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Invited Commentary

Assumptions, models and data: a comment on Richardson and Zuk

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To test theoretical models (e.g. Kokko and Mappes 2005) and allied verbal arguments, Richardson and Zuk (2022) (RZ) conducted a meta-analysis to see if virgins are less choosy than mated females when presented with potential mates. Spoiler alert: they found no statistically significant difference. This is reassuring as most experimental mate choice studies either use only one type of female or ignore female mating status. Nonetheless, RZ raise questions about how to test theory using meta-analysis.

First, testing for within-species differences using across-species comparisons is risky. Researchers might be more likely to use mated females in species where they are known, or assumed, to be choosy (e.g. due to cumulative material benefits to mate choice). More generally, confounding inherent differences among species could obscure the true effect of mating on female choosiness. Ideally we need within-species, or even within-study, effect sizes from females randomly assigned as virgin or mated. Experimental studies that compare the choosiness of such females exist (e.g. Aich et al. 2020), but are rare (RZ, Figure 3).

Second, can we generalize from RZ's datasets? Female choosiness was based on avoiding: 1) hybrid mating (e.g. heterospecifics males); 2) close relatives; 3) males with STDs. However, hybridization often leads to maladapted or non-viable offspring, strongly selecting for choosiness, even by virgins; evidence for mate choice for inbreeding avoidance is weak (de Boer et al. 2021), and theory predicts that inclusive fitness can favor inbreeding (Kokko and Ots 2006); and while a potentially valid test, the data set for avoiding males with STD is small (n = 16 studies) so the meta-analysis is underpowered. Also, STDs could elevate male mating effort (a "terminal investment"), which might confound simple predictions that females should avoid infected males. For example, parasitized stickleback can, albeit briefly, be redder and more attractive than healthy males. RZ acknowledge some of those limitations, and we agree that a meta-analysis of mate choice for ornaments or body size would be a better test of theory.

Third, in the "trade-up hypothesis" modeled by Kokko and Mappes (2005), virgins are less choosy because remaining unmated carries a cost in terms of lost opportunities to reproduce. In contrast, mated females can start to produce offspring, but improve on their previous mate's quality by being choosier when remating. As RZ note, however, the hypothesis has some key assumptions. For example, in external fertilizers even non-virgins must mate to fertilize each new batch of eggs. Consequently, changes in choosiness based on risking the failure to breed cannot apply. Moreover, the trade-up hypothesis cannot be tested with data from simultaneous choice experiments (e.g. two choice tests). Choosing the highest quality male does not elevate the risk of remaining unmated. There is no trade-off between mate quality and fertilization insurance, hence no expectation that virgins and mated females will differ in their choice. Even if mated females more often refuse the available males than do virgin females, this is not captured by effect sizes that only use data from "successful" trials where a choice was made. This undermines RZ's statement that "in no-choice designs both virgin and mated females may anticipate a lower chance of remating *which may reduce any differences between them in mate choice* [emphasis added]". We suggest that the trade-up hypothesis only applies to data from no-choice experiments in internal fertilizers. If so, RZ should present the analysis with the most suitable dataset available.

Another key assumption of Kokko and Mappes's (2005) model is that a female can produce offspring as soon as she mates for the first time, and at a rate that is independent of the duration of her pre-mating period. Any delay in mating is costly as it lowers lifetime offspring production. There are, however, species with life histories that mitigate such costs. For example, when females mate long before breeding commences, then virgins can be choosy without delaying the onset of reproduction. Similarly, if females use the pre-mating period to acquire resources that elevate fecundity, they may end up with the same fecundity as a less choosy, earlier mating counterparts. This could weaken selection on virgins to mate quickly and indiscriminately. In sum, RZ have identified a neglected topic and provided a valuable meta-analysis. But to build on their findings we need: 1) new theoretical models that explore how varying key assumptions of existing models alter predictions; and 2) to then test them using more targeted datasets.

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