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Commentary

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

Paul E. Smaldino^{a,*}, Lesley Newson^{b,c}^a Center for Advanced Modeling in the Social, Behavioral, and Health Sciences, Johns Hopkins University, Baltimore, MD, USA^b Department of Environmental Science and Policy, University of California, Davis, CA, USA^c College of Life and Environmental Sciences, University of Exeter, UK

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ABSTRACT

van den Berg, Fawcett, Buunk, and Weissing [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] have recently presented a model purporting to explain the evolution of parent-offspring conflict in human mate choice. We show that their model's behavior stems from a number of problematic assumptions and does not yield a satisfactory explanation of the evolution of this human behavior.

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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.

* Corresponding author. Center for Advanced Modeling in the Social, Behavioral, and Health Sciences Johns Hopkins University, Baltimore, MD 21209, USA.

E-mail address: paul.smaldino@gmail.com (P.E. Smaldino).

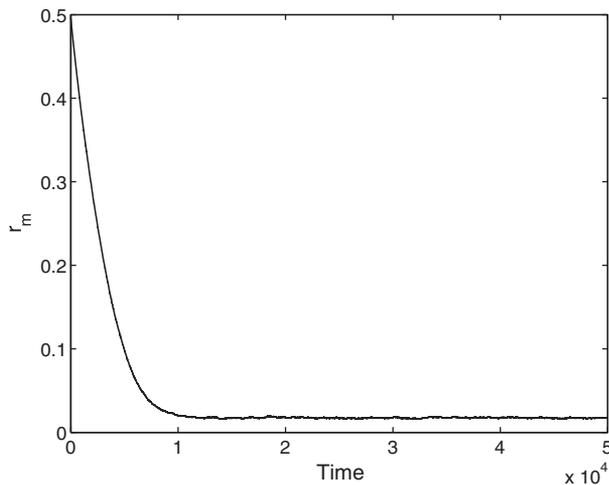


Fig. 1. Neutral selection on male provisioning ability, r_m , using the mutation parameters in van den Berg et al. (2013). Plot shows the population mean, $N = 2500$.

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 child-rearing 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.

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 (Hrdy, 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.

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