



Invited Commentaries

Two research avenues for future mate-choice copying studies: a comment on Davies et al.

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Since the early 1990s, when Pruett-Jones (1992) revised and formally defined the concept of mate-choice copying, this type of nonindependent mate choice has been consistently studied and a handful of experimental, theoretical, and conceptual works has been published every year. The accumulated amount of experimental studies is now allowing researchers to use meta-analytical methods to characterize mate-choice copying both in humans (Gouda-Vossos et al. 2018) and in nonhuman animals (Jones and DuVal 2019; Davies et al. 2020). The literature search of the two meta-analyses in nonhuman animals was carried out 1 month apart, showing that many researchers in the field today consider this analysis necessary. And, because the two studies show enough methodological differences, both are useful and complementary. Additionally, Davies et al. (2020) consistently discuss their results with those of Jones and Duval (2019), guiding the reader toward the nuances of both studies that, otherwise, could be confusing.

Davies et al. (2020) found two factors influencing significantly mate-choice copying across studies: the taxonomic group and the design type. For the taxonomic group, the effect of mate-choice copying is stronger in mammals and progressively less strong in birds, fish, and arthropods. Given that mate-choice copying is a form of social learning, this result may indicate general cognitive differences between taxonomic groups, but the authors caution against the overinterpretation of the data given the still small number of species that can be analyzed by group. Indeed, most studies on mate-choice copying have only been carried out on a small number of species, so it is still difficult to understand what factors—ecological, social, or cognitive—really affect the occurrence and strength of this behavior.

Regarding design type, Davies et al. (2020) show that mate-choice copying is stronger when focal individuals can make an initial choice before the demonstration (the “before-and-after” design) compared to when they can only choose after the demonstration (the “no pretest” design). This is important information to be considered by researchers in future experiments; however, it is also relevant to point out that most studies of mate-choice copying in

arthropods use the “no pretest” design, and they are also found to be the less prone to copy by the authors. Given that the taxonomic group and the design type were analyzed in separate meta-analytical models, it is not possible to rule out the hypothesis that these two moderators are dependent on each other.

Meta-analyses are extremely important tools to point out where research is lacking and Davies et al. (2020) propose two research avenues for future studies: how mate-choice copying operates within a species and how widespread it is across taxonomic groups. We believe that these are indeed relevant recommendations and would like to expand on them. The first avenue leads to using model species, taking advantage of the tools available for them, to more deeply understand the mechanisms affecting the occurrence and strength of mate-choice copying. It implies using new designs adapted to the specific questions being asked. The second avenue leads to using nonmodel species with contrasting ecologies and life histories to investigate the factors that could predispose mate-choice copying evolution. It should imply using standard designs to make the results of different species more comparable. For example, the first study of mate-choice copying in the model species *Drosophila melanogaster* (Mery et al. 2009) uses, in one of its experiments, the standard before-and-after design only with the setup adaptations to a small animal as the fruit fly. Its second experiment and the studies that were published subsequently are about how mate-choice copying operates within the species and so use design adaptations to answer specific questions, such as mate-choice copying generalization (Mery et al. 2009), sperm depletion (Loyau et al. 2012), conformity (Danchin et al. 2018), costly variants (Nöbel et al. 2018), and neuronal mechanisms (Monier et al. 2018), among others.

More studies following these two research avenues would greatly help future meta-analyses to better characterize the occurrence, strength, and mechanisms of this fascinating behavior across species. Moreover, because mate-choice copying is likely to generate cultural evolution (Danchin et al., 2018) and affect the diversification processes of populations and species (Varela et al. 2018), studies are also needed to help characterize its evolutionary potential.

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First evidence for a significant effect of the regression to the mean fallacy in mate copying: a comment on Davies et al.

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Davies et al.'s (2020) meta-analysis on mate copying shows a series of suggestive, interesting results. Here, we elaborate on their discussion by emphasizing two conceptual points and one technical point.

“MATE-CHOICE COPYING” OR “MATE COPYING”

The widespread distribution of mate copying suggests an ancient origin or multiple convergent evolutions, raising the question of its benefits. These benefits are tightly linked to the deep nature of the information provided by the demonstration. The classical view is that the information lies in the choice of the demonstrator. Hence, its usual name of mate-choice copying. However, as already suggested (Wagner and Danchin 2010), we think that the information in fact lies in the performance of one male—and not the other(s)—in copulating

with other females. We, thus, prefer calling it mate copying, a term that avoids putting the stress on the demonstrator female's choice.

THE TWO FORMS OF MATE COPYING

We agree with Davies et al. (2020) that it is crucial to distinguish two forms of copying. Females can learn to prefer (or avoid) a given male over another: this is individual-based mate copying. Although interesting, this basic form of mate copying has limited evolutionary impacts as it only persists for as long as the individual males survive. Females may rather learn to prefer any male with a given trait: this is what Davies et al. (2020) call generalized copying, although it is more appropriate to call it trait-based mate copying (Bowers et al. 2012). Only trait-based mate copying can lead to the emergence of persistent cultural traditions that can affect sexual selection and evolution over generations. We recommend incorporating this distinction into future studies on mate copying.

DAVIES ET AL.'S RESULTS MAY REVEAL THE EFFECT OF THE REGRESSION TO THE MEAN IN BEFORE-AND-AFTER DESIGNS

Although technical, a nice result of Davies et al. (consistent with Jones and DuVal 2019) is their finding that “before-and-after” designs lead to stronger copying than “no pretest” designs. A biological explanation may be that social information is more striking to the observer when it contradicts the observer's prior preference or that observers may be cognitively “turned on” by the pretest, leading to better learning scores. However, here, we would like to provide a purely technical explanation. There are two kinds of before-and-after designs: the male that receives positive information during the demonstration is decided by the experimenter either a priori (before-and-after-a) independently from the result of the first preference test or only after (before-and-after-b) the first test so that demonstrations are positive for the male that was nonpreferred during the first test. Both of these designs, and particularly so before-and-after-b, are subject to the regression to the mean (RTM) statistical fallacy that is rampant as soon as the same individuals or lineages are tested twice (Danchin et al. 2014).

RTM emerges when the same measurement occurs twice per entity, which is the case in before-and-after designs. These measurements have a certain distribution with a mean and a norm (the most common value). Pick a first measurement with an extreme value (large or small) and draw the second measurement randomly from that distribution. This second measurement will tend to be closer to the most common value (usually close to the mean) just for purely statistical reasons. This generates a placebo effect in that, after an extreme value of, say, cholesterol that you measured in the first step, the second measurement is now closer to normal (and healthy), independently from any treatment, just by chance. In the treatment group that received a drug, or saw a demonstration, part of the change, thus, results from the treatment (a drug against cholesterol or the demonstration) but another part will be due to the RTM effect.

In the case of mate copying, RTM occurs when females that have shown, by chance, a strong preference for a given option is tested again after a demonstration providing positive information for the other option to assess any reversal in her preference. Because the first preference would be stronger than expected, the after-demonstration preference will seem to show some reversion even in the absence of any effect of social information.