## Forum

## Mate choice copying and mate quality bias: are they different processes?

## Klaudia Witte<sup>a</sup> and Jean-Guy J. Godin<sup>b</sup>

<sup>a</sup>Department of Biology and Didactics, University of Siegen, Adolf-Reichwein-Strasse 2, D-57068 Siegen, Germany and <sup>b</sup>Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada

Mate preferences can be highly variable within populations (Andersson 1994; Jennions and Petrie 1997). Part of this variation is owing to flexibility in mating preferences expressed by individuals during their lifetime (Jennions and Petrie 1997). Of increasing interest over the past 2 decades has been the potential role of individual social experiences underlying such flexibility in mate choice decisions (e.g., Gibson and Höglund 1992; Dugatkin 1996; Witte 2006). It is now well established that individuals can acquire social information from conspecifics about potential mates, which can subsequently influence their choice of mates and lead to nonindependent mate choice (e.g., Pruett-Jones 1992; Dugatkin 1996; Westneat et al. 2000; Witte 2006). One form of nonindependent choice is mate choice copying (Wade and Pruett-Jones 1990; Dugatkin 1992, 1996; Gibson and Höglund 1992; Pruett-Jones 1992; Westneat et al. 2000; Witte 2006).

Although there has been some disagreement and confusion over which phenomena or processes constitute mate choice copying, it is now generally accepted that mate choice copying is operationally a form of nonindependent mate choice resulting from social learning, in which an individual gains social information about potential mates by observing sexual interactions between nearby male and female conspecifics and uses this learned-association information later in choosing a mate. Mate choice copying is considered to have occurred if a focal individual's observation of a sexual interaction between a male and a female increases its likelihood of subsequently preferring or rejecting the individual observed mating (Pruett-Jones 1992; Dugatkin 1996; Kraak 1996; Westneat et al. 2000; Witte 2006). Mate choice copying can be exhibited by females and males, but it appears to be more prevalent in females (Dugatkin 1996; Westneat et al. 2000; Witte 2006). Therefore, we restrict our consideration here to mate choice copying by females.

A sexual interaction between a male and a female produces cues (arising from the male, the model female, or from the interaction between the model female and the male) that, if perceived by a nearby focal female, could result in a change in the probability that she accepts that particular male as a mate (Kraak 1996; Westneat et al. 2000). There are a number of potential mechanisms of how such cues could produce a change in that probability; these mechanisms can be broadly categorized into either nonindependent choices via nonlearned responses or nonindependent choices via learning (Kraak 1996; Westneat et al. 2000). The weight of empirical evidence indicates that mate choice copying best corresponds to an associative learning (association to male) mechanism, wherein a focal female associates a cue from the model female

© The Author 2009. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oxfordjournals.org with the accepted or rejected male involved. Subsequently, the focal female's likelihood of mating with that particular male is changed, even if the cue is no longer present (Westneat et al. 2000).

In their Forum article, Vakirtzis and Roberts (2009) proposed a new term for a nonindependent mate choice strategy, which they assert differs from mate choice copying. They coined the term "mate quality bias" to describe a process whereby the quality of a prospective male mate is assessed by an observer (copier) female not based on the number of females that male had previously attracted but on the quality of females he had attracted, and subsequently she uses this social information to choose a mate. Vakirtzis and Roberts (2009, p. 908) maintain that this particular process "fits into neither the definition nor the theoretical framework of mate choice copying" and that it should therefore be distinguished from the process of mate choice copying. We respectfully disagree. We question whether the proposed new term "mate quality bias" actually describes a new mechanism of nonindependent mate choice that is fundamentally different from that of mate choice copying. In other words, does this new term offer a new understanding of the mechanism(s) of nonindependent mate choice in females in general? We argue below that it does not.

The proposed "mate quality bias" term of Vakirtzis and Roberts stems from their interpretation of a paper by Hill and Ryan (2006), who interpreted their findings in the context of mate choice copying. In their study, Hill and Ryan gave (observer) sailfin molly females (Poecilia latipinna) a binary choice between 2 conspecific males as potential mates. One of the males was viewed interacting with the gynogenetic hybrid species, the Amazon molly (Poecilia formosa), whereas the other male was viewed interacting with a conspecific P. latipinna female. Subsequently, sailfin molly females preferred to associate with males that they had previously seen interacting with a conspecific female. Although Hill and Ryan (2006) interpreted their result within the context of mate choice copying, Vakirtzis and Roberts propose an underlying mechanism which they claim is different from mate choice copying to explain the findings of Hill and Ryan (2006). Vakirtzis and Roberts argue that, in this case, P. latipinna females based their mate choice decision exclusively on the perceived quality of the model female (i.e., a conspecific model female = high quality; conversely, a heterospecific model female = low quality) observed consorting with a male. In their opinion, this process is different from mate choice copying and, therefore, a new term "mate quality bias" is warranted to describe it.

As emphasized by Westneat et al. (2000), considerable empirical evidence supports the general view that mate choice copying best corresponds to an associative learning mechanism, wherein a focal (observer) female associates a cue from the model female with the accepted or rejected male involved. Such an association to a male could occur regardless of the type of cue received by the observer female (Westneat et al. 2000). Potential types of cue arising from the model female consorting with a male are varied and include, for example, her courtship behavior, copulation/spawning behavior, age, and body size (Westneat et al. 2000). Indeed, in addition to the study of Hill and Ryan (2006), previous experimental

studies have demonstrated that observer females attend to and use (in making subsequent mate choice decisions) cues from the model female that indicate her quality. For example, Amlacher and Dugatkin (2005) performed an experiment in which observer (copier) female guppies (Poecilia reticulata) could choose between a male seen together with an older female and a male together with a younger female. Test females preferred to associate with the male they have seen together with older females. Similarly, Dugatkin and Godin (1993) presented (copier) female guppies with 2 males consorting with model females of different quality; either small (young) female that were probably inexperienced in mate choice or large (older) females that were likely experienced in mate choice. Observer females copied only the choice of larger (presumably higher quality) model females. Vukomanovic and Rodd (2007) repeated and extended the study of Dugatkin and Godin (1993) by testing 4 model/copier female combinations (i.e., large/large, small/small, large/small, and small/large) in the guppy. Their results corroborate those of Dugatkin and Godin (1993) and, additionally, they found that large female guppies copy the choice of large model females, but small guppy females did not copy the choice of small model females. Vukomanovic and Rodd (2007, p. 583) noted that "this evidence provides support for the notion that females are more likely to copy when they perceive that there is an imbalance between their assessment ability and that of another female." Thus, they concluded that females used the quality of the model female as a cue in mate choice copying.

The results of the latter studies, including those of Hill and Ryan (2006), can be explained by the process of mate choice copying. The generally accepted operational definition and theoretical framework of mate choice copying (reviewed in Dugatkin 1996; Westneat et al. 2000; Witte 2006) explicitly include the notion that observer (copier) females can obtain social information about the quality of a prospective mate by observing a sexual interaction between that male and another (model) female. In doing so, the copier female can potentially assess the quality of the male, the quality of the model female, or both and use this information subsequently in her mate choice decisions. Therefore, in our opinion, it is not necessary to invoke a new process (i.e., mate quality bias, sensu Vakirtzis and Roberts 2009) as the underlying mechanism for the use of social information by an observer female about the quality of females that a male had previously attracted in her assessing the quality of that male as a potential mate. As noted above, the process of mate choice copying already provides for such a mechanism. The notion of "mate quality bias" thus adds nothing new to our understanding of nonindependent mate choice that is not already incorporated in the concept of mate choice copying. To the contrary, this

proposed new term could potentially lead to more confusion than clarity in the research area of mate choice copying.

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*Key words:* mate choice, mate choice copying, sexual selection, social learning.

Address correspondence to K. Witte. E-mail: witte@biologie.uni-sie-gen.de.

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