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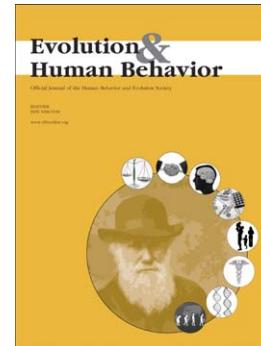
Conflict over resources generates conflict over mate choice: Reply to Smaldino & Newson

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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*  
 59 *al.*, 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  $0.940 \pm 0.001$  [step 1];  $0.937 \pm 0.001$  [step 2];  $0.899 \pm 0.001$  [step 3];  $0.895 \pm 0.001$  [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 alpha 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  
192 Fig. 2. Parent–offspring conflict over mate choice still emerges when male quality is not heritable (and  
193 therefore not subject to a negative mutation bias). In this modified version of our model, male quality is  
194 randomly drawn from a uniform distribution between 0 and 1 at birth. Means and standard errors over 50  
195 replicate simulations are shown.

