

Original Article

Social information use may lead to maladaptive decisions: a game theoretic model

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Because animals rely on the actions of others to make behavioral decisions in various contexts and social information use has important evolutionary implications, numerous theoretical studies have addressed the question of when it should occur. Despite several predictions of these models are supported by experimental findings, they have focused mainly on animals that can copy others' decisions, without paying a cost. Yet, the acquisition or exploitation of social information is likely to be costly in many cases, notably when animals compete for depleting resources: social learners then cannot directly copy the decision of others but instead acquire generalized preferences through observation and hence suffer a risk of being unable to use the information previously collected. To explore the conditions that should favor this form of copying (i.e., acquisition of generalized preferences), we developed a mate-choice model with 2 strategies: selective females assess potential partners until they have found an acceptable mate, whereas copier females observe their mating decisions and then search for a male similar in appearance to the accepted mates. Our results indicate that the extent to which animals should rely on personal information logically increases with the costs entailed by social information use, and the proportion of asocial learners can even reach fixation. Furthermore, as the costs of using both personal and social information are frequency dependent on the proportion of social and asocial learners, there are conditions where both strategies coexist within the population, although social information use may lead to maladaptive decisions. *Key words*: acquisition of generalized preferences, cultural transmission, frequency dependence, mate-choice copying, social learning. [*Behav Ecol* 23:225–231 (2012)]

INTRODUCTION

The social environment of animals strongly affects their behavior, and in various contexts, individuals rely on both the personal information they have collected about the value of the alternatives and the actions or performances of others. For instance, there are many evidences that animals use social information to detect the presence of a predator, learn to avoid toxic foods, choose a location to forage, or select a mating partner (reviewed by Danchin et al. 2004; Galef and Laland 2005; Witte and Nöbel 2011). Social learning can have important evolutionary implications, notably by affecting the opportunity for sexual selection (Wade and Pruett-Jones 1990; Kirkpatrick and Dugatkin 1994; Laland 1994; Agrawal 2001), and numerous theoretical studies, therefore, have addressed the question of when it should occur (e.g., Boyd and Richerson 1985; Feldman et al. 1996; Laland et al. 1996; Wakano et al. 2004). Among them, several game theoretic models on mate-choice copying have attempted to predict the relative frequency of females that should either choose a partner based on their own assessment of the quality of potential mates or copy the mating decisions of other females (e.g., Losey et al. 1986; Dugatkin 1992, 2005; Pruett-Jones 1992; Dugatkin and Höglund 1995; Stöhr 1998; Sirot 2001; also see Valone 2007). Copying is expected to be most prevalent when mate assessment is costly because this behavior would allow females to acquire more

information about the quality of potential partners or to increase the rate at which they gain this information (Stöhr 1998). Several theoretical works, also, have suggested that this behavior would occur exclusively when females differ in their ability to discriminate among potential mates and only females with poor mate assessment abilities should benefit from copying the mating preferences of more experienced females (Dugatkin 1992; Stöhr 1998). Thus, even if individual learning is costly, in terms of energy required to build and maintain the structures involved in learning and memory (Johnston 1982), social learners should not copy indiscriminately the behavior of others. Social information use, therefore, should not lead to maladaptive decisions (i.e., decisions that reduce the fitness of the learner relative to alternative behaviors). Supporting these expectations, younger female guppies (*Poecilia reticulata*) have been found to copy the mate choice of older females, whereas older females were not influenced by the mate choice of younger models (Dugatkin and Godin 1993; Amlacher and Dugatkin 2005; Vukomanovic and Rodd 2007). Also, experiments with minnows (*Phoxinus phoxinus*) have reported that individuals increasingly relied on social learning when the level of predation, and hence the cost of collecting personal information, was increased (Webster and Laland 2008).

On the other hand, a number of experimental studies failed to demonstrate social information use (e.g., Gibson et al. 1991; McComb and Clutton-Brock 1994; Fiske et al. 1996; Lafleur et al. 1997; Brooks 1998; Widemo 2006; Auld et al. 2009), whereas others did not report enhanced use of social information under conditions where personal sampling was costly (Briggs et al. 1996; Galef and Whiskin 2006). One potential explanation for these findings is that the acquisition or exploitation of social information may be costly too, hence

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Table 1
Definition of the parameters used in the model

Symbol	Meaning
N	Number of males (N_M) and females (N_F): total of each sex. Range of tested values: 50–200
p	Proportion of selective females
$1 - p$	Proportion of copier females
T	Maximum number of potential males sampled by selective females during a breeding season. Range of testes values: 1–5
x_t	Proportion of high-quality males available at time t . Range of tested values: 0.1–0.9
$1 - x_t$	Proportion of low-quality males available at time t
ε	Risks of assessment error, noted, respectively, ε_s and ε_c for selective and copier females. Range of tested values: 0–0.5
W	Mean reproductive success of a female reproducing with a high-quality male. Range of tested values: 5–50
w	Mean reproductive success of a female reproducing with a low-quality male. Default value: 4
C_A	Cost of mate assessment. Range of tested values: 0–1
m	Mortality rate of offspring produced late in the season (i.e., after the T sampling processes). Range of tested values: 0–1
d	Density of females. Range of tested values: 0–1
$S_U(t)$	Number of selective females that are still unpaired at time t
$S_H(t)$	Number of selective females that form a pair bond with a high-quality male at time t
$S_L(t)$	Number of selective females that form a pair bond with a low-quality male at time t
$M_U(t)$	Number of males that are still unpaired at time t
y	Proportion of selective females paired with a high-quality male
C_H	Number of copier females paired with a high-quality male after having observed the mating decision of at least one selective female
C_L	Number of copier females paired with a low-quality male after having observed the mating decision of at least one selective female
R_H	Number of copier females that reproduce randomly, after the T sampling processes are completed, with a high-quality male
R_L	Number of copier females that reproduce randomly, after the T sampling processes are completed, with a low-quality male
I_S	Mean reproductive success of selective females
I_C	Mean reproductive success of copier females

For all parameters, the default value or the range of tested values is specified.

diminishing the rate at which it should be used. Notably, according to recent theoretical analyses on the evolution of reliance on social learning (Wakano et al. 2004; Rendell et al. 2010), the proportion of asocial learners should increase in frequency, until they eventually reach fixation, when the rate of environmental variability increases. This is because social learners are highly vulnerable of acquiring outdated or inappropriate information when environmental conditions change frequently. In addition to environmental stochasticity, other mechanisms, whose importance has not been explored yet, could also contribute to favor reliance on personal information by affecting over time the value of the information previously acquired from others. When animals compete for depleting resources, in particular, we would expect individuals relying on social information less frequently under most conditions because the benefits of social learning are then frequency dependent on the proportion of social and asocial learners: social learners necessarily need to observe the behavior of at least one asocial individual before making their own choice; consequently, as the proportion of asocial learners increases, the quantity of remaining resources decreases, thereby increasing the risk that social learners are unable to use the information socially acquired. Such a situation may occur, for instance, when animals compete for food or even for mates in socially monogamous species, because both males and females then have only one partner in a season and hence become unavailable for other individuals once they have formed a pair. In that case, copying females cannot reproduce with the same males as those previously chosen by selective females, but they could instead use this information to acquire a generalized preference for the phenotype of the most frequently chosen males. Although there is experimental evidence that females can gain a preference for generalized traits rather than particular males only (White and Galef 2000; Witte and Noltemeier 2002; Godin et al. 2005; Swaddle et al. 2005; Drullion and Dubois 2008), no theoretical study has been conducted yet to explore the conditions under which this form of social information use should occur.

To address this issue, we developed a two-strategy game: selective females (i.e., asocial learners) assess potential partners until they have found an acceptable mate to reproduce with, whereas copier females (i.e., social learners) observe the mating decisions of selective females and then search for a male similar in appearance to the most frequently accepted individuals. Despite our model specifically applies to mate-choice copying in socially monogamous species, conclusions from our study not only can be extended to any other depleting resources but have also important implications for understanding the potential contributions of copying to the cultural evolution of preferences. Indeed, even in polygynous species in which males have little to offer to females aside from sperm and the risk of sperm depletion is very low, females must acquire, too, generalized preferences for male traits, for copying to result in the cultural inheritance of mating preferences within populations (Boyd and Richerson 1985; Brooks 1998). Understanding the conditions favoring this mechanism is therefore critical for understanding the role of social environment on the transmission and maintenance of learned behavior.

THE MODEL

Assumptions of the model

All parameters of the model are listed in Table 1. We consider a socially monogamous breeding population with N_M males and N_F females. As in Dubois (2007), we focus on the mating decisions of females, and so, we consider males as the non-discriminating sex. Thus, only males vary in quality, and for simplicity, we set male quality as a discrete variable: males may be either of high or low quality, with parameters x_0 and $(1 - x_0)$ representing, respectively, the initial proportion of each category of males within the population. The quality of each male is fixed throughout its life, and we denote by W and w the breeding success of a female (estimated in number of offspring produced) that reproduces with a high- or low-quality male, respectively, with $W > w$.

Females can adopt 2 different strategies to choose a breeding partner: selective females base their decision on the personal information they gain about potential partners, whereas copier females observe the mating decisions of selective females and then copy their preferences by searching to reproduce with a male of the same type than the most frequently chosen individuals. Because mate assessment is time and energy consuming, we assume that selective females 1) cannot assess the quality of more than T potential mates during a breeding season and 2) suffer a fixed assessment cost C_A that reduces their breeding performance each time they assess a potential partner. After every sample, selective females decide either to accept to reproduce with the male sampled if he has been assessed as a high-quality individual or to continue searching for a mate, otherwise. Thus, although selective females accept to reproduce only with males that are considered as high-quality individuals, they can nevertheless reproduce with both types of males, as assessment is error prone. Accordingly, the parameter ε_S represents the probability that a selective female makes an error when assessing the quality of a given male, whereas $(1 - \varepsilon_S)$ represents the probability of assessing without error. We assume that the probability of making an error does not depend on male quality and that selective females, therefore, have the same probability ε_S of rejecting a high-quality male or accepting to reproduce with a low-quality male. The time invested in mate assessment also implies that copier females are capable of discriminating between selective and copier females and so can copy only the decision of the females they have observed during the mate assessment period. On the other hand, we assume that observing females have only access to the mating decision and not to the success of their conspecifics. Copying females, therefore, ignore when they observe the choice of a selective female whether she made a right or a wrong decision and so may copy an erroneous decision. Finally, we assume that, contrary to selective females, copier females that are still unpaired at the end of the breeding season (i.e., after selective females have sampled T potential partners) can reproduce randomly with the remaining available mates, whatever their quality, but with less success. This is because conditions are less favorable for reproduction late in the season, and offspring that are produced following random pairing, consequently, survive less. We denote by m , the rate of mortality of late-season offspring.

Procedure

To calculate the mean gain expected by selective and copier females for a given season, we successively consider each of the T sampling processes, and for each of them, we assume that the process of mate selection is sequential: selective females first have to assess the quality of potential partners so that copier females can observe and then copy their decision. We do that because males become unavailable for mating after forming a pair bond. Consequently, both the number of unpaired females and the number of potential males, among which they can choose, decrease over the course of the breeding season. We denote by $S_U(t)$, $C_U(t)$, and $M_U(t)$ the number of selective females, copier females, and males, respectively, that are still unpaired at time t , that is after selective females have assessed t potential mates (where t is an index that varies from 0 to T). If the parameters p and $(1 - p)$ represent the proportion of selective and copier females, respectively, then the number of unpaired selective females at the beginning of the sampling process (i.e., $t = 0$) is equal to $S_U(0) = pN_F$, whereas the number of available males is $M_U(0) = N_M$.

To simplify the equations, we give the formula only for the first sampling process, but the same procedure is used for the following samples. As each male cannot be assessed by more than one selective female during a given sample, the number

of selective females that can estimate the quality of one potential partner at the beginning of the sampling process (i.e., $t = 0$) is $S_U(0)$ if $S_U(0) \leq M_U(0)$ or $M_U(0)$ if $S_U(0) > M_U(0)$. Males are randomly encountered, and a selective female therefore encounters a high- or a low-quality male with a probability x_0 and $(1 - x_0)$, respectively. Because each female has a risk ε_S of making an assessment error, the number of selective females paired with a high- or a low-quality male after the first sample (i.e., $t = 1$) is $S_H(1)$ and $S_L(1)$, respectively, with:

$$S_H(1) = \begin{cases} S_U(0) \times x_0 \times (1 - \varepsilon_S) & \text{if } S_U(0) \leq M_U(0) \\ M_U(0) \times x_0 \times (1 - \varepsilon_S) & \text{if } S_U(0) > M_U(0) \end{cases},$$

and

$$S_L(1) = \begin{cases} S_U(0) \times (1 - x_0) \times \varepsilon_S & \text{if } S_U(0) \leq M_U(0) \\ M_U(0) \times (1 - x_0) \times \varepsilon_S & \text{if } S_U(0) > M_U(0) \end{cases}.$$

The number of remaining potential partners and the proportion of high-quality males among them can be deduced from previous equations, and thus, we can estimate the number of copier females that will at their turn mate with a high- or low-quality partner. We assume that copier females can acquire a preference for one or the other type of males only if they observe the mating decision of at least one selective female. This probability $f(1)$ depends on both the number of selective females that accept a breeding partner during the sampling process (i.e., $S_H(1)$ and $S_L(1)$ for females paired with a high- or low-quality male) and the density of females within the population d with $0 \leq d \leq 1$:

$$f(1) = \left(\frac{S_H(1) + S_L(1)}{N_F} \right)^{1-d}.$$

In addition, copier females acquire a preference for high- or low-quality males, on the basis of their relative pairing success. Copier females that observe the mating decision of at least one selective female, therefore, acquire a preference for high-quality males with a probability $y(1)$:

$$y(1) = \frac{S_H(1)}{S_H(1) + S_L(1)},$$

and conversely a preference for low-quality individuals, with probability $[1 - y(1)]$.

Like selective females, copier females can make an error when they make a choice, and so, we denote by ε_C the probability that a copier female accepts to reproduce with a male that is not of her preferred type. Based on the number of copier females that acquire a preference for high-quality males and their rate of error, we can calculate the maximum number of copier females that might pair with a high-quality male after the first sample:

$$\hat{C}_H(1) = C_U(0) \times f_1 \times [y(1) \times (1 - \varepsilon_C) + [1 - y(1)] \times \varepsilon_C].$$

Whether copier females succeed or not in finding a high-quality male to reproduce, however, depends on the availability of potential mates of each type in the population, and the actual number of copier females that will be paired with a high-quality male after the first sample, therefore, equals:

$$C_H(1) = \begin{cases} \hat{C}_H(1) & \text{if } \hat{C}_H(1) \leq x_1 M_U(1) \\ x_1 M_U(1) & \text{if } \hat{C}_H(1) > x_1 M_U(1) \end{cases}.$$

Similarly, the maximum number of copier females that might pair with a low-quality male is:

$$\hat{G}_L(1) = C_U(0) \times f_1 \times [y(1) \times \varepsilon_C + [1 - y(1)] \times (1 - \varepsilon_C)],$$

although the number of copier females that will effectively reproduce with a low-quality male equals:

$$C_L(1) = \begin{cases} \hat{G}_L(1) & \text{if } \hat{G}_L(1) \leq (1 - x_1)M_U(1) \\ (1 - x_1)M_U(1) & \text{if } \hat{G}_L(1) > (1 - x_1)M_U(1) \end{cases}.$$

The number of remaining potential partners, as well as the proportion of high-quality males, is then deduced from previous equations, and the same procedure is iterated for the subsequent T samples, in order to estimate, after each new sample, the number of additional selective and copier females paired with a high- or a low-quality male.

After the T sampling processes are completed, copier females that are still unpaired because either they have failed to get social information from selective females or did not find a male of their preferred type, reproduce randomly with the first encountered available male. The number of copier females that choose at random a high- or a low-quality male to reproduce with is noted R_H and R_L with:

$$R_H = \begin{cases} C_U(T) \times x_T & \text{if } C_U(T) \geq M_U(T) \\ M_U(T) \times x_T & \text{if } C_U(T) < M_U(T) \end{cases},$$

and

$$R_L = \begin{cases} C_U(T) \times (1 - x_T) & \text{if } C_U(T) \geq M_U(T) \\ M_U(T) \times (1 - x_T) & \text{if } C_U(T) < M_U(T) \end{cases}.$$

Finally, at the end of the season, we can calculate the average gain expected by each type of females. As there is an assessment cost that reduces the breeding performance of selective females each time they estimate the quality of one potential partner, their mean reproductive success is equal to:

$$I_S = \frac{\sum_{t=1}^T [S_H(t) \times (W - t \times C_A) + S_L(t) \times (w - t \times C_A)]}{pN_F},$$

whereas the mean reproductive success of copier females is equal to:

$$I_C = \frac{\sum_{t=1}^T [C_H(t) \times W + C_L(t) \times w] + (1 - m) \times [R_H \times W + R_L \times w]}{(1 - p)N_F}.$$

The first part of the numerator corresponds to the gain expected by copier females that have selected their mate by copying the choice of other females, whereas the second part represents the mean expected gain of females that have paired randomly late in the season. In this later case, the rate of offspring mortality is m , whatever is the quality of their father.

To find the solution to the game, we estimate, for all values of p between 0 and 1, the mean gain expected by selective and copier females. Next, we check whether a population of selective females can be invaded by a mutant copier female, and vice versa, to test whether one strategy or the other is the evolutionarily stable strategy (ESS). If neither strategy is a pure ESS, we seek the value of p for which the mean expected gain of a selective female equals that of a copier female, that is the proportion of selective females p^* that satisfies $I_S = I_C$.

PREDICTIONS

Risk of assessment error and availability of potential mates

The model predicts that the selective strategy should be favored when females employing this tactic make few errors, compared

with copier females, but this effect is more pronounced when the number of males is equal or larger to the number of females (Figure 1). The risk for selective females to assess erroneously the quality of a given male (ε_S) also has different effects on the expected proportion of selective and copier females at equilibrium, depending on the relative number of available males (Figure 1). More precisely, when the sex ratio is female biased, increasing the risk of assessment error first leads to a decrease and then a slight increase in the expected proportion of selective females (Figure 1a,b). Inversely, when the number of males is either equal or larger to the number of females, selective females should first increase and then decrease in frequency as their probability of making errors increases (Figure 1c,d).

The expected proportion of copier females at equilibrium reflects a trade-off between the risks of 1) choosing a low-quality male and 2) failing to reproduce that both vary with the accuracy of assessment of males by selective females (Figure 2). For instance, when the sex ratio is female-biased and selective females make very few errors, our model predicts that females do not gain from observing and copying the mating decisions of selective females because copier females then have a high risk of being still unpaired at the end of the T sampling processes. Indeed, under such conditions, selective females provide reliable information about the quality of potential partners. However, given that males become unavailable for other females following pair formation, copier females are then unlikely to find a high-quality male to reproduce with before the end of the sampling processes and have to reproduce randomly at the end of the season with the remaining available males that are almost low-quality individuals. When the risk of assessment error of selective females is low, the proportion of copier females is then expected to be very low given that they have almost no chance of pairing with a high-quality male compared with selective females (Figure 2a). Increasing the risk of assessment errors of selective females increases the probability that copier females succeed in finding a high-quality partner because high-quality males are then more frequently rejected by selective females, and copier females therefore have, even by chance late in the season, a higher probability of encountering a good-quality partner (Figure 2a). This effect should theoretically lead to an increase in the use of mate-choice copying. However, increasing the risk of assessment errors also leads to an increase in the proportion of copier females that fail to reproduce (Figure 2b), thereby diminishing the benefits of using this strategy. This is the reason why increasing further ε_S slightly decreases the expected proportion of copier females (Figure 1b).

The prediction is different when the number of males is either equal or larger to the number of females (Figure 1c,d) because the number of males that are still available at the end of a given season is always sufficient to fertilize all the females. Copier females, consequently, have no risk of remaining unpaired (Figure 2b), contrary to selective females who have a high probability of not reproducing, particularly when they make very few errors. Thus, increasing ε_S under such conditions, first favors selective females by reducing their risk of remaining unpaired. Increasing the rate of assessment error, however, also increases the probability that selective females accept low-quality males to reproduce with, which in turn allows copier females to reproduce more frequently with high-quality males (Figure 2a). This is the reason why the expected proportion of selective decreases as their error rate has attained a critical value at the expense of copier females who can even reach fixation when they do not suffer an addition mortality cost (Figure 1c).

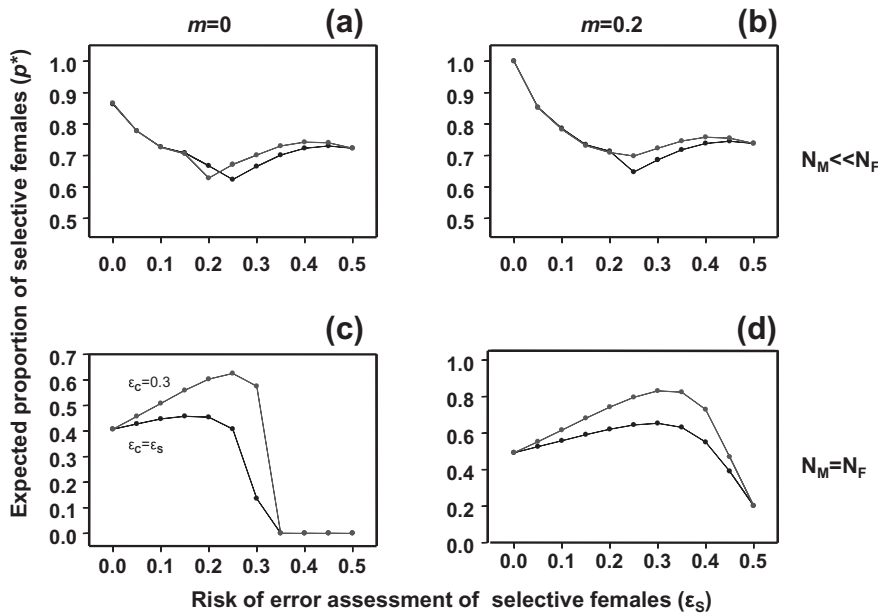


Figure 1
 Expected proportion of selective females at equilibrium (p^*) in relation to the probability that selective females make assessment errors (ϵ_s) when the risk of errors of copier females is either $\epsilon_C = 0$ or $\epsilon_C = \epsilon_S$. Panel (a): $N_M = 70$, $N_F = 100$, $m = 0$; Panel (b): $N_M = 70$, $N_F = 100$, $m = 0.2$; Panel (c): $N_M = 100$, $N_F = 100$, $m = 0$; and Panel (d): $N_M = 100$, $N_F = 100$, $m = 0.2$. In all panels, $C_A = 0.1$, $W = 10$, $w = 4$, $T = 3$, $x_0 = 0.5$, and $d = 0.2$.

Population density, cost of mate assessment, and difference in mate quality

The probability that copier females fail to reproduce before the end of the sampling processes, and hence, their risk of choosing a low-quality male among the remaining males, also

depend on their likelihood of observing at least one selective female that accepts a male as a mate. Among other parameters, the probability to acquire social information for copier females depends on female density, and increasing female density therefore should decrease the proportion of selective females (Figure 3). Inversely, the cost associated with personal information acquisition reduces the proportion of females that choose a partner independently of others, and so, the model predicts, unsurprisingly, that the proportion of selective females should be highest when the cost of mate assessment is low (Figure 3). Finally, because there is a cost of mate assessment, females can benefit from being selective only if males vary widely among each other in their breeding performance, and selective females have a low probability of not reproducing at all. Thus, selective females should increase in frequency with the difference in breeding performance between high- and low-quality males as well as with the initial proportion of males that are of good quality (Figure 4).

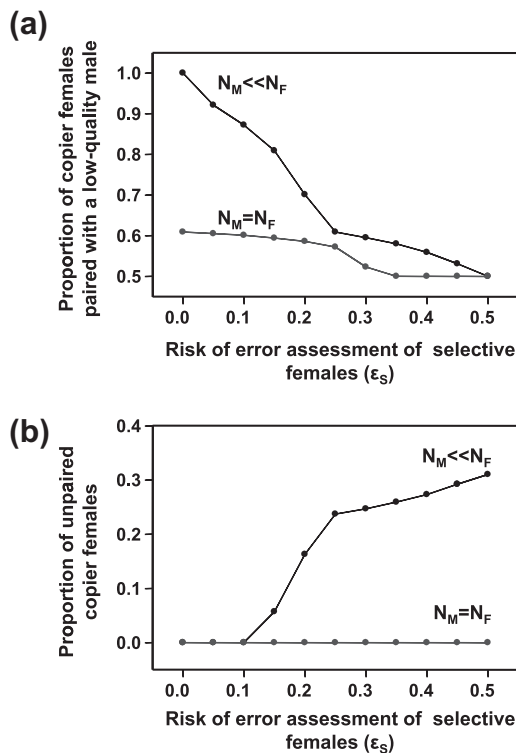


Figure 2
 Proportion of copier females at equilibrium (a) paired with a low-quality male and (b) unpaired, in relation to the risk of assessment error of selective females, when the number of males is either $N_M = 70$ or $N_M = 100$. In this figure, $N_F = 100$, $\epsilon_C = 0$, $C_A = 0.1$, $W = 10$, $w = 4$, $T = 3$, $x_0 = 0.5$, $d = 0.2$, and $m = 0$.

DISCUSSION

Costs of social and asocial learning

Like previous theoretical studies on mate-choice copying (Pruett-Jones 1992; Dugatkin and Höglund 1995; Sirot 2001), our model predicts that the extent to which social information should be used strongly depends on the costs of collecting personal information. Indeed, we found that the expected proportion of copier females increased with the time and energy required for assessing the quality of potential mates. Also, because selective females have an increased risk of failing to reproduce compared with copier females, personal information use can be totally inappropriate, and there are conditions where all the females should mate randomly. On the other hand, despite the proportion of asocial learners can reach zero, the proportion of copier females predicted by our model is relatively weak under most circumstances, compared with previous studies, and selective females can even exist as a pure ESS, as well. Such a difference arises because our model considers not only the cost of collecting personal information but also those associated with the acquisition and exploitation of social information. Essentially,

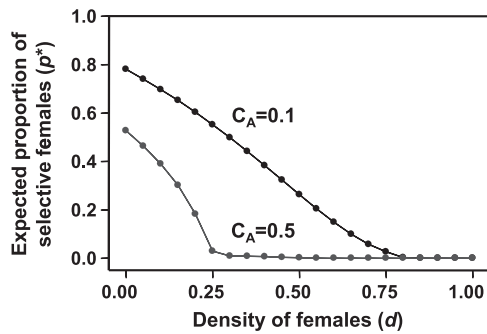


Figure 3

Expected proportion of selective females at equilibrium (p^*) in relation to the density of females (d) when the cost of mate assessment is either $C_A = 0.1$ or $C_A = 0.5$. In this figure, $N_M = N_F = 100$, $x_0 = 0.5$, $\varepsilon_S = 0.2$, $\varepsilon_C = 0.2$, $W = 10$, $w = 4$, $T = 3$, and $m = 0$.

there are 2 types of costs that may reduce the use of social information: it can be too difficult to extract or unusable. For instance, our model predicts that copying is not advantageous when female density is very low because these conditions likely prevent females from observing the mating decisions of others and hence from acquiring a mating preference for a male phenotype. Also, given that males have only one mating partner in a season, copier females have an additional risk of not reproducing early in the season (while the conditions are the most favorable for reproduction), if they do not find a mate of their preferred type when it is time for them to make a choice. Thus, even when selective females make no mistake and hence provide reliable information about male quality, there may be no interest to use social information. This is the case notably when the sex ratio is biased toward females because there is then a strong competition among females for access to mating partners, favoring those that make their decision early in the season, and these individuals are individuals of better condition and/or with better fitness in a population. Thus, as pointed out by Kendal et al. (2005), our model emphasizes the importance of considering not only the costs of collecting personal information but also those entailed by the use of social information to understand the role of social interactions in the acquisition of learned behaviors.

Social transmission of maladaptive information

An important consequence of having considered depleting resources (i.e., socially monogamous males) in our model is that the costs of using both personal and social information are frequency dependent on the proportion of social and asocial learners, which may favor the social transmission of maladaptive information in certain conditions. Indeed, one of the most frequently invoked advantages of using socially acquired information is that it reduces uncertainty about alternatives, thereby allowing more adaptive choices (Valone 2007). Thus, it is generally believed that individuals should rely on social information only when asocial learners acquire and display accurate information about their environment. Consequently, the only reason why social learning processes could result in the transmission of maladaptive information is because the environment is very unstable, and the information that is transmitted is then outdated or locally inappropriate (Boyd and Richerson 1985; Feldman et al. 1996; Laland et al. 1996; Laland and Williams 1998; Wakano et al. 2004). Contradicting these conclusions, our model predicts that copier females are most frequently maintained within the population when they face a high risk of acquiring a preference for low-quality males

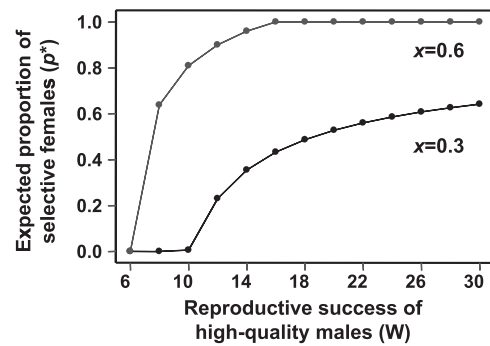


Figure 4

Expected proportion of selective females at equilibrium (p^*) in relation to the difference in breeding performance between high (W) and low (w) quality males when the initial proportion of high-quality males is either $x_0 = 0.3$ or $x_0 = 0.6$. In this figure, $N_M = N_F = 100$, $C_A = 0.1$, $\varepsilon_S = 0.2$, $\varepsilon_C = 0.2$, $w = 4$, $T = 3$, $d = 0.2$, and $m = 0$.

and may even increase in frequency with the rate of assessment errors of selective females. Because of the risk of copying a wrong decision, the expected proportion of copier females paired with a low-quality male was very large in certain circumstances compared to the proportion of females that would have reproduced with a low-quality individual if they had paired randomly. So, there are conditions where females would benefit from copying an erroneous decision. This arises for instance when the number of males is less than that of females: if selective females discriminate accurately among males, then copier females have almost no chance of reproducing because all high-quality males, unanimously preferred, are already paired when they can make a choice. Conversely, if selective females may do assessment errors, rejected high-quality mates can be further chosen by copier females. When animals compete for depleting resources, we then predict that the relative proportion of asocial and social learners would reflect a trade-off between the reliability of the information socially acquired and the ease with which it can be used.

Implications for sexual selection

Our finding that maladaptive information can be socially transmitted has important evolutionary implications: if copying can be beneficial when social information is unreliable, then mate-choice copying would not necessarily lead to reduced variance in male traits, as predicted by previous studies (Wade and Pruett-Jones 1990). Inversely, as copier females can observe an erroneous choice and then generalize their preferences to any male with the same phenotype, social information use might contribute to maintaining phenotypic variability among males. Although most experimental studies on mate-choice copying have focused to date on the mean change in female preferences induced by the apparent mating decision of a conspecific model (reviewed by Dugatkin 2000; White 2004; Witte 2006; Witte and Nöbel 2011), there is recent evidence that females may vary considerably in the importance they give to personal and social information (Drullion and Dubois 2008). If our predictions are correct, then such differences would arise because females adjust their behavior not only to the reliability of the information gained from personal experience or from observing others but also to their perceived risk of being unable to use subsequently the information socially acquired, which depends notably on the intensity of competition among females for access to mating partners.

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