

# Mate choice copying and nonindependent mate choice: a critical review

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The past two decades have witnessed an explosion of interest in nonindependent mate choice, i.e. female choice that is influenced by the choices of other females. This research has focused overwhelmingly on mate choice copying, which occurs when a female is more likely to mate with a previously mated male and reject a previously rejected male. I review the theoretical constructs of nonindependent mate choice and mate choice copying, and evaluate the general hypotheses that have been proposed to account for the adaptive significance of mate choice copying, namely that it serves to bypass the costs of mate choice or improve the discrimination accuracy of females. I discuss the standard experimental protocols that are employed in the study of mate choice copying and review empirical studies that have been conducted to date. Strengths and weaknesses of the mate choice copying research program are highlighted, as well as possible directions for future research.

While the suggestion that females may be influenced by each other's mate choice has appeared sporadically in the literature since at least the 1970s (e.g. Wiley 1973, Lill 1974, Bradbury & Gibson 1983), the systematic study of mate choice copying did not begin until the early 1990s. It was then that a string of seminal papers (Wade & Pruett-Jones 1990, Dugatkin 1992, Pruett-Jones 1992) formalized our conceptual understanding of this phenomenon and laid the foundations for the large body of research that has since followed. Here, I will critically summarize the main findings of the literature, evaluate the progress achieved so far and suggest avenues for future research.

## The definition

The standard definition of mate choice copying has been given by Pruett-Jones (1992), and involves two distinct probabilities that a male will be chosen by a female. The absolute probability of choice results from the female's evaluation with her standard (or independent) adaptations for assessment. The conditional probability results when the female has knowledge of other females' choices. According to this definition, "Copying occurs when the conditional probability of choice of a given male by a female is either greater or less than the absolute probability of choice depending on whether that male

mated previously or was avoided, respectively.” (Pruett-Jones 1992: p. 1001).

In other words, a female’s knowledge of a male having mated with another female increases the probability that she will subsequently also select him as a mate, and knowledge of his having been rejected lowers the probability that she will subsequently select him. Intuitively the idea is straightforward. If a male has been selected or avoided by a female there is probably good reason for it, and a third female would do well to be sensitive to this information as she searches for a mate. Unfortunately, the above definition as it stands can accommodate various phenomena that have nothing to do with mate choice. For example the well-known tendency of animals to move in groups or use conspecifics as cues for habitat selection (Kiester 1979) can lead to phenomena which outwardly conform to the above definition, but for which the term mate choice copying would be misleading. Such is the case in fallow deer (*Dama dama*), where the tendency of females to stay in groups as a method of avoiding harassment by males while visiting leks can add to the skew in the distribution of male mating success (Clutton-Brock *et al.* 1989). The first female on a male’s territory can attract subsequent females, which in turn attract more females and so on (Clutton-Brock *et al.* 1989). When on the territory, the females are then more likely to mate with the male, if for no other reason than proximity. This, however, could be more constructively viewed as a byproduct of a mechanism that has evolved for reasons other than mating, in particular protection from harassment, rather than mate choice copying *per se* (Clutton-Brock & McComb 1993, McComb & Clutton-Brock 1994, Brooks 1998). It was problems like this that led Dugatkin (1996a) to amend Pruett-Jones’ definition: “Mate choice copying occurs when: The conditional probability of choice of a given male by a female is greater than the absolute probability of choice depending upon whether that male mated previously. Further, the information about a male’s mating history (or some part of it) must be obtained by the female via observation” (Dugatkin 1996a: p. 87).

While in the context of this stand-alone definition it is not immediately obvious, the last

sentence is meant to mean that observing the mate choices of other females must be the *causal factor* of the difference between the absolute and conditional probabilities (*see* Dugatkin 1996a: pp. 86–88)

Some brief remarks before concluding this section. Mate choice copying is a type of *non-independent mate choice*, meaning female choice that is affected by the actions of other females (Pruett-Jones 1992, Westneat *et al.* 2000). The example of female aggregation discussed above is another instance of nonindependent choice, though, unlike copying, the nonindependence is not the direct result but rather the byproduct of an adaptation, and one that is not even related to mate choice. While the idea of nonindependent mate choice is helpful in highlighting the fact that copying is not the only way females can influence one another, vigorously pursuing this idea to its logical boundaries can lead to an extensive list of generic phenomena, the biological importance of which is debatable to say the least. Westneat *et al.*’s (2000) list includes stimulus enhancement, stimulus reduction, contagion, inhibition, stimulus response, association-to-location, association-to-male, association-to-trait and finally a category they call ‘cognition’ [for explanation of these terms see Westneat *et al.* (2000)]. For example in stimulus enhancement, copulation can attract, due to its conspicuous nature (loud, with violent motions etc.), the attention of a third female, which is thus more likely to accidentally take notice and subsequently copulate with this particular male. The authors conclude by criticizing the literature’s narrow focus on mate choice copying (which in their conceptual scheme corresponds roughly to what they term association-to-male) and calling for a more ‘balanced’ consideration of alternative mechanisms of nonindependent mate choice. It is difficult to see how random non-adaptive processes like stimulus enhancement or other generic phenomena could justify the same degree of scientific scrutiny as an elaborate adaptation that systematically exploits social information for the benefit of its bearers. More importantly, it is difficult to imagine any other outcome to such a research program than an unexciting catalogue of stochastic across-species phenomena. Tellingly perhaps, Westneat

*et al.*'s proposal for a more balanced approach has gone largely unheeded, and the research on nonindependent mate choice continues to focus overwhelmingly on mate choice copying.

## The evolution of copying

### A cost avoidance adaptation

Two general explanations have been offered to explain the evolution of mate choice copying. The first views it as a cost-avoidance or short-cut strategy (Pomiankowski 1990), whereby the copying female enjoys the benefits accruing to actively choosing females but avoids the sampling costs associated with active mate choice (Wade & Pruett-Jones 1990, Gibson & Höglund 1992, Pruett-Jones 1992). These costs include the time and energy that must be spent evaluating potential mates, the risks of predation and harassment by rejected males, parasite exposure and sexually transmitted diseases (Pomiankowski 1987, Reynolds & Gross 1990, Andersson 1994, Dugatkin & Höglund 1995).

It is easy to show that a population consisting solely of choosers ( $x$ ) will be vulnerable to invasion by a single copying mutant (Pruett-Jones 1992). We can describe the average fitness  $E$  of the choosers as  $E(x) = W + f - k$ , where  $W$  is the mean heritable fitness of males,  $f$  the extra fitness benefits choosers gain due to their discrimination, and  $k$  the sampling costs (Pruett-Jones 1992). Obviously it is a condition that  $f > k$  for discrimination to have evolved in the first place. A single copying mutant ( $y$ ) will find herself in the fortunate position of copying in a population that is 'uncontaminated' by other copiers and gain the fitness advantage that accrues to choosers without paying the sampling costs:  $E(y) = W + f > E(x)$ , and copying invades the population. Similarly, a population consisting solely of copiers will end up making random choices, and  $E(y) = W$ . A single mutant chooser will invade, provided  $f > k$ .

The ESS will therefore involve a mixed population of choosers and copiers. These two strategies need not be embodied in distinct genotypes but can manifest themselves within individuals at some optimum frequencies (Pruett-Jones

1992). The values for these frequencies will obviously depend on a variety of complicating factors. For example, starting from the assumption that females visit prospective mates in pairs, Pruett-Jones arrives at a chooser frequency of  $p = 1 - (k/f)$ . We can see in this equation the gross mechanics of mate choice copying: the lower the costs  $k$  relative to the benefits  $f$ , the more it will pay for females to go through the trouble of choosing their mate independently. On the other hand high sampling costs will favor a copying strategy.

The cost-avoidance framework of mate choice copying provides researchers with a set of broad research avenues which surprisingly have remained almost entirely unexplored. One straightforward deduction from this framework is that mate choice copying is most likely to be found in species where females incur great mate choice costs, but to date no direct tests of this prediction have been made. Strong corroboration for this prediction could be obtained, if, for example, a comparative study of closely related species that differ greatly in the costs of female choice revealed differences in mate choice copying in the expected direction.

Another element of the cost-avoidance framework is the co-existence in a population of the frequency-dependent behavioral polymorphism of choosers and copiers, so that copying is displayed by some but not all females, the rest engaging in active choice. Presumably, as discussed above, this frequency-dependent behavioral polymorphism can manifest within the same female. Alternatively, and this would certainly constitute a more exciting finding, a proportion of females could be genetically disposed to copying and the rest genetically disposed to choosing. We would, in other words, observe some females that always copy and others that never do so. Again, this research avenue has remained unexplored.

The only empirical studies to date that could be construed as bearing directly on the cost-avoidance framework have been conducted in the guppy (*Poecilia reticulata*). In a laboratory setting Briggs *et al.* (1996) sought to experimentally manipulate predation risk by placing a predator fish in an aquarium adjacent to female guppies in some but not all trials of a mate

choice copying experiment. Their hypothesis was that females should copy more frequently when a predator was present, as a way of minimizing perceived predation costs. The results did not bear out this prediction, and females were no more likely to copy in the presence of a predator than they were in its absence. In another study (Dugatkin & Godin 1998), researchers tried to experimentally manipulate the time costs of mate choice by inducing hunger in some female guppies while allowing unlimited access to food for others. The hypothesis was that hungry females should exhibit more copying behavior than satiated ones, in an attempt to minimize the time costs of mate choice and allocate any time thus economized into the search for food. Again, the results did not bear this prediction out. Only the most well-fed females engaged in mate choice copying, while the hungry ones apparently ignored the choices of other females (Dugatkin & Godin 1998).

Does this mean that the cost-avoidance hypothesis has been empirically disconfirmed? The results must be interpreted with caution for a number of reasons. Firstly, these experiments have been conducted on a single species, so it could be premature to generalize. Secondly, the artificiality of the laboratory settings may have affected the females in ways different to what would have been the case in the wild. A predator restrained behind a Plexiglas partition in an adjacent aquarium may represent an entirely different entity in the female's perception to a predator swimming freely down the stream. Thirdly, and perhaps more importantly, the time frame of these studies may differ greatly from that through which mate choice copying mechanisms are 'calibrated' in natural conditions. For example, assume that the general hypothesis is true and that increased predation risk in a natural population raises the frequency of mate choice copying. The most adaptive way in which females could take this increased risk on board would be developmentally, observing predation risks over the long run, not on a day-to-day and largely variable basis. At maturation they would thereby have a more accurate global estimate of ambient predation risk and could adjust their mate choice tactics accordingly, presumably for life. In those instances where a predator did

happen to be present, we should expect females to be more concerned with avoiding the predator rather than selecting sexual partners. An analogous argument could be made for the study that employed experimental manipulation of hunger (Dugatkin & Godin 1998). Perhaps more important than the negative results of these two studies is the cost-avoidance hypothesis' inability to generate fruitful empirical research, something which is not the case for the second approach to mate choice copying.

### **Copying as an adaptation to facilitate discrimination**

According to this framework, mate choice copying might be better understood by avoiding the classical cost-benefit analysis and focusing instead on the uncertainty or error component in the mate assessment process (Gibson & Höglund 1992, Nordell & Valone 1998, Uehara *et al.* 2005). Females try to estimate male quality via various physical, behavioral and social cues, but their estimate is subject to error, and wrong decisions are often made (Ryan *et al.* 2007). Under conditions of increased uncertainty, any additional information that can contribute to better assessment should be used. Such is the case when, for instance, the males under consideration are closely matched for the relevant traits (size, coloration, courtship behavior, etc.). Another instance of increased uncertainty concerns young and sexually inexperienced females, which are perhaps not mature enough to evaluate males correctly, even if the males differ considerably in quality. Under such circumstances, copying the choices of others is preferable to independent choice, even if poor decisions are occasionally copied (Wade & Pruett-Jones 1990, Gibson & Höglund 1992, Nordell & Valone 1998). Without the benefit of copying, a female that cannot decide between two or more males has to make what is essentially a random choice. In the rest of the population, however, at least some of the females will be making successful decisions, so that copying others' choices is necessarily equal to or better than random choice, no matter how small the fraction of females that are choosing successfully. This perspec-

tive therefore provides a convincing solution to what was always the most obvious problem with mate choice copying, namely that there is a risk of copying poor decisions (Giraldeau *et al.* 2002). Note that in this framework there is generally no tension between choosers and copiers, frequency-dependent or not. All females are selected to rely primarily on their own independent assessment, and resort to copying only under conditions of uncertainty. Copying is therefore viewed as a facultative adaptation, and the relative rarity with which this phenomenon manifests might be due to the rarity with which the necessary conditions obtain in nature.

The predictions of this framework have been confirmed. It has been shown (in guppies and sailfin mollies, *Poecilia latipinna*) that females resort to copying when offered a choice between two closely matched males, but choose independently when the males differ greatly in quality (Dugatkin 1996b, Witte & Ryan 1998). This result is now so widely accepted that most studies of mate choice copying use closely matched males so as to maximize the probability of eliciting copying behavior. Furthermore it has proven possible to manipulate the intensity of mate choice copying in a highly predictable manner by manipulating not only the difference in quality between two potential mates but also the amount of information provided by other females (Dugatkin 1998, Witte & Noltemeier 2002). This second variable can be manipulated in two ways, namely by having more than one female choose a certain male and by having one female spend increasing amounts of time with him. In addition, it has been shown that while younger female guppies copy the choices of older females, the latter do not copy the choices of the former (Dugatkin & Godin 1993). When given an opportunity to choose between copying an older or a younger female's mate choice, a younger female guppy tends to copy the older female's choice (Amlacher & Dugatkin 2005). Overall, the choices of younger females are disregarded by older and other young females alike, whereas the choices of older females appear to influence both young and older females (Vukomanovic & Rodd 2007). It should, however, be noted that Ophir and Galef (2004) found no evidence that virgin Japanese quail (*Coturnix*

*japonica japonica*) females were more likely to copy than sexually experienced females.

In recent years, there has been a tendency to place mate choice copying in the much broader context of public information theory (e.g. Nordell & Valone 1998, Valone & Templeton 2002, Danchin *et al.* 2004, Kavaliers *et al.* 2006, Valone 2007, Mery *et al.* 2009). Public information is an instance of inadvertent social information (ISI), or information that is provided inadvertently by animals as they engage in efficient performance of their activities (Danchin *et al.* 2004). In particular, public information is a type of ISI that pertains to the quality of a resource (other types of ISI pertain to different kinds of information, Danchin *et al.* 2004). The concept was originally applied to foraging (Valone 1989, Templeton & Giraldeau 1995): an animal which after a brief inspection departs from a poor foraging patch, though merely tending to its own energy needs, inadvertently provides information to nearby animals about the poor quality of the patch. Likewise, animals that experience success in a particular patch persist in its exploitation and inadvertently signal the existence of a high quality patch. The difference between ISI and other kinds of social information (like signals) is that ISI is not produced intentionally. Individuals that generate public information are selected to perform as efficiently as possible, not communicate any information to others (Danchin *et al.* 2004). The information is therefore highly reliable, as the risk of deception is minimized, but animals are predicted to rely more on public information in conditions of increased uncertainty (Nordell & Valone 1998, Valone & Templeton 2002, van Bergen *et al.* 2004).

This general copying strategy, applicable also to contexts outside mating, has been called *copy-when-uncertain* (Laland 2004). The connection between public information and mate choice copying is straightforward; females selecting or rejecting a male can be viewed as generating public information about the male's quality, and other females are expected to be sensitive to this highly reliable information when their own private information is insufficient or unreliable (Nordell & Valone 1998). Apart from foraging and mate choice, the concept of public information has been extended to various other domains

like breeding habitat selection and opponent assessment in fighting interactions (Valone & Templeton 2002, Valone 2007).

The importance of public information theory as an analogy that places mate choice in the big picture, alongside other domains like foraging and agonistic interactions, is obvious. At the same time, it is important to stress that mate choice is a unique adaptive problem, with special kinds of demands that clearly set it apart from other animal behaviors. As such, there can be no substitute for theory that is targeted specifically to mate choice copying, and, descending to an even lower level of analysis, theory tailored to specific ecologies, mating systems and species (e.g. Dugatkin & Höglund 1995, Stöhr 1998).

### **Mate choice copying: social or genetic?**

A widespread but inaccurate distinction in the literature pertains to an alleged ontological chasm between mate choice copying on the one hand and the standard or independent mate choice mechanisms on the other. According to this distinction, mate choice copying constitutes a social, and consequently ‘non-genetic’ influence on mate choice, while independent mate choice preferences constitute ‘genetic’ and consequently non-social influences on mate choice (e.g. Dugatkin 1996b, 1998, Applebaum & Cruz 2000, Witte & Noltemeier 2002, Witte 2006). Manifest mate choice is therefore shaped by two distinct forces that act independently of each other, the genetic and the social, and the interesting question concerns the possible outcomes of situations where these two independent forces conflict with one another. If the influence exerted by mate choice copying is strong enough, then its non-genetic/social influence can ‘override’ the fixed genetic preferences that otherwise generally prevail (Dugatkin 1996b, 1998, Witte & Noltemeier 2002, Witte & Ueding 2003, Witte 2006).

The following example will help illustrate this line of reasoning. Female guppies have evolved a preference for orange body coloration in males, so that they generally prefer males with larger orange areas over those with smaller

ones (Houde 1987, 1988). Dugatkin (1996b) placed a model female next to the less orange of two males, and allowed a focal female that had observed this simulated choice to subsequently choose between the two males. He found that when the males differed by 12% or 24% on their total body orange area, the focal female copied the simulated choice of the model female, but did not copy when the males differed by 40%. Dugatkin couches these results in terms of a conflict between genes and the social environment, suggesting that when the males differed by 12%–24%, cultural cues overrode genetic preferences, but when the difference was 40%, genetic preferences masked any cultural effects. He concludes by suggesting that the experimental protocol used in the study could be modified so as to examine the ‘relative strength of genetic and nongenetic factors’ on a variety of traits across species (Dugatkin 1996b: p. 2773, *see* also Dugatkin 1998, Witte 2006 for similar discussions of these results).

This reasoning is based on the flawed premise that an animal’s environment is somehow independent of its genes. In reality an animal’s genes also determine its environment (Tooby & Cosmides 1992, Tooby *et al.* 2003). Since the environment (including the social environment) is infinite, selection, operating necessarily through genes, also must indirectly determine which part of the environment becomes relevant to the central nervous system (CNS) and consequently the behavior of an animal (Tooby & Cosmides 1992). An animal’s environment, social or not, is therefore inextricably linked to and determined by its genes, and the suggestion that the two are not only independent, but can even somehow go against each other, is not valid.

The notion of guppies that are caught in a battle between their genes and the environment, each pulling on opposite sides of the same rope, thus presents a misleading picture of Dugatkin’s (1996b) fascinating results. A more plausible interpretation of Dugatkin’s results would be that the genes underlying the mate choice copying adaptations in the guppy have evolved to the point that female guppies are now highly selective as to the conditions under which they are influenced by conspecifics’ choices. When two males differ widely in coloration, the guppy

CNS does not allow the information about conspecifics' choices to integrate with the information arising from independent assessment, and the guppy does not copy. When the males are closely matched for orangeness, the guppy CNS responds to this similarity by transmitting the information about conspecifics' choices to those regions that underlie independent assessment, and the two streams of information are integrated to produce a final evaluation, which then determines manifest behavior. To achieve this level of sophistication in the guppy CNS more genetic information is required, not less, regardless of whether on any given trial the guppy copies or not. The fact that this adaptation depends on the social environment for its inputs does not alter the fact that it is as 'genetic' in origin as any independent mate choice mechanism or preference.

## The empirical record

I have compiled the available empirical evidence for mate choice copying in different species, along with their predominant mating system and unusual features (Table 1). Individual studies are classified as providing or not providing evidence for mate choice copying, with a separate category reserved for inconclusive studies. In arriving at these classifications I have mainly relied on the respective authors' evaluations of their results. Earlier studies that were not conducted on the basis of a copying hypothesis but have been subsequently suggested as possible evidence for mate choice copying are not included here (see Pruett-Jones 1992, Jamieson 1995, and references therein).

An examination of the table shows that with the exception of the zebra finch (*Taeniopygia guttata*) all species where results consistent with mate choice copying have been obtained present with an element of polygyny or promiscuity. By far the best-studied model species are the guppy, sailfin molly and Japanese quail. The volume of operational replications and highly predictable nature of the results (see above) leave little doubt that mate-choice copying behavior in these species is subserved by evolved cognitive specializations. It should be noted, however, that in the

guppy this phenomenon appears to manifest in some, but not all populations (Brooks 1996, Lafleur *et al.* 1997, Brooks 1999). In addition to these species, preliminary evidence for copying exists in the mouse (*Mus musculus*), the Norway rat (*Rattus norvegicus*), deep-snouted pipefish (*Syngnathus typhle*), black grouse (*Tetrao tetrix*), brown-headed cowbird (*Molothrus ater*), whitebelly damselfish (*Amblyglyphidodon leucogaster*) humpback limia (*Limia nigrofasciata*), Mexican molly (*Poecilia mexicana*), Amazon molly (*Poecilia formosa*), a Gulf of California marine isopod (*Paracerceis sculpta*) and the ocellated wrasse (*Symphodus ocellatus*). In contrast to the aforementioned species, the pied flycatcher (*Ficedula hypoleuca*), fallow deer (*Dama dama*), sand goby (*Pomatoschistus minutus*), common goby (*Pomatoschistus microps*), great snipe (*Gallinago media*) and Perugia's limia (*Limia perugiae*) probably don't copy. The Japanese medaka (*Oryzias latipes*), three-spined stickleback (*Gasterosteus aculeatus*) and sage grouse (*Centrocercus urophasianus*) present a mixed picture, and more results are needed before definite conclusions can be drawn. Two very recent studies on different *Drosophila* species (*melanogaster* and *serrata*) have also produced conflicting results (Auld *et al.* 2009, Mery *et al.* 2009, see also Leadbeater 2009), and it will be interesting to see whether this is due to actual differences in copying behavior or the different methodologies employed in the studies.

Though the idea of mate choice copying first developed through field observations of lekking species (Bradbury & Gibson 1983, Losey *et al.* 1986, Höglund *et al.* 1990, Gibson *et al.* 1991, Marks *et al.* 1994), the table shows that empirical studies are now overwhelmingly laboratory-based, concentrating mostly on fish (Witte 2006), and to a lesser extent birds and mammals. This shift in emphasis is due largely to the ease with which certain model fish species can be studied in aquaria, and the increased control over confounding variables these laboratory studies afford (see Amudsen 2003). Added to this, many fish (like the poeciliids so commonly used in mate choice copying studies) adapt well to captivity and their sexual behaviors are not adversely affected by the artificiality of their aquarium environment (Amudsen 2003). Studies

**Table 1.** Compilation of empirical studies on mate choice copying in non-human animals. Unless noted otherwise, studies listed test for mate choice copying in females; those suggesting mate choice copying in males are indicated with an asterisk (\*). Similarly, \*\* denotes studies that suggest generalized trait copying (i.e. copying of general male traits, not individual males), those marked with \*\*\* suggest mate choice copying via chemical signals, and † denotes field studies.

Species	Evidence for mate choice copying	Studies not supporting mate-choice copying	Inconclusive studies	System
Guppy ( <i>Poecilia reticulata</i> )	Dugatkin 1992, 1996b, 1998, 2007, Dugatkin <i>et al.</i> 2002, 2003, Dugatkin & Godin 1992, 1993, 1998; Godin <i>et al.</i> 2005**, Vukomanovic & Rodd 2007, Amlacher & Dugatkin 2005, Godin & Hair 2009†,	Brooks 1996, 1999, Lafleur <i>et al.</i> 1997		Promiscuous, no parental care
Sailfin molly ( <i>Poecilia latipinna</i> )	Schlupp <i>et al.</i> 1994, Schlupp & Ryan 1997*, Witte & Ryan 1998, 2002†, Witte & Noltemeier 2002**, Witte & Massmann 2003, Witte & Ueding 2003, Hill & Ryan 2006, Heubel <i>et al.</i> 2008			Promiscuous, no parental care
Japanese medaka ( <i>Oryzias latipes</i> )	Grant & Green 1996	Howard <i>et al.</i> 1998		Promiscuous, no parental care
Deep-snouted pipefish ( <i>Syngnathus typhle</i> )	Widemo 2006*			Reversed sex roles
Japanese quail ( <i>Coturnix coturnix japonica</i> ); for reviews see White 2004, Galef 2008	Galef & White 1998*, White & Galef 2000a**, 2000b*, Ophir & Galef 2003, 2004, Persaud & Galef 2005		White & Galef 1999b	Uncertain, probably mixed (polygamous/monogamous) with some degree of paternal care
Zebra finch ( <i>Taeniopygia guttata</i> ); for discussion see Brown & Fawcett 2005	Swaddle <i>et al.</i> 2005**, Drullion & Dubois 2008**	Doucet <i>et al.</i> 2004		Monogamous, with life-long pairbonding and biparental investment
Black grouse ( <i>Tetrao tetrix</i> )	Höglund <i>et al.</i> 1995†		Höglund <i>et al.</i> 1990†	Lekking
Pied flycatcher ( <i>Ficedula hypoleuca</i> )		Slagsvold & Vijugrein 1999		Mostly monogamous with biparental care
Norway rats ( <i>Rattus norvegicus</i> )	Galef <i>et al.</i> 2008***			Promiscuous, no paternal care



Fallow deer ( <i>Dama dama</i> )		Clutton-Brock & McComb 1993, McComb & Clutton-Brock 1994	Lekking
Marine isopod ( <i>Paracerceis sculpta</i> )	Shuster & Wade 1991 <sup>†</sup>		Territorial, polygynous
Whitebelly damselfish ( <i>Amblyglyphidodon leucogaster</i> )	Goulet & Goulet 2006 <sup>†</sup>		Promiscuous with male territoriality
Sand goby ( <i>Pomatoschistus minutus</i> )		Forsgren <i>et al.</i> 1996	Promiscuous with paternal care
Three-spined stickleback ( <i>Gasterosteus aculeatus</i> )	Frommen <i>et al.</i> 2008	Patrinquin-Meldrum & Godin 1998	Promiscuous with paternal care
Perugia's limia ( <i>Limia perugiae</i> )		Applebaum & Cruz 2000	Promiscuous, no parental care
Humpback limia ( <i>Limia nigrofasciata</i> )	Munger <i>et al.</i> 2004		Promiscuous, no parental care
Ocellated wrasse ( <i>Symphodus ocellatus</i> )	Alonzo 2008 <sup>†</sup>		Promiscuous, with paternal care and male territoriality
Mouse ( <i>Mus musculus</i> )	Kavalliers <i>et al.</i> 2006 <sup>***</sup>		Polygynous, territorial
Great snipe ( <i>Callinago media</i> )		Fiske <i>et al.</i> 1996 <sup>†</sup>	Lekking
Mexican molly ( <i>Poecilia mexicana</i> )	Heubel <i>et al.</i> 2008		Promiscuous
Amazon molly ( <i>Poecilia formosa</i> )	Heubel <i>et al.</i> 2008		Gynogenetic
Common goby ( <i>Potamoschistus microps</i> )		Reynolds & Jones 1999	Promiscuous with paternal care
Sage grouse ( <i>Centrocercus urophasianus</i> )	Gibson <i>et al.</i> 1991		Lekking
Fruit fly ( <i>Drosophila serrata</i> )		Spurrer <i>et al.</i> 1994	Promiscuous
Fruit fly ( <i>Drosophila melanogaster</i> ); for discussion see Leadbeater <i>et al.</i> 2009	Mery <i>et al.</i> 2009 <sup>**</sup>	Auld <i>et al.</i> 2009	Promiscuous
Brown-headed cowbird ( <i>Molothrus ater</i> )	Freed-Brown & White 2010		Brood parasite with no parental care, uncertain mating system

in leks, on the other hand, are more expensive and logistically demanding, often involve rather limited datasets and are notorious for their difficulty in controlling confounding variables.

The standard experimental design is a binary forced-choice task that takes place in an aquarium or cage (Dugatkin 1992). A 'focal' female, constrained in a transparent canister in the centre of the apparatus, is typically made to choose between two closely-matched (for size, coloration, etc.) males that are restrained in transparent compartments on opposite ends of the apparatus. One of these males is confined alone in one side, while on the other side the second male courts a 'model' female that is also restrained in an adjacent transparent compartment. From her vantage point in the centre of the apparatus, the focal female can thus observe what appears to be a single, or unsuccessful, male on one side and a successful one on the other. After the focal female has observed this scene for some time (often 10 or 30 minutes) the model female is removed from her compartment, the transparent canister restraining the focal female is lifted, and she is allowed to swim freely around the tank for a predetermined amount of time. The prediction of the mate choice copying hypothesis is that the focal female will spend more time close to the successful male, a proxy measure of her interest and willingness to mate with him (Bischoff *et al.* 1985, Kodric-Brown 1993, White & Galef 1999a). Repeated trials of this experiment with different individuals can reveal significant deviations of the number of trials in which subjects prefer successful males from what would be predicted by the null hypothesis that successful and unsuccessful males have an equal probability of being selected (e.g. Dugatkin 1992, Dugatkin 1996b, Forsgren *et al.* 1996). The percentage of time or the absolute amount of time spent closer to either male can also serve as the dependent variable (e.g. Dugatkin & Godin 1993, Dugatkin 2007).

An alternative and increasingly popular experimental protocol that is used with the above apparatus is the preference reversal task (Dugatkin & Godin 1992). Here both males are first presented alone, and the focal female expresses her affiliative preference in the absence of a

model female (i.e. on the basis of her independent assessment). Once the focal female's preference has been established, she is restrained in the transparent canister in the center of the apparatus, and a model female is introduced into a compartment adjacent to the male that the focal female did not initially prefer. The experimental design thus simulates a choice by the model female that apparently contradicts the focal female's preference. After the focal female has observed this scene for some time, the model female is removed and the focal female is re-tested to see if her affiliative preference remains the same or has reversed in the face of contradictory information by the model female. The latter case implies mate choice copying. Again, as in the standard protocol described above, a number of measures can be used as the dependent variable. For example, a parallel test-retest series of trials can be run in the absence of any model female to see how consistent focal females' preferences would otherwise tend to be across two consecutive trials. The frequencies of consistent choices in the mate-choice copying and control trials are then compared to test for significant differences (e.g. Dugatkin & Godin 1992). Measures of absolute and relative time spent with the two males can also be used (e.g. Galef & White 1998, White & Galef 2000b, Witte & Massmann 2003).

So far the discussion has focused solely on females, but the empirical record suggests that, given the appropriate conditions, males can also copy (Schlupp & Ryan 1997, White & Galef 2000b, Witte & Ryan 2002, Widemo 2006). Widemo (2006) found that male but not female pipefish appear to copy, a result that presents no challenge to mate choice copying theory, since in this species the roles of the sexes are reversed and males are choosier. Sailfin molly males, like their female conspecifics, also copy each other's choices, which can be understood in light of the short time-window of female sexual activity (Schlupp & Ryan 1997, Witte & Ryan 2002). Because of this constraint males are under great pressure to assess a female's sexual receptivity, and mate choice copying could constitute a partial solution to this problem, with courting and mating serving as cues of sexual availability.

Male molly copying might therefore contribute to the mating frenzies that are observed in the wild, when several males attempt to copulate with a female at the same time (Schlupp & Ryan 1997). Also, a study with Japanese quail found that males significantly increased the amount of time they spent near previously non-preferred females after having observed them mating with another male 48 hours ago (White & Galef 2000b).

An important feature of the empirical record concerns the findings that guppy (Godin *et al.* 2005), sailfin molly (Witte & Noltemeier 2002) zebra finch (Swaddle *et al.* 2005, Drullion & Dubois 2008), Japanese quail (White & Galef 2000a) and fruit fly *Drosophila melanogaster* (Mery *et al.* 2009) females may copy not only other females' preferences for certain males, but generalize these preferences to other males with similar traits. In other words, a model female's preference for a male with a certain trait predisposes focal females to prefer all males with that trait, a process that if widespread could theoretically lead to cultural inheritance of mating preferences (Brooks 1998). How generalized trait copying of this sort could evolve is not yet certain, but a simple haploid, two-locus model (one locus coding for copying, the other for the male trait) suggests this could be indirectly, through genetic hitchhiking on high-fitness genotypes (Servedio & Kirkpatrick 1996). Studies have often employed artificial, experimentally manipulated male traits, like colored leg bands and glued feathers, but Godin *et al.* (2005) found mate choice copying can even affect female guppies' preferences for male orange coloration, a natural trait that is known to affect mate choice (Houde 1987, 1988). Witte and Noltemeier (2002) also found that mate choice copying can affect female mollies' preferences for male size, a trait known to contribute to female molly choice (Marler & Ryan 1997). The extent to which generalized trait copying manifests in nature, as well as its actual impact, if any, on cultural evolution, remains unknown. Theoretical studies have shown that female copying of a male trait could have diverse consequences on the evolution of the trait, depending on the set of underlying assumptions (Kirkpatrick & Dugatkin 1994, Agrawal 2001).

## Directions for future research

### Mate choice copying through non-visual modalities

Recent studies in rodents, animals heavily reliant on olfaction, suggest that mate choice copying in these species is mediated not by visual observation but by olfactory cues (Kavaliers *et al.* 2006, Galef *et al.* 2008). This bypasses what is one of the most restrictive prerequisites of mate choice copying, namely that copying females must be in spatio-temporal proximity to third party copulations (Losey *et al.* 1986). Kavaliers *et al.* (2006) showed that naïve female mice prefer odors of males that are associated with the odor of an estrous female over those of matched males that are not thus associated. This preference for male odors associated with odors of estrous females can even negate females' instinctive aversion to odors of parasitized males. Females exposed to odors of parasitized males associated with odors of estrous females preferred them to those of non-parasitized males that were presented alone. These socially-induced responses to male odors appear to be mediated by the oxytocin system, since they are absent in females with deletions of the oxytocin gene (Kavaliers *et al.* 2006). Evidence of chemically mediated mate choice copying also exists for Norway rats, where it was found that focal females prefer to mate with males that had recently engaged in sexual activity over males that had not, even though they had not witnessed the mating (Galef *et al.* 2008). This effect was blocked when the focal females were rendered anosmic (Galef *et al.* 2008).

Recently, a study with brown-headed cowbirds provided the first evidence of acoustic mate choice copying (Freed-Brown & White 2009). Females of this species emit a characteristic chatter sound when being successfully courted by males, and this vocalization makes it easy, in principle, for other females to gauge a male's success. Researchers played back to focal females male courtship songs that were either followed or not followed by female chatter, and found that focal females displayed more copulation solicitation displays (species-typical postures) when the male songs were followed by

chatter (Freed-Brown & White 2009). Results like this and those discussed in rodents above highlight the potential for a fruitful research program that will examine mate choice copying via non-visual modalities in various species, perhaps even in hitherto unimaginable ways.

### Copying rejection

It is interesting to note that, with a single exception (Witte & Ueding 2003), all empirical studies to date have focused on the first part of the definition of mate choice copying, namely the acceptance of a male. There are, however, strong reasons to believe that females should also be sensitive to the rejection of a male (Pruett-Jones 1992, Witte 2006). The reason this research avenue has not been pursued probably has to do with the increased difficulty of satisfactorily simulating the rejection of a male in the lab, and the inability of existing protocols to accommodate this scenario. Witte and Ueding (2003) tackled this problem by using video playbacks instead of live males. In a modification of the preference reversal protocol discussed above, focal females first chose between playbacks of males displayed on two opposing video monitors. After affiliative preference was established females were exposed, on one monitor, to pre-recorded video playbacks of a model female escaping the preferred male, while on the other monitor the original playback of the non-preferred male was again displayed. After this, females were retested by exposure to both of the original male playbacks. The results suggested that females modified their preferences on the basis of the information contained in the rejection scene, spending significantly less time near the monitors displaying images of the previously preferred male. More than half of the focal females even reversed their original preferences entirely. Future studies that address this problem with similar or different methodologies will tap into a practically unexplored area of empirical research that could prove at least as equally rewarding as what has been investigated so far.

### The genetics of copying

As discussed above, no empirical study to date has examined whether copiers *vs.* non-copiers constitute two different morphs within the same population, a difference that if found, could perhaps signal the existence of underlying genetic variation.

I am aware of only one empirical study in the literature that has examined the genetics of copying (Dugatkin & Druen 2007). This did not conceptualize copying *versus* choosing as discrete behavioral categories, but rather viewed copying as a tendency that varies on a continuum from no copying to extreme copying, and examined whether there is heritable genetic variation in this trait by comparing copying in mother guppies to that of their female offspring. There was very little support for a heritable component in copying behavior (Dugatkin & Druen 2007).

It is easy however to see the benefit of studies on the genetics of copying by contemplating the questions that would be raised if a future study, perhaps in another species, were to uncover a heritable component in copying behavior. Is the variability indeed maintained by frequency dependent selection or is it the result of correlated variation in the ability of females to discriminate quality? Is there any other, perhaps hitherto unnoticed trait that correlates with this heritability? Will the results generalize predictably to other species? Alternatively, if no heritable component is found, yet discrete behavioral morphs are established, what are the developmental events which spur development one way or another? Considerations like this suggest that insights into the genetics of copying will undoubtedly feed back into studies of behavior, and enrich our understanding of this phenomenon in ways that may not be forthcoming simply from behavioral studies alone.

### Mate choice copying and genetic compatibility

Experimental studies of copying generally make no attempt to identify the precise nature of the benefits that copying confers. Given how-

ever that most studies are conducted with non-resource based mating systems, the implicit assumption has probably been that genetic benefits in the form of ‘good genes’ are the driving force behind the evolution of copying. What happens when mate choice is based not on ‘good genes’ but on compatible genes, as for example when females seek mates that will lead to heterozygous offspring (Brown 1997, Tregenza & Wedell 2000, Roberts & Little 2008)? In this case the optimal male differs from female to female, and assuming the only benefits are genetic we should never observe copying, unless perhaps the model female is a close relative. In principle, the presence of copying behavior should constitute evidence against a compatible genes hypothesis and in favour of more universal mate choice criteria.

### **Beyond mate choice copying: nonindependent mate choice in monogamy**

A synopsis of all empirical studies conducted to date (Table 1) shows that with the exception of the zebra finch, results consistent with mate choice copying have not obtained in monogamous species. It is worth noting that even in the zebra finch the results have been mixed, with one study failing to find a copying effect (Doucet *et al.* 2004). Vakirtzis and Roberts (2009, 2010a) have recently suggested that this paucity of copying-type effects in monogamous species is not accidental, but directly related to relevant features characteristic of monogamous species. These authors have argued that mate choice copying is highly unlikely to evolve in monogamous species due to (1) the increasing costs of female competition that copying females would be likely to suffer (2) the diminishing paternal care for their offspring that copying females would suffer (3) the generally low male mating skew which renders the frequency of a male’s mates an ineffective cue in discrimination (4) unequal model female mate value (e.g. is it worth copying the choice of unattractive females?) and (5) an ambiguous relationship between a male’s quality and the number of his

mates (*see* Vakirtzis & Roberts 2010a for discussion, Dubois 2007 for a different view). Their proposed alternative to mate choice copying in monogamy is a process they have termed *mate quality bias*. Ideally, the process takes place in a serially monogamous species where all males are mated and there is a frequent turnover of mates. Added to this, the assessment of the model female must offer some kind of advantage for focal females to move beyond independent mate choice (a point sometimes overlooked). As the name implies, the female adjusts her assessment of the male in accordance with the mate value of his mate, so that males mated with high-quality mates increase their probability of choice, whereas those that are mated with low-quality females decrease it.

Results with humans, a species where female mate value is more heavily dependent on visual cues of attractiveness compared with males (e.g. Townsend 1989, 1998), generally support these predictions. Most experimental studies (using photographic stimuli of men and their supposed partners which are presented to female raters) have failed to find a classical copying effect, i.e. a female preference for men in relationships versus single men (Uller & Johansson 2003, Milonoff *et al.* 2007, Waynforth 2007, but *see* Eva & Wood 2006, Parker & Burkley 2009). The model female’s attractiveness is of paramount importance: women raters give higher desirability (e.g. attractiveness, interest in pursuing a relationship, etc.) ratings to men who are presented with attractive mates and lower ratings to those presented with unattractive mates (Waynforth 2007, Little *et al.* 2008, Vakirtzis & Roberts 2010b, Yorzinski & Platt 2010). Indeed, a male can often suffer a reduced desirability rating when presented with an unattractive mate compared to when he is presented alone (Waynforth 2007, Yorzinski & Platt 2010). The effect is contingent on the attractiveness of the male himself (*see* Vakirtzis & Roberts 2010b): phenotypically attractive males require a more attractive mate to retain their high ratings, whereas relatively unattractive men tend to increase their ratings regardless of the model female’s attractiveness (Waynforth 2007). It will be interesting to see if results like these can generalize to

other species, and particularly those with serially monogamous systems (Vakirtzis & Roberts 2009, 2010a).

## Conclusion

The past two decades have witnessed an explosion of interest in mate choice copying. Theoretical elaboration notwithstanding, mate choice copying is essentially a very simple idea, easily testable in the lab, and research in this area is almost certain to accelerate. Particularly encouraging is the tendency of the field to outgrow itself and expand in previously unforeseen directions (e.g. Nordell & Valone 1998, Kavaliers *et al.* 2006, Waynforth 2007, Galef *et al.* 2008). The concept of copying others' choices has proved so successful in mate choice studies that scientists are slowly beginning to apply it to areas outside mate choice, like habitat selection and even decisions about whom to parasitize (Gonçalves *et al.* 2003, Wagner & Danchin 2003). Despite of all the progress achieved so far however, I have shown here that scientists have only begun to scratch the surface of this unique phenomenon. The future is therefore certain to greatly improve our knowledge and understanding of why, how and when females copy the choices of others.

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