parents, in contrast, use their influence on mate
88 choice to ensure that the *realized* preference ($p + q$) has the same value as it would have had in the
89 absence of parental involvement, because this represents the optimal compromise for them between the
90 costs and benefits of choosiness.

91 **4. Evolving parental compensation**

92 S&N suggest that our main result (Fig. 3 in Van den Berg *et al.*, 2013) is caused by an entirely different
93 mechanism than the one we put forward. However, their argument is based on misconceptions about the
94 workings of our model, in particular the incorrect assertion that “the average resource contribution to
95 childrearing from partnered males was negligible” (see section 2).

96 Our explanation for the evolution of compensatory parental resource allocation strategies is
97 straightforward: if there are diminishing returns on investment, it pays more to invest in daughters that
98 have fewer resources from their partner. If, instead, returns on investment are accelerating, parents evolve
99 an augmenting resource-allocation strategy (see Fig. S2 in Van den Berg *et al.*, 2013). This latter pattern
100 would not evolve if the alternative explanation proposed by S&N were correct.

101 **5. Comparison with other hypotheses**

102 S&N find it implausible that sibling competition for parental resources would be strong enough to weaken
103 the female preference for high-investing mates. Yet there is overwhelming evidence in a range of other
104 contexts that sibling competition is a potent evolutionary force with some striking consequences,
105 including chick begging, siblicide, and genomic imprinting (Kilner & Hinde, 2012; Roulin & Dreiss,
106 2012). We maintain that our model provides a potentially valid hypothesis that deserves further attention.

107
108 S&N mention two alternative hypotheses for the evolution of parent-offspring conflict over mate choice.
109 The first hypothesis, already alluded to by Trivers (1974), rests on the observation that a female's mate
110 often provides resources not only to their own children, but also to those of her sisters and cousins. Such
111 behavior seems more beneficial to the female's parents than to the female herself, so potentially it could
112 lead to parent-offspring conflict over mate choice. This is an interesting hypothesis, but it leads to a new
113 problem: why would males divert resources from their own children to less related family members?

114 S&N's second hypothesis is that parents are more experienced, and therefore better able to choose a mate
115 for their offspring. This may be true, but it does not explain the conflict; why would offspring disagree if
116 their parents know best?

117
118 Our model (Van den Berg *et al.*, 2013) explains, from an evolutionary point of view, why parents and
119 offspring should not necessarily agree over the latter's choice of a mate. We did not claim that it is the
120 only possible explanation for this conflict, nor even the best one, and we welcome alternative hypotheses

121 as well as constructive criticism of our model. To discriminate between competing hypotheses, it is
122 essential to examine the logic closely and derive clear, testable predictions. Evolutionary computer
123 simulations have a vital role to play in this regard.

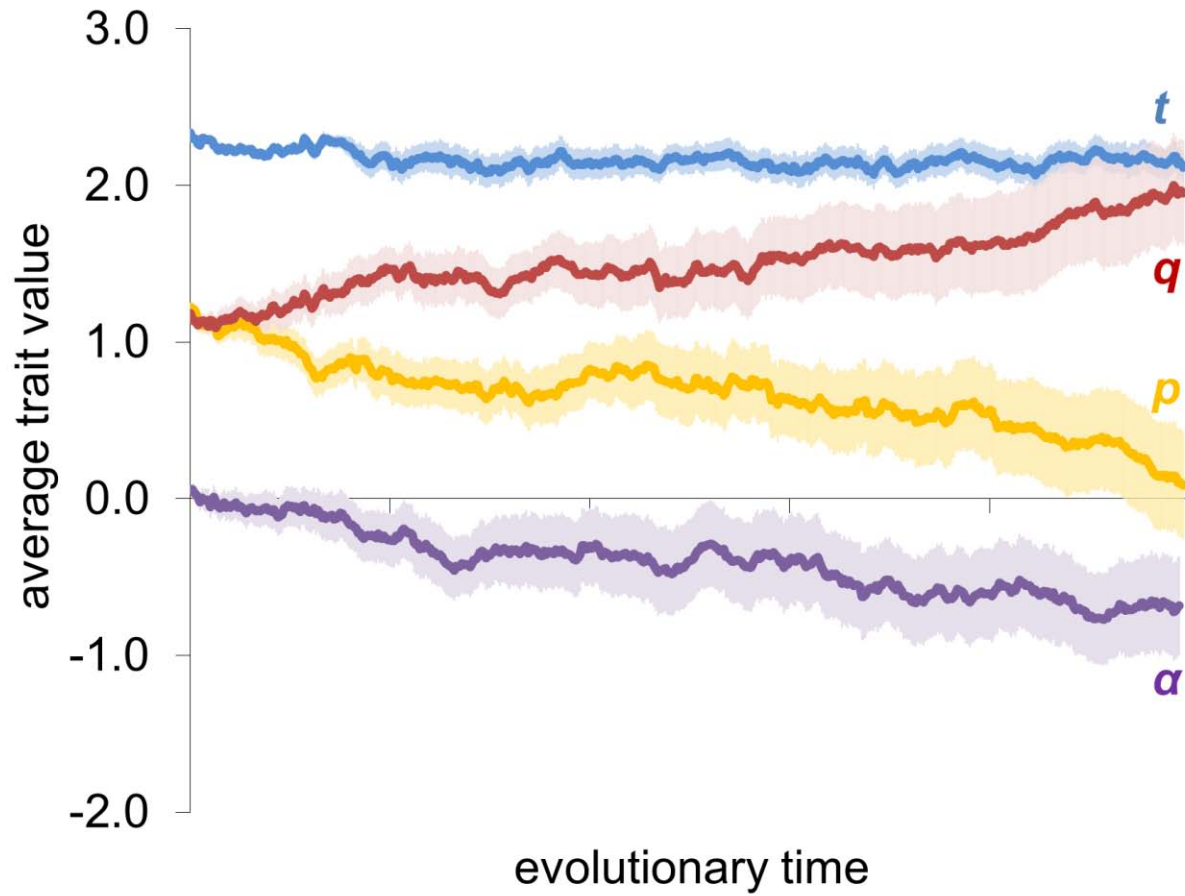
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185 Fig. 1. Parent–offspring conflict over mate choice still emerges when high-quality males pay reduced
186 signaling costs. In this modified version of our model, male survival probability (v_m) is dependent on the
187 genetic value for signaling intensity (t) rather than the expressed trait value (t_e), according to
188 $v_m = \exp -ct^2$. To achieve the same level of trait expression t_e , lower-quality males require a higher
189 value of t (as in our original model) and therefore incur higher survival costs. Means and standard errors
190 over 50 replicate simulations are shown.

191 Fig. 2. Parent–offspring conflict over mate choice still emerges when male quality is not heritable (and
192 therefore not subject to a negative mutation bias). In this modified version of our model, male quality is
193 randomly drawn from a uniform distribution between 0 and 1 at birth. Means and standard errors over 50
194 replicate simulations are shown.
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