

Sex and the public

Social eavesdropping, sperm competition risk and male mate choice

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Mate choice can be sensitive to social cues from neighboring individuals, e.g., animals can copy mate choice decisions. Males that are at risk of being copied by others may respond to this with reduced preference expression (“audience effects”). We review the various pathways by which sperm competition risk affects (1) male mate copying behavior and (2) audience effects. For example, a recent study suggests that males gather complex social information on rivals’ sexual competitiveness (sexual activity and attractiveness to females) and respond with reduced expression of mating preferences only “when it matters,” i.e., when a sexually competitive rival is present.

Sexual selection, e.g., through mate choice, is an important evolutionary driver and individuals may integrate a wide range of information in their assessment of mate quality.¹ Mate choice is not only based on external characteristics (morphological, behavioral or other) of potential mating partners, but also the social environment in which mating occurs plays an essential role (non-independent mate choice²⁻⁴). Especially in group-living animals⁵ communication events—such as communicatory interactions between sending (courting) males and receiving (choosing) females—typically do not occur in privacy, but in a public domain.⁶⁻¹¹ Living in a social (or communication) network¹¹⁻¹⁴ enables animals to eavesdrop on other individuals’ mating decisions and utilize the extracted information.^{8,10,15-17} The most intensely studied type of social eavesdropping is mate choice copying,^{2,3,18-21} but also males that are at risk of being copied by others may respond to this with reduced preference expression (“audience effects”^{14,22-24}). In livebearing fishes (family Poeciliidae), where females often mate multiply,^{25,26} sperm competition risk (SCR) is a decisive factor affecting males’ fitness (reproductive success), but its role for non-independent mate choice was largely unknown. We demonstrate that SCR plays a significant role for (1) male mate copying behavior (with males copying less when SCR is high²⁷) and (2) audience effects. For instance, SCR leads males to deceive rivals about their actual mating preferences.²⁸

Moreover, a recent study²⁹ uncovered a surprisingly complex case of social information use: males eavesdrop on rivals’ sexual competitiveness (sexual activity and attractiveness to females) and respond with reduced preference expression only “when it matters,” i.e., when being observed by a sexually competitive rival.

Sexual selection theory often assumes that mate choice decisions are based on genetically inherited internal factors (i.e., innate search images) that enable individuals to select among several potential mates¹ (Fig. 1A) and accordingly, an increasing body of literature provides direct (e.g., through parent-offspring comparisons)^{30,31} or indirect evidence (e.g., from the investigation of common garden reared individuals)³²⁻³⁴ for a genetic basis of mating preferences. Still, several studies exemplified that mate choice in nature is a complex process that also involves the acquisition of information from the social environment^{2,3,21,35} (Fig. 1B). This does not come as a surprise as animal behavior in general typically is a product of both innate (genetic) and environmental factors.^{36,37}

Much research has been conducted on female mate choice, and various theories have been forwarded to explain the adaptive significance of female mating preferences.^{1,38-40} However, it is well established that also males express mating preferences,⁴¹⁻⁴⁵ especially if mating or sperm production is costly⁴⁶⁻⁴⁹ and if females differ in their resource value,^{50,51} such as numbers of oocytes in the female ovary.⁵² In modern bony fishes (Teleostei), for example, female fecundity is typically a correlate of body size, and males prefer to mate with larger, more fecund females (e.g., in two-spotted gobies, *Gobiusculus flavescens*,⁵³ guppies, *Poecilia reticulata*,⁵⁴ Atlantic mollies, *P. mexicana*,^{44,45,55} and haplochromine cichlids, *Astatotilapia flavijosephi*).⁵⁶

Male teleosts assess females’ quality not only on the basis of body size, but a range of other phenotypic traits may also be relevant.^{50,57,58} However, in stark contrast to female mate choice, sperm competition risk (SCR) and intensity (SCI) can affect male mate choice.⁵⁹⁻⁶² Obviously, a male’s reproductive fitness is at stake when sperm from two or more males compete for fertilization of a clutch,^{63,64} or—in internally fertilizing species—within a single female’s genital tract.^{26,65,66} In this review, we provide a brief overview of recent findings in the field of socially influenced (non-independent) male mate choice. We emphasize the role played by SCR for various aspects of non-independent male mate choice.

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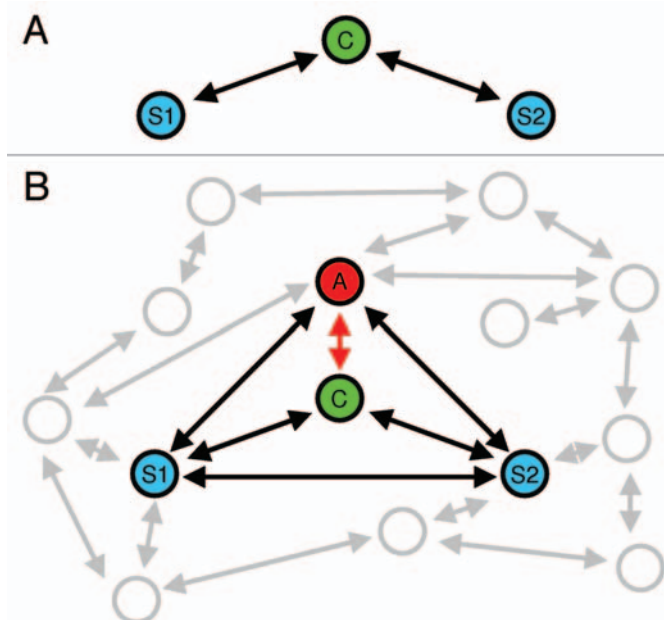


Figure 1. (A) Schematic view of an idealized mate choice situation in a classical binary choice test. Mate choice is thought of as a process of mate quality assessment involving the choosing individual (C) and two potential mating partners (stimuli, S1 and S2). (B) Mate choice in a communication network involving multiple senders and receivers of information. For simplicity, most studies to date have focused on interactions between four individuals. In this example, a by-standing individual (the audience, A) may affect the focal individual's mate choice, but also interactions between S1 and S2, and between A and both stimuli are acknowledged.

Especially in internal fertilizing species, such as livebearing fishes (family Poeciliidae), where females mate multiply,⁶⁷ and females can store sperm for several consecutive broods,^{26,68,69} sperm competition is intense. Poeciliid broods are typically sired by several males (e.g., *P. reticulata*;^{26,70} sailfin molly, *P. latipinna*;^{71,72} green swordtails, *Xiphophorus hellerii*⁷³), which may be due, in part, to benefits for females of mating multiply,²⁵ but also to coercive male mating behavior, i.e., forced copulations.⁷⁴⁻⁷⁷ Obviously, females' behavior (i.e., their past and anticipated future sexual interactions) and especially the behavior of surrounding males can have a profound effect on SCR and thus, are likely to affect males' fitness (reproductive success). It seems straightforward to predict that the SCR a male is facing while choosing a mate is likely to affect his mate choice,^{23,61,62,78} and males are predicted to evolve counter-strategies to reduce SCR.⁷⁹

Social Eavesdropping: Males Copy Other Males' Choices

Social eavesdroppers are by-standing individuals that may extract information about the quality of the observed individuals by using information of signaling interactions^{3,16} (Fig. 2A). In the context of mate choice the most intensely studied form of social eavesdropping is mate choice copying, which has been defined as a process during which a female's probability of choosing a given

male increases if other females have previously chosen that male¹⁸ (Fig. 2B). Most studies on mate choice copying have focused on females,^{2,21,35} but also males copy other males' choices (*P. latipinna*;^{80,81} pipefish, *Syngnathus typhle*;⁸² three-spined stickleback, *Gasterosteus aculeatus*⁸³).

The adaptive significance of male mate choice copying in poeciliids could be linked to reduced costs for searching a receptive female.⁸⁰ Poeciliid females are receptive only as virgins or for few days post partum^{68,84,85} and accordingly, only a small proportion of females in a population are receptive at a time.^{39,69} As poeciliid males need to approach females to test their receptivity by nipping at the female's genital opening,⁸⁶ copying other males' mate choice may allow saving considerable energetic and opportunity costs (sensu⁸⁰).

Nevertheless, male mate choice copying in internally fertilizing species—like livebearing fishes—remains a conundrum, as males incur increased SCR when choosing another male's previous mate. In a recent study, we therefore asked whether male Atlantic mollies (*P. mexicana*) would copy less under increased SCR.²⁷ We created two copying situations with different levels of SCR: a fraction of the focal males were allowed to copy from visual interactions between a stimulus female and a model male (representing low SCR) while another fraction of males could observe direct (sexual) interactions (leading to increased SCR). As predicted, males from the latter group copied less, demonstrating that *P. mexicana* males indeed respond to perceived SCR when copying each other's mate choice.²⁷

Audience Effects: Risk of Being Copied Affects Mate Choice

Audience effects are defined as behavioral changes induced by the presence of other (by-standing) individuals that may or may not extract information from the observed communication events^{23,24} (Fig. 2C). Beside audience induced changes in signaling and courtship behavior,^{87,88} the presence of a conspecific audience also has the potential to affect males' mate choice decisions.^{23,28,29,62,89-91} *Poecilia mexicana* males, e.g., cease expressing mating preferences and reduce their sexual activity when another male is present,⁸⁹ which may be a response to avoid unintended interception of information about their mating preferences.^{23,62} On top of that, it appears that *P. mexicana* males deceive rivals about their mating preferences by directing their first sexual interaction (directly after they were presented with the audience male) towards the female they had rejected beforehand,^{28,91} (Fig. 3). This behavior was interpreted as an attempt employed by males to lead the rival away from their preferred mate, thereby exploiting mate choice copying through dishonest signaling.²³ Ultimately, these behaviors may thus help to reduce the level of SCR.

As SCR is clearly linked to the present motivational state of the by-stander, we asked whether *P. mexicana* males are able to assess and remember rivals' sexual motivation and attractiveness to females, and if they might integrate this information strategically into their mating behavior.²⁹ Male-dyads were allowed to familiarize with one another in two adjacent compartments of a tank that was separated by a transparent Plexiglas divider. One of them was

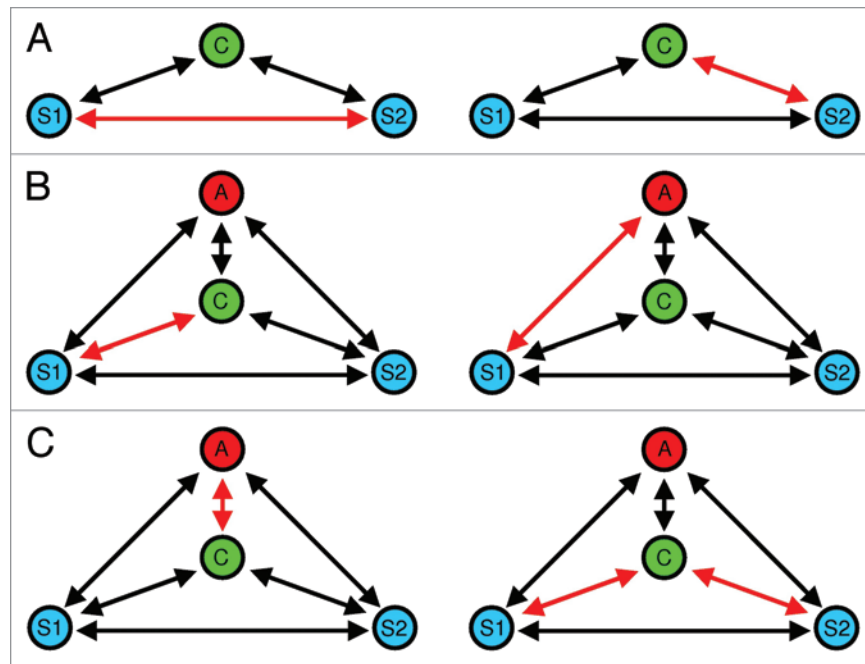


Figure 2. Different forms of social eavesdropping during mate choice in communication networks. (A) Eavesdropping on interactions between two potential mating partners: the choosing individual (C) extracts information about mate quality by observing aggressive^{92,93} or acoustic interactions¹⁷ between two potential mating partners (S1 and S2). (B) A special form of social eavesdropping is mate choice copying, where a by-standing individual (A) extracts information about mate quality from observing sexual interactions. In the present example, A is more likely to approach S1 after having observed (C) sexually interact with S1. (C) Audience-induced changes in mate choice. The mere presence of a by-stander (the audience, A) affects the mate choice behavior of the choosing individual (C), which may be interpreted as a strategy to reduce sperm competition risk, as A might copy C's mate choice at a later point in time.

kept together with a female and thus, was perceived by the other male as sexually active, while the other male was alone and thus, perceived as sexually inactive. In subsequent mate choice tests with different stimulus females, the males from each dyad served as focal and audience males, and vice versa. Focal males ceased to show mating preferences only when they had perceived their rivals as sexually active (Fig. 4A). In addition, focal males that were observed by a sexually active rival showed a stronger behavioral response when rivals were larger and thus, more attractive to females²⁹ (Fig. 4B). This suggests that male fish are indeed able to remember and strategically exploit information about rivals when performing mate choice; in essence, males respond to an audience only “when it matters.”

Altogether, the aforementioned studies exemplify the various effects of social eavesdropping on male mate choice. Males make use of socially acquired information (mate choice copying), but also males that are at risk of being copied respond to this (audience effects), which may be a strategy to reduce SCR.

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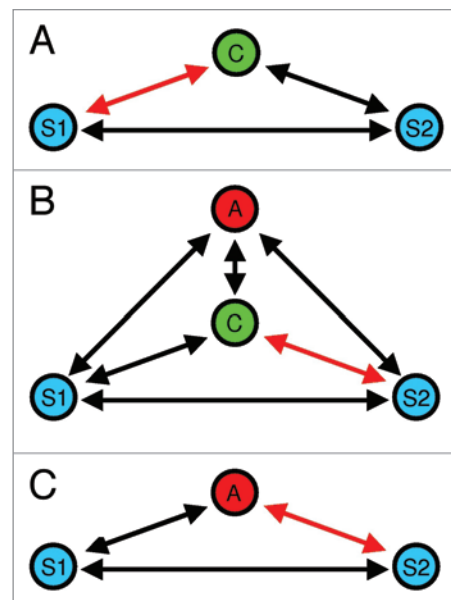


Figure 3. Deceptive signaling during male mate choice.²⁸ In (A) the choosing male (C) exhibits a mating preference for S1. (B) When an audience male (A) enters the mate choice arena, C initially interacts with S2, (C) which will be copied by (A).

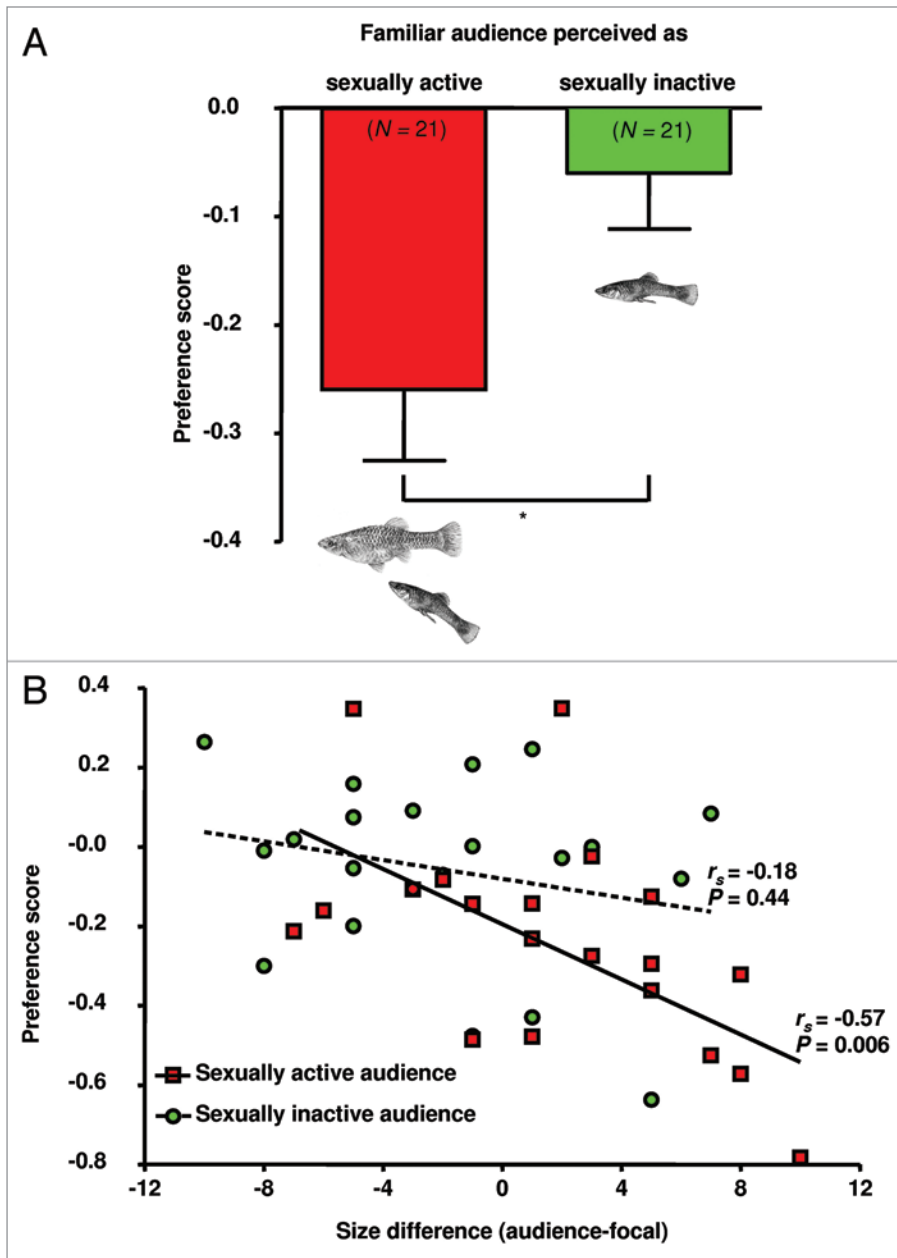


Figure 4. Changes in *P. mexicana* male mating preferences induced by the presence of a familiar audience male.²⁹ Males of a dyad (one sexually active and one sexually inactive male) were tested for their preferences while successively serving both as focal and audience males. (A) A comparison of preference scores (fraction of time near preferred female during 2nd-1st test parts, means \pm SEM) reveals that male preferences were more affected when the rival was perceived as sexually active (paired *t*-test; **p* < 0.05). (B) Correlation between body size differences and changes in male mating preferences (preference scores). Body size differences in the tested male dyads (*N* = 21) were determined as the audience male's standard length (SL)—focal male's SL. *r_s*- and *p*-values are from Spearman rank order tests. The strength of male preferences decreased with increasing rival body size when the audience was perceived as sexually active, but not in the case of sexually inactive audience males.

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