incomplete—and potentially even misleading—understanding of how female choice decisions play out in the real world. In addition, Richardson and Zuk's (2022) review touched on the potential role of male mating behaviors in mediating the response of virgin and non-virgin females. Here, we extend on this discussion by delving more deeply into the importance of male mating status and male reproductive strategies, and how these, in turn, might interact with female mating status to affect female choice outcomes.

MALE EXPERIENCE MATTERS

Like female experience, male mating history can also affect female choice. In general, females might prefer non-virgin males because of the potential advantages of mating with a sexually experienced partner that can provide females with better resources. For example, in the nereidid polychaete *Neanthes acuminata*, females prefer males with a more extensive mating history as experienced males were better fathers (Fletcher et al. 2009). Also, while virgin males might be more invested in their mating effort, experienced males are often more successful in mating (Aich et al. 2021). In contrast, males with a higher mating history might become sperm-limited, and mating with them could lower female fertilization success. In such cases, females should benefit by discriminating against non-virgin males, as demonstrated, for example, in the European grapevine moth *Lobesia botrana* (Muller et al. 2016). Therefore, in the context of female mating history, virgin and non-virgin females could differ in their mating preferences based on male mating history. Thus, we recommend that future studies, ideally, should focus on teasing apart both male and female mating history, either experimentally or statistically, to determine how they might interact to influence female mate choice (see Aich et al. 2020).

AND MALE BEHAVIORS TOO

The effects of female mating status on her mate choice decisions are also expected to be affected by male mating strategies. As mentioned in Richardson and Zuk's (2022) review, males could benefit from mating with virgin females if virgins are more receptive, and, in pursuing such females, males end up achieving higher fertilization success. Thus, if virgin females are preferred by males, then this could lead to more mating effort being directed by males toward virgin females. For instance, in the terrestrial isopod *Armadillidium vulgare*, males prefer virgin over mated females, even if the latter are infested with parasites (Fortin et al. 2018). Indeed, emerging evidence suggests that males do adjust their mating behavior based on female mating status. For example, in species with alternative reproductive tactics, such as guppies *Poecilia reticulata*, males engage in more courtship behaviors toward virgin females, but direct more coercive, sneaky copulations toward non-virgins (Guevara-Fiore et al. 2009). Such biases in male mating behavior toward females differing in mating status could potentially result in variation in female mate perception, preference, and, ultimately, mating opportunities. Unfortunately, only a handful of studies have looked at the effect of female mating status on male mating investment, especially in vertebrates. Here, there is scope for future studies to test the effects of female mating experience on male mating strategies in a broader range of taxa. Results from such studies will help us to better understand the substantial variation in mating preferences in both virgin and non-virgin females.

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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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Keeping the Virgin in her niche: a commentary on Richardson and Zuk

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ONE MATING DOES NOT A CHOOSER MAKE

Richardson and Zuk (2022)'s important and novel study calls attention to a widespread problem with mate-choice studies. They argue that by excluding subjects with a mating history, studies of female mate-choice may misrepresent the strength and direction of female mate preferences and therefore their influence on mating outcomes.

The authors followed several theoretical models and prominent empirical papers to predict that virgin females should be less choosy than non-virgins, and thoroughly tested this prediction with a comprehensive meta-analysis. The data failed to show an effect of mating status (virgin/non-virgin) on choosiness, which the authors attributed partly to confounding effects of age and experience.

Indeed, whether a female has experienced a mating or not is part of a broader spectrum of variation in female physiology and social experience that shapes not only how females make sexual decisions, but the fitness consequences of those decisions. All reproductive females were once virgins, and one's first mating is simply one facet of her history. The importance of that first mating to female lifetime fitness varies from one species to the other, as do the constraints and consequences of (not) being choosy.

Accordingly, mating status may often be secondary to a host of other factors that affect choosiness but do not involve mating. Typical measures of choosiness are confounded with boldness and exploratory behavior (David and Cézilly 2011). As predicted for both mate-searching and general risk-taking, choosiness is sensitive to ecological factors like nutritional condition and predation risk. Choosiness and preference are also ubiquitously influenced by social experience before and after maturity (Rosenthal and Ryan 2022).

MATING STATUS IS CONFOUNDED WITH SOCIAL EXPERIENCE

Social interactions outside of mating can have extreme effects on mate-choice phenotypes. Remarkably, the same experiences can