



Correspondence

Parent-offspring conflict in mate choice: a commentary on the study by van den Berg, Fawcett, Buunk, and Weissing

In a recent *Evolution and Human Behavior* paper, van den Berg, Fawcett, Buunk, and Weissing (2013) used a computational model to address the problem of how parent–offspring conflict in human mate choice might have evolved. This paper will be referred to henceforth in this commentary as BFBW.

Parent–offspring conflict in mate choice is a uniquely human concern and has important ramifications for understanding our social evolution, yet its existence has only recently been recognized and it remains poorly understood. The problem of understanding its evolution lends itself to analysis through computational modeling. However, the model presented in BFBW relies on a number of unrealistic assumptions. Our analysis of their model design suggests that the paper's conclusion – that the evolution of parent–offspring conflict in mate choice is driven by sibling competition for parental resources in childrearing – is not supported. We describe below the assumptions of a model which we are questioning and propose an explanation for how they generated the results reported in the paper.

Relation between male signaling and mate quality

In the BFBW model, the cost of exhibiting the costly trait (in terms of survival and mating rates), is *higher* for male individuals of higher mate quality. We question this because, as noted by Iwasa and Pomiankowski (1999), “For increasing handicap trait size to increase with male quality to be an evolutionary outcome..., the marginal cost of producing a larger trait must be smaller for individuals with higher quality.” In other words signaling quality must incur a cost which only quality individuals can afford. The BFBW model ignores this well accepted common sense rule of costly signaling.

The evolution of male provisioning ability

A number of traits in the BFBW model are heritable and mutable. Although negative or positive mutation was equally likely for most traits, the male provisioning ability, r_m , was assumed to mutate negatively with three times the likelihood of mutating positively. The authors justify this assumption with the claim that it “is consistent with the idea that most mutations will decrease provisioning ability..., and ensures the maintenance of population-level variation in male provisioning ability” (p. 407).

We find this justification questionable because, although it is true that most genetic mutations are harmful, the resulting negative consequences generally manifest before reproductive age; most mutations are harmful because they interfere with proper development (Wimsatt, 1986). The predominance of harmful mutations should not, in general, contribute so substantially to variance among adults of reproductive age. Moreover, this justification relies on another assumption, which the authors do not address: that the

influences of social learning and cumulative culture, which should stabilize variation in ability (Henrich, 2004; Smaldino & Richerson, 2014), can be ignored.

In the BFBW model, the combination of a high mutation rate with a strong tendency for negative mutations quickly pushes a population under neutral selection toward almost insignificant levels of male provisioning ability. To illustrate this, we ran a simulation with a population of $N = 2500$ asexually reproducing individuals (corresponding to the initial number of males in BFBW's model). We initialized each individual in the population with a trait, r_m , randomly drawn from a uniform distribution between 0 and 1, as in BFBW. We then simulated 50,000 generations of evolution – one-tenth of the length of simulations in BFBW – using the same mutation parameters as BFBW. We found that the mean value of this trait quickly sank from 0.5 to nearly zero, kept only slightly positive through mutation (Fig. 1). Moreover, the population variance on this trait went from 0.0812 at the start to 0.000729 by the end, casting doubt on the claim that a high mutation rate maintained variation in the population.

A negative trajectory on a trait through neutral drift can be countered by positive natural selection. However, as discussed above, positive trait values actually *decreased* male fitness. In short, in the BFBW model, strongly negative selection drove down male provisioning levels so that the average resource contribution to childrearing from partnered males was negligible. This means that nearly all resource contributions related to childrearing came from the focal female's parents. The strong reliance on parental resources for childrearing that is dictated by the model partly explains BFBW's results. More insight can be gained by examining how the model dictates that parents will allocate resources to their daughters.

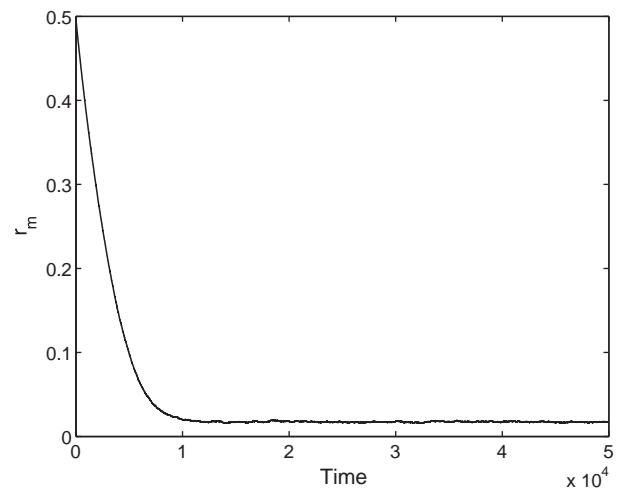


Fig. 1. Neutral selection on male provisioning ability, r_m , using the mutation parameters in van den Berg et al. (2013). Plot shows the population mean, $N = 2500$.

Parental allocation strategies

BFBW initially considers two strategies through which parents unequally allocate resources to their daughters, “augmenting” and “compensatory”. No empirical ethnographic literature was cited to illustrate the use of these strategies. In addition, we are surprised that the authors do not consider the fact that the fitness-optimizing strategy for resource allocation to offspring will vary with the total available resources. An augmenting strategy will be more likely to prevail as resources become scarcer. A compensatory strategy is likely to prevail as resources become more abundant.

More importantly, however, the mathematical specification of the compensatory and augmenting allocation strategies guaranteed the results obtained in the fixed allocation scenario. Consider an example in which a parent has two daughters, such that daughter A’s husband provides her with double the resources provided to daughter B by her husband. Under the compensatory allocation strategy, the parents will allocate *four times* as many resources to daughter B compared to daughter A. The reverse is true for the augmenting allocation strategy (daughter A will get four times more parental resources than her sister). Thus, parental allocation *overcompensates* (or *overaugments*) for disparities in mate-provided resources. In the compensatory allocation condition, selection will favor daughters who choose low quality mates, since this guarantees them more parental resources. Thus, compensatory allocation will select for lower p , and augmenting allocation will select for high p .

BFBW does not include an explanation for why parental preference for their offsprings’ mate quality balances their offsprings’ preferences, leading to consistent values of $(p + q)$. A likely explanation is that because almost all reproductive resources come from parents, parents who have more offspring have to divide those resources more widely. This results in fewer resources – and therefore lower fecundity – per daughter. Strong selection is therefore exerted on parents to have fewer viable daughters. The sum $(p + q)$ therefore remains stable across simulations and q increases among parents who use compensatory allocation. The optimal $(p + q)$ balances the need for having enough surviving daughters to continue the gene line but also few enough so that they remain competitive in terms of resource distribution.

Evolving parental compensation

We showed above that by overweighing the allocation strategies in the fixed allocation runs, the design of the BFBW model inevitably generated the results of differential preferences in parents and offspring. However, in runs of the model which allowed parental allocation strategies to evolve, a compensatory allocation strategy emerged, apparently supporting the conclusion that evolution favors such a parental strategy and thereby yields differential preferences for mate quality between parents and offspring. This result stems primarily from costly female preferences for “high quality” males (even though males provide few resources). The negative relationship between mating success and strong preferences for “high quality” male mates should initially select for lowered preferences in both offspring and parents, which is what was found (BFBW Fig. 3). Because preferences for one’s own mate, p , influence one’s mating success more than preferences for the mate of one’s offspring, q , negative selection will be stronger on p . The proliferation of parents who use an augmenting allocation strategy will be correlated with offspring who favor more attractive mates. Likewise, daughter preferences for less attractive mates will be correlated with parents who compensate them for these choices. All things being equal, however, preferences for lower quality males will have a selective advantage over preferences for high quality males, due to the role of these preferences in mating success. Selection will therefore favor compensatory parental allocation strategies. The disparities between offspring and parental mate preferences will subsequently evolve as discussed above.

Discussion

The problematic assumptions of the BFBW model do not necessarily invalidate its conclusions altogether. We would be interested to see the model run with what we consider to be a more realistic mutation on male provisioning and a more appropriate relation between male quality and signal cost. First, male provisioning ability and its associated indicator trait should incur a positive cost on survival. Second, mutation on male provisioning ability should either be neutral, or the authors should more thoroughly justify their decision to bias mutation on this (and only this) trait so strongly. It is hypothetically possible that the qualitative shape of its results could still hold, but we would be interested in the effect size. We predict that it will be small. Additionally, it would be helpful to see a more thorough analysis of the model with plots illustrating the evolutionary trajectory of male provisioning ability in the full model.

Even if the explanation for parent-offspring conflict in mate choice offered in BFBW were (weakly) supported by a computational model, we would remain skeptical of its external validity. It is implausible that competition for parental resources can be strong enough to create an evolved preference in reproductive age females for mates who will be poor providers of resources as a means of extorting more resources from their parents. Understanding parent-offspring conflict in mate choice, its evolution, and its cultural variation is, as the authors recognize, an important problem for evolutionary science. We suggest two alternative explanations not considered in BFBW.

First, it is well known that human childrearing relies heavily on resources (e.g., food, care, education and, more recently, money) from individuals other than the child’s parents. This includes grandparents but also aunts, uncles, siblings, cousins, friends and, more recently, employees (Hrady, 2009). The mate of a focal female is often observed to provide not only for his own offspring, but also for the offspring of her siblings and cousins. It is possible that some parent-offspring conflict in mate choice may stem from competition between a focal female’s primary concern for her own offspring and her older family members’ concerns for more equal allocation of resources to the children of her siblings and cousins. We have recently presented a modeling framework that incorporates family structure, mate choice, and cooperative breeding (Smaldino, Newson, Schank, & Richerson, 2013), with which such questions may be investigated. A second possibility, not mutually exclusive with the first, is that the institution of parental influence is a group-beneficial trait (Smaldino, *in press*). Parents have wisdom and experience and may simply make better choices that benefit both themselves and their offspring. In this case, the bounded rationality of mate-seeking offspring may be compensated by influence from older family members with shared interests.

Paul E. Smaldino
Center for Advanced Modeling in the Social
Behavioral, and Health Sciences
Johns Hopkins University, Baltimore, MD, USA
E-mail address: paul.smaldino@gmail.com

Lesley Newson
Department of Environmental Science and Policy
University of California
Davis, CA, USA
College of Life and Environmental Sciences
University of Exeter, UK

<http://dx.doi.org/10.1016/j.evolhumbehav.2013.12.003>

References

- Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *American Antiquity*, 69, 197–214.

- Hrdy, S. B. (2009). *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Harvard University Press.
- Iwasa, Y., & Pomiankowski, A. (1999). Good parent and good genes models of handicap evolution. *Journal of Theoretical Biology*, 200, 97–109.
- Smaldino, P. E. (in press). The cultural evolution of emergent group-level traits. *Behavioral and Brain Sciences*.
- Smaldino, P. E., & Richerson, P. J. (2014). Human cumulative cultural evolution as a form of distributed computation. In P. Michelucci (Ed.), *Handbook of human computation*. New York: Springer.
- Smaldino, P. E., Newson, L., Schank, J. C., & Richerson, P. J. (2013). Simulating the evolution of the human family: cooperative breeding increases in harsh environments. *PLoS ONE*, 8(11), e80753.
- van den Berg, P., Fawcett, T. W., Buunk, A. P., & Weissing, F. J. (2013). The evolution of parent-offspring conflict over mate choice. *Evolution and Human Behavior*, 34, 405–411.
- Wimsatt, W. C. (1986). Developmental constraints, generative entrenchment, and the innate-acquired distinction. In W. Bechtel (Ed.), *Integrating scientific disciplines* (pp. 231–273). Dordrecht, The Netherlands: Martinus-Nijhoff.

Conflict over resources generates conflict over mate choice: reply to Smaldino and Newson

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

Relation between male signaling and mate quality

S&N claim that, in our model, males of higher quality pay a higher cost of exhibiting the trait. This is not true. In our model there is no direct relation between male quality (i.e. provisioning ability) and survival cost; instead, a male's survival depends solely on his expression of the indicator trait (t_e). But it is true that for the same genetic value of trait expression (t), we assumed that higher-quality males signal at higher intensity and hence pay higher survival costs. Based on this, S&N conclude that we have ignored the “well accepted common sense rule of costly signaling” that “signaling quality must incur a cost which only quality individuals can afford.” However, standard theory on sexual selection shows that costly preferences can evolve if higher-quality males produce stronger signals for the same genetic value of trait expression (Fawcett et al., 2007; Iwasa, Pomiankowski, & Nee, 1991). This is the form of costly signaling we implemented in our model. That the handicap principle works in this case is evident from the results in Step 1 of our model, which is a standard sexual selection model without parental involvement:

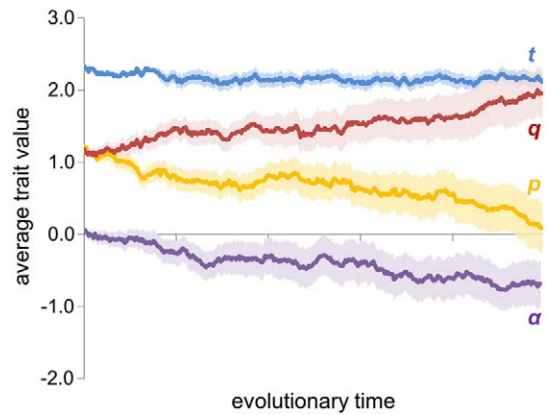


Fig. 1. Parent-offspring conflict over mate choice still emerges when high-quality males pay reduced signaling costs. In this modified version of our model, male survival probability (v_m) is dependent on the genetic value for signaling intensity (t) rather than the expressed trait value (t_e), according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

Fig. 1A in Van den Berg et al. (2013) shows stable exaggeration of a costly female preference for a costly indicator of male quality. More importantly, our findings are robust to the specific assumptions of our model; if we assume, as S&N recommend, that low-quality males pay higher costs of trait expression, we still predict the emergence of parent-offspring conflict over mate choice (Fig. 1).

The evolution of male provisioning ability

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

It is not surprising that male provisioning ability rapidly declines to zero if a negative mutation bias is the only force affecting its evolution (as in S&N's Fig. 1), but in our model this mutation bias is opposed by two selection pressures. First, males of higher quality have more resources to invest in their offspring, and therefore on average obtain higher reproductive success. Second, evolved female preferences for males with a larger indicator trait also favor higher-quality males. As a result, male parenting ability is maintained at high levels in our simulations (averages \pm s.e.m. over the last generation of all replicates: 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 “negligible” contribution to child-rearing. This incorrect assertion appears to be at the root of most of the issues raised by S&N. Nonetheless, to address concerns about our assumptions, we have investigated a modified version of our model without biased mutations (Fig. 2); here, too, we predict the emergence of parent-offspring conflict over mate choice.

Parental allocation strategies

S&N suggest that parent-offspring conflict emerges in our model because the parents' compensatory resource-allocation strategy “overcompensates (or overaugments) for disparities in mate-provided resources.” This is not the case; in Fig. 3 in Van den Berg et al. (2013), where allocation strategies are free to evolve, the onset of

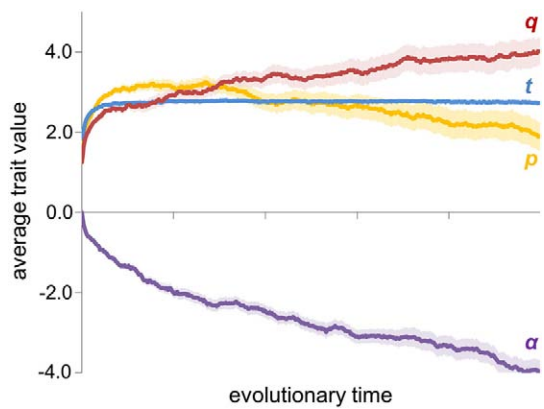


Fig. 2. Parent–offspring conflict over mate choice still emerges when male quality is not heritable (and therefore not subject to a negative mutation bias). In this modified version of our model, male quality is randomly drawn from a uniform distribution between 0 and 1 at birth. Means and standard errors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

parent–offspring conflict already occurs before parents overcompensate (i.e., while the evolved value of alpha is still smaller than -1). This is confirmed by one of the modified versions of our model presented here (Fig. 1), in which undercompensation evolves but the conflict over mate choice is still strong.

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

Evolving parental compensation

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

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

Comparison with other hypotheses

S&N find it implausible that sibling competition for parental resources would be strong enough to weaken the female preference for high-investing mates. Yet there is overwhelming evidence in a range of other contexts that sibling competition is a potent evolutionary force with some striking consequences, including chick begging, siblicide, and genomic imprinting (Kilner & Hinde, 2012;

Roulin & Dreiss, 2012). We maintain that our model provides a potentially valid hypothesis that deserves further attention.

S&N mention two alternative hypotheses for the evolution of parent–offspring conflict over mate choice. The first hypothesis, already alluded to by Trivers (1974), rests on the observation that a female’s mate often provides resources not only to their own children, but also to those of her sisters and cousins. Such behavior seems more beneficial to the female’s parents than to the female herself, so potentially it could lead to parent–offspring conflict over mate choice. This is an interesting hypothesis, but it leads to a new problem: why would males divert resources from their own children to less related family members? S&N’s second hypothesis is that parents are more experienced, and therefore better able to choose a mate for their offspring. This may be true, but it does not explain the conflict; why would offspring disagree if their parents know best?

Our model (Van den Berg et al., 2013) explains, from an evolutionary point of view, why parents and offspring should not necessarily agree over the latter’s choice of a mate. We did not claim that it is the only possible explanation for this conflict, nor even the best one, and we welcome alternative hypotheses as well as constructive criticism of our model. To discriminate between competing hypotheses, it is essential to examine the logic closely and derive clear, testable predictions. Evolutionary computer simulations have a vital role to play in this regard.

Pieter van den Berg
Theoretical Biology Group
University of Groningen, The Netherlands
Evolutionary Social Psychology Group
University of Groningen, The Netherlands

Tim W. Fawcett
Theoretical Biology Group
University of Groningen, The Netherlands
Evolutionary Social Psychology Group
University of Groningen, The Netherlands
Modelling Animal Decisions Group
University of Bristol, United Kingdom

Abraham P. Buunk
Evolutionary Social Psychology Group
University of Groningen, The Netherlands
Royal Netherlands Academy of Arts and Sciences

Franz J. Weissing
Theoretical Biology Group
University of Groningen, The Netherlands
E-mail address: f.j.weissing@rug.nl

<http://dx.doi.org/10.1016/j.evolhumbehav.2013.12.004>

References

- DeAngelis, D. L., & Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36, 147–168.
- Fawcett, T. W., Kuijper, B., Pen, I., & Weissing, F. J. (2007). Should attractive males have more sons? *Behavioral Ecology*, 18, 71–80.
- Fawcett, T. W., Kuijper, B., Weissing, F. J., & Pen, I. (2011). Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *Proceedings of the National Academy of Sciences USA*, 108, 15925–15930.
- Hamblin, S. (2012). On the practical usage of genetic algorithms in ecology and evolution. *Methods in Ecology and Evolution*, 4, 184–194.
- Iwasa, Y., & Pomiankowski, A. (1999). Good parent and good genes models of handicap evolution. *Journal of Theoretical Biology*, 200, 97–109.
- Iwasa, Y., Pomiankowski, A., & Nee, S. (1991). The evolution of costly mate preferences: II. The “handicap” principle. *Evolution*, 45, 1431–1442.
- Kilner, R. M., & Hinde, C. A. (2012). Parent–offspring conflict. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 119–132). Oxford, UK: Oxford Univ Press.

- Kokko, H. (2007). *Modelling for field biologists and other interesting people*. Cambridge, UK: Cambridge Univ Press.
- Kotiaho, J., LeBas, N. R., Puurtinen, M., & Tomkins, J. L. (2008). On the resolution of the lek paradox. *Trends in Ecology and Evolution*, 23, 1–3.
- Kuijper, B., Pen, I., & Weissing, F. J. (2012). A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 287–312.
- Peck, S. L. (2004). Simulation as experiment: a philosophical reassessment for biological modeling. *Trends in Ecology and Evolution*, 19, 530–534.
- Pomiankowski, A., Iwasa, Y., & Nee, S. (1991). The evolution of costly mate preferences: I Fisher and biased mutation. *Evolution*, 45, 1422–1430.
- Roulin, A., & Dreiss, A. N. (2012). Sibling competition and cooperation over parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 133–147). Oxford, UK: Oxford Univ Press.
- Smaldino, P. E., & Newson, L. (2013). Parent–offspring conflict in mate choice: a comment on Van den Berg et al. *Evolution and Human Behavior* XXX, XXX–XXX.
- Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist*, 14, 249–264.
- Van den Berg, P., Fawcett, T. W., Buunk, A. P., & Weissing, F. J. (2013). The evolution of parent–offspring conflict over mate choice. *Evolution and Human Behavior*, 34, 405–411.
- Van Doorn, G. S., Edelaar, P., & Weissing, F. J. (2009). On the origin of species by natural and sexual selection. *Science*, 326, 1704–1707.
- Van Doorn, G. S., & Weissing, F. J. (2004). The evolution of female preferences for multiple indicators of male quality. *American Naturalist*, 164, 173–186.
- Van Doorn, G. S., & Weissing, F. J. (2006). Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist*, 168, 742–757.