

choice because, even though all prospective mates might satisfy this criteria, the individual still invests resources in mate assessment. Crucially, this is not merely a technical nuance that can be dismissed. It is biologically relevant to consider that the expression of a low acceptance threshold will still entail mate assessment because this represents a cost of choice.

For this reason, I suggested depicting variation in a threshold, or other horizontal variation in a preference function, as “what” is preferred rather than by “how much” it is preferred, the latter being represented in the slope of a preference function (Edward 2015). When a threshold is lowered, the proportion of prospective mates that satisfy acceptance criteria is increased because the criteria defining “what” is preferred becomes relaxed. This is why mating rate can increase. Yet, when an acceptance threshold shifts, the slope of the preference function remains unchanged. The choosing individual remains equally and absolutely strict in not accepting any mates that fall below a threshold, irrespective of its value.

K&J suggest a pragmatic approach to describing an individual as nonchoosy would be to define a frame of reference, such as when all members of the opposite sex exceed a mating threshold. I would question this for a number of reasons. First, as described above, an individual expressing even a low threshold will still assess prospective mates, a biologically important cost of expressing choice. Second, unless the height of the preference function above the threshold is permitted to vary (e.g., Fitzpatrick and Servedio 2015), this definition unnecessarily restricts nonchoosy individuals to accepting every prospective mate. Third, this approach cannot be universally applied to all preference functions, for example, when defining an absence of mate choice relative to choice expressed as a unimodal curve. Finally, using an arbitrary frame of reference to describe the absence of choice could exacerbate confusion. This is because a different frame of reference would be relevant to different studies. Although the exemplified frame of reference is relevant to studying intersexual mate choice within a species, an alternative would be appropriate when, for example, studying mate choice among distinct geographic or demographic populations, in the context of same sex sexual behaviour or in the context of interspecific mate choice.

All these shortcomings can be overcome by adopting a very simple definition for the absence of choice: a flat preference function across all trait values (Edward 2015). K&J make the point that a complete absence of mate choice is untenable as all individuals will ultimately not attempt to mate with all animate and inanimate objects. A truly flat preference function might then be considered a technical nicety. However, although all individuals will show choice over at least some traits, it does not follow that choice will be expressed for all possible traits. A truly flat preference function is therefore not merely a theoretical and technical nuance but both a practical and biologically pragmatic benchmark to describe the absence of choice.

The key issues that seem to distinguish our alternative perspectives are 1) the parameters of a preference function that are used to describe choice and 2) the terminology associated with these parameters. K&J highlight the value of an acceptance threshold to describe choice, attaching labels of “choice” and “choosiness” to this parameter. I agree that an increased threshold will, all else being equal, reduce the number of accepted mates. By attaching the labels of “choice” and “choosiness” to this variation, these terms might then be interpreted the same. However, I would argue that using these labels is confusing when the expression of even a very low threshold necessarily incurs costs of mate assessment, and variation in this

parameter of a preference function will never produce a truly flat preference function. For these reasons, I would strongly advocate that, in addition to the threshold or any other horizontal variation in a preference function, we should also recognize variation in the slope of a preference function. I have suggested an approach to describing mate choice in which horizontal variation in a preference function is termed “preference” and variation in the slope of a preference function is termed “choosiness” (Edward 2015). Perhaps this is not the best answer, but there is still a valid question. If not “choosiness,” what label should we reserve for describing variation in the slope of a preference function?

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Mate choice and mating decisions: a response to comments on Dougherty & Shuker

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We would here like to respond to several invited commentaries on our recent review (Dougherty and Shuker 2015). We would like to start by thanking all the authors for their wide-ranging comments and Edward (2015) for his much-needed synthesis of descriptions of mate choice.

Rowe and Arnqvist (2015) highlight the fact that the role of mate rejection costs in generating the difference in preference between choice and no-choice designs still needs to be demonstrated empirically. We agree that although many studies showing reduced choosiness at low encounter rates in a no-choice setting do give some support for this assertion, convincing measures of rejection costs remain elusive. We suggest that in some systems, it may be possible to simulate a high mate encounter rate prior to a trial, so that subjects become choosy even in a no-choice setting as the cost of rejection becomes comparable to choice designs. An alternative may be to explore in more detail the proportion of females that fail to find a mate (e.g., Rhoads 2010). Indeed, failure to be inseminated may be more common than we think although quantifying it in a way that controls for various other ecological variables may well remain challenging.

Kokko and Jennions (2015) suggest that the lack of a significant difference in the strength of mating preferences between males and females in our sample may be due to research bias. If

there is a tendency for mate choice experiments (in either sex) to be performed only in those species for which choice is likely and/or apparent, then this is not a truly representative sample. This is an important point and highlights a common problem with meta-analysis. Moreover, no-choice studies may be more likely to include sexually nonresponsive subjects, as these tend to be removed prior to analysis of choice tests (Kokko and Jennions 2015). We surveyed the studies in our review and found that this was the case in 8 of 38 studies. This number is perhaps lower than expected, for at least 2 reasons. First, several of the studies in our sample considered mating frequency as the preference outcome, and thus, nonreceptive individuals are in a sense “included” in the analysis. Second, in many studies, all subjects used in choice trials did make a choice, although in most cases this was not stated explicitly but had to be inferred from the methods and results. Repeating our analysis after removing these 8 potentially problematic studies (leaving 162 effect sizes) did not significantly alter our overall results: preferences were still significantly larger when tested using a choice design compared with a no-choice design (weighted least-squares regression, study and species as random effects, main effect of paradigm: $F_{1,125} = 10.01$, $P = 0.002$).

No-choice designs may underestimate the strength of mating preferences in species in which multiple mates are encountered simultaneously, such as lek-breeding species (Kokko and Jennions 2015; Ryan and Taylor 2015). However, in many of the species included in our sample, good data on the ecology of mate encounter are sorely lacking, and in these cases, we suggest that a no-choice design should be considered a null hypothesis (we would also rather underestimate the strength of selection than overestimate it). Moreover, it still needs to be shown empirically that comparative evaluation occurs in these species: the potential for comparison is not enough. In some species, mate assessment may be sequential even when simultaneous comparison is possible (e.g., see Gibson 1996).

This brings us on to a potential cognitive explanation for the difference in preference strength seen in the 2 designs. Ryan and Taylor suggest that the cognitive processes used in making mating decisions may differ between choice and no-choice scenarios. We would agree that this is likely to be the case in some species, but we caution about generalizing across all taxa and making a priori assumptions about cognitive mechanisms. This is particularly true given the large variation in both the animals doing the choosing and, as Ryan and Taylor note, the stimuli being chosen in each case. Such variation is why we have tended to prefer an ecological explanation (the costs of mate rejection) for the differences seen between choice designs. That said, the role of cognition in sexual selection, both as a target of sexual selection and as a facilitator of mate choice, is receiving increasing attention. However, behavioral ecologists need to be wary of how they measure “cognition” and how

they interpret their findings: generalized “cognition” tests may not prove informative in the context of sexual selection (Rowe and Healy 2014).

For us, many of these comments highlight that the links between mate sampling and mate choice remain underdeveloped. The laboratory has proved a successful testing ground for many aspects of sexual selection theory, but we typically struggle to replicate meaningful mate-sampling problems. This moves the onus onto field studies, but in many cases, serious logistical problems still often arise. Leks may provide some of the best opportunities for studies of mate sampling in the field, but one might argue that even leks are going to be unrepresentative of most situations in the field. Instead, we need more empirical studies of the ecology of mate choice (e.g., Deb and Balakrishnan 2014). These studies would also inform inferences about cognitive mechanisms of choice. The distinction between encountering one mate or many is a simple one, but there are many other factors that may be important (such as the time available for assessment: Ryan and Taylor). However, we need to face up to these difficulties and design studies that test both mate sampling and mate choice theory. Reid and Stamps (1997) provide an inspiring illustration of what one can achieve.

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