

Mate-choice copying: Status quo and where to go

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Abstract Mate-choice copying is a fascinating and widespread mate-choice strategy. Individuals gather public information about potential mates by observing others during sexual interactions and choose or reject the same individual as a mate as the observed individual did before. The influence of copying behavior on an individual's mate choice can be so strong that socially acquired information can override genetically based preferences for certain phenotypes. Thus, mate-choice copying enforces dynamic processes in sexual selection. Here, we review the current state of research on mate-choice copying and focus on sex-specific aspects. We present evidence that mate-choice copying can support the evolution of novel sexual ornaments, and we discuss potential costs of mate-choice copying when public information is not reliable. Moreover, we discuss the conflict faced by males that copy since mate-choice copying increases sperm competition. In conclusion we suggest interesting topics for future research in mate-choice copying [Current Zoology 61 (6): 1073–1081, 2015].

Keywords Mate-choice copying, Public information, Audience effect, Sperm competition, Novel ornaments

Most models of sexual selection assume that males and females exhibit genetically based mate preferences (Bakker and Pomiankowski, 1995; Iwasa and Pomiankowski, 1999; Mead and Arnold, 2004; Andersson and Simmons, 2006). Forming mate preferences is a complex process in which not only genetic factors but also non-genetic factors like social learning are involved. Social learning is widespread in the animal kingdom and not restricted to vertebrates (Boyd and Richerson, 1985; Heyes and Galef, 1996; Leadbeater and Chittka, 2007). It covers any learning in which an individual receives information about other conspecifics or heterospecifics by observing them interacting with others or with environmental resources and thus, using socially provided information (Danchin et al., 2004). Forms of social learning have now been recognized as meaningful mechanisms for the non-genetic inheritance, i.e. the cultural transmission of mate preferences (Brooks, 1998; Witte and Noltemeier, 2002; Godin et al., 2005). The cultural transmission of mate preferences via mate-choice copying leads to high dynamic processes in the evolution of mate preferences. Mate preferences will change faster (e.g. resulting in preference of a specific phenotype) and will change reproductive success of individuals within populations faster than any changes in mate preferences through genetic factors. Thus mate-choice copying increases the dynamic of processes in sexual selection.

Mate-choice copying (hereafter abbreviated as MCC) is one form of social learning. Since Lee A. Dugatkin (1992) provided the first experimental evidence that guppy females *Poecilia reticulata* do not choose a mate independently of other females but copy the mate choice of others, a “boom” of experimental and theoretical studies on MCC started. Research on this topic is still ongoing in invertebrates and vertebrates including humans (e.g. Vakirtzis and Roberts, 2012). The first prerequisite and necessary condition for MCC to occur is that individuals must be able to observe the mate choice of other conspecifics (Losey et al., 1986). To qualify as MCC, it must be the sexual interaction, and not the consequence of the choice of a female or a male (e.g. eggs in a nest), that influences mating decisions of others. Following the definition of Pruett-Jones (1992) “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. The outcome of female copying is that if one female mates with or avoids a specific male, successively choosing females will be accordingly more or less likely to mate with that male than they would otherwise have been”. The same is true for male mate choice. Thus, MCC can lead to a socially determined preference for specific mates or a rejection of specific mates (Witte and Ueding, 2003). The influence of MCC

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on mate choice can be so strong that socially acquired information can override genetically based preferences for certain male phenotypes in females (e.g. guppies, Dugatkin, 1996, 1998; Godin et al., 2005; sailfin mollies *Poecilia latipinna*, Witte and Noltemeier, 2002). Sailfin molly females maintain the socially learned mate preference (via MCC) for smaller males and can, therefore, serve as model females for other conspecific females. Additionally, sailfin molly females remember an observed sexual interaction for at least one day and can thus copulate with the same male, not only immediately after the observed females, but at a safer moment regarding predation risk and/or sperm depletion in males (Witte and Massmann, 2003).

So far, there are six studies showing experimentally that MCC occurs in the wild: black grouse *Lyrurus tetrrix* (Höglund et al., 1995), sailfin molly (Witte and Ryan, 2002), whitebelly damselfish *Amblyglyphidodon leucogaster* (Goulet and Goulet, 2006), ocellated wrasse *Symphodus ocellatus* (Alonzo, 2008), and the Trinidadian guppy (Godin and Hair, 2009). Thus, MCC is a biologically relevant mate-choice strategy. Although MCC seems to be widespread in animals (Vakirtzis, 2011), the specific conditions and mechanisms underlying MCC are still not well understood, and so far, no fitness advantages through MCC have been shown.

Vakirtzis (2011) has given a good overview regarding the theoretical background of MCC and the empirical evidence in different mating systems. However, some important and interesting aspects of MCC have not been investigated and discussed in-depth so far. These include sex-specific aspects as well as individual advantages/disadvantages and evolutionary consequences of MCC. Thus, we will focus on the following aspects of MCC: The first section will highlight sex-specific aspects of MCC. The second section will illustrate the role of MCC in supporting the evolution of novel sexual ornaments. In the third section we will discuss the context dependence and costs of MCC when public information is not reliable, i.e. the ‘audience effect’ in MCC, and in the fourth section we will focus on the conflict in males because MCC increases sperm competition. In the outlook, we would like to suggest topics for future research in MCC.

1 Sex-Specific Aspects of Mate-Choice Copying

So far, studies investigating MCC in females are far more numerous than those investigating MCC in males.

This is probably because females are considered to be the choosier sex (Trivers, 1972) in most species because they usually face higher reproductive investment. High reproductive investment is expected to select for increased choosiness (Kokko and Johnstone, 2002) and copying should reduce the cost of choosiness (Dugatkin, 2005). Therefore, females are thought to be more prone to use public information (Danchin et al., 2004) than males. However, there are also studies demonstrating that males use this mating strategy as well (e.g. Schlupp and Ryan, 1997; White and Galef, 2000a; Witte and Ryan, 2002; Widemo, 2006; Auld and Godin, 2015). Copying might be beneficial for males if mating or sperm production is costly (Kokko and Jennions, 2008) or if males provide parental care. Only few studies have focused on both sexes within one species and have discovered sex-specific aspects of MCC.

In the deep-snouted pipefish *Syngnathus typhle*, a sex role reversed species, in which males are choosier than females, males but not females copy the mate choice of their conspecifics (Widemo, 2006). Moreover, Moran et al. (2013) found that male but not female darters of *Etheostoma flabellare* show MCC. In this species, males provide parental care by guarding a nest site under a rock and caring for developing eggs. However, Moran et al. (2013) found that in another darter species, *Etheostoma zonale*, in which neither sex provides parental care, both sexes show MCC. The same was found in sailfin mollies (reviewed in Witte and Nöbel, 2011) and Atlantic mollies *Poecilia mexicana* (females: Heubel et al., 2008; males: Bierbach et al.; 2011). When both sexes face high costs of reproduction as in the stickleback *Gasterosteus aculeatus*, both sexes use mate-choice copying (Frommen et al., 2009). Moreover, in the socially monogamous zebra finch *Taeniopygia guttata castanotis*, in which both sexes provide parental care, Kniel et al. (2015a) showed that females, but not males copy the mate choice of their conspecifics. In the Japanese quail *Coturnix japonica* an interesting sex difference was found. Female quail copied the mate choice of other females (White and Galef, 1999a) and the attractiveness of males remained enhanced even 48h after females had seen them mate (White and Galef, 2000a). Males, however, avoided females they have seen mating (White and Galef, 1999b), but only for a short time period, since White and Galef (2000a) found that they no longer avoided those females after 48 h. Avoidance of recently mated females might be a strategy to reduce or avoid sperm competition (see section 4).

Whether males and/or females use MCC does not

seem to depend solely on their mating system. Hence, a prediction of whether or not males and/or females of a certain species will copy the mate choice of their conspecifics remains difficult, which makes it even more important for future studies to consider both sexes. However, sex differences may be difficult to detect as even within a sex there may be differences between populations (overview in Vakirtzis, 2011). In the guppy, for example, MCC was found in some, but not all populations (Brooks, 1996, 1999). *Poecilia latipinna* females show heterospecific mate-choice copying (they copy *Poecilia formosa*, gynogenetic, all-female), but only in sympatric populations, not in allopatric populations (Heubel et al., 2008).

Finally, another difference in MCC between the sexes is that, by now, generalization, i.e. copying the choice for a phenotype instead of an individual, has only been demonstrated in females (see section 2).

2 Mate-Choice Copying and the Evolution of Novel Ornaments

As demonstrated in various studies (overview in Vakirtzis, 2011) copying the mate choice of others can lead individuals to choose opposite-sex individuals whose phenotype differs from their genetically determined preferences. Hence, the idea formed that MCC can play a role in the evolution of new secondary sexual traits. A theoretical study by Agrawal (2001) considers MCC an efficient mechanism for the evolution of new traits (but see Kirkpatrick and Dugatkin, 1994). Agrawal showed that MCC can support the spread of a novel trait within a population and that it can drive females to prefer rare and novel male phenotypes. Santos et al. (2014) took a step further by including negative public information, i.e. the rejection of a mate, in their model. They stated that a novel (rare and fitter) phenotype will spread in a population if positive and negative information about the common phenotype cancel each other out, or when the negative information prevails.

A requirement for this mechanism is that copiers generalize between potential mates, i.e. copy the choice for a phenotype and not for an individual. Generalization is a prerequisite for cultural inheritance of socially driven mate choice (Brooks, 1998). Variation in the choice between naturally occurring phenotypes due to MCC has been demonstrated. For example, Godin et al. (2005) demonstrated that female guppies showed MCC and that they generalized the preference for a natural color phenotype to other male individuals of the same

phenotype. Witte and Noltemeier (2002) found that sailfin molly females generalized a learned preference for smaller males between individual males. However, it remains difficult to distinguish between learned and genetically based preferences. In order to set those apart, new artificial phenotypes have to be created for which there is no latent preference. And indeed, a number of studies have demonstrated that even the choice for artificially created phenotypes can be copied.

In birds, Swaddle et al. (2005) demonstrated that female zebra finches copied the choice of other females and preferred males of the same artificial phenotype (leg band color) as the observed female's mate. Additionally, Drullion and Dubois (2008) found that female zebra finches copied and generalized the choice for males wearing different leg bands (orange and white) if the received information was consistent. Another experimental study in the zebra finch showed that female MCC can support the spread of a new male trait, a red feather on the forehead (Kniel et al., 2015a). White and Galef (2000b) found that female Japanese quail copied the mate choice of other females and generalized between males of the same artificial phenotype (blue or red food coloring on male breast feathers). In fish, an experimental study on sailfin mollies showed that MCC in females can support the spread of a new male trait (an artificial yellow plastic sword with a black border; Witte, 2006). Even in insects, MCC for artificial traits was demonstrated. Mery et al. (2009) found that female *Drosophila melanogaster* not only show MCC, but that they generalized and preferred males of the same color type (manipulated by dusting males with green or pink powder) as the male they had previously observed mating.

So far, generalization in MCC has only been demonstrated in females. To our knowledge, there is only one study that has investigated whether males generalize in MCC. Kniel et al. (2015a) have tested generalization in male MCC in zebra finches with a negative result. Copying the choice of a specific female phenotype does not make sense in males to evaluate the reproductive stage of a female, and indeed, MCC of a phenotype has never been observed in males. However, there is no evidence that male zebra finches copy the choice for an individual female.

Up to now, studies showed that MCC can support the spread of a new ornament within a population. Due to the sex-specific ability to generalize and copy the choice of specific phenotypes instead of individuals, it is more likely that MCC supports the evolution of new traits in the male sex than in females or in both sexes.

Thus, MCC can lead to stronger sexual dimorphism within a species.

3 Context-Dependence of Mate-Choice Copying and the Audience Effect

MCC is a rather facultative and not an obligate mate choice strategy (Witte and Ryan, 1998). Individuals should always decide whether, when and whom to copy. Thus, MCC is a context-dependent mate choice strategy. Animals that show MCC behavior use public information (Danchin et al., 2004) for their mate-choice decisions. This leads to the question whether public information is always reliable. The social environment does not only influence the behavior of the copier but it can also influence the behavior of the 'model' individual (i.e. the individual that will be or is copied) in case the latter notices that he or she is being observed. Such a change in behavior due to the presence of an observing individual is termed 'audience effect' or 'bystander effect' (McGregor, 2005). During the last three decades, audience effects have been investigated in different contexts and in diverse animal taxa (insects: Tachon et al., 1999, Fitzsimmons and Bertram, 2013; fish: Matos and McGregor, 2002; Dziewieczynski et al., 2012, 2014; Bierbach et al., 2011b; Nöbel and Witte, 2013; Auld et al. 2015; birds: Baltz and Clark, 1994, 1997; Ung et al., 2011; Hoi and Griggio, 2012; Kniel et al., 2015b; mammals: Townsend and Zuberbühler, 2009; Overduin-Devries et al., 2012).

Where males show MCC behavior, it is assumed that an audience effect during mate choice most likely results from the threat of sperm competition (Plath et al., 2008, see section 4). Behavioral experiments, in which males had to choose between two females, revealed that sailfin molly males (Nöbel and Witte, 2013), as well as Atlantic molly males conceal their mate preference (Plath et al., 2008; Ziege et al., 2009) when a male audience is present, or they even trick their observers by interacting with the previously non-preferred female (Plath et al., 2008; Nöbel and Witte, 2013). Bierbach et al. (2011b) showed that guppy males ceased to show a mating preference when a familiar male was present that had been perceived as sexually active. However, they showed no such audience effect when they had perceived their audience as sexually inactive and thus as no sperm competitor. Moreover, audience effects were stronger when the audience male was larger and thus more attractive to females. Auld et al. (2015) showed that male Trinidadian guppies lowered their mating ef-

fort and exhibited fewer conspicuous courtship displays when other males, i.e. potential rivals, were around.

Plath et al. (2010) reported differences in the expression of audience effects within a species: While surface-dwelling males of the Atlantic molly deceive their rivals about mating preferences, sending misleading signals was not found in the cave-dwelling form of the species. The difference in behavior has been discussed to result from an evolutionary regression in the cave-dwelling population. Since MCC (at least if it is based on visual cues) is unlikely to occur under dark conditions, there is no need to conceal a mate preference (Plath et al., 2010).

In recent experiments with Atlantic mollies, a pretended mate choice of a 'model' fish indeed misleads males: Audience males copied their conspecifics even if these directed their mating behavior towards less attractive individuals (Nöbel et al., manuscript in preparation). Further, Nöbel and Witte (2013) showed that *P. latipinna* males, that were aware of being observed by an audience male, transferred more sperm during copulation. Thus, model males might compensate the risk of a reduced reproductive success due to sperm competition by providing the female with more sperm. This in turn should lower the reproductive success of the copying male (or encourage copying males to enhance their sperm transfer as well; see section 4).

However, audience effects in the context of mate choice do not necessarily result from the risk of being copied. Other explanations for a change in mate choice when an audience is present might be the avoidance of agonistic interactions or simply a distraction of the choosing individual ('split-attention hypothesis', Plath and Schlupp, 2008).

Dubois and Belzile (2012) as well as Kniel et al. (2015b) found an audience effect in males of the socially monogamous zebra finch where MCC in males does not occur (Kniel et al., 2015a). Here, males probably change their preference in order to reduce the risk of being rejected by their preferred mate, since the female might choose the audience male as a mating partner. Hence, males might invest more time in courting a formerly non-preferred female to avoid remaining unpaired (Dubois and Belzile, 2012).

One could expect that females also show an audience effect that prevents other females from copying their mate choice. Concealing a mate preference might ensure that the preferred male does not run out of sperm due to copulations with other females. Further, in species where females generalize observed interactions and copy the preference for a certain phenotype (White and

Galef, 2000b; Witte and Noltemeier, 2002; Godin et al., 2005, Swaddle et al., 2005), females could hide their own preferred phenotype to avoid an enhanced attraction of other females to this male phenotype, especially if this male phenotype is rare within the population. In that case, other females might try to attract the focal female's mate as an extra-pair mate. This may lead to unfertilized eggs for the focal female. Plath et al. (2009) investigated audience effects in female Atlantic mollies. They found a slightly weaker expression of female mate preferences when an audience female was present. The effect was much weaker than the audience effect found in males. These results have been explained by a lower strength of competition between females compared to males as well as by the fact that females usually form female-biased shoals and thus, are used to the permanent presence of other females. In zebra finches, Kniel et al. (2015b) found no change in female mate preferences when an audience female was present. But females reduced their choosing motivation. This decrease in choosing motivation might be interpreted as a weak audience effect since females might try not to reveal their mating preference to their audience.

The here summarized findings suggest that the expression of an audience effect is no obligate and inflexible strategy but that it is an optional strategy that individuals only show under certain social conditions and contexts. As explained by Gross (1996), most strategies that include alternative mating tactics can be regarded as conditional strategies: They are genetically fixed and status-dependent (with or without frequency-dependent selection). The animal has to choose a tactic and, therefore, needs to assess its own status as well as its social environment. Similarly to the expression of an audience effect, the expression of MCC might also not (or not in every species showing this behavior) be an inflexible strategy in males. Rather, it might be a facultative strategy that depends on certain circumstances such as the perceived level of sperm competition (see section 4).

The investigation of complex interactions provided by the social environment between actors and observers in the context of mate choice has just started. There is need for more innovative experiments to understand the role of each participant in this dynamic public information network, as well as under what circumstances public information should be used (Dubois et al., 2012).

4 Mate-Choice Copying and Sperm Competition

Copying the mate choice of their conspecifics might

be a beneficial strategy for males. However, it also bears some costs, since it increases sperm competition, especially for copier males. Males usually face strong intra-sexual competition and are rather selected to fertilize as many female ova as possible. In this context, many studies in the last three decades have put emphasis on the strong force of sperm competition in sexual selection (overview in Birkhead and Møller, 1998; Simmons, 2001). Males evolved diverse tactics to avoid or cope with sperm competition such as mate-guarding (Conner and Itagaki, 1984; Morbey, 2002), removal of alien sperm (Córdoba-Aguilar et al., 1993), insertion of mating plugs (Masumoto, 1993), enhanced sperm transfer (Nöbel and Witte, 2013), or a mating preference for virgin females (Carazo et al., 2004). Sperm competition avoidance in some way contradicts MCC, since copying males accept to mate with a female that most probably received another male's sperm shortly before. MCC should thus only occur if the benefits are higher than the costs of sperm competition. Experiments testing this idea should compare reproductive success of copier and non-copier males in situations of different degrees of sperm competition.

In the family *Poeciliidae*, where MCC in males occurs in several species (Witte and Ryan, 2002; Munger et al., 2004; Heubel et al., 2008), MCC has been suggested to save time and energy associated with the thorough investigation of a female's fertility status (Schlupp and Ryan, 1997). In some contradiction to the finding that they show MCC, sailfin molly males show higher rates of sexual behavior towards virgin females than towards gravid females (Farr and Travis, 1986). This behavior indicates that sperm competition is indeed an issue in this species since a preference for virgin females can be regarded as a tactic to avoid sperm competition.

In a recent study, Auld and Godin (2015) found that males of the closely related guppy show MCC behavior. However, in an earlier study, it was shown that guppy males do not show MCC, but prefer to mate with females they have not seen in a sexual interaction with other males before (Dosen and Montgomerie, 2004). Avoidance of recently mated females has, for example, also been observed in males of the Japanese quail (White and Galef, 1999b). Least killifish males *Heterandria formosa* prefer smaller females over larger ones, an observation that has been interpreted as an active mechanism to avoid sperm competition, since smaller females are usually younger and therefore more likely virgins. The authors assumed that least killifish males

gain a reproductive advantage if they are the first mating partner of a female ('first-male precedence', Ala-Honkala et al., 2010). In contrast, other studies on Poeciliids reported paternity bias to be skewed towards the last male to mate with a female during her fertile period ('last-male precedence'; Hildemann and Wagner, 1954; Constanz, 1984; Farr and Travis, 1986; Evans and Magurran, 2001). Under last-male precedence, sperm competition should be more severe for the first male (i.e. the 'model male') than for the copying male, while copying should be less efficient under first-male precedence. However, not only the order, but also the interval between two copulations seems to be important for the reproductive success of a male. In guppies, the proportion of offspring sired by the first of two males was found to increase as the interval between the first and the second copulation increased (Evans and Magurran, 2001). Hence, copying males should try to keep this interval as short as possible. In contrast, male Japanese quail avoided females only shortly after they had seen them mating. No further avoidance was observed after 48 hours (White and Galef, 2000a). Here, sperm competition might be more severe for the second male to mate with a female within a short period of time than for the first male.

Under strong sperm competition, males might favor unoccupied females, while they might show MCC behavior if sperm competition is rather weak. For instance, males might refuse to copy when they observe a female interacting with several males (increased sperm competition) or when the model male is of higher quality and thus expected to succeed during sperm competition. Alternatively, males might stick to MCC even if the level of sperm competition is high, but increase the amount of sperm transferred during copulation. As predicted in theoretical studies (e.g. Parker, 1974; Parker et al., 1997), empirical work showed that male mating behavior and/or the amount of sperm transferred can be adjusted to the perceived risk of sperm competition in various animal species (e.g. Cuadrado, 2000; Price and Rodd, 2006; Wigby et al., 2009; Kureck et al., 2011). In line with these findings, sailfin molly males have been reported to transfer more sperm during copulation when they are observed by a competitor (Nöbel and Witte, 2013; see section 3). Hence, copying males might try to compensate a potential reproductive disadvantage by transferring a large amount of sperm. Support for a behavioral adaptation of copying behavior to the perceived risk of sperm competition was given by Bierbach et al. (2011a). Atlantic molly males copied the mate

choice of a model male if they had seen him associated with a previously non-preferred female. But MCC was weaker when the tested males witnessed not only an association but a physical interaction of the two (i.e. increased risk of sperm competition). In order to clarify whether males indeed adapt their copying behavior to their competitive environment, experimental studies with males in different mating situations are required. Moreover, the reproductive success of copying males and 'model' males should be compared in species in which MCC in males occurs.

5 Outlook: Mate-Choice Copying – and Where to Go

Although inspiring theoretical models and experimental studies on MCC have discovered fascinating aspects of this mate-choice strategy in the last 23 years, there are still important issues that have to be explored.

5.1 What is the fitness advantage of mate-choice copying for the copier and the copied individual?

Unfortunately, the fitness advantage of MCC is still unknown. Do females and/or males that copy the mate choice of others have a higher reproductive success than non-copying individuals? This is a fundamental question for assessing the evolutionary consequences of MCC. For the copied individual, theoretical models predict that males that are copied as mates by females have a higher reproductive success than other males (Wade and Pruett-Jones, 1990). This leads to a skew distribution in the number of offspring in males. However, this idea has not been tested yet.

5.2 Does mate-choice copying have a genetic background?

Social learning in general requires a genetic predisposition for the ability to learn from other conspecifics. All theoretical models on MCC assume a genetical component. In relation to a potential fitness advantage of MCC it is crucial to know whether it is at least partly genetically determined. We do not expect to identify genes determining copying behavior, but there might be a higher likelihood that descendants of copying individuals show stronger copying behavior than descendants of non-copying individuals. A study by Dugatkin and Druen (2007) did not find support for the assumption that MCC has a heritable component in guppies. More studies are needed to assess whether MCC has a genetic background.

5.3 Information matters – but what information?

Although MCC appears to be quite common, there are still important aspects missing that could shed light

on the underlying mechanism of this fascinating mate-choice strategy. In a copying situation, the observer will be part of an information network. Therefore, two of the central questions are: what is the biologically relevant information and from whom will the observer gain this information, since there are different sources (Westneat et al., 2000). S/he will receive information about the quality of the fe/male interacting with his/her mate, the so-called ‘model’. Further, s/he will receive information about the quality of the ‘model’, and additional information about the two individuals by observing their interaction. How are these information qualities and quantities connected with each other? To identify the crucial information quality and information quantity that leads to a change in mate choice decisions, it is necessary to isolate specific interactions from others and analyze each of them separately. Those studies will provide new insights into the mechanism of information gathering and cognitive performances in animals in general.

5.4 The role of the ‘model’

So far, many different aspects of MCC have been investigated regarding the role of the ‘model’. We know that the size of the ‘model’ female matters and that females copy the mate choice of bigger females which are, therefore, probably older and more experienced in mate choice, but not vice versa (Dugatkin and Godin, 1992; Amlacher and Dugatkin, 2005; Vukomanovic and Rodd, 2007). We also know that sailfin molly females only copy the mate choice of conspecific females and not the mate choice of closely related Amazon molly females (Hill and Ryan, 2006). Thus, females seem to assess the quality of a ‘model’ female and decide whether to copy or not to copy. Size/age and species identity are only two factors regarding the quality of a ‘model’ for the copying individuals. Does the personality of a ‘model’, its position and role in a social group or a shoal matter for copying individuals? Are ‘leaders’ in a shoal better ‘models’ for MCC than ‘followers’, and ‘bold models’ better than ‘shy models’? These are only some ideas for future investigations to understand the role of the ‘model’ in MCC.

So far, we just started to understand the mechanism and function of this complex mating strategy, and we hope that many researchers will continue to or start studying MCC.

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