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

have opposite effects on preferences and choosiness in sister species (Verzijden et al. 2012) or even recently diverged populations (Bailey and Zuk 2012). Females that have never mated will inevitably have different social experiences than mated females, confounding what we mean by "virgins".

We need to pay close attention to how studies are "making virgins". Has a "virgin" female had sexual experience—without gamete transfer—in the past? How are females prevented from mating? Publications often omit details. In poecilid fishes, standard practice is to collect fry early in life and raise age cohorts, while removing males that show signs of maturity. Females therefore grow up lacking social experience with males or indeed any adults.

Experimental evidence suggests social experience, rather than mating status, may play a primary role in females' failure to be choosy. Delclos et al. (2021) raised age cohorts of swordtails (*Xiphophorus birchmanni*) with and without visual and olfactory cues of adults during ontogeny—but prevented from mating. Females from age cohorts without adult experience had smaller brains and failed to develop preferences for conspecific mate-choice. "Making virgins" may yield individuals with especially impoverished social and environmental experience relative to their wild counterparts.

ARE VIRGINS REALLY THAT SPECIAL?

The expectation that females should be less choosy about their first mating, and indeed that a single mating marks a fundamental change in status, holds true only for some systems. Male mate-choice, density changes, and shifting operational sex ratios mean that females often have more opportunity for choice earlier in a breeding season. The fitness consequences of mate-choice—even of preferring conspecific or unrelated males—can also often hinge on dynamic ecological variables that have nothing to do with mating status (Rosenthal and Ryan 2022). The first mating itself may be relatively unimportant not only as a proximate trigger to changes in choosiness, but also as a source of variation in fecundity.

Just as human experience biases our expectations of inbreeding avoidance (Dorsey and Rosenthal 2022)—another mate-choice phenomenon not supported by thorough meta-analyses—so too does the human fixation on female virginity (Hastrup 1993). Females are more than their mating status, and working with virgin or mated females is only one of the many aspects to consider in mate-choice research. The authors used *virgin* for clarity and convenience, but perhaps it is time to retire a term (along with *easy*, while we are at it) whose emotional and social valence in human society may overinflate its importance across animals.

By focusing on a single event, we dismiss how mate-choice mechanisms and the fitness consequences they generate are dynamic over the course of individual life-histories. The conceptual leap suggested by Richardson and Zuk is to start thinking about female mating decisions over their lifetimes, where the first mating—the "loss of virginity"—is just one discrete milestone in a lifetime of experiences and sexual interactions.

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The value of *not* trusting intuition: a response to comments on Richardson and Zuk

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We are grateful for the five commentaries on Richardson and Zuk (2022). We are encouraged to see that others find the topic of female mating status in studies of female choice to be a valuable and interesting one.

Our meta-analysis found no evidence that virgin females were less choosy than mated females. However, as several comments point out, this result does not call for researchers to happily ignore female mating status in mate choice studies. After all, absence of evidence should not be taken as evidence of absence. We agree with those commenters who point out that (1) differences between virgin and mated females will differ among systems and (2) myriad other factors besides virginity influence female choosiness. For example, Pärssinen and Kvarnemo (2022) point out that virgin females may be less choosy in systems where females compete for males. Meanwhile, Fascinetto-Zago and Rosenthal (2022) highlight the importance of social experience which is often confounded with mating status.

It was also not our goal to settle the question of whether future studies of mate choice should use virgin or mated females. As pointed out by Dougherty (2022), this decision ultimately relies on testing (and then publishing!) the effects of female mating status in a given species. Our suggestion that researchers should choose females that are the most ecologically relevant rather than relying on conventional wisdom is perhaps unsatisfying, but we see little alternative. Parssinen and Kvarnemo (2022) offer a useful suggestion for dealing with the problem of female mating status: use large numbers of wild-caught females that represent the best sample of who is doing the choosing.