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

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

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15 Males of several species have been shown to alter their mate preference in the presence of an

16 eavesdropping rival. This evasive tactic has been interpreted as an attempt by the courting

17 male to drive the attention of the rival away from the preferred female. The fitness return of

18 this deceptive strategy will depend on the costs of cheating for the actor (the displayer) and

19 the benefits for the rival (the bystander) of copying the choice of the displayer. We developed

20 a two-person nonzero sum game between two males that compete for mating with one of two

21 receptive females. Males could assess female quality with a varying level of uncertainty,

22 which was modelled using a Bayesian statistical decision theory approach. We explored the

23 actor and bystander payoffs under different levels of uncertainty in mate assessment and

24 difference in quality between females. We found that when being eavesdropped on is costly

25 (i.e. when females differ largely in quality), males are expected to cheat to reduce the amount

26 of public information that is available to the unintended audience. However, under these

27 circumstances, the value of the public information is low and the bystander is not expected to

28 copy the choice of the actor. Our model suggests that deceptive male choice may evolve only

29 under relatively restricted conditions and suggest that other explanations, such as, for

30 example, a reduction in the risk of precopulatory male–male competition may be more likely.

31 Future theoretical and empirical work will be necessary to test alternative interpretations of

32 the audience effects in male mate choice.

33 Keywords: audience effects; computational mate choice; deception; game-theoretic model;

34 male mate choice; mate choice copying; *Poecilia*; public information; sperm competition.

35

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).

61

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

86 polyandrous species a female's mating probability is expected to decrease as the number of

87 previous matings increases. For example, in an experiment with guppies, only 64% of 55

88 females that mated with one male and were presented with a second male after the initial

89 mating did actually remate (Evans & Magurran, 2001). Assuming that this remating

90 probability remains constant across successive encounters with males, about 29% of the

91 females would be expected to mate with more than five males. This figure is very similar to

92 the proportion observed in another guppy population, using a slightly different mating design,

93 in which about 26% of the females mated with more than five males (frequency estimated

94 from Figure 2 in Evans & Gasparini, 2013), supporting the generally assumed notion that

95 guppy female mating rate declines with the number of previous matings. The decline in

96 female mating probability after mating may be due to increased costs and/or decreased

97 benefits of successive matings (Jennions & Petrie, 2000) or to conflict with males (e.g. Scott,

98 1986).

99

100 The costs of being copied also differ between males and females. A male whose choice is

101 copied will suffer the same costs, associated with the increased probability of pre- and

102 postcopulatory competition, faced by the copier. Accordingly, male sexual behaviour is often

103 altered by the presence of a bystander (e.g. Vignal, Mathevon, & Mottin, 2004) and the public

104 information extracted from intersexual communication can be used to guide the behaviour of

105 eavesdropping individuals (Matos & Schlupp, 2005). Audience effects in a male choice

106 context have been studied in detail in fish (Dzieweczynski & Rowland, 2004; Herb, Biron, &

107 Kidd, 2003), and in particular in poeciliids (Auld & Godin, 2015; Fisher & Rosenthal, 2007;

108 Makowicz, Plath, & Schlupp, 2010; Plath, Blum, Schlupp, & Tiedemann, 2008; Plath,

109 Richter, Tiedemann, & Schlupp, 2008). In these fish, it has been shown that the initial

110 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

136   control his manifested preferences for a high- over a low-quality female. The observer can

137   eavesdrop on the actor's mating behaviour and strategically use (or decide not to use) this

138   public information in mating decisions.

139

140   # Methods

141   ## The model

142   The game is a two-person nonzero sum game between two males that compete for mating

143   with one of two receptive females. The two males are of similar quality, but play different

144   roles: the actor has the priority of choosing and, eventually, of mating with one of the two

145   females; the bystander can observe the behaviour of the actor and, only after the actor has

146   made his move, he can make his own. To provide the actor with the possibility of cheating,

147   the model assumes that the bystander can assess the mating preferences, but not the mate

148   choice of the actor (see below). Unlike males, females are assumed to differ in quality (e.g.

149   the number or dimensions of eggs). We name the high-quality female H and the low-quality

150   female L.

151

152   ## The Actor strategy: the use of private information

153   The actor assesses the females' quality with uncertainty. To model this, we adopt a Bayesian

154   statistical decision theory approach (McNamara & Dall, 2010). We describe the perceived

155   female values with one of two stochastic variables: (1) $H = \mu_H + \varepsilon$, when the female is of

156   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

157   true female qualities, whereas ε is a normally distributed random variable with zero mean and

158   variance σ^2. We define $h(x) = P(x|H)$ and $l(x) = P(x|L)$ the probability density functions

159   of H and L, respectively.

160

161   First, we consider the behaviour of the actor when the bystander is absent. Suppose that, at a

162   given time i, the actor is assessing the high-quality female, which he perceives of quality x_i.

163   The actor has no prior information, but he is assumed to 'know' the likelihoods of perceiving

164   x_i when a female is either of high or of low quality and to be able to 'compute' the relative

165   posterior probability:

166

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

168

169   If $P(H|x_i) > 0.5$ then the male will court the female until time i+1; otherwise he will move to

170   and start courting the other female. Note that, at any time step i, the posterior probabilities are

171   assumed to be independent of previous assessments, that is, the male is thought not to use

172   prior private information.

173

174   The proportion of time spent by the actor with the high-quality female is the expression of his

175   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

176   preference for the high-quality female is:

177

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

179

180   Analogously, $A_L = 1 - A_H$, is the preference for the low-quality female.

181   Second, we consider what happens when the actor perceives the presence of the bystander.

182   We assume that the bystander does not affect the perceived preferences (A_H) of the actor, but

183   only his manifested preferences (M_H). In other words, we allow the actor to cheat. This means

184   that, when there is a bystander, the actor can move away from a female even if he perceives

185 her of high quality or he can court a female even if he perceives her of low quality.

186 Specifically, we assume that the manifested preferences for the high- and low-quality females

187 are, respectively, $M_H = (1 - K_A)A_H$, and $M_L = 1 - M_H = K_A + (1 - K_A)A_L$.

188

189 K_A can vary between 0 and 1 and it describes the strategy of the actor. When K_A is zero, the

190 actor adopts a honest strategy and the perceived and the manifested preferences coincide.

191 Conversely, when $K_A = 1$, the actor is fully dishonest in that he will court the female he

192 perceives of low quality.

193

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

195 When waiting for his turn, the bystander obtains the females' quality information both

196 directly, by assessing them, and indirectly, by eavesdropping on the actor's behaviour. Thus,

197 when he eventually has access to the females, he is assumed to make an optimal use of the

198 previously acquired public information, as predicted by Bayes's theorem. The posterior

199 probability of the hypothesis that the assessed female is of better quality than the other (i.e.

200 the probability that she is the H female) will depend not only on her perceived quality (x_i),

201 but also on her prior probability $P(H)$ that this hypothesis be true:

202

203 $P(H|x_i) = \frac{h(x_i)P(H)}{h(x_i)P(H)+l(x_i)P(L)}.$ (3)

204

205 The prior probability depends on how the bystander evaluates and responds to the manifested

206 preference of the actor. Specifically, we assume that the bystander's strategy is defined by

207 two variables: (1) K_B, which depends on the assumed reliability of the actor's manifested

208 preference and affects the amount of public information that is actually used in the decision

209 process; (2) b, a binary variable which describes the way the bystander uses public

9

210   information: when $b = 1$, the actor's manifested preferences and $P(H)$ are positively

211   associated, whereas when $b = 0$, they are negatively associated:

212

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

214

215   When $K_B = 0$, the bystander perceives the public information as fully unreliable and $P(H) =$

216   0.5, independent of the value of b. When $K_B = 1$, the bystander perceives the public

217   information as fully reliable. In this case, if $b = 0$ then $P(H) = M_H$, whereas if $b = 1$ then

218    $P(H) = 1 - M_H$. The bystander, by strategically adjusting K_B between 0 and 1, can control

219   the risk of being deceived by the actor, whereas, by controlling b, he can increase or decrease

220   the probability of mating with the female preferred by the actor. As we shall see, b plays an

221   important role in determining the bystander's optimal decision strategy, when unmated

222   females should be preferred over recently mated females, independent of their qualities.

223

224   As for the actor, we assume that the proportion of time spent by the bystander with a female is

225   the probability of obtaining $P(H|x) > 0.5$ when assessing that female and it is an expression

226   of his preference. It may be shown that $P(H|x) > 0.5$ when the perceived quality is greater

227   than the threshold ϕ, which depends not only on μ_H and μ_L, but also on the uncertainty level

228   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

229   analytical derivation of ϕ). Thus, the bystander's preference for H is:

230

231    $B_H = \int_\phi^\infty h(x)\, dx;$ \qquad (5a)

232   and his preference for L is:

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

234

235   **\<H2\>Payoffs**

236   As mentioned above, μ_H and μ_L are the reproductive resources (i.e. the number of eggs) made

237   available by the high- and the low-quality females. Let $\pi_A = f(K_A)$ and $\pi_B = f(K_B, b)$ the

238   strategies of the actor and of the bystander, respectively. We define the payoffs $W(\pi_A, \pi_B)$ as

239   the amount of reproductive resources that the actor is expected to obtain when playing π_A

240   against the bystander playing π_B. Conversely, $W(\pi_B, \pi_A)$ are the payoffs of the bystander

241   playing π_B against an actor playing π_A. Besides the total amount of resources (μ_H and μ_L),

242   three other parameters affect the payoffs matrix: (1) the costs of cheating (γ); (2) the

243   probability that a female that has mated with the actor will mate again with the bystander (δ);

244   (3) the effect of mating order on fertilization success (φ).

245

246   The costs of cheating paid by the actor are represented by his decreased probability of mating

247   with the high-quality female. For fully honest actors, the model assumes that the probability

248   of mating with either the high- or the low-quality female is, respectively, M_H and M_L. When

249   the actor is cheating (that is, when $M_H < A_H$), he is expected to experience a reduced

250   probability of mating with H, which is not compensated for by an increase in the probability

251   of mating with L. Specifically, we assume that his probability of mating with H is $A_H(1 - $

252     $K_A)^\gamma$, where γ is the parameter defining the cost of cheating. The probability of mating with L

253   is still M_L.

254

255   For the bystander, mating probability depends on his preferences and on whether the chosen

256   female has previously mated with the actor. We assume that recently mated females are less

257   prone to remate and the parameter δ defines the probability that a mated female will remate

258     $(0 \leq \delta \leq 1)$.

259

260   When both males mate with the same female, sperm competition occurs. In this case, we

261   assume that between-male differences in fertilization success depend only on the mating order

262   and we define with φ (with $0 \leq \varphi \leq 1$) the proportion of eggs that are expected to be

263   fertilized by the bystander (i.e. by the second of the two males to mate with the female).

264

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

266

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

268

269   and

270

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

272

273   In words, the expected benefits of the actor are the sum of two terms: (1) the resources (μ_H)

274   expected from the high-quality female, H, multiplied by the probabilities that the actor mates

275   with H and the bystander chooses either L or H, corrected for the bystander's probability of

276   mating or siring her eggs, and (2) the resources (μ_L) expected from the low-quality female, L,

277   multiplied by the probabilities that the actor mates with H and the bystander chooses either H

278   or L, corrected for the bystander's probability of mating or siring her eggs. Analogously, the

279   payoffs of the bystander are the sum of the expected resources obtained from the high- and

280   the low-quality females multiplied by the probabilities that he mates with them and fertilizes

281   their eggs.

12

282

<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 $2n$

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 $\bar{K}_B^* = \sum_{i=1}^n \sum_{j=1}^2 \pi_B^*(i,j)K_B(i)$.

296

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.

301

<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

13

307   assessing female quality) and priors (i.e. public information obtained by observing the actor's

308   mating preferences) optimally, as described by Bayes's principle. From this assumption, it

309   follows that the influence of the public information on the bystander's choice depends on the

310   accuracy of direct assessment. If the bystander obtains strong direct evidence that a female is

311   of high quality, then the public information (the priors) plays only a marginal role on his final

312   mating decision. In contrast, when he cannot assess the female with high accuracy, his mating

313   decision may be strongly affected by eavesdropping on the actor. Since the actor can control

314   the type and the amount of (public) information that is available to the bystander, his

315   deceiving possibilities are expected to increase with decreasing assessment accuracy. For

316   example, when the direct assessment is accurate and the actor perceives a 0.75, but shows a

317   0.375 preference for the high-quality female (i.e. $K_A = 0.5$), the trustful-copying bystander

318   (i.e. $K_B = 1$ and $b = 1$) will reduce his preference from 0.75 to 0.61 (Fig. 1a, b). In contrast,

319   when the direct assessment is less accurate so that the actor's preference for the high-quality

320   female is 0.65, the same level of deception is enough to make a trustful bystander reverse his

321   preference and show a 0.71 mating preference for the low-quality female (Fig. 1c,d).

322

323   **<H2>Fertilization success and cheating costs**

324   Although uncertainty in female quality assessment is a key parameter of the game, we start by

325   considering the ideal case, in which there is no uncertainty and, thus, no possibility of

326   deception. Since deception is fully ineffective, the actor is forced to play the 'honest' strategy,

327    $K_A = 0$. The bystander's best reply to this strategy depends on his fertilization success ($\delta\varphi$).

328   When $\delta\varphi < \mu_L/\mu_H$, the bystander maximizes his payoffs by mating with the low-quality

329   female. Under this condition, the bystander will adopt the 'trustful-not-copying' strategy

330   ($K_B = 1; b = 0$), which makes him use the public information against the female preferred by

331   the actor. When $\delta\varphi > \mu_L/\mu_H$, in contrast, the bystander maximizes his payoffs by mating

332   with the high-quality female even if she has already mated with the actor. In this case, the

333   bystander will adopt the 'trustful-copying' strategy ($K_B = 1$; $b = 1$), which strongly penalizes

334   the actor.

335

336   Now, we introduce uncertainty into the game. In Fig. 2, we show the effect of the bystander's

337   fertilization success and of the actor's cheating costs on the Nash equilibrium strategies, under

338   a condition of low ($\sigma = 0.7$) and high ($\sigma = 3$, Fig. 2a, b) uncertainty. In these simulations,

339   female qualities are kept constant at $\mu_H = 15$ and $\mu_L = 12$ (but see the Python Notebook for

340   results under different conditions, http://penelope.unito.it/matecopying).

341

342   When assessment uncertainty is low (Fig. 2a, b) and $\delta\varphi < \mu_L/\mu_H$, the 'honest' actor and the

343   'trustful-not-copying' bystander are still pure Nash equilibrium strategies. In contrast, when

344    $\delta\varphi > \mu_L/\mu_H$ the bystander always copies the actor ($b = 1$), who, in turn, would benefit by

345   deceiving the bystander into preferring the low-quality female. However, since uncertainty is

346   low, deception is ineffective and the costs it imposes on the actor usually exceed the benefits.

347   Under these conditions, the actor is forced to play the 'honest' strategy, the bystander

348   perceives the actor's behaviour as fully reliable and the 'honest-trustful-copying' strategy is a

349   pure Nash equilibrium pair. There are, however, a few exceptions, which occur when the

350   bystander's fertilization success is extremely high and the costs of cheating very low. Under

351   these conditions, the game has only mixed equilibrium strategies, in which the actor is no

352   longer fully honest ($0 < \bar{K}_A^* < 1$) and the bystander no longer fully trustful ($0 < \bar{K}_B^* < 1$).

353

354   In Fig. 2c, d, we show the solutions of the game when female quality assessment is highly

355   uncertain. The 'honest/trustful-not-copying' pair of strategies is still a Nash equilibrium, but

356   only for a fertilization success much lower than μ_L/μ_H. Indeed, the fertilization success

357   threshold above which 'copying' is the most remunerative strategy for the bystander

358   decreases with increasing assessment uncertainty: for $\sigma = 3$ the threshold is $\delta\varphi \cong 0.55$ (Fig.

359   2d), for $\sigma = 4$ is $\delta\varphi \cong 0.45$, and for $\sigma = 5$ is $\delta\varphi \cong 0.35$ (see the Python notebook).

360

361   As explained above, when sperm competition penalizes the bystander, he should adopt the

362   'not-copying' strategy to minimize the risk of mating with an already mated female. If the

363   bystander knows with certainty which female the actor prefers, then he would be able to

364   minimize the risks of sperm competition by mating with the disfavoured female. However,

365   when the uncertainty of quality assessment increases, the actor's mating preference decreases

366   and the bystander's risk of mating with an already mated female increases. For example, if the

367   honest actor showed a preference for the high-quality female of $M_H = 0.6$, the bystander that

368   adopted the 'trustful-not-copying' strategy would show a preference for the low-quality

369   female of $B_L = 0.62$. In this case, there would be a 0.48 probability that the bystander and

370   the actor mate with the same female and a 0.52 probability that the chosen female is the low-

371   quality one. But, if the bystander cannot prevent sperm competition, then he would do better

372   trying to compete for the eggs of the high-quality rather than for those of the low-quality

373   female. For this reason, the threshold from the 'not-copying' to the 'copying' strategy

374   decreases when the uncertainty of female quality assessment increases.

375

376   When the bystander switches from the 'not-copying' to the 'copying' strategy, the actor no

377   longer benefits from playing honestly, unless the deception costs prevent him from cheating.

378   In fact, the 'honest-trustful-copying' equilibrium pair of strategies is only found when the

379   costs of cheating are greater than a certain threshold, which increases with the bystander's

380   fertilization success. For example, for $\delta\varphi = 0.6$, there are honest equilibrium pairs only when

381     $\gamma \geq 0.5$, whereas for $\delta\varphi = 0.7$ only when $\gamma \geq 0.7$, and the honesty threshold increases to

382　$\gamma = 0.9$ for $\delta\varphi = 0.8$ (Fig. 2c). In all other cases, the game has no pure equilibrium pairs, but

383　only one or more mixed equilibrium strategies. Under these conditions, deception is more

384　effective when the cheating costs are high ($\gamma \geq 0.5$) than when they are low. In fact, Fig. 2c,

385　d shows that the mixed equilibrium strategies of the bystander tend to underestimate the

386　honesty of the actor (i.e. $\overline{K}_B^* > 1 - \overline{K}_A^*$) when the costs of cheating are low and to overestimate

387　it (i.e. $\overline{K}_B^* < 1 - \overline{K}_A^*$) when the costs are high. Independent of the costs, however, the level of

388　deception is always relatively low, being always $\overline{K}_A^* < 0.3$. For these values of $\overline{K}_A^*$, the

389　manifested preference of the actor for the highest-quality female is decreased but still higher

390　than 0.5. Thus, the actor seems more likely to retain honest information than to provide the

391　bystander with dishonest information.

392

393　**<H1>Discussion**

394　When being copied by an eavesdropper imposes a cost on the male making a mating decision,

395　the latter is expected to adjust his behaviour in order to limit or prevent the use of public

396　information (Nordell & Valone, 1998). However, since these changes in behaviour are likely

397　to be costly, the behavioural adjustment is expected to make an optimal trade-off between

398　these two types of costs. Our game-theoretic model has been devised to study this trade-off.

399　Specifically, the model asks when it pays a courting male to reduce his manifested preference

400　for the high-quality female in order to decrease the probability that a bystander male will mate

401　with her. A similar question has been addressed recently by Dubois (2015). In her game,

402　males can adopt one of four tactics: (1) unselective males, which mate with both high- and

403　low-quality females indiscriminately; (2) copier males, which use social information, when

404　available, or mate indiscriminately, when unavailable; (3) selective-insensitive males, which

405　prefer high- over low-quality females, without changing these preferences in the presence of

406　an audience; or (4) selective and sensitive males, which prefer high-quality females and

407 change their preference in the presence of an audience. The results of the model indicate that

408 the four tactics form a mixed equilibrium strategy when last-male sperm precedence is strong,

409 the cost of female assessment large and the risk of eavesdropping high. The selective-

410 sensitive tactic, however, is never a pure strategy.

411 Our model differs from Dubois's model (2015) both in the assumptions and in the

412 methodology and derives, to a large extent, different results. The main methodological

413 difference is that our model is based on the computational mechanisms and rules of mating

414 decisions (Castellano, 2009, 2010). The computational mechanisms (1) explain how the

415 decision maker processes private and public information, (2) are part of the assumptions of

416 the model and, consequently, (3) act as a constraint on the set of possible behavioural

417 strategies. Following the 'behavioural gambit' approach (Fawcett, Hamblin, & Giraldeau,

418 2013), Dubois's model considers the alternative strategies as independent phenotypes, which

419 can be interpreted as either polymorphic traits in the population or plastic traits at the

420 individual level. Given these tactics, the solution of the game is the set of phenotypic

421 frequencies that are evolutionarily stable. In contrast, in our model, the alternative tactics are

422 not independent traits, but the expression of the same decisional mechanism. Our model

423 explains behavioural variation in terms of variation in the parameters that govern the

424 computational mechanisms and it assumes that selection acts on these parameters (Castellano,

425 2009, 2015; McNamara & Houston, 2009). We think that this approach might help to capture

426 the very essence of the biological problem under study by favouring a close integration of

427 decision mechanism and behaviour function.

428 Our model identified three main factors that are expected to affect the strategic manipulation

429 of public information: (1) the strength of the conflict between the eavesdropping and the

430 eavesdropped males; (2) the manipulative potential of the eavesdropped male, which depends

431   on the intrinsic value of public information; and (3) the cost of public information

432   manipulation.

433

434   **<H2>The strength of the conflict**

435   The most important factor that affects the strategic use of public information is the strength of

436   the conflict between the individual that provides public information (the actor) and the

437   individual that can use this information (the bystander) (Nordell & Valone, 1998; Valone,

438   2007). In our model, the strength of the conflict depended on (1) the difference in fertilization

439   success between the actor and the bystander and (2) the difference in quality between the two

440   contended resources (females).

441   When the fertilization success of the bystander is lower than the ratio between the low- and

442   the high-quality females, there is no conflict between the actor and the bystander, because

443   both maximize their reproductive success by choosing different females: the actor, which has

444   the priority in mating decision, will do best by choosing the high-quality female, whereas the

445   bystander will do best by choosing the low-quality female. In this case, public information

446   might be better seen as being about the costs, rather than the benefits, for the bystander of

447   choosing the high-quality resource: the actor benefits from providing public information

448   about these costs and the bystander benefits from exploiting the public information provided

449   by the actor. This is what has been observed in a context of interspecific competition for food

450   between eusocial stingless bees that eavesdrop on recruitment signals of other species to

451   guide their foraging strategy (Lichtenberg, Zivin, Hrncir, & Nieh, 2014). Since eavesdroppers

452   may fight to access the food, they have been observed to avoid more conspicuous signals

453   because they indicate higher competitive costs. Analogously, our model suggests that, when

454   the bystander has a low fertilization success (i.e. when last-male sperm precedence is weak

455   and/or female remating probability is low), he should do better by reversing rather than by

456   copying the actor's preference.

457   Interestingly, the model also suggests that uncertainty in female quality assessment affects the

458   strength of the conflict. In fact, other things being equal, high assessment uncertainty reduces

459   the strength of the actor's preference and hence the intrinsic value of public information.

460   However, when the bystander is uncertain about the choice of actor, our model predicted that

461   his optimal strategy is to use public information as an indication of expected benefits of

462   copying, rather than of expected costs. In fact, if uncertainty makes sperm competition

463   unavoidable, the bystander should do better by competing for the high- than for the low-

464   quality resources. Although in our game the actor could only reduce but not increase his

465   perceived preferences (i.e. K_A was forced to vary between 0 and 1), we can predict that if he

466   has a strong sperm competition advantage over the bystander, then he would be favoured by

467   exaggerating his manifested preferences (i.e. $K_A > 1$). In this way, the risk of sperm

468   competition would decrease and both the actor and the bystander would benefit. Indeed, as

469   suggested by Lichtenberg et al. (2014), when the public information is about the costs of

470   accessing a resource, both signallers and eavesdroppers benefit from the increase in the

471   information quality (i.e. an increase in signal conspicuousness is expected).

472   When the fertilization success of the bystander is greater than the ratio between the low- and

473   the high-quality females, the conflict between the bystander and the actor is strong, because

474   both benefit from choosing the high-quality female. In this case, the model predicted mixed

475   equilibrium strategies, with partially unreliable actors and partially untrusting bystanders. At

476   the equilibrium, both the actual and the perceived reliability of public information depended

477   on the potential benefits and on the expected costs of its manipulation (see below).

478

<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

504 resources for reproduction or when these resources are not limited (Berglund, Magnhagen,

505 Bisazza, Konig, & Huntingford, 1993), there is unlikely to be any substantial cost for the

506 female whose choice is copied. In contrast, model males pay a cost of being copied. The

507 results of our model suggests that the manipulation of public information is more likely to

508 occur when the difference in quality between the mating options is small. However, under

509 these conditions, the benefits of manipulation are also necessarily low.

510 The intrinsic value of public information also depends on the accuracy of mate quality

511 assessment. This, in turn, will affect the relative costs of using private and public information.

512 When private information is more costly to acquire than public information, it might be

513 beneficial to make a quick and inaccurate evaluation of the alternatives and to base the mating

514 decision mainly on public information. For example, in agonistic interactions, the direct

515 assessment of the competitive value of rivals might be costly, because it exposes the decision

516 maker to the risk of fighting. In these cases, the decision maker should trust the 'reputation' of

517 the opponent, rather than directly assess his value (Valone, 2007). In a mate choice context,

518 this is similar to what may be observed in species in which cryptically coloured females that

519 assess directly conspicuous mates expose themselves to the risk of being predated (Gibson &

520 Bachman, 1992; Pocklington & Dill, 1995). When the predation risk associated with direct

521 mate assessment is high, female mate choice copying is more likely to evolve. In males, in

522 contrast, it is unlikely that the costs of assessing female quality are so high that they would

523 exceed either the costs of copying or the benefits of accurate evaluations.

524

525 **<H2>The costs of manipulating public information**

526 The results of our model suggest that the actor's strategic manipulation of public

527 information may evolve when the conflict between the actor and the bystander is so

528 strong that it pays the bystander to copy the actor's choice and the intrinsic value of

529 public information is high. In our game, this was represented by a reduction in the actor's

530 manifested preference for high-quality females in the presence of an audience. However,

531 a reduction in courtship effort is likely to decrease the actor's attractiveness and his

532 probability of mating with the high-quality female. The results of our model indicated

533 that the higher the manipulation costs the higher the reliability of public information at

534 equilibrium. If, in contrast, the actor pays no costs for manipulating public information

535 (i.e. his probability of mating with the high-quality female is not reduced), his best move

536 is to make his manifested preference for the high-quality female unreliable, so that the

537 bystander no longer benefits from using public information. The manipulation costs,

538 thus, can prevent the complete corruption of public information in social networks and

539 promote mixed equilibrium strategies that make actors only partially reliable and

540 bystanders only partially trustful.

541

542 **<H2>Conclusions**

543 Our model showed that when being eavesdropped on is costly, an animal is expected to

544 plastically adjust its behaviour to reduce the amount of public information that is available to

545 the unintended audience. However, unless the costs of being eavesdropped on are extremely

546 high and those of manipulating public information extremely low, such an audience-mediated

547 plasticity is unlikely to be so pronounced that it results in an effective manipulation of the

548 audience. In other words, males are not expected to cheat about their real mating preference to

549 deceive bystanders, unless under very limited (and extreme) conditions. The results of our

550 model conflict with the empirical evidence that male poeciliids reverse their mating

551 preference in the presence of a male audience (but see Callander, Backwell, & Jennions, 2012

552 for contrasting results; Plath, Blum, et al., 2008; Plath, Richter, et al., 2008; Ziege et al.,

553 2009). We argue that this audience effect may therefore have alternative functional

554 explanations. For example, males may plastically modify their perceived preferences for the

555 high-quality female to reduce the costs associated with direct, precopulatory, male–male

556 competition (Auld, Jeswiet, & Godin, 2015; Mautz & Jennions, 2011; Plath, Richter, et al.,

557 2008). While clearly the audience effect can be interpreted as a male strategy to maximize his

558 reproductive success when rival males are present, the two interpretations are radically

559 different. The deception hypothesis rests on the assumption that the audience effect does not

560 affect mate choice, but only the manifested preferences. The alternative hypothesis, which

561 could be named the 'flexible decision' hypothesis, assumes that both mating preferences and

562 mating decisions are flexibly adjusted to the social environment in which mate choice is

563 carried out. A large difference in body size between the actor and the bystander should not

564 influence the actor's behaviour under the deception hypothesis (Plath, Richter, et al., 2008),

565 whereas it should have a large effect if the actor's strategy aims at reducing the costs of

566 aggressive male–male interactions. Similar predictions may be made for the difference in

567 male ornamentation. In contrast, the deception hypothesis predicts a larger audience effect

568 when the actor can choose between females that are very different in quality, whereas a male

569 may decide to pay the costs of an aggressive interaction with the bystander, and hence keep

570 his initial preference, if the audience effect is mainly driven by the costs of aggressive

571 interactions. More empirical studies on the effects of social environments on both mating

572 preferences and mating decisions (Mautz & Jennions, 2011) will be necessary to provide

573 insights into the functional role of the audience effect.

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584   References

585

586   Auld, H. L., & Godin, J. G. J. (2015). Sexual voyeurs and copiers: social copying and the

587   audience effect on male mate choice in the guppy. *Behavioral Ecology and*

588   *Sociobiology, 69*, 1795-1807.

589   Auld, H. L., Jeswiet, S. B., & Godin, J. G. J. (2015). Do male Trinidadian guppies adjust their

590   alternative mating tactics in the presence of a rival male audience? *Behavioral*

591   *Ecology and Sociobiology, 69*, 1191-1199.

592   Berglund, A., Magnhagen, C., Bisazza, A., Konig, B., & Huntingford, F. (1993). Female-

593   female competition over reproduction. *Behavioral Ecology, 4*, 184-187.

594   Bierbach, D., Makowicz, A. M., Schlupp, I., Geupel, H., Streit, B., & Plath, M. (2013).

595   Casanovas are liars: Behavioral syndromes, sperm competition risk, and the evolution

596   of deceptive male mating behavior in live-bearing fishes. *F1000Research, 2*, 75.

597   Brooks, R. (1996). Copying and the repeatability of mate choice. *Behavioral Ecology and*

598   *Sociobiology, 39*, 323-329.

599   Callander, S., Backwell, P. R. Y., & Jennions, M. D. (2012). Context-dependent male mate

600   choice: the effects of competitor presence and competitor size. *Behavioral Ecology,*

601   *23*, 355-360.

602   Castellano, S. (2009). Towards an information-processing theory of mate choice. *Animal*

603   *Behaviour, 78*, 1493-1497.

604 Castellano, S. (2010). The computational mechanisms of mate choice. *Ethology, 116*, 283-

605   291.

606 Castellano, S. (2015). Bayes' rule and bias roles in the evolution of decision making.

607   *Behavioral Ecology, 26*, 282-292.

608 Clark, D. L., Roberts, J. A., & Uetz, G. W. (2012). Eavesdropping and signal matching in

609   visual courtship displays of spiders. *Biology Letters, 8*, 375-378.

610 Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005).

611   Information and its use by animals in evolutionary ecology. *Trends in Ecology &*

612   *Evolution, 20*, 187-193.

613 Dubois, F. (2015). When being the centre of the attention is detrimental: copiers may favour

614   the use of evasive tactics. *Behavioral Ecology and Sociobiology, 69*, 183-191.

615 Dugatkin, L. A. (1992). Sexual selection and imitation: Females copy the mate choice of

616   others. *The American Naturalist, 139*, 1384-1389.

617 Dugatkin, L. A. (1996a). Copying and mate choice. In C. Heyes & B. G. Galef (Eds.), *Social*

618   *learning and imitation: the roots of culture* (pp. 85-105). London, U.K.: Academic

619   Press.

620 Dugatkin, L. A. (1996b). Interface between culturally based preferences and genetic

621   preferences: Female mate choice in *Poecilia reticulata*. *Proceedings of the National*

622   *Academy of Sciences of the USA, 93*, 2770-2773.

623 Dugatkin, L. A. (1998). Genes, copying, and female mate choice: shifting thresholds.

624   *Behavioral Ecology, 9*, 323-327.

625 Dugatkin, L. A., & Godin, J. G. J. (1992). Reversal of female mate choice by copying in the

626   guppy *(Poecilia reticulata)*. *Proceedings of the Royal Society B-Biological Sciences,*

627   *249*, 179-184.

628   Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate copying in the guppy (*Poecilia*

629   *reticulata*): Age-dependent effects. *Behavioral Ecology, 4*, 289-292.

630   Dzieweczynski, T. L., & Rowland, W. J. (2004). Behind closed doors: use of visual cover by

631   courting male three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour,*

632   *68*, 465-471.

633   Evans, J. P., & Gasparini, C. (2013). The genetic basis of female multiple mating in a

634   polyandrous livebearing fish. *Ecology and Evolution, 3*, 61-66.

635   Evans, J. P., & Magurran, A. E. (2001). Patterns of sperm precedence and predictors of

636   paternity in the Trinidadian guppy. *Proceedings of the Royal Society B-Biological*

637   *Sciences, 268*, 719-724.

638   Fawcett, T. W., Hamblin, S., & Giraldeau, L.-A. (2013). Exposing the behavioral gambit: the

639   evolution of learning and decision rules. *Behavioral Ecology, 24*, 2-11.

640   Fisher, H. S., & Rosenthal, G. G. (2007). Male swordtails court with an audience in mind.

641   *Biology Letters, 3*, 5-7.

642   Frommen, J. G., Rahn, A. K., Schroth, S. H., Waltschyk, N., & Bakker, T. C. M. (2009).

643   Mate-choice copying when both sexes face high costs of reproduction. *Evolutionary*

644   *Ecology, 23*, 435-446.

645   Galef, B. G., Lim, T. C. W., & Gilbert, G. S. (2008). Evidence of mate choice copying in

646   Norway rats, *Rattus norvegicus*. *Animal Behaviour, 75*, 1117-1123.

647   Galef, B. G., & White, D. J. (1998). Mate-choice copying in Japanese quail, *Coturnix*

648   *coturnix japonica*. *Animal Behaviour, 55*, 545-552.

649   Gibson, R. M., & Bachman, G. C. (1992). The costs of female choice in a lekking bird.

650   *Behavioral Ecology, 3*, 300-309.

651   Gibson, R. M., Bradbury, J. W., & Vehrencamp, S. L. (1991). Mate choice in lekking sage

652   grouse revisited: The roles of vocal display, female site fidelity, and copying.

653   *Behavioral Ecology, 2*, 165-180.

654   Godin, J. G. J., Herdman, E. J. E., & Dugatkin, L. A. (2005). Social influences on female

655   mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying

656   behaviour. *Animal Behaviour, 69*, 999-1005.

657   Grafe, T. U. (2005). Anuran choruses as communication networks. In P. McGregor (Ed.),

658   *Animal communication networks* (pp. 277-299). Cambridge, U.K.: Cambridge

659   University Press.

660   Herb, B. M., Biron, S. A., & Kidd, M. R. (2003). Courtship by subordinate male siamese

661   fighting fish, *Betta splendens*: Their response to eavesdropping and naive females.

662   *Behaviour, 140*, 71-78.

663   Hoglund, J., Alatalo, R. V., Gibson, R. M., & Lundberg, A. (1995). Mate-choice copying in

664   black grouse. *Animal Behaviour, 49*, 1627-1633.

665   Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic

666   benefits. *Biological Reviews of the Cambridge Philosophical Society, 75*, 21-64.

667   Kniel, N., Dürler, C., Hecht, I., Heinbach, V., Zimmermann, L., & Witte, K. (2015). Novel

668   mate preference through mate-choice copying in zebra finches: sexes differ.

669   *Behavioral Ecology, 26*, 647-655.

670   Lichtenberg, E. M., Zivin, J. G., Hrncir, M., & Nieh, J. C. (2014). Eavesdropping selects for

671   conspicuous signals. *Current Biology, 24*, R598-R599.

672   Loyau, A., Blanchet, S., Van Laere, P., Clobert, J., & Danchin, E. (2012). When not to copy:

673   female fruit flies use sophisticated public information to avoid mated males. *Science

674   Report, 2*.

675   Makowicz, A. M., Plath, M., & Schlupp, I. (2010). Male guppies (*Poecilia reticulata*) adjust

676   their mate choice behaviour to the presence of an audience. *Behaviour, 147*, 1657-

677   1674.

678   Mangasarian, O. L., & Stone, H. (1964). Two-person nonzero-sum games and quadratic

679   programming. *Journal of Mathematical Analysis and Applications, 9*, 348-355.

680   Matos, R. J., & Schlupp, I. (2005). Performing in front of an audience: signallers and the

681   social environment. In P. K. McGregor (Ed.), *Animal communication networks* (pp.

682   63-83). Cambridge, U.K.: Cambridge University Press.

683   Mautz, B. S., & Jennions, M. D. (2011). The effect of competitor presence and relative

684   competitive ability on male mate choice. *Behavioral Ecology, 22*, 769-775.

685   McNamara, J. M., & Dall, S. R. X. (2010). Information is a fitness enhancing resource. *Oikos,*

686   *119*, 231-236.

687   McNamara, J. M., & Houston, A. I. (2009). Integrating function and mechanism. *Trends in*

688   *Ecology and Evolution, 24*, 670-675.

689   Mery, F., Varela, S. A. M., Danchin, É., Blanchet, S., Parejo, D., Coolen, I., & Wagner, R. H.

690   (2009). Public versus personal information for mate copying in an invertebrate.

691   *Current Biology, 19*, 730-734.

692   Milner, R. N. C., Booksmythe, I., Jennions, M. D., & Backwell, P. R. Y. (2010). The battle of

693   the sexes? Territory acquisition and defence in male and female fiddler crabs. *Animal*

694   *Behaviour, 79*, 735-738.

695   Nöbel, S., & Witte, K. (2013). Public information influences sperm transfer to females in

696   sailfin molly males. *PLoS One, 8*, e53865.

697   Nordell, S. E., & Valone, T. J. (1998). Mate choice copying as public information. *Ecology*

698   *Letters, 1*, 74-76.

699 Ojanguren, A. F., & Magurran, A. E. (2004). Uncoupling the links between male mating

700   tactics and female attractiveness. *Proceedings of the Royal Society B-Biological*

701   *Sciences, 271*, S427-S429.

702 Parker, G. A., & Smith, J. M. (1990). Optimality theory in evolutionary biology. *Nature, 348*,

703   27-33.

704 Plath, M., Blum, D., Schlupp, I., & Tiedemann, R. (2008). Audience effect alters mating

705   preferences in a livebearing fish, the Atlantic molly, *Poecilia mexicana*. *Animal*

706   *Behaviour, 75*, 21-29.

707 Plath, M., Richter, S., Tiedemann, R., & Schlupp, I. (2008). Male fish deceive competitors

708   about mating preferences. *Current Biology, 18*, 1138-1141.

709 Pocklington, R., & Dill, L. M. (1995). Predation on females or males: Who pays for bright

710   male traits? *Animal Behaviour, 49*, 1122-1124.

711 Pruett-Jones, S. (1992). Independent versus non-independent mate choice: Do females copy

712   each other? *The American Naturalist, 140*, 1000-1009.

713 Santos, M., Matos, M., & Varela, S. A. M. (2014). Negative public information in mate

714   choice copying helps the spread of a novel trait. *The American Naturalist, 184*, 658-

715   672.

716 Schlupp, I., & Ryan, M. J. (1997). Male sailfin mollies (*Poecilia latipinna*) copy the mate

717   choice of other males. *Behavioral Ecology, 8*, 104-107.

718 Scott, D. (1986). Inhibition of female *Drosophila melanogaster* remating by a seminal fluid

719   protein (Esterase 6). *Evolution, 40*, 1084-1091.

720 Vakirtzis, A. (2011). Mate choice copying and nonindependent mate choice: A critical

721   review. *Annales Zoologici Fennici, 48*, 91-107.

722 Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos, 56*,

723   357-363.

724 Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others:

725   a review of public information use. *Behavioral Ecology and Sociobiology, 62*, 1-14.

726 Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to

727   partner's voice. *Nature, 430*, 448-451.

728 Webster, M. M., & Laland, K. N. (2013). Local enhancement via eavesdropping on courtship

729   displays in male guppies, *Poecilia reticulata*. *Animal Behaviour, 86*, 75-83.

730 Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I., & Hein, W. K. (2000).

731   Alternative mechanisms of nonindependent mate choice. *Animal Behaviour, 59*, 467-

732   476.

733 Widemo, M. S. (2006). Male but not female pipefish copy mate choice. *Behavioral Ecology,*

734   *17*, 255-259.

735 Witte, K., Kniel, N., & Kureck, I. M. (2015). Mate-choice copying: Status quo and where to

736   go. *Current Zoology, 61*, 1073-1081.

737 Witte, K., & Massmann, R. (2003). Female sailfin mollies, *Poecilia latipinna*, remember

738   males and copy the choice of others after one day. *Animal Behaviour, 65 Part 6*, 1151-

739   1159.

740 Witte, K., & Nöbel, S. (2011). Learning and mate choice. In C. Brown, K. N. Laland & J.

741   Krause (Eds.), *Fish cognition and behaviour (2nd ed.)* (pp. 81-107). Oxford, U.K.:

742   Blackwell.

743 Witte, K., & Noltemeier, B. (2002). The role of information in mate-choice copying in female

744   sailfin mollies (*Poecilia latipinna*). *Behavioral Ecology and Sociobiology, 52*, 194-

745   202.

746 Witte, K., & Ryan, M. J. (1998). Male body length influences mate-choice copying in the

747   sailfin molly *Poecilia latipinna*. *Behavioral Ecology, 9*, 534-539.

748   Witte, K., & Ryan, M. J. (2002). Mate choice copying in the sailfin molly, *Poecilia latipinna*,

749   in the wild. *Animal Behaviour, 63*, 943-949.

750   Ziege, M., Mahlow, K., Hennige-Schulz, C., Kronmarck, C., Tiedemann, R., Streit, B., &

751   Plath, M. (2009). Audience effects in the Atlantic molly (*Poecilia mexicana*)–prudent

752   male mate choice in response to perceived sperm competition risk? *Frontiers in*

753   *Zoology, 6*, 17.

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756   **Appendix**

757   The model assumes that a male would choose to court (and eventually to mate with) a female

758   if the posterior probability that this female is of high quality is greater than 0.5. Here, we

759   derive the value of perceived female quality (ϕ), above which the female is accepted as an

760   appropriate mate and below which she is rejected.

761   Let $P(H)$ and $P(L) = 1 - P(H)$ be the prior probabilities that the assessed female is of either

762   high or low quality, respectively.

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

764   high quality is:

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

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

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

768   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

769   density functions $P(x|H)$ and $P(x|L)$, respectively.

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

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

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

773   If the choosing male uses only private information (i.e. $P(H) = P(L) = 0.5$), then $\phi = \phi_0 =$

774     $\frac{\mu_H + \mu_L}{2}$. If he integrates private and public information and if public information is honest (i.e.

775     $P(H) > P(L)$), then $\phi < \phi_0$ and the male's preferences for the high-quality female increase.

776   Finally, if the male uses dishonest public information (i.e. $P(H) < P(L)$), then $\phi > \phi_0$ and his

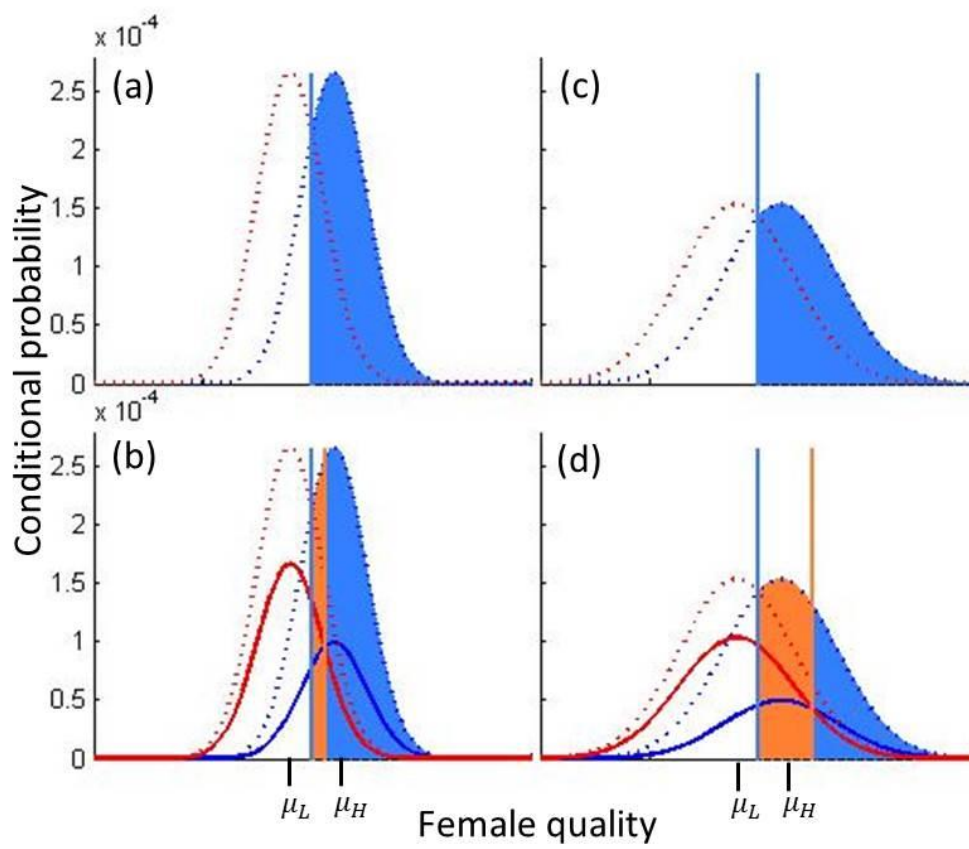777   preferences for the high-quality female decrease.

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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

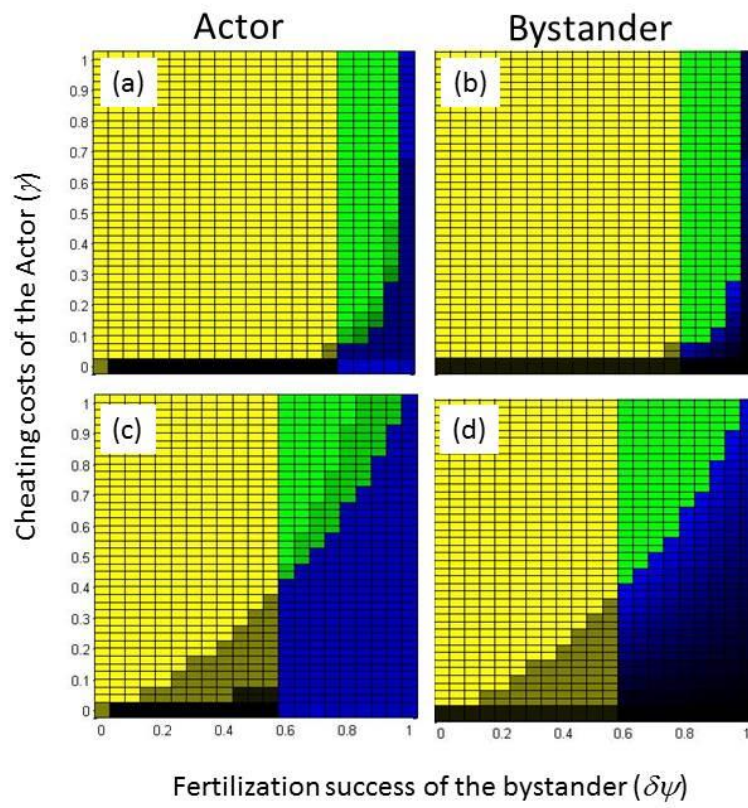half the preference manifested when using private information only.

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'

806   strategies (i.e. $K_O = 1$) and the green gradient with the 'not-copying' strategies (i.e. $K_O = 0$).

807   Plain yellow and plain green in the Actor panels ((a) and (c)) correspond to the honest

808   strategy ($K_A = 0$), whereas in the Bystander panels ((c) and (d)) plain yellow corresponds to

809   the 'trustful-not-copying' strategy ($K_O = 1$ and $b = 0$) and plain green to the 'trustful-

810   copying' strategy. Blue indicates the absence of pure Nash equilibrium strategies and the

811   tonality of blue is proportional to the honesty (for the Actor) or the perceived reliability (for

812   the Bystander) of the strategy (black dishonesty or unreliability). See

813   http://penelope.unito.it/matecopying for further details.

814

815 Figure 1.

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821   Figure 2.

Fertilization success of the bystander ($\delta\psi$)

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