

Forum: Ideas

Nonindependent mate choice in monogamy

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Individuals usually mate with opposite-sex others based on their own assessment of prospective mates' suitability (reviews in Kempenaers 2007; Roberts and Little 2008), but this assessment can also be modulated by observing decisions of others—so-called nonindependent mate choice. We have proposed the term “mate quality bias” to describe the type of nonindependent mate choice that occurs when a female biases her own evaluation of a male in accordance with his mate's quality (Vakirtzis and Roberts 2009). This type of nonindependent choice should be expected to occur in monogamous or relatively monogamous species where, due to mutual choice, there will usually exist a high correlation between a male's quality and his mate's quality (Trivers 1972; Burley 1977; Johnstone 1997). In these species, the most desirable males will tend to mate with the most desirable females and less desirable individuals will be left to mate among themselves (Burley 1983; Jones and Ratterman 2009). In principle, this selective mapping between male and female quality will not obtain in promiscuous and polygynous species, where, due to minimal male choice and high male mating skew, the top males will mate with all willing females, whereas lower quality males will achieve fewer or no mating opportunities. In these species, it is thus unlikely that an observing female will deduce reliable information about the male from the quality of his mate; rather, the frequency of partners and/or copulations may be a more useful cue. Use of such cues in mate assessment is known as mate choice copying (Pruett-Jones 1992; Dugatkin 1998).

This is not to say that observing females in these nonmonogamous species should copy the choices of all females in the population. For example, focal females should ignore the choices of model females who are young and sexually inexperienced and may thus have an intolerably high error component in their choice of mates (Dugatkin and Godin 1993; Nordell and Valone 1998). The outcome of such facultative copying will be that the males with whom these immature females mate experience a conditional probability of choice that approximately equals their absolute probability (for definitions, see Pruett-Jones 1992). In other words, their probability of being chosen after being observed with the immature female should neither increase nor decrease in comparison to what it would be had they been observed alone (Dugatkin and Godin 1993; Amlacher and Dugatkin 2005; Vukomanovic and Rodd 2007). Mate quality bias and this type of facultative mate choice copying therefore both involve aspects of female quality (Witte and Godin 2010). However, the idea of mate quality bias is based on a particular set of assumptions and conditions that will usually be found in monogamy, where, in contrast to more promiscuous mating systems, mate choice copying is unlikely to evolve (see Table 1). Because mate choice copying and mate quality bias start from different background assump-

tions, they inevitably lead to different predictions (though there will be cases where they produce superficially similar results).

To see this, let a male enjoy an absolute probability of choice by a given female equal to P_b , a constant between 0 and 1. In mate quality bias, we move from independent choice to a limited set of contexts in which the female, instead of assessing the quality of the male, evaluates instead the more easily assessable quality of his mate (for examples of these contexts, see Vakirtzis and Roberts 2009 and below). This results in a conditional probability that is, theoretically, a continuous and monotonically increasing function h of female quality that ranges from 0 to 1, with $h'(x) > 0$ for all x . By the intermediate value theorem, there must be a value x_0 of female quality for which $h(x_0) = P_b$. Moreover, because the function is monotonically increasing, x_0 must be unique. All values of female quality larger than x_0 will therefore satisfy $h(x) > P_b$, whereas $h(x) < P_b$ for every $x < x_0$. There exists therefore in mate quality bias the potential for a male's mating success (with a certain range of females) to actually lower his probability of choice, a possibility that is absent from mate choice copying, facultative or not. Recall that in copying the only way a male can lower his probability of choice is if he is rejected by a female (Pruett-Jones 1992; Witte and Ueding 2003); in mate quality bias, this will happen when a male is accepted by a female.

This analysis leads to the following prediction:

In mate quality bias, the larger the male's absolute probability of choice, the larger the proportion of the entire female population that, when mated to the male, decreases his probability of choice. (Equivalently, the smaller the male's absolute probability of choice, the larger the proportion of the entire female population that, when mated to the male, increases his probability of choice.)

Put another way, the higher the quality of the male the higher the corresponding “parity value” of female quality over which the male starts to increase his probability of choice and under which he starts to lower it. Symbolically, for every $P_h > P_b$, there must exist an $x_1 > x_0$ for which $h(x_1) = P_h$, and letting F represent the cumulative distribution function of female quality in the population, it follows that $F(x_0) < F(x_1)$ (see Figure 1).

Is there empirical support for this prediction? Yes. Waynforth (2007) had a sample of men's facial photographs rated for attractiveness by female subjects (a measure of absolute probability). Two weeks later, the female subjects re-rated the male images, but this time they also were simultaneously shown a facial image of each man's supposed girlfriend (conditional probability). The female stimuli that were used as girlfriends had been randomly assigned to each male stimulus and covered a wide attractiveness range from very attractive to very unattractive. Waynforth initially tested whether the attractiveness ratings of men presented with a girlfriend increased compared with when they had been presented alone, as a mate choice copying hypothesis would predict. He could find no change, a negative result which corroborates earlier studies that had used different methodologies (Uller and Johansson 2003; Milonoff et al. 2007). A meaningful pattern in the data only emerged when Waynforth examined the effect of the

Table 1

Five reasons why the concept of mate choice copying has proved so successful in the lekking/promiscuous species where it has mostly been studied (left half of the table), with the corresponding reasons why it is almost certain to fail in monogamy (right half)

Lekking/promiscuous species →	Why mate choice copying can evolve	Monogamous/socially monogamous species →	Why mate choice copying cannot evolve
1. No paternal care	No risk of diminished paternal care	Paternal care	Copying females will suffer diminished paternal care for their offspring
2. No female competition	No costs from female competition	Female competition	Copying females will suffer costs of female competition from male's current mate
3. High male mating skew	The top males will easily stand out from the rest	Low male mating skew	Because all males will tend to have one mate at a time, this cue will not be a useful aid in discrimination (Vakirtzis and Roberts 2009)
4. No male choice	Copying females can treat a male's mates as homogeneous units, summing them up to obtain a gauge of his overall success	Substantial male choice	Simply tracking the frequency of a male's mates will not suffice due to substantial differences in female mate value. From the vantage point of a male, one high-quality female might even be preferable to 2 low-quality females
5. Unambiguous, monotonically increasing relation between a male's quality and the number of his mates	Copying females can be confident that the more mates a male has the higher his quality	No clear relation between number of mates and quality of male	1) Various males might allocate differential effort to parenting versus mating, and which allocation is preferable will depend on a female's needs. 2) Although it can generally be expected that males of higher genetic quality will engage in more extra-pair copulations, these will be covert matings of which copying females will probably have no knowledge. 3) Males in successful breeding pairs will have no reason to dissolve them, whereas the opposite will be true for males that find themselves in unsuccessful relationships, perhaps even leading to an inverse correlation between male quality and lifetime number of mates (e.g., Linden 1991; Dubois and Cézilly 2002).

supposed girlfriends' attractiveness and found that the difference in individual men's attractiveness rating between the 2 conditions was primarily attributable to their girlfriend's attractiveness. Men presented with attractive girlfriends tended to increase their baseline attractiveness ratings, whereas men who were presented with unattractive girlfriends lowered their attractiveness ratings (see also Sigall and Landy 1973; Little et al. 2008). Interestingly, and in support of the predictions we derive above, Waynforth (2007, p. 268) gives a graphical summary of his results, which breaks down the change in ratings for the male stimuli (between test and retest) by the attractiveness of the men (low, medium, and high attractiveness). The results show that the large majority of girlfriends caused a decrease in the attractiveness ratings of highly attractive men and that these men could only retain, but not increase, their initial attractiveness when they were paired to attractive partners. Unattractive men, on the other hand, gained in attractiveness regardless of who they were paired with, though when paired with unattractive girlfriends the positive change in attractiveness is so small that it is probably statistically insignificant. The pattern for men of intermediate attractiveness falls between the 2 extremes, and these men unmistakably lost in attractiveness by being paired with unattractive girlfriends but gained by being paired with attractive ones.

The qualitative predictions derived above are not altered if we loosen the assumption that the male's conditional probability of choice will be a function exclusively of his mate's quality and allow the male's own fixed quality into the model. It is not even necessary to assume that his conditional probability of choice will span the entire range from 0 to 1; assuming it is constrained to span a narrower range around his absolute probability of choice leads to the same predictions.

As we previously suggested (Vakirtzis and Roberts 2009), nonindependent mate choice is almost certainly more difficult to evolve in monogamy compared with other systems. For example, in mate choice copying, it is easy to see why assessing simply whether or not a male is mating can be a less challenging task than assessing his quality directly. Mate quality bias by definition involves something more subtle than merely the presence or absence of a female mate (viz. her quality), and as we suggested, the evaluation of the female must offer some advantage over the evaluation of the male for this process to evolve. Adding to this, there must be a turnover of mates for any kind of nonindependent mate choice to operate, which immediately excludes monogamous species that bond for life. Given these limitations, it is likely that females in the majority of monogamous species choose mates independently. The goal of future theoretical work could be, on the basis of the

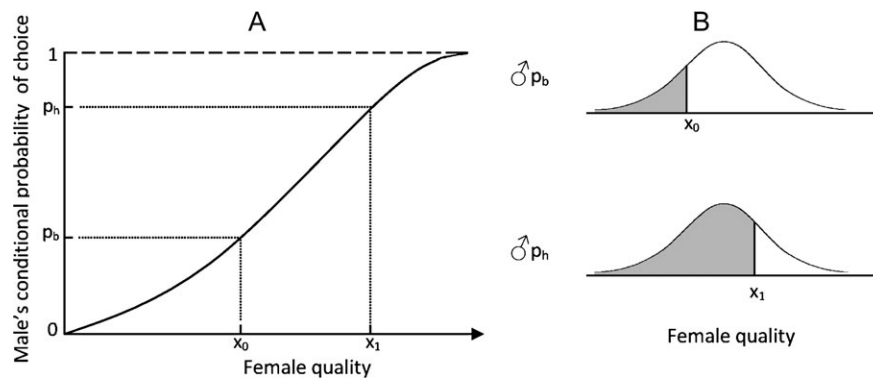


Figure 1

(A) The conditional probability of a male being chosen as a function of his past mate's quality. Two values of conditional probability ($P_h > P_b$) are plotted with their corresponding values of female quality ($x_1 > x_0$). (B) The effects of mate quality bias on 2 males of differing quality, the first having an absolute probability of choice equal to P_b (top) and the second a higher absolute probability of choice equal to P_h (bottom). The shaded area of the female quality distribution (assumed here to be normal) corresponds to those females in the population that, if mated to the males, would lower their attractiveness as mates for an observing female. The higher quality male suffers a reduced probability of choice in most cases, whereas the opposite is true for the low-quality male. This analysis leads to obvious predictions about when these males should "flaunt" their mates and when they should not.

bivariate normal distribution which theoretically describes assortative mating in terms of quality, to determine the boundaries of the parameter space in which mate quality bias could evolve, with emphasis on the correlation coefficient between male and female quality and its relation to the putative "advantage parameter," symbolizing the advantage gained by females that engage in mate quality bias (Vakirtzis and Roberts 2009). There almost certainly exists a state of tension between the correlation coefficient and the advantage parameter, with lower values of the former necessitating higher values of the latter and vice versa, and the goal of future theoretical work could be to more precisely describe this relation.

In humans, the advantage lies in the much greater contribution physical attractiveness makes to female as compared with male mate value (the latter being more heavily dependent on nonphysical characteristics like social status and resource-holding potential), which renders the mate value of a man's mate much easier to visually assess than his own (Buss 1994; Uller and Johansson 2003; Waynforth 2007). Given that there is some cross-cultural variation in the relative importance women assign to men's physical attractiveness versus nonphysical characteristics (due, perhaps, to pathogen prevalence or other hitherto unidentified factors, see Gangestad and Buss 1993; Eagly and Wood 1999; Gangestad and Simpson 2000), it is straightforward to assume that the significance of mate quality bias should correlate negatively with this relative importance. In other words, the greater the importance of men's physical attractiveness in a particular society the lesser the advantage offered by mate quality bias and the weaker its effect should be. Conversely, the more significance women assign to nonphysical characteristics the greater the advantage offered by mate quality bias and, therefore, the more powerful its influence on women's assessments should be.

Finally, we offer 2 important caveats with regard to human nonindependent mate choice. First, although humans are relatively monogamous, there is evidence of a moderately polygynous past (Alexander et al. 1979; Harcourt et al. 1981), so that the general model developed here might in the future need to be modified somewhat to take account of these deviations from monogamy. The 2 processes of nonindependent choice are not necessarily mutually exclusive, and as the boundaries between monogamy and promiscuity/polygyny become blurred, elements of both processes might be found.

Second, studies of mate quality bias, either in humans or in other species, should always be conducted bearing in mind that male choice might prevent females' experimentally manipulated desires from resulting in actual matings because high-quality males might reject the advances of low-quality females.

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Key words: mate choice copying, mate quality bias, monogamy, nonindependent mate choice.

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REFERENCES

- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. In: Chagnon NA, Irons W, editors. *Evolutionary biology and human social behavior*. North Scituate (MA): Duxbury Press. p. 402–435.
- Amlacher J, Dugatkin LA. 2005. Preference for older over younger models during mate-choice copying in young guppies. *Ethol Ecol Evol*. 17:161–169.
- Burley N. 1977. Parental investment, mate choice, and mate quality. *Proc Natl Acad Sci USA*. 74:3476–3479.
- Burley N. 1983. The meaning of assortative mating. *Ethol Sociobiol*. 4:191–203.
- Buss D. 1994. *The evolution of desire: strategies of human mating*. New York: Basic Books.
- Dubois F, Cézilly F. 2002. Breeding success and mate retention in birds: a meta-analysis. *Behav Ecol Sociobiol*. 52:357–364.
- Dugatkin LA. 1998. Genes, copying, and female mate choice: shifting thresholds. *Behav Ecol*. 9:323–327.
- Dugatkin LA, Godin J-GJ. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age dependent effects. *Behav Ecol*. 4:289–292.
- Eagly AH, Wood W. 1999. The origin of sex differences in human behavior: evolved dispositions versus social roles. *Am Psychol*. 54:408–423.
- Gangestad SW, Buss DM. 1993. Pathogen prevalence and human mate preferences. *Ethol Sociobiol*. 14:89–96.

- Gangestad SW, Simpson JA. 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behav Brain Sci.* 23:573–587.
- Harcourt AH, Harvey PH, Larson SG, Short RV. 1981. Testis weight, body weight and breeding system in primates. *Nature.* 293: 55–57.
- Johnstone RA. 1997. The tactics of mutual mate choice and competitive search. *Behav Ecol Sociobiol.* 40:51–59.
- Jones AG, Ratterman NL. 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proc Natl Acad Sci USA.* 106: 10001–10008.
- Kempenaers B. 2007. Mate choice and genetic quality: a review of the heterozygosity theory. *Adv Study Behav.* 37:189–278.
- Linden M. 1991. Divorce in great tits—chance or choice? An experimental approach. *Am Nat.* 138:1039–1048.
- Little AC, Burriss RP, Jones BC, DeBruine LM, Caldwell CA. 2008. Social influence in human face preference: men and women are influenced more for long-term than short-term attractiveness decisions. *Evol Hum Behav.* 29:140–146.
- Milonoff M, Nummi P, Nummi O, Pienmunne E. 2007. Male friends, not female company, make a man more attractive. *Ann Zool Fenn.* 44:348–354.
- Nordell SE, Valone TJ. 1998. Mate choice copying as public information. *Ecol Lett.* 1:74–76.
- Pruett-Jones S. 1992. Independent versus nonindependent mate choice: do females copy each other? *Am Nat.* 140:1000–1009.
- Roberts SC, Little AC. 2008. Good genes, complementary genes and human mate preferences. *Genetica.* 132:309–321.
- Sigall H, Landy D. 1973. Radiating beauty: effects of having a physically attractive partner on person perception. *J Pers Soc Psychol.* 28: 218–224.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and the descent of man, 1871–1971.* Chicago (IL): Aldine. p. 136–179.
- Uller T, Johansson LC. 2003. Human mate choice and the wedding ring effect: are married men more attractive? *Hum Nat.* 14:267–276.
- Vakirtzis A, Roberts SC. 2009. Mate choice copying and mate quality bias: different processes, different species. *Behav Ecol.* 20:908–911.
- Vukomanovic J, Rodd H. 2007. Size-dependent female mate copying in the guppy (*Poecilia reticulata*): large females are role models but small ones are not. *Ethology.* 113:579–586.
- Waynforth D. 2007. Mate choice copying in humans. *Hum Nat.* 18:267–271.
- Witte K, Godin J-GJ. 2010. Mate choice copying and mate quality bias: are they different processes? *Behav Ecol.* 21:193–194.
- Witte K, Ueding K. 2003. Sailfin molly females (*Poecilia latipinna*) copy the rejection of a male. *Behav Ecol.* 14:389–395.