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Forum

Mate choice copying and mate quality bias: different processes, different species

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WHAT IS MATE QUALITY BIAS?

Nonindependent mate choice occurs when a female is influenced in her choices by the actions of other females (Westneat et al. 2000). Mate choice copying is a form of nonindependent mate choice in which the probability of a male being selected as a mate increases if he has previously mated with another female and decreases if he has previously been rejected (Dugatkin 1992; Pruett-Jones 1992; Witte and Ueding 2003). Mate choice copying may evolve for 2, not mutually exclusive, reasons (Gibson and Höglund 1992). First, it could serve as a shortcut strategy whereby a female avoids the costs of active mate choice like time, energy, and predation risk (e.g., Pomiankowski 1987; Reynolds and Gross 1990), by observing and imitating the actions of other females that have paid the costs of active mate choice and are presumably making relatively successful mating decisions (Pomiankowski 1990; Pruett-Jones 1992). Second, given an error component in the mate assessment process, it could improve the discrimination accuracy of a female, and particularly if she is prone to errors in assessment, as happens for example with young and sexually inexperienced females (Gibson and Höglund 1992; Nordell and Valone 1998; Danchin et al. 2004). Mate choice copying has been studied experimentally and in natural conditions in a variety of fish and bird species (reviewed in Dugatkin 1996a; Galef and White 2000).

A recent experiment (Hill and Ryan 2006) in *Poecilia latipinna* (sailfin molly) has added a new dimension to the study of mate choice copying. *Poecilia formosa* (Amazon molly) is an all-female species arising from the hybridization of *P. latipinna* and *Poecilia mexicana* (Turner 1982; Avise et al. 1991). These females reproduce asexually but require sperm from a male of their bisexual parent species to stimulate embryogenesis (Hubbs CL and Hubbs LC 1932). Although sperm does not fertilize the already diploid *P. formosa* eggs, *P. latipinna* males appear to benefit from these pseudomatings by becoming more attractive to *P. latipinna* females (Schlupp et al. 1994). Extending this finding, Hill and Ryan (2006) examined whether copying females are sensitive to the other female's mate value, a variable that had not been manipulated in previous studies of mate choice copying. They hypothesized that because *P. latipinna* males prefer conspecific females to the parasitic *P. formosa* females and males compete for mates, the quality of a male's mate (*P. latipinna* vs. *P. formosa*) could serve as an indicator of the male's quality (Woodhead and Armstrong 1985; Ryan et al. 1996; Hill and Ryan 2006). Employing a binary choice design they simultaneously presented female *P. latipinna* with conspecific males that were consorting with either a *P. formosa* or a *P. latipinna* female. Their results provide strong support for the idea that *P. latipinna* females are sensitive to this difference in female mate value and prefer males that are chosen by conspecifics over males chosen by *P. formosa* females.

Though the authors describe these results as mate choice copying, their study brings to light a type of nonindependent mate choice that fits into neither the definition nor the theoretical framework of mate choice copying (Wade and Pruett-Jones 1990; Gibson and Höglund 1992; Pruett-Jones 1992). The relevant contrast is now not between mated and unmated males (or between the number of mates each male has secured), but between the quality of a male's mate and the quality of other males' mates (Hill and Ryan 2006). Although the former involves necessarily discrete and often binary variables, the latter involves variables that can potentially manifest in fine continuous gradations, and the concept of "copying" something simply does not apply.

What the phenomenon described by Hill and Ryan (2006) shares with mate choice copying proper is that selection exploits a valuable source of biological information, namely, the sexual histories of prospective mates and in particular the females that make up these histories. We feel that this, among other things, may lead some authors (up until recently ourselves included) to lump these 2 distinct processes together. Due to the significance of the aforementioned differences, however, these processes should urgently be distinguished, and we propose that "mate quality bias" be used to describe this particular phenomenon (Hill and Ryan 2006), with mate choice copying (Pruett-Jones 1992) reserved for the plethora of studies that conform to the definition and conceptual framework of mate choice copying proper.

CONDITIONS FAVORING MATE QUALITY BIAS

It is no accident that the study of mate choice copying has focused mostly on promiscuous and lekking species, where the male's primary concern lies in securing as many mates as possible (e.g., Dugatkin 1992; Clutton-Brock and McComb 1993; Höglund et al. 1995; Grant and Green 1996; Witte and Ryan 2002). The marked skews in male mating success, as well as the significant proportion of males that fail to secure any matings at all, provide ample relevant information for selection to work on. To see why this is so, consider that in order for a male trait to adaptively guide female choice, there needs to be meaningful variation in that trait, so that females can reliably discriminate between males on the basis of that trait. The traits with the widest meaningful variation should be most favored; on the other hand, traits that manifest uniformly across all males would be useless. In mate choice copying, the "trait" is quantitative sexual success in the form of frequency of sexual partners or copulations. Because this trait varies most among males in promiscuous and polygynous species, these will usually be the types of mating systems most conducive to copying. In these systems, there are, in other words, a sufficient proportion of unmated males to repay a female's interest in the mated ones (Figure 1). Pursuing the idea of mate choice copying in different kinds of mating systems, and particularly those that lack significant variance in male mating success (e.g., in monogamous systems), will probably turn out to be a largely futile enterprise. In these kinds of systems, given certain conditions we describe below, mate

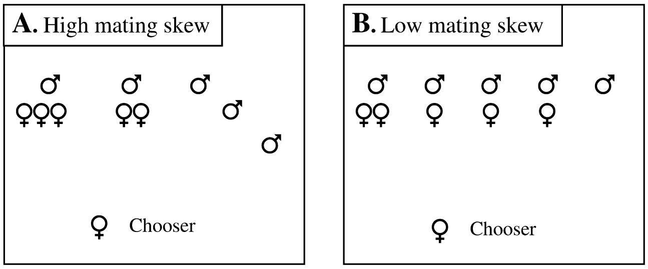

Figure 1
Mating skew and potential for mate choice copying. In A, the mating status (mated vs. unmated) of males is a cue that reveals the high quality males. This is not the case in B, where the great majority of males are mated. Mate choice copying is less likely to occur in B.

quality bias might be favored by selection, whereas mate choice copying would appear to be a relatively weak aid to mate choice.

So as to simplify the discussion that follows, we will confine it to the most common scenario, where the female furnishes most parental investment and is the choosier of the sexes (Trivers 1972). Obviously, where these prevailing conditions are reversed, the roles of the sexes in relation to mate quality bias might also be reversed (Trivers 1972; Widemo 2006). In order for mate quality bias to evolve, at a minimum the following conditions must be satisfied:

1. An evolutionarily exploitable positive correlation between a random female's quality and her partner's quality. The most common way through which this might come about is probably an element of male choice coupled to the stronger female choice.
2. A difference in the ease, speed, or accuracy with which the quality of male or female individuals can be assessed, with the assessment of females being preferable (i.e., easier, faster, or more accurate) to that of males. Given the general pattern of dullness and averageness in the female compared with the variation in elaborate secondary sex characters and condition-dependent badges of males (Darwin 1871; Andersson 1994), we should not be surprised if mate quality bias turns out to be a less common biological phenomenon than mate choice copying. As the example of *P. latipinna* shows, however, such cases do exist. Note that in this instance (Hill and Ryan 2006), the assessment of the female was a vastly easier task: Although assessing the male could potentially involve a diverse array of traits (Bisazza 1993; Marler and Ryan 1997; MacLaren et al. 2004), assessing the female reduced to simple heterospecific recognition.
3. The advantage arising from the exploitation of condition 2) must be sufficiently large to overcome the drawback arising from the imperfect correlation in condition 1).

The first 2 conditions should generally be easy to evaluate across species, whereas the third will pose a more serious challenge to the researcher. At any rate, the empirical finding of mate quality bias in a species that satisfies the first 2 conditions should provide indirect evidence for the satisfaction of the third.

Due to the open-endedness of condition 2) above, the evolutionary mechanics of mate quality bias might be explored in a variety of ways. For example, assume that what is selected for is maximal accuracy in assessing the male's quality, that is, minimization of error. It is a reasonable assumption that the length of time that can be spent assessing mates is often variable across females and at different times of the breeding period. If, within the constraints of a particularly brief assessment time, a female's quality can be more accurately evaluated in relation to that of her mate's, it would pay a choosing female to be sensitive to the female's quality, assuming that the expected error component due to the imperfect correlation of male and female quality on the population level is relatively small. Mate quality bias could therefore be an auxiliary or facultative strategy, complementary to the independent assessment machinery of a species' females (as in mate choice copying, Nordell and Valone 1998). Furthermore, such a process would be well suited to situations where females aggregate, spending the majority of the season in close proximity, a context that would allow ample opportunity for one to evaluate the other. If the time spent with males occupies a relatively small part of the entire season, we can, assuming certain basic cognitive faculties of individual identification and memorization, see that it could be beneficial for females to pay attention to one another's quality during the remainder of the season when they are aggregated. This could be done at virtually no cost, as the females go about their daily business, but the additional information might improve the accuracy of females' assessments of males.

STUDYING MATE QUALITY BIAS

Clearly, the mating system most conducive to mate quality bias is serial monogamy. Not only will serial monogamy very frequently satisfy condition 1) above, but, unlike lifelong monogamy, it will also permit the evolution of mate quality bias by allowing a male's potential partner to act on the information furnished by the previous partner. In lifelong monogamy, where once bonded a male is rarely released into the mating market again, unmated females simply cannot act on this information, even if it is readily available. Birds, and especially those species with the highest divorce rates, could therefore be a starting point in testing for mate quality bias (Ens et al. 1996).

Converging lines of evidence indicate that mate quality bias also operates in *Homo sapiens*. Although females are the choosier of the sexes, male choice does operate and is mediated by a number of cognitive adaptations (Miller and Todd 1998). Indeed, the study of male choice and its relation to such female qualities as nubility, ovulation, body shape, and facial attractiveness (e.g., Symons 1995; Thornhill and Gangestad 1999; Roberts et al. 2004; Gangestad and Scheyd 2005; Rhodes 2006; Roberts and Little 2008), forms one of the most exciting research areas in what has emerged in recent years as human evolutionary psychology (Buss 1999; Barrett et al. 2002). One of the most consistent findings in the literature pertains to the marked contrasts in mate choice criteria across genders (reviewed in Buss 1994, 1999). Although the mate value of women is determined primarily by visual cues of attractiveness, the mate value of men is more heavily dependent on relatively complex cues like social status, resource holding potential, and willingness to invest in the female, which are considerably more difficult to evaluate than simple visual cues of appearance and attractiveness. The requirement of assortative mating in relation to quality (condition 1) above) is also satisfied, as it is well documented that more attractive women tend to mate with more desirable (i.e., of higher socioeconomic, financial and educational status) men (Elder 1969; Udry and Eckland 1984; Townsend 1998). In addition, against a background of substantial variability in human mating systems and behavior (Alexander et al. 1979; Buss and Schmitt 1993; Pillsworth and Haselton 2006), serial pair-bonding appears to be nearly universal across cultures (Fisher 1989). Particularly relevant here apart from the universality of serial pair-bonding is the relatively low variance in male mating success, with the percentage of men who marry in every American birth cohort since the 19th century exceeding 90%. In a cross-cultural sample of 97 countries, the mean percentage of men who have married by the age of 49 has been estimated at nearly 92% (Fisher 1989; 1994).

Given the above, it should come as no surprise that attempts to show that women engage in mate choice copying (as delimited here) have produced mostly negative results (Uller and Johansson 2003; Eva and Wood 2006; Milonoff et al. 2007; Waynforth 2007). In what appears to be a more promising line of research, recent controlled experimental studies have started to focus more on partner attractiveness rather than the presence or absence of a partner per se. The most consistent finding to emerge is that women find men more attractive when they are presented as being paired with relatively attractive partners, compared with men with relatively unattractive partners (Waynforth 2007; Little et al. 2008). Waynforth (2007) has found that the perceived attractiveness of a man presented with a relatively unattractive girlfriend actually decreases in comparison to the baseline attractiveness ratings he receives when presented alone.

We suggest that although women engage in mate quality bias rather than mate choice copying, men are less likely to display either form of nonindependent choice (but see Little et al. 2008). Two considerations motivate this position. Firstly, as discussed above, men can acquire most of the information relating to female quality through readily available visual cues, so any form of nonindependent mate choice would not be particularly helpful. Secondly, attraction to mated women risks the costs of sperm competition and physical aggression by romantic rivals (Hill and Buss 2008). This last consideration does not constitute a problem the other way around, when women are attracted to mated men.

A final note. As conceptualized here, mate quality bias can serve both to reduce the costs involved with mate choice and to improve discrimination accuracy, depending on the particulars of condition 2) above. These are the same adaptive functions that have been suggested with regard to mate choice copying (Gibson and Höglund 1992). It is interesting to note that to date a substantial number of studies support the improved discrimination accuracy view of mate choice copying (e.g., Dugatkin and Godin 1993; Dugatkin 1996b; Witte and Ryan 1998; Amlacher and Dugatkin 2005). It has been found, for example, that when males are closely matched for quality, females tend to copy the choices of other females, but when males differ markedly in quality, females do not copy but rely instead on their own independent evaluation of the males (Dugatkin 1996b; Witte and Ryan 1998). Findings like this suggest that copying is a facultative strategy, complementary to females' independent assessment of males and that females resort to copying only when they have trouble discriminating between males on the basis of their quality (Nordell and Valone 1998). This does not fit well with the view of mate choice copying as a cost avoidance strategy, whereby certain females choose to avoid the costs of active mate choice altogether by parasitizing the efforts of other females (Pruett-Jones 1992); indeed the cost avoidance hypothesis of mate choice copying has received little empirical support to date (Briggs et al. 1996; Dugatkin and Godin 1998). It will be interesting to see if a similar pattern applies to mate quality bias.

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