The audience effect and the role of deception in the expression of male mating preferences

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The audience effect and the role of deception in the expression of male mating preferences

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Males of several species have been shown to alter their mate preference in the presence of an eavesdropping rival. This evasive tactic has been interpreted as an attempt by the courting male to drive the attention of the rival away from the preferred female. The fitness return of this deceptive strategy will depend on the costs of cheating for the actor (the displayer) and the benefits for the rival (the bystander) of copying the choice of the displayer. We developed a two-person nonzero sum game between two males that compete for mating with one of two receptive females. Males could assess female quality with a varying level of uncertainty, which was modelled using a Bayesian statistical decision theory approach. We explored the actor and bystander payoffs under different levels of uncertainty in mate assessment and difference in quality between females. We found that when being eavesdropped on is costly (i.e. when females differ largely in quality), males are expected to cheat to reduce the amount of public information that is available to the unintended audience. However, under these circumstances, the value of the public information is low and the bystander is not expected to copy the choice of the actor. Our model suggests that deceptive male choice may evolve only under relatively restricted conditions and suggest that other explanations, such as, for example, a reduction in the risk of precopulatory male–male competition may be more likely. Future theoretical and empirical work will be necessary to test alternative interpretations of the audience effects in male mate choice.

Keywords: audience effects; computational mate choice; deception; game-theoretic model; male mate choice; mate choice copying; *Poecilia*; public information; sperm competition.

Animals can improve their assessment of the quality of conspecifics or environmental resources by using public information. This is a form of ‘inadvertent social information’ (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005) that can be acquired by noting the performance of other individuals or their behavioural decisions (Valone, 1989; Valone, 2007). Evidence for the acquisition of public information from the behavioural decisions of others comes mostly from studies of female mate copying behaviour (Dugatkin, 1992; Dugatkin & Godin, 1992; Nordell & Valone, 1998; Pruett-Jones, 1992). Mate choice copying occurs when an individual’s initial mating preference between two potential partners is reversed after having witnessed another individual displaying a preference for the initially nonpreferred partner (Dugatkin & Godin, 1992; Santos, Matos, & Varela, 2014). Mate choice copying was first found in the guppy, *Poecilia reticulata* (e.g. Dugatkin, 1992). Since then it has been reported in several vertebrate (Galef, Lim, & Gilbert, 2008; Galef & White, 1998; Gibson, Bradbury, & Vehrencamp, 1991; Hoglund, Alatalo, Gibson, & Lundberg, 1995) and invertebrate species (Loyau, Blanchet, Van Laere, Clobert, & Danchin, 2012; Mery et al., 2009). It is typically observed in females (Dugatkin, 1996a; Vakirtzis, 2011; Westneat, Walters, McCarthy, Hatch, & Hein, 2000) and can be so strong that it overrides females’ innate preferences (Dugatkin, 1996b, 1998; Godin, Herdman, & Dugatkin, 2005; Witte & Noltemeier, 2002). Females may benefit from copying because this reduces their sampling time (Witte & Nöbel, 2011) and their choice error, in particular when they are inexperienced in mate choice (Dugatkin & Godin, 1993). Furthermore, male displays are often conspicuous to predators and predation risk associated with mate evaluation (Gibson & Bachman, 1992; Pocklington & Dill, 1995) may therefore be reduced if, by copying, females can avoid being directly courted before mating and mate when predation risk is reduced. Indeed, female sailfin mollies, *Poecilia latipinna*, remember males and can copy the mate choice of other females up to 1 day after they have observed their sexual interaction (Witte & Massmann, 2003).

The evolutionary scenario for mate choice copying is more complicated in the case of males. Although mate choice copying has also been reported for males, in particular in fishes (Frommen, Rahn, Schroth, Waltschyk, & Bakker, 2009; Schlupp & Ryan, 1997; Widemo, 2006; Witte & Ryan, 2002), the benefits of this mating strategy for males are less clear. It has been suggested that such benefits may be associated with male mate-searching behaviour in species that court within communication networks (Webster & Laland, 2013). For example, males seeking mates have been shown to eavesdrop on conspicuous courtship behaviour of rival males to locate mates (e.g. Clark, Roberts, & Uetz, 2012; Grafe, 2005; Milner, Booksmythe, Jennions, & Backwell, 2010; Webster & Laland, 2013) and fertility status of females (Schlupp & Ryan 1997). Furthermore, males may observe other males' courtship behaviour to indirectly assess the relative quality of different mates, for example to locate higher quality females if male courtship rate varies with the quality of the available mates (Ojanguren & Magurran, 2004). However, when a male can choose between two different females, copying the choice of another male may be associated with nontrivial costs. Typically, mate choice copying is accompanied by an increased risk of directly or indirectly competing with the male whose choice has been copied (Witte, Kniel, & Kureck, 2015). Accordingly, mate choice copying is less frequent in the sex in which mate competition is stronger (see Kniel et al., 2015; Widemo, 2006 for a reversed sex role species and for a species with traditional sex roles, respectively). Intrasexual competition deriving from mate choice copying can occur before and after mating. In monandrous species, a male copying the mate choice of another male will face an increased risk of losing the contest with the rival and/or of being rejected by the female. When females are polyandrous, choosing another male's previous mate will result in an increased level of sperm competition (Nöbel & Witte, 2013). Furthermore, the cost of being rejected by the female cannot be discounted, as even in polyandrous species a female’s mating probability is expected to decrease as the number of previous matings increases. For example, in an experiment with guppies, only 64% of 55 females that mated with one male and were presented with a second male after the initial mating did actually remate (Evans & Magurran, 2001). Assuming that this remating probability remains constant across successive encounters with males, about 29% of the females would be expected to mate with more than five males. This figure is very similar to the proportion observed in another guppy population, using a slightly different mating design, in which about 26% of the females mated with more than five males (frequency estimated from Figure 2 in Evans & Gasparini, 2013), supporting the generally assumed notion that guppy female mating rate declines with the number of previous matings. The decline in female mating probability after mating may be due to increased costs and/or decreased benefits of successive matings (Jennions & Petrie, 2000) or to conflict with males (e.g. Scott, 1986).

The costs of being copied also differ between males and females. A male whose choice is copied will suffer the same costs, associated with the increased probability of pre- and postcopulatory competition, faced by the copier. Accordingly, male sexual behaviour is often altered by the presence of a bystander (e.g. Vignal, Mathevon, & Mottin, 2004) and the public information extracted from intersexual communication can be used to guide the behaviour of eavesdropping individuals (Matos & Schlupp, 2005). Audience effects in a male choice context have been studied in detail in fish (Dzieweczynski & Rowland, 2004; Herb, Biron, & Kidd, 2003), and in particular in poeciliids (Auld & Godin, 2015; Fisher & Rosenthal, 2007; Makowicz, Plath, & Schlupp, 2010; Plath, Blum, Schlupp, & Tiedemann, 2008; Plath, Richter, Tiedemann, & Schlupp, 2008). In these fish, it has been shown that the initial preference of the focal male between two potential female partners is attenuated or even reversed when he is observed by a competitor male (Plath, Blum, et al., 2008; Plath, Richter, et al., 2008; Ziege et al., 2009). This behaviour has been interpreted as an attempt by the focal male to deceive the audience male about his real mating preference: if the audience male copies the focal male's mate choice (Auld & Godin, 2015), the latter will reduce the risk of sperm competition when later mating with the initially preferred female ('deception hypothesis', Bierbach et al., 2013; Plath, Richter, et al., 2008).

The deception hypothesis rests on the assumption that the costs of deceiving are smaller than its benefits. Costs and benefits for the deceiving male will depend on the response of the bystander to his deceptive signals. In turn, the response of the bystander will depend on the costs or benefits that the bystander is expected to obtain if he uses the focal-male mating preferences as a source of public information about the qualities of prospective female mates. Benefits of copying for the bystander are expected to vary in relation to (1) the difference in quality between two potential female mates; in particular, a bystander male should be able to make an independent mate quality assessment when the difference in quality between two potential mates is large (Witte & Ryan, 1998); (2) the probability that a female will remate after having mated with another male; in particular it can be expected that this probability is always <1, otherwise a female will remate indefinitely (Evans & Gasparini, 2013); (3) the fertilization success in relation to mating order; unless there is a significant last male precedence effect, mate choice copying should not evolve.

To investigate the hypothesis that audience-mediated flexibility in male mating preferences evolved to deceive potential competitors about the quality of prospective females, we developed a game-theoretic model between two players: a focal male (the actor) and an observer (the bystander). The actor has the priority in mating decisions and can strategically control his manifested preferences for a high- over a low-quality female. The observer can eavesdrop on the actor's mating behaviour and strategically use (or decide not to use) this public information in mating decisions.

<H1>Methods

<H2>The model

The game is a two-person nonzero sum game between two males that compete for mating with one of two receptive females. The two males are of similar quality, but play different roles: the actor has the priority of choosing and, eventually, of mating with one of the two females; the bystander can observe the behaviour of the actor and, only after the actor has made his move, he can make his own. To provide the actor with the possibility of cheating, the model assumes that the bystander can assess the mating preferences, but not the mate choice of the actor (see below). Unlike males, females are assumed to differ in quality (e.g. the number or dimensions of eggs). We name the high-quality female H and the low-quality female L.

<H2>The Actor strategy: the use of private information

The actor assesses the females' quality with uncertainty. To model this, we adopt a Bayesian statistical decision theory approach (McNamara & Dall, 2010). We describe the perceived female values with one of two stochastic variables: (1) $H = \mu_H + \varepsilon$, when the female is of high quality and (2) $L = \mu_L + \varepsilon$, when she is of low quality. μ_H and μ_L (with $\mu_H > \mu_L$) are the true female qualities, whereas ε is a normally distributed random variable with zero mean and variance σ^2. We define $h(x) = P(x|H)$ and $l(x) = P(x|L)$ the probability density functions of H and L, respectively.

First, we consider the behaviour of the actor when the bystander is absent. Suppose that, at a given time *i*, the actor is assessing the high-quality female, which he perceives of quality x_i. The actor has no prior information, but he is assumed to ‘know’ the likelihoods of perceiving x_i when a female is either of high or of low quality and to be able to ‘compute’ the relative posterior probability:

$$P(H|x_i) = \frac{h(x_i)}{h(x_i)+l(x_i)}. \qquad (1)$$

If $P(H|x_i) > 0.5$ then the male will court the female until time *i*+1; otherwise he will move to and start courting the other female. Note that, at any time step *i*, the posterior probabilities are assumed to be independent of previous assessments, that is, the male is thought not to use prior private information.

The proportion of time spent by the actor with the high-quality female is the expression of his preference. Since $P(H|x_i) > 0.5$ when $x_i > \frac{1}{2}(\mu_H + \mu_L)$, (see Fig. 1a,c), the actor’s perceived preference for the high-quality female is:

$$A_H = \int_{\frac{\mu_H+\mu_L}{2}}^{\infty} h(x)\,dx. \qquad (2)$$

Analogously, $A_L = 1 - A_H$, is the preference for the low-quality female.
Second, we consider what happens when the actor perceives the presence of the bystander. We assume that the bystander does not affect the perceived preferences (A_H) of the actor, but only his manifested preferences (M_H). In other words, we allow the actor to cheat. This means that, when there is a bystander, the actor can move away from a female even if he perceives

her of high quality or he can court a female even if he perceives her of low quality. Specifically, we assume that the manifested preferences for the high- and low-quality females are, respectively, $M_H = (1 - K_A)A_H$, and $M_L = 1 - M_H = K_A + (1 - K_A)A_L$.

K_A can vary between 0 and 1 and it describes the strategy of the actor. When K_A is zero, the actor adopts a honest strategy and the perceived and the manifested preferences coincide. Conversely, when $K_A = 1$, the actor is fully dishonest in that he will court the female he perceives of low quality.

<H2>The Bystander's strategy: the use of public information

When waiting for his turn, the bystander obtains the females' quality information both directly, by assessing them, and indirectly, by eavesdropping on the actor's behaviour. Thus, when he eventually has access to the females, he is assumed to make an optimal use of the previously acquired public information, as predicted by Bayes's theorem. The posterior probability of the hypothesis that the assessed female is of better quality than the other (i.e. the probability that she is the H female) will depend not only on her perceived quality (x_i), but also on her prior probability $P(H)$ that this hypothesis be true:

$$P(H|x_i) = \frac{h(x_i)P(H)}{h(x_i)P(H)+l(x_i)P(L)}. \qquad (3)$$

The prior probability depends on how the bystander evaluates and responds to the manifested preference of the actor. Specifically, we assume that the bystander's strategy is defined by two variables: (1) K_B, which depends on the assumed reliability of the actor's manifested preference and affects the amount of public information that is actually used in the decision process; (2) b, a binary variable which describes the way the bystander uses public information: when $b = 1$, the actor's manifested preferences and $P(H)$ are positively associated, whereas when $b = 0$, they are negatively associated:

$$P(H) = \begin{cases} if\ b = 0 \text{ then } \left(1 - {M_H}^{K_B} \left(\frac{1}{2}\right)^{1-K_B}\right) \\ if\ b = 1 \text{ then } {M_H}^{K_B} \left(\frac{1}{2}\right)^{1-K_B} \end{cases} \tag{4}$$

When $K_\mathrm{B} = 0$, the bystander perceives the public information as fully unreliable and $\mathrm{P}(H) = 0.5$, independent of the value of b. When $K_\mathrm{B} = 1$, the bystander perceives the public information as fully reliable. In this case, if $b = 0$ then $P(H) = M_H$, whereas if $b = 1$ then $P(H) = 1 - M_H$. The bystander, by strategically adjusting K_B between 0 and 1, can control the risk of being deceived by the actor, whereas, by controlling b, he can increase or decrease the probability of mating with the female preferred by the actor. As we shall see, b plays an important role in determining the bystander's optimal decision strategy, when unmated females should be preferred over recently mated females, independent of their qualities.

As for the actor, we assume that the proportion of time spent by the bystander with a female is the probability of obtaining $P(H|x) > 0.5$ when assessing that female and it is an expression of his preference. It may be shown that $P(H|x) > 0.5$ when the perceived quality is greater than the threshold ϕ, which depends not only on μ_H and μ_L, but also on the uncertainty level σ^2 and on the $\log\left(\frac{P(L)}{P(H)}\right)$ (see Fig. 1b, d for a graphical representation and the Appendix for an analytical derivation of ϕ). Thus, the bystander's preference for H is:

$$B_H = \int_{\phi}^{\infty} h(x)\, dx; \tag{5a}$$

and his preference for L is:

$B_L = 1 - B_H$. (5b)

<H2>Payoffs

As mentioned above, μ_H and μ_L are the reproductive resources (i.e. the number of eggs) made available by the high- and the low-quality females. Let $\pi_A = f(K_A)$ and $\pi_B = f(K_B, b)$ the strategies of the actor and of the bystander, respectively. We define the payoffs $W(\pi_A, \pi_B)$ as the amount of reproductive resources that the actor is expected to obtain when playing π_A against the bystander playing π_B. Conversely, $W(\pi_B, \pi_A)$ are the payoffs of the bystander playing π_B against an actor playing π_A. Besides the total amount of resources (μ_H and μ_L), three other parameters affect the payoffs matrix: (1) the costs of cheating (γ); (2) the probability that a female that has mated with the actor will mate again with the bystander (δ); (3) the effect of mating order on fertilization success (φ).

The costs of cheating paid by the actor are represented by his decreased probability of mating with the high-quality female. For fully honest actors, the model assumes that the probability of mating with either the high- or the low-quality female is, respectively, M_H and M_L. When the actor is cheating (that is, when $M_H < A_H$), he is expected to experience a reduced probability of mating with H, which is not compensated for by an increase in the probability of mating with L. Specifically, we assume that his probability of mating with H is $A_H(1 - K_A)^\gamma$, where γ is the parameter defining the cost of cheating. The probability of mating with L is still M_L.

For the bystander, mating probability depends on his preferences and on whether the chosen female has previously mated with the actor. We assume that recently mated females are less prone to remate and the parameter δ defines the probability that a mated female will remate ($0 \leq \delta \leq 1$).

When both males mate with the same female, sperm competition occurs. In this case, we assume that between-male differences in fertilization success depend only on the mating order and we define with φ (with $0 \leq \varphi \leq 1$) the proportion of eggs that are expected to be fertilized by the bystander (i.e. by the second of the two males to mate with the female).

We define the payoffs matrices of the (π_A, π_B) game as:

$$W(\pi_A, \pi_B) = \mu_H A_H (1 - K_A)^\gamma (1 - \delta\varphi B_H) + \mu_L A_L (1 - \delta\varphi B_L) \qquad (6a)$$

and

$$W(\pi_B, \pi_A) = \mu_H B_H \big(1 - A_H (1 - K_A)^\gamma (1 - \delta\varphi)\big) + \mu_L B_L \big(1 - A_L (1 - \delta\varphi)\big). \qquad (6b)$$

In words, the expected benefits of the actor are the sum of two terms: (1) the resources (μ_H) expected from the high-quality female, *H*, multiplied by the probabilities that the actor mates with *H* and the bystander chooses either *L* or *H*, corrected for the bystander's probability of mating or siring her eggs, and (2) the resources (μ_L) expected from the low-quality female, *L*, multiplied by the probabilities that the actor mates with *H* and the bystander chooses either *H* or *L*, corrected for the bystander's probability of mating or siring her eggs. Analogously, the payoffs of the bystander are the sum of the expected resources obtained from the high- and the low-quality females multiplied by the probabilities that he mates with them and fertilizes their eggs.

<H2>Solutions of the game

To solve this game, we transformed the variables K_A and K_B from continuous to discrete, by letting them assume *n* equidistant values between 0 and 1 (extremes included). A strategy is represented by the discrete probability distributions of the variables that define it: the actor's strategy is a vector of *n* elements, whereas the bystander's strategy is a matrix with 2*n* elements. The discrete game was obtained by evaluating the actor's and bystander's payoffs at the $2n^2$ points. From the payoff matrix, we derive the Nash equilibrium pairs, that is, pairs of strategies (π_A^*, π_B^*) that satisfy the conditions $W_A(\pi_A, \pi_B^*) \leq W_A(\pi_A^*, \pi_B^*)$ and $W_B(\pi_A^*, \pi_B) \leq W_B(\pi_A^*, \pi_B^*)$. A pure equilibrium pair occurs when both the actor and the bystander play only one tactic. Conversely, a mixed equilibrium pair occurs when the actor's and bystander's optimal strategies involve several tactics with different probabilities. In both pure and mixed equilibrium strategies, the level of the actor's honesty and bystander's perceived reliability can be described, respectively, by $\bar{K}_A^* = \sum_i^n \pi_A^*(i) K_A(i)$ and $\bar{K}_B^* = \sum_{i=1}^n \sum_{j=1}^2 \pi_B^*(i,j) K_B(i)$.

To find mixed equilibrium pairs, we used the bimat.m function (Bapi Chatterjee 2009), which finds one mixed Nash equilibrium strategy, using the quadratic-programming method of Mangasarian and Stone (1964). A full description of the model, a downloadable version of the Python notebook and the user manual can be found at http://penelope.unito.it/matecopying.

<H1>Results

<H2>Uncertainty and deception

In our model, we assume that the mechanism of mating decision is analogous to the computation of the posterior probability that a prospective mate is an appropriate partner. The bystander, thus, is assumed to use direct evidence (i.e. private information from directly assessing female quality) and priors (i.e. public information obtained by observing the actor's mating preferences) optimally, as described by Bayes's principle. From this assumption, it follows that the influence of the public information on the bystander's choice depends on the accuracy of direct assessment. If the bystander obtains strong direct evidence that a female is of high quality, then the public information (the priors) plays only a marginal role on his final mating decision. In contrast, when he cannot assess the female with high accuracy, his mating decision may be strongly affected by eavesdropping on the actor. Since the actor can control the type and the amount of (public) information that is available to the bystander, his deceiving possibilities are expected to increase with decreasing assessment accuracy. For example, when the direct assessment is accurate and the actor perceives a 0.75, but shows a 0.375 preference for the high-quality female (i.e. $K_A = 0.5$), the trustful-copying bystander (i.e. $K_B = 1$ and $b = 1$) will reduce his preference from 0.75 to 0.61 (Fig. 1a, b). In contrast, when the direct assessment is less accurate so that the actor's preference for the high-quality female is 0.65, the same level of deception is enough to make a trustful bystander reverse his preference and show a 0.71 mating preference for the low-quality female (Fig. 1c,d).

<H2>Fertilization success and cheating costs

Although uncertainty in female quality assessment is a key parameter of the game, we start by considering the ideal case, in which there is no uncertainty and, thus, no possibility of deception. Since deception is fully ineffective, the actor is forced to play the 'honest' strategy, $K_A = 0$. The bystander's best reply to this strategy depends on his fertilization success ($\delta\varphi$). When $\delta\varphi < \mu_L/\mu_H$, the bystander maximizes his payoffs by mating with the low-quality female. Under this condition, the bystander will adopt the 'trustful-not-copying' strategy ($K_B = 1$; $b = 0$), which makes him use the public information against the female preferred by the actor. When $\delta\varphi > \mu_L/\mu_H$, in contrast, the bystander maximizes his payoffs by mating with the high-quality female even if she has already mated with the actor. In this case, the bystander will adopt the 'trustful-copying' strategy ($K_B = 1$; $b = 1$), which strongly penalizes the actor.

Now, we introduce uncertainty into the game. In Fig. 2, we show the effect of the bystander's fertilization success and of the actor's cheating costs on the Nash equilibrium strategies, under a condition of low ($\sigma = 0.7$) and high ($\sigma = 3$, Fig. 2a, b) uncertainty. In these simulations, female qualities are kept constant at $\mu_H = 15$ and $\mu_L = 12$ (but see the Python Notebook for results under different conditions, http://penelope.unito.it/matecopying).

When assessment uncertainty is low (Fig. 2a, b) and $\delta\varphi < \mu_L/\mu_H$, the 'honest' actor and the 'trustful-not-copying' bystander are still pure Nash equilibrium strategies. In contrast, when $\delta\varphi > \mu_L/\mu_H$ the bystander always copies the actor ($b = 1$), who, in turn, would benefit by deceiving the bystander into preferring the low-quality female. However, since uncertainty is low, deception is ineffective and the costs it imposes on the actor usually exceed the benefits. Under these conditions, the actor is forced to play the 'honest' strategy, the bystander perceives the actor's behaviour as fully reliable and the 'honest-trustful-copying' strategy is a pure Nash equilibrium pair. There are, however, a few exceptions, which occur when the bystander's fertilization success is extremely high and the costs of cheating very low. Under these conditions, the game has only mixed equilibrium strategies, in which the actor is no longer fully honest ($0 < \overline{K}_A^* < 1$) and the bystander no longer fully trustful ($0 < \overline{K}_B^* < 1$).

In Fig. 2c, d, we show the solutions of the game when female quality assessment is highly uncertain. The 'honest/trustful-not-copying' pair of strategies is still a Nash equilibrium, but only for a fertilization success much lower than μ_L/μ_H. Indeed, the fertilization success threshold above which ‘copying’ is the most remunerative strategy for the bystander decreases with increasing assessment uncertainty: for $\sigma = 3$ the threshold is $\delta\varphi \cong 0.55$ (Fig. 2d), for $\sigma = 4$ is $\delta\varphi \cong 0.45$,and for $\sigma = 5$ is $\delta\varphi \cong 0.35$ (see the Python notebook).

As explained above, when sperm competition penalizes the bystander, he should adopt the ‘not-copying’ strategy to minimize the risk of mating with an already mated female. If the bystander knows with certainty which female the actor prefers, then he would be able to minimize the risks of sperm competition by mating with the disfavoured female. However, when the uncertainty of quality assessment increases, the actor’s mating preference decreases and the bystander’s risk of mating with an already mated female increases. For example, if the honest actor showed a preference for the high-quality female of $M_H = 0.6$, the bystander that adopted the ‘trustful-not-copying’ strategy would show a preference for the low-quality female of $B_L = 0.62$. In this case, there would be a 0.48 probability that the bystander and the actor mate with the same female and a 0.52 probability that the chosen female is the low-quality one. But, if the bystander cannot prevent sperm competition, then he would do better trying to compete for the eggs of the high-quality rather than for those of the low-quality female. For this reason, the threshold from the ‘not-copying’ to the ‘copying’ strategy decreases when the uncertainty of female quality assessment increases.

When the bystander switches from the ‘not-copying’ to the ‘copying’ strategy, the actor no longer benefits from playing honestly, unless the deception costs prevent him from cheating. In fact, the ‘honest-trustful-copying’ equilibrium pair of strategies is only found when the costs of cheating are greater than a certain threshold, which increases with the bystander’s fertilization success. For example, for $\delta\varphi = 0.6$, there are honest equilibrium pairs only when $\gamma \geq 0.5$, whereas for $\delta\varphi = 0.7$ only when $\gamma \geq 0.7$, and the honesty threshold increases to

$\gamma = 0.9$ for $\delta\varphi = 0.8$ (Fig. 2c). In all other cases, the game has no pure equilibrium pairs, but only one or more mixed equilibrium strategies. Under these conditions, deception is more effective when the cheating costs are high ($\gamma \geq 0.5$) than when they are low. In fact, Fig. 2c, d shows that the mixed equilibrium strategies of the bystander tend to underestimate the honesty of the actor (i.e. $\overline{K}_B^* > 1 - \overline{K}_A^*$) when the costs of cheating are low and to overestimate it (i.e. $\overline{K}_B^* < 1 - \overline{K}_A^*$) when the costs are high. Independent of the costs, however, the level of deception is always relatively low, being always $\overline{K}_A^* < 0.3$. For these values of $\overline{K}_A^*$, the manifested preference of the actor for the highest-quality female is decreased but still higher than 0.5. Thus, the actor seems more likely to retain honest information than to provide the bystander with dishonest information.

<H1>Discussion

When being copied by an eavesdropper imposes a cost on the male making a mating decision, the latter is expected to adjust his behaviour in order to limit or prevent the use of public information (Nordell & Valone, 1998). However, since these changes in behaviour are likely to be costly, the behavioural adjustment is expected to make an optimal trade-off between these two types of costs. Our game-theoretic model has been devised to study this trade-off. Specifically, the model asks when it pays a courting male to reduce his manifested preference for the high-quality female in order to decrease the probability that a bystander male will mate with her. A similar question has been addressed recently by Dubois (2015). In her game, males can adopt one of four tactics: (1) unselective males, which mate with both high- and low-quality females indiscriminately; (2) copier males, which use social information, when available, or mate indiscriminately, when unavailable; (3) selective-insensitive males, which prefer high- over low-quality females, without changing these preferences in the presence of an audience; or (4) selective and sensitive males, which prefer high-quality females and change their preference in the presence of an audience. The results of the model indicate that the four tactics form a mixed equilibrium strategy when last-male sperm precedence is strong, the cost of female assessment large and the risk of eavesdropping high. The selective-sensitive tactic, however, is never a pure strategy.

Our model differs from Dubois's model (2015) both in the assumptions and in the methodology and derives, to a large extent, different results. The main methodological difference is that our model is based on the computational mechanisms and rules of mating decisions (Castellano, 2009, 2010). The computational mechanisms (1) explain how the decision maker processes private and public information, (2) are part of the assumptions of the model and, consequently, (3) act as a constraint on the set of possible behavioural strategies. Following the 'behavioural gambit' approach (Fawcett, Hamblin, & Giraldeau, 2013), Dubois's model considers the alternative strategies as independent phenotypes, which can be interpreted as either polymorphic traits in the population or plastic traits at the individual level. Given these tactics, the solution of the game is the set of phenotypic frequencies that are evolutionarily stable. In contrast, in our model, the alternative tactics are not independent traits, but the expression of the same decisional mechanism. Our model explains behavioural variation in terms of variation in the parameters that govern the computational mechanisms and it assumes that selection acts on these parameters (Castellano, 2009, 2015; McNamara & Houston, 2009). We think that this approach might help to capture the very essence of the biological problem under study by favouring a close integration of decision mechanism and behaviour function.

Our model identified three main factors that are expected to affect the strategic manipulation of public information: (1) the strength of the conflict between the eavesdropping and the eavesdropped males; (2) the manipulative potential of the eavesdropped male, which depends on the intrinsic value of public information; and (3) the cost of public information manipulation.

<H2>The strength of the conflict

The most important factor that affects the strategic use of public information is the strength of the conflict between the individual that provides public information (the actor) and the individual that can use this information (the bystander) (Nordell & Valone, 1998; Valone, 2007). In our model, the strength of the conflict depended on (1) the difference in fertilization success between the actor and the bystander and (2) the difference in quality between the two contended resources (females).

When the fertilization success of the bystander is lower than the ratio between the low- and the high-quality females, there is no conflict between the actor and the bystander, because both maximize their reproductive success by choosing different females: the actor, which has the priority in mating decision, will do best by choosing the high-quality female, whereas the bystander will do best by choosing the low-quality female. In this case, public information might be better seen as being about the costs, rather than the benefits, for the bystander of choosing the high-quality resource: the actor benefits from providing public information about these costs and the bystander benefits from exploiting the public information provided by the actor. This is what has been observed in a context of interspecific competition for food between eusocial stingless bees that eavesdrop on recruitment signals of other species to guide their foraging strategy (Lichtenberg, Zivin, Hrncir, & Nieh, 2014). Since eavesdroppers may fight to access the food, they have been observed to avoid more conspicuous signals because they indicate higher competitive costs. Analogously, our model suggests that, when the bystander has a low fertilization success (i.e. when last-male sperm precedence is weak and/or female remating probability is low), he should do better by reversing rather than by copying the actor's preference.

Interestingly, the model also suggests that uncertainty in female quality assessment affects the strength of the conflict. In fact, other things being equal, high assessment uncertainty reduces the strength of the actor's preference and hence the intrinsic value of public information. However, when the bystander is uncertain about the choice of actor, our model predicted that his optimal strategy is to use public information as an indication of expected benefits of copying, rather than of expected costs. In fact, if uncertainty makes sperm competition unavoidable, the bystander should do better by competing for the high- than for the low-quality resources. Although in our game the actor could only reduce but not increase his perceived preferences (i.e. K_A was forced to vary between 0 and 1), we can predict that if he has a strong sperm competition advantage over the bystander, then he would be favoured by exaggerating his manifested preferences (i.e. $K_A > 1$). In this way, the risk of sperm competition would decrease and both the actor and the bystander would benefit. Indeed, as suggested by Lichtenberg et al. (2014), when the public information is about the costs of accessing a resource, both signallers and eavesdroppers benefit from the increase in the information quality (i.e. an increase in signal conspicuousness is expected).

When the fertilization success of the bystander is greater than the ratio between the low- and the high-quality females, the conflict between the bystander and the actor is strong, because both benefit from choosing the high-quality female. In this case, the model predicted mixed equilibrium strategies, with partially unreliable actors and partially untrusting bystanders. At the equilibrium, both the actual and the perceived reliability of public information depended on the potential benefits and on the expected costs of its manipulation (see below).

<H2>The intrinsic value of public information

The potential benefits obtained by manipulating public information depend on its intrinsic value. Our model assumed that the male mating preference between two females is equivalent to the posterior probability that one female is perceived of higher quality than the other. Consistent with the optimality approach of the normative models in behavioural ecology (Parker & Smith, 1990), our model also assumed that posterior probabilities are computed by integrating direct evidence with priors, as explained by the Bayes' principle (Castellano, 2009, 2015). According to our model, the intrinsic value of public information (i.e. the manipulative potential of the actor) is therefore the effect of priors on the posterior probabilities. This effect is strong only when the value of private information (acquired by the direct assessment of female qualities) is low. For example, if the direct assessment provides no information (i.e. $P(x|H) = 0.5$), then the posterior and the prior probabilities coincide and, thus, the manipulative potential of the actor is maximum. High intrinsic values of public information might be observed either (1) when the direct assessment is inaccurate and the alternatives cannot be effectively discriminated from each other or (2) when the direct assessment is accurate but costly to carry out.

In our game, when the difference in quality between the two females and the assessment accuracy were both high, then the effect of public information on the bystander's mating preferences was low. In contrast, when the difference in quality was small and the assessment accuracy was low, the value of public information was potentially high. Empirical evidence supports this prediction. For example, in species in which females use public information in mate choice, 'copying' occurs more commonly when males have similar quality (Dugatkin, 1992; Dugatkin & Godin, 1992), than when they show a large difference in quality (Brooks, 1996; Dugatkin, 1996a). Furthermore, inexperienced (e.g. young) females tend to copy the choice of more experienced females (Dugatkin & Godin, 1993). When males do not provide resources for reproduction or when these resources are not limited (Berglund, Magnhagen, Bisazza, Konig, & Huntingford, 1993), there is unlikely to be any substantial cost for the female whose choice is copied. In contrast, model males pay a cost of being copied. The results of our model suggests that the manipulation of public information is more likely to occur when the difference in quality between the mating options is small. However, under these conditions, the benefits of manipulation are also necessarily low.

The intrinsic value of public information also depends on the accuracy of mate quality assessment. This, in turn, will affect the relative costs of using private and public information. When private information is more costly to acquire than public information, it might be beneficial to make a quick and inaccurate evaluation of the alternatives and to base the mating decision mainly on public information. For example, in agonistic interactions, the direct assessment of the competitive value of rivals might be costly, because it exposes the decision maker to the risk of fighting. In these cases, the decision maker should trust the ‘reputation’ of the opponent, rather than directly assess his value (Valone, 2007). In a mate choice context, this is similar to what may be observed in species in which cryptically coloured females that assess directly conspicuous mates expose themselves to the risk of being predated (Gibson & Bachman, 1992; Pocklington & Dill, 1995). When the predation risk associated with direct mate assessment is high, female mate choice copying is more likely to evolve. In males, in contrast, it is unlikely that the costs of assessing female quality are so high that they would exceed either the costs of copying or the benefits of accurate evaluations.

<H2>The costs of manipulating public information

The results of our model suggest that the actor’s strategic manipulation of public information may evolve when the conflict between the actor and the bystander is so strong that it pays the bystander to copy the actor’s choice and the intrinsic value of public information is high. In our game, this was represented by a reduction in the actor's manifested preference for high-quality females in the presence of an audience. However, a reduction in courtship effort is likely to decrease the actor's attractiveness and his probability of mating with the high-quality female. The results of our model indicated that the higher the manipulation costs the higher the reliability of public information at equilibrium. If, in contrast, the actor pays no costs for manipulating public information (i.e. his probability of mating with the high-quality female is not reduced), his best move is to make his manifested preference for the high-quality female unreliable, so that the bystander no longer benefits from using public information. The manipulation costs, thus, can prevent the complete corruption of public information in social networks and promote mixed equilibrium strategies that make actors only partially reliable and bystanders only partially trustful.

<H2>Conclusions

Our model showed that when being eavesdropped on is costly, an animal is expected to plastically adjust its behaviour to reduce the amount of public information that is available to the unintended audience. However, unless the costs of being eavesdropped on are extremely high and those of manipulating public information extremely low, such an audience-mediated plasticity is unlikely to be so pronounced that it results in an effective manipulation of the audience. In other words, males are not expected to cheat about their real mating preference to deceive bystanders, unless under very limited (and extreme) conditions. The results of our model conflict with the empirical evidence that male poeciliids reverse their mating preference in the presence of a male audience (but see Callander, Backwell, & Jennions, 2012 for contrasting results; Plath, Blum, et al., 2008; Plath, Richter, et al., 2008; Ziege et al., 2009). We argue that this audience effect may therefore have alternative functional explanations. For example, males may plastically modify their perceived preferences for the high-quality female to reduce the costs associated with direct, precopulatory, male–male competition (Auld, Jeswiet, & Godin, 2015; Mautz & Jennions, 2011; Plath, Richter, et al., 2008). While clearly the audience effect can be interpreted as a male strategy to maximize his reproductive success when rival males are present, the two interpretations are radically different. The deception hypothesis rests on the assumption that the audience effect does not affect mate choice, but only the manifested preferences. The alternative hypothesis, which could be named the 'flexible decision' hypothesis, assumes that both mating preferences and mating decisions are flexibly adjusted to the social environment in which mate choice is carried out. A large difference in body size between the actor and the bystander should not influence the actor's behaviour under the deception hypothesis (Plath, Richter, et al., 2008), whereas it should have a large effect if the actor's strategy aims at reducing the costs of aggressive male–male interactions. Similar predictions may be made for the difference in male ornamentation. In contrast, the deception hypothesis predicts a larger audience effect when the actor can choose between females that are very different in quality, whereas a male may decide to pay the costs of an aggressive interaction with the bystander, and hence keep his initial preference, if the audience effect is mainly driven by the costs of aggressive interactions. More empirical studies on the effects of social environments on both mating preferences and mating decisions (Mautz & Jennions, 2011) will be necessary to provide insights into the functional role of the audience effect.

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Appendix

The model assumes that a male would choose to court (and eventually to mate with) a female if the posterior probability that this female is of high quality is greater than 0.5. Here, we derive the value of perceived female quality (*ϕ*), above which the female is accepted as an appropriate mate and below which she is rejected.

Let $P(H)$ and $P(L) = 1 - P(H)$ be the prior probabilities that the assessed female is of either high or low quality, respectively.

From Bayes's theorem, it derives that the posterior probability that the assessed female is of high quality is:

$$P(H|x) = \frac{P(x|H)P(H)}{P(x|H)P(H) + P(x|L)P(L)},$$

and the posterior probability that she is of low quality is:

$$P(L|x) = \frac{P(x|L)P(L)}{P(x|H)P(H) + P(x|L)P(L)}.$$

Let $h(x) = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(x-\mu_H)^2}{2\sigma^2}}$ and $l(x) = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(x-\mu_L)^2}{2\sigma^2}}$ be the two conditional probability density functions $P(x|H)$ and $P(x|L)$, respectively.

We define with ϕ the value of x where $P(H|\phi) = P(L|\phi) = 0.5$.

Since $\frac{h(\phi)}{l(\phi)} = \frac{P(L)}{P(H)}$,

$\phi = \frac{\mu_H + \mu_L}{2} + \frac{\sigma^2}{\mu_H - \mu_L} Log\left(\frac{P(L)}{P(H)}\right)$.

If the choosing male uses only private information (i.e. $P(H) = P(L) = 0.5$), then $\phi = \phi_0 = \frac{\mu_H + \mu_L}{2}$. If he integrates private and public information and if public information is honest (i.e. $P(H) > P(L)$), then $\phi < \phi_0$ and the male’s preferences for the high-quality female increase. Finally, if the male uses dishonest public information (i.e. $P(H) < P(L)$), then $\phi > \phi_0$ and his preferences for the high-quality female decrease.

Figure Captions

Figure 1. The effectiveness of the actor's deception depends on the bystander's uncertainty in the direct assessment of female quality. In (a) and (b), the uncertainty is relatively low ($\sigma = 1.5\frac{\mu_H-\mu_L}{2}$). In (a), the bystander uses only private information. The two normal curves are the conditional probability distributions of the perceived qualities when the female is of either low (dotted red curve, $P(x|L)$) or high quality (dotted blue curve, $P(x|H)$)). The bystander preference for the high-quality female is the cumulative probability of perceiving the female above the blue threshold ($\phi = \frac{\mu_H+\mu_L}{2}$) and is $B_H = 0.75$ (i.e. the integral represented by the blue area). In (b), the bystander also uses public information by observing the actor's courtship behaviour. The actor, however, is assumed to deceive ($K_A = 0.5$) so that his manifested preference is $M_H = 0.75(1 - K_A) = 0.375$. The red and blue solid curves are, respectively, $P(x|L) * P(L)$ and $P(x|H) * P(H)$. The actor's deception decreases the bystander's preference for the high-quality female because it increases the quality threshold (ϕ) above which $P(H|x) > 0.5$ (i.e. the orange line, where the solid red and the solid blue curves intersect). Under these conditions, the bystander's preference is $B_H = 0.61$ (the blue surface). In (c) and (d), the uncertainty is higher than in (a) and (b), being $\sigma = 2.5\frac{\mu_H-\mu_L}{2}$. In (c), the bystander uses only private information and his preference for the high-quality female is $B_H = 0.65$ (blue surface). In (d), the bystander uses public information and the actor deceives ($K_A = 0.5$), as in (b). In this case, however, deception is much more effective than in (b) and the bystander's preference for the high-quality female is $B_H = 0.29$, which is less than half the preference manifested when using private information only.

Figure 2. The effect of the fertilization success and the cheating cost on the equilibrium strategies of the actor and the bystander. The yellow gradient is associated with the 'copying'

strategies (i.e. $K_O = 1$) and the green gradient with the ‘not-copying’ strategies (i.e. $K_O = 0$). Plain yellow and plain green in the Actor panels ((a) and (c)) correspond to the honest strategy ($K_A = 0$), whereas in the Bystander panels ((c) and (d)) plain yellow corresponds to the ‘trustful-not-copying’ strategy ($K_O = 1$ and $b = 0$) and plain green to the ‘trustful-copying’ strategy. Blue indicates the absence of pure Nash equilibrium strategies and the tonality of blue is proportional to the honesty (for the Actor) or the perceived reliability (for the Bystander) of the strategy (black dishonesty or unreliability). See http://penelope.unito.it/matecopying for further details.

Figure 1.

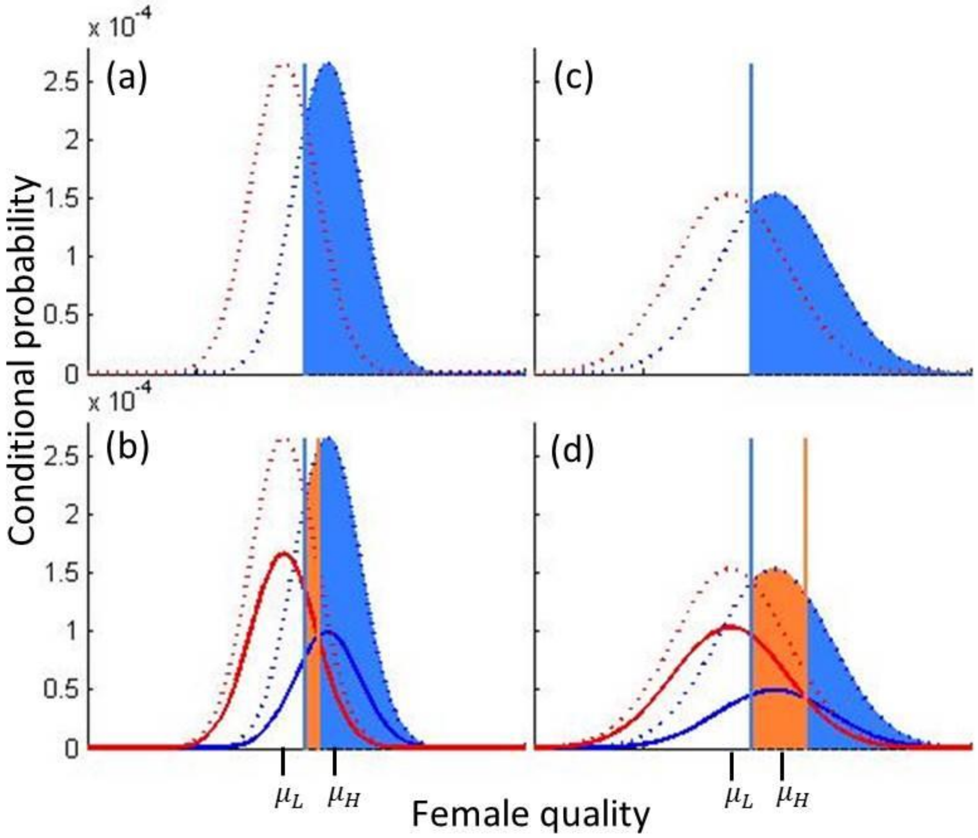
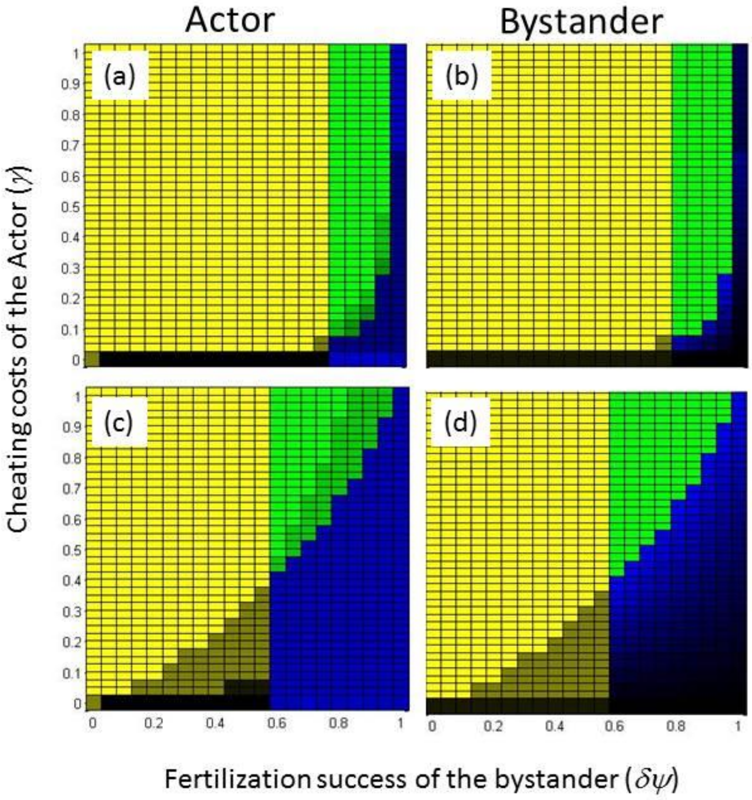

$\times 10^{-4}$
(a)
(c)
$\times 10^{-4}$
(b)
(d)
2.5
2
1.5
1
0.5
0
Conditional probability
μ_L
μ_H
μ_L
μ_H
Female quality

Figure 2.


Actor
Bystander
(a)
(b)
(c)
(d)
Cheating costs of the Actor (γ)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.2
0.4
0.6
0.8
1
Fertilization success of the bystander ($\delta\psi$)