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Negative Public Information in Mate Choice Copying Helps the Spread of a Novel Trait

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ABSTRACT: Numerous field and laboratory experiments have shown that many species have the capacity for social learning, including mate choice decisions that can be influenced by witnessing the mating decisions of others. Here we develop a numerical model of mate choice copying that follows the population genetics tradition, consisting in tracking allele frequencies in a population over time under various scenarios. In contrast to previous evolutionary models, we consider both positive social information and negative social information because many mating systems are driven by males in pursuit of a mate and female refusal of copulation may provide negative social information. The inclusion of negative social information to mate choice copying helps the spread of a novel trait, even if female innate mate choice preference is biased toward the common male type. We argue that the presence or absence of copying might simply mirror the associated cost-benefit relationship of the mating system of a given species and suggest how to test this prediction.

Keywords: copying, mate choice, negative information, polyandry, social learning.

Introduction

Numerous field and laboratory experiments have shown that many species have the capacity for social learning, the ability one individual has to extract information from interactions with, or observations of, other individuals' behaviors (Galef and Laland 2005; Leadbeater and Chittka 2007; Blanchet et al. 2010). Guppies learn how to get to food from other guppies (Laland and Williams 1997), octopuses learn to identify prey from other octopuses (Fiorito and Scotto 1992), fathead minnows learn to recognize predator cues from other minnows (Ferrari et al. 2005), female quails learn whom to mate with from other females (Galef and White 1998), many songbirds learn their song

from other adult birds (Marler and Tamura 1964), and so on. Social learning provides a quick and cheap shortcut to acquire adaptive information related to what to eat, what to prey on, what to fear, whom to mate with, and so on, without going into the costly and painful process of individual trial-and-error learning (Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Rendell et al. 2010; Mesoudi 2011).

The focus here is on a particular type of social influence on mate choice. A range of studies report that individuals' mate choice decisions are influenced by witnessing the mating decisions of others (reviewed in Dugatkin 1996a; Westneat et al. 2000; Vakirtzis 2011). Such nonindependent behavior has been termed "mate choice copying," or "copying" for short (Losey et al. 1986; Pruett-Jones 1992). Theoretical work on the evolutionary consequences of copying has shown that it can cause a strong positive frequency-dependent bias that eliminates novel or rare male traits, even if these males are fitter than the common males in the population (Laland 1994; Kirkpatrick and Dugatkin 1994; but see Agrawal 2001). From this point of view, though the evolution of copying can be viewed as a mechanism that allows females to improve their accuracy in assessing male quality (Pomiankowski 1990; Pruett-Jones 1992; Nordel and Valone 1998; Vakirtzis 2011), copying is a maladaptive behavior in the long term. This frequency-dependent bias, or the pressure to conform to the majority view, has long been recognized by social psychologists as an important barrier to the spread of novel cultural traits (Sherif 1936; Asch 1951).

Our aim here is to develop a model to test whether the inclusion of negative public information can overcome the previously suggested inability of novel traits to invade a system with mate choice copying. So far, theoretical models discussed only positive public information, with observer females changing or strengthening their preferences by witnessing mate choices by model females (Kirkpatrick

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and Dugatkin 1994; Agrawal 2001). This is probably because the systematic study of mate choice copying began in the early 1990s, when some seminal articles suggested that copying could explain the high variance in male mating success in lekking species, species where males aggregate and the females survey potential partners for copulation (Wade and Pruett-Jones 1990; Höglund and Alatalo 1995; Stöhr 1998). However, mate choice copying by females has also been described in species whose mating system is mainly driven by males in pursuit of mates. For instance, Mery et al. (2009) showed that even the small-brained (approximately 100,000 neurons; Weiner 2000) fruit fly *Drosophila melanogaster* can copy mating preferences. Fieldwork with *Drosophila* and other species reveals that a high proportion of males attempting to copulate repeatedly are rejected by females (Santos et al. 1988), suggesting that negative public information may play an important role. The only study to date dealing with negative public information in copying was carried out by Witte and Ueding (2003), who showed that sailfin molly females can reverse their choice after having observed a previously attractive male being rejected by another female.

This is odd because the potential effect of negative cues was explicitly acknowledged in the standard definition of copying as “a type of non-independent choice in which the probability that a female chooses a given male increases if other females have chosen that male and decreases if they have not” (Pruett-Jones 1992, p. 1000). A similar situation happens in the field of foraging behavior in social insects, where a key property of individual scouts is to gather information about food sources and share it with nestmates through recruiting signals (Detrain and Deneubourg 2008). The successful scout emits positive recruitment signals to guide nestmates to food; however, the use of negative signals to mark unrewarding foraging paths while the scouts explore and thus increase the success rate of foraging (Stickland et al. 1999) has been largely ignored until recently (Robinson et al. 2005).

Some considerations are in order before extrapolating lab results of mate choice copying to natural populations. First, spatial subdivision of male-female interactions is a ubiquitous phenomenon in many sexual organisms. Many species, including *Drosophila*, can be characterized by the Levene migration pattern (Levene 1953), that is, a patchy population structure not truly subdivided on the demographic timescale (Harrison and Hastings 1996), where adults randomly disperse from a common pool to find a discrete and suitable patch to feed, mate, and breed (Shorrocks 1982; Lacy 1983; Santos et al. 1988, 1999). Sampling effects in the effective number of locally breeding adults result in Wright's $F_{ST} > 0$, which here should be interpreted as due to the sampling of families across patches in one

generation, not the long-term outcome of drift (Santos 1997a). This raises the following problem: because the average number of locally mating/breeding flies per patch is generally small (Santos et al. 1988; Santos 1997b), say, five pairs, a simple calculation using the binomial distribution shows that a rare male phenotype with a population frequency of 5% will be absent in 77% of the patches. Following the standard definition of copying (Pruett-Jones 1992), it seems to exist only in presence of behavioral alternatives. In 77% of the patches above there will not be alternative male phenotypes to choose, which is in contradiction with the idea of copying as it is usually understood and empirically tested (e.g., Dugatkin 1992; Dugatkin and Godin 1993).

Consider, for example, the experiment by Mery et al. (2009) showing that females do learn to copy preferences for phenotypic traits (see also Kirkpatrick and Dugatkin 1994). The authors artificially generated two male phenotypes by dusting individuals with green or pink powder. An observer female witnessed a (e.g.) green male copulating with a model female and then a (e.g.) pink male that did not copulate because the model female was non-receptive. After this double demonstration, the observer female was presented with two new colored males, and she preferably mated with males dusted with the color associated with successful copulation. What is not clear from this experiment is what would have happened after a single positive (acceptance of colored mate) or negative (rejection of colored mate) demonstration. If copying behavior is still possible in such a situation, the probability that copier females will choose the most common male type should be weighted by the positive and negative cues provided by model females, according to Pruett-Jones's (1992) definition of copying.

Second, consider now an alternative view of copying as a “strategy that is used mainly when public information contradicts, rather than supports, personal information” (Mery et al. 2009, p. 733; see also Dugatkin and Godin 1993; Sirot 2001; Vukomanovic and Rodd 2007). Suppose that all females are born with an innate preference for the common male phenotype in the population. In patches where copier females will observe matings only with the preferred male type (most patches, at the invasion period), there is no contradiction between their natural tendencies and what they observe: they will not change their innate preference but perhaps only reinforce it, meaning that they will be less likely to change preference in the future. But what happens in patches where both male phenotypes are present and a fraction of matings occur with the rare male type? Copier females will witness matings with this new phenotype, and, therefore, there will be a contradiction between their innate preference and the public information they receive. Some copier females may then change

their preference, possibly allowing the fitter male phenotype to spread. In this verbal scenario, copying may not be maladaptive after all.

Here, we will stick to the standard definition of mate choice copying (Pruett-Jones 1992). The question then is, can negative public information lessen the strong positive frequency-dependent bias triggered by copier females acquiring information on prospective mates, to the extent that an uncommon but fitter male phenotype can invade the population? Intuitively, the answer seems to be yes, but this verbal intuition has to be quantitatively substantiated to the mating system of the species involved. Assuming a patchy population structure, we developed a numerical model that consists of tracking allele frequencies over time under various scenarios. We center our attention on females rather than on males, because mate choice copying appears to be more frequent in females (Dugatkin 1996a; Westneat et al. 2000). Depending on the parameter values, we show that the inclusion of negative public information helps the spreading of a novel trait, even if female innate mate choice preference is biased toward the common male type in the population. We discuss the idea that mate choice copying is a widespread strategy and suggest that it might reflect the mating system only of the particular species under study.

The Model

In constructing our model, we have relied on the empirical information available on population structure and mating systems in *Drosophila*. This should not be taken as a lack of generality of the model, because the *Drosophila* genus includes about 2,000 known species (Powell 1997) that display a large diversity of reproductive strategies (including lek behavior in Hawaiian *Drosophila*), thus offering a versatile genus to study mating system evolution and sexual selection (Spieth 1974; Markow 1996). Wild populations comprise individuals with variable genotypes, phenotypes, ages, and mating histories. Incorporating all life-history features would result in an intractable model, and, therefore, we have tried to keep the relevant details to a reasonable minimum without compromising the salient features.

Polyandry is an important ingredient in the model. It is frequent in insects, with some species more prone to mating multiple times in a short period of time (Markow 1996; Arnqvist and Nilsson 2000; Markow et al. 2012). Female receptivity is closely associated with depletion of their supply of stored sperm (e.g., Manning 1962; Wedell 2005), and females will not usually remate for some time (varying according to the species) after insemination. Therefore, any male trying to mate a nonreceptive female will be rejected and probably provide negative public in-

formation to observer females. Although adaptive use of learning by males can enhance mating success and reduce time and effort in pursuing less desirable females (Dukas and Dukas 2012), we have observed a high proportion of field *Drosophila buzzatii* males rejected by females (Santos et al. 1988). This was likely due to males trying to mount and copulate nonreceptive females, which can remate between 1.6 and 3.1 times as an average within 4 h of observation (Bundgaard and Barker 2000).

Model Description and Software Implementation

Following Marin (1991), we use the factors that determine the final frequencies of mating: (i) female receptivity; (ii) male competitive ability, which can be related to body size, courtship vigor, pheromone production, and so on; and (iii) female acceptance, which depends on mate choice. Importantly, we assume that male competitive ability is genetically determined and that female mate choice preferences have a dual component: an innate component with no genetic variation and a nongenetic component that is socially determined. We follow Kirkpatrick and Dugatkin (1994) and consider mate choice copying as the source of socially acquired information, which, in our context, is information inadvertently produced when males mate successfully to, or when rejected by, model females (Danchin et al. 2004; Wagner and Danchin 2010) and can eventually prevail over the fixed genetic preferences of observer females (see, e.g., Vakirtzis 2011).

Each generation consists of two types of females: mature, or model, females that can repeatedly mate and produce offspring and immature, or observer, females whose observations of copulations (positive public information) and of males rejected by model females (negative public information) will alter their mating preferences (Mery et al. 2009). The model incorporates a diploid population segregating for an autosomal locus with two alleles, A and a . Assume allele A is dominant over a . Male type x has genotypes AA and Aa , and male type y has genotype aa . These alleles do not produce different female types. At the start of generation t_0 an adult population comprising N_m mature males, N_{mf} model females, and N_{of} observer females is randomly generated with allele frequencies $f(A) = p$ and $f(a) = 1 - p$ in Hardy-Weinberg proportions. Generations are discrete, and the number of breeding adults at each generation is $N = N_m + N_{mf}$. Viability selection is not introduced in the model: males can differ in their competitive ability, and female preference does not affect survival, although it can affect fertility depending on the type of male that sires her offspring (see below). The reason for not including juvenile viability selection in the model is that it would imply following the distribution of sib groups across patches, and the effective selection is

reduced by $1/(1 - 2F_{ST})$ assuming soft selection (Santos 1997a). As we will explain below, the model implicitly assumes that no density regulation occurs in each breeding site.

Individuals disperse at random through the available patches, independent of category (i.e., mature males, model females, and observer females); their numbers per patch and category are taken from a Poisson distribution with parameter $\lambda > 0$. Male-female encounters happen randomly on each patch, and the number of matings is obtained from a Poisson distribution using m times the number of model females in the patch as the parameter for the distribution (when $m > 1$, some females will necessarily remate). Copulations are assumed to be sequential and dependent on the male's courtship vigor, female receptivity, and female mate preference (Marin 1991) as follows.

Courtship vigor (i.e., maximum number of courtship displays by a male when attempting to copulate with a female) is c_x (c_y) for a type x (y) male. Female receptivity decreases with the number of times she mates and is given by

$$FR_{i,j} = \exp\left(-\alpha \frac{tfm}{c_i}\right), \tag{1}$$

where $FR_{i,j}$ is the receptivity of females toward the i th type (x, y) male in the j th patch, c_i is male courtship vigor, tfm is the number of times the female has mated, and α is a constant. The choice of an exponential fitness function is

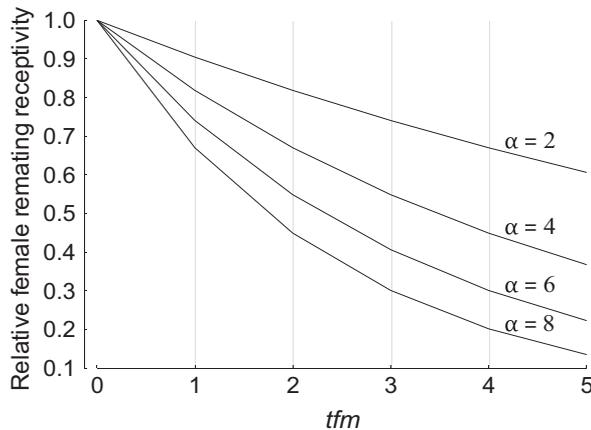


Figure 1: Females' remating receptivity toward common (e.g.) y males relative to their receptivity for males carrying the novel x trait. The courtship vigor of y males is assumed to be 80% that of x males ($c_y = 4, c_x = 5$). tfm is the number of times the female has mated. Relative receptivity drops with increasing α (see eq. [5]) from its maximum value equal to one for virgin females. These females have the same receptivity regardless of males' courtship vigor, which is a conservative assumption in the model.

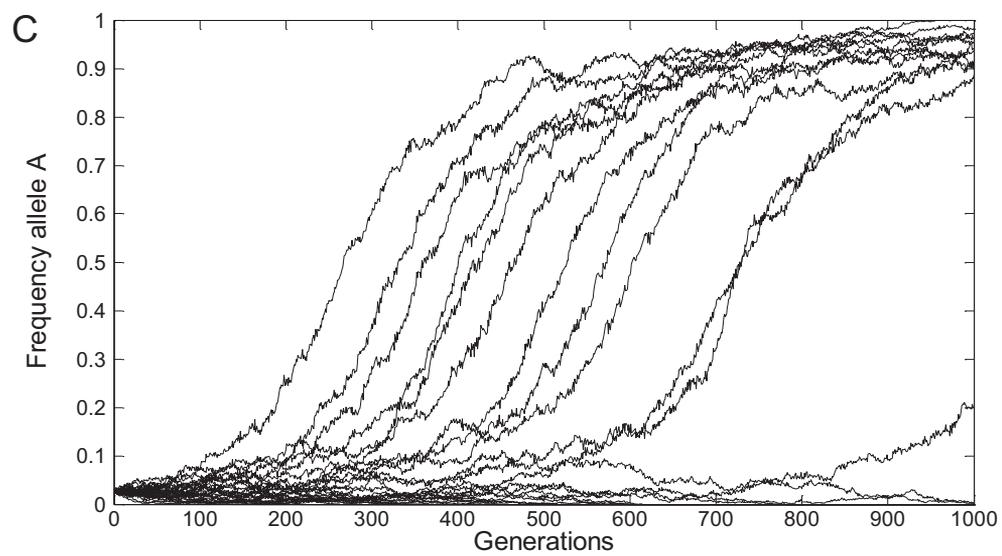
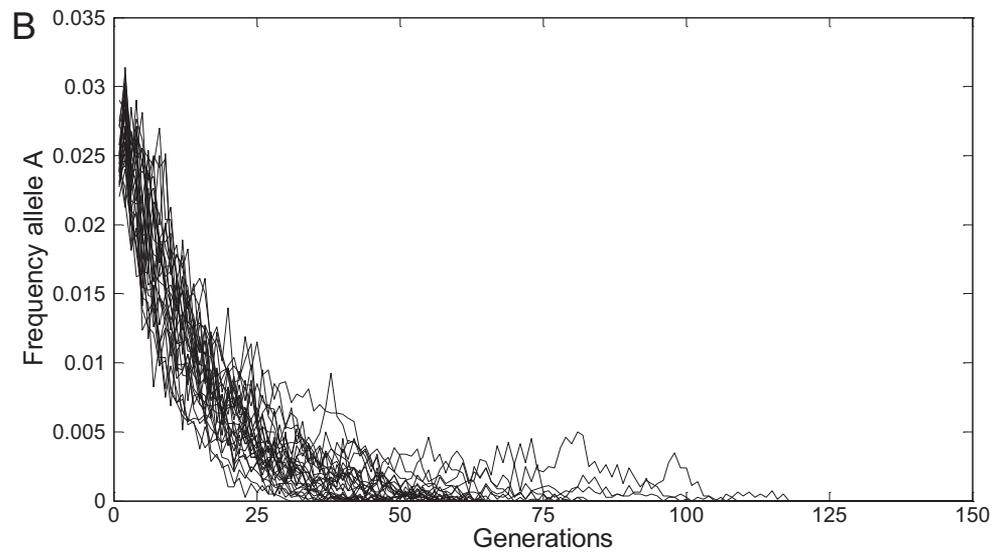
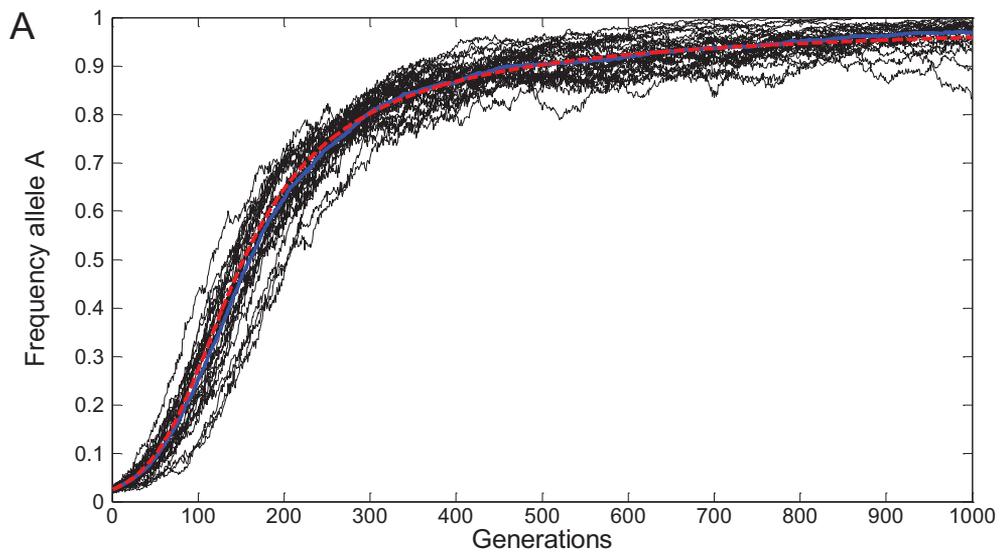
arbitrary, but it captures the essential idea that female receptivity decreases as the supply of stored sperm increases. Note that virgin females are fully receptive (i.e., $FR_{i,j} = 1$ when $tfm = 0$) and that the receptivity of a nonvirgin female is $FR_{x,j} > FR_{y,j}$ ($FR_{x,j} < FR_{y,j}$) when male courtship vigor $c_x > c_y$ ($c_x < c_y$). The assumption that receptivity of virgin females is independent of male courtship vigor is conservative because it will hamper the spread of a rare allele that increases male competitive ability.

Innate female preference is pm_i ; random choice means $pm_x = pm_y = 0.5$. All females have an innate preference for the most common male type in the population. Preference of observer females changes according to the mate choices of model females in the patch as $pm_{i,j}^* = pm_i + \Delta pm_{i,j}$ ($0 \leq pm_{i,j}^* \leq 1$ is the "effective preference" as termed by Kirkpatrick and Dugatkin 1994), where

$$\Delta pm_{i,j} = \begin{cases} \pm k \times \frac{\text{matings}_{i,j}}{\text{matings}_j} & \text{if only PPI} \\ \pm k \times \frac{\text{matings}_{i,j} - w \times \text{rejections}_{i,j}}{\text{courtships}_j} & \text{if both PPI and NPI} \end{cases}, \tag{2}$$

where PPI is positive public information, NPI is negative public information, and k is the weight of copying. (The reason for the plus-minus sign is because when the ratio of, e.g., successful males type x to all successful males in the j th patch is higher than 0.5, then $\Delta pm_{x,j} > 0$, which implies $\Delta pm_{y,j} < 0$ given that $pm_{x,j}^* + pm_{y,j}^* = 1$.) When only positive public information is considered, $\Delta pm_{i,j}$ is the change in female mate choice preference that happens in the j th patch according to the mating frequencies of the i th type male, and k is a constant ($0 \leq k \leq 0.5$; $k = 0$ corresponds to no copying). If both positive public information and negative public information are taken into account, successful courtships provide positive public information, and rejections provide negative public information; $0 < w < 1$ is the weight given to this negative public information (see below). Also, when only positive public information is available and with innate random choice ($pm_x = pm_y = 0.5$), the effective preference of observer or copier females toward the most common males will reach the maximum value when $k = 0.5$ and only that male is present in a patch.

A short digression is in order here. Because we assume that all females have an innate preference for the most common male type, it might have been reasonable to consider parameter k as dependent on male phenotype. As discussed above, it is more likely that a change in preference goes in the direction opposite innate preference, which means that k for a mating with the abundant male should be smaller than k for a mating with the uncommon



male type. As this would increase the likelihood that the novel trait spreads in the population, we have decided to keep the model simple and give the same weight to both types of matings when updating the mate choice preferences of observer females.

The rationale for considering $0 < w < 1$ in equation (2) is because “the information about a male’s mating history (or some part of it) must be obtained by the [observer] female via observation” (Dugatkin 1996a, p. 87; our addition in brackets). Mating time (positive public information) is usually longer than rejection time (negative public information), which means that, in terms of duration time, the probability that a copier female observes a successful male is higher than that of observing a rejected male. For example, copulation duration shows large variation among *Drosophila* species, from 30 s to more than 2 h, although the majority of species mate for 10 min or less (Markow 1996). However, species with higher remating times tend to have a shorter copulation time and a shorter remating interval. This suggests that w is a decreasing function of mating time but the term $w \times \text{rejections}_j \approx \text{constant}$ because the frequency of rejections by females increases with their copulation latency time. Equation (2) uses a local mass-copying rule (Kirkpatrick and Dugatkin 1994); that is, it assumes that all copier females in a patch observe the mate choices (and rejections) made by model females.

The probability of copulation by the i th type male in the j th patch is then the product of female receptivity times female effective preference:

$$P_{i,j} = \text{FR}_{i,j} \times \text{pm}_{i,j}^* \tag{3}$$

After all matings in the patches have occurred, each inseminated female produces n eggs that produce $n \times \exp(-0.7 \times \text{tfm})$ adult flies (numbers were rounded down to the lower integer) according to the number of times females mated (tfm). Parenthetically, recall that if a female can mate up to three times, $\text{tfm} = 0,1,2$ in equation (1) for female receptivity (prior to copulation); the corresponding values are $\text{tfm} = 1,2,3$ for fertility (after copulation). Also, notice that $\sum_{\text{tfm}=1}^{\infty} \exp(-0.7 \times \text{tfm}) = 0.99$. The decreasing exponential function for fertility was introduced to somehow mimic the average direct fitness

gain of multiple matings, estimated around 30%–70%. For example, suppose $n = 50$ and a female that had mated with three males: she will have 24 adult offspring with the first male, 12 with the second, and 6 with the third. Therefore, it certainly pays for a male to court and mate a virgin female (Dukas and Dukas 2012).

This framework allows introducing fertility selection by varying the number of eggs (n_i) in conjunction with mating type as

$$\psi_i = n_i \times \exp(-0.7 \times \text{tfm}), \tag{4}$$

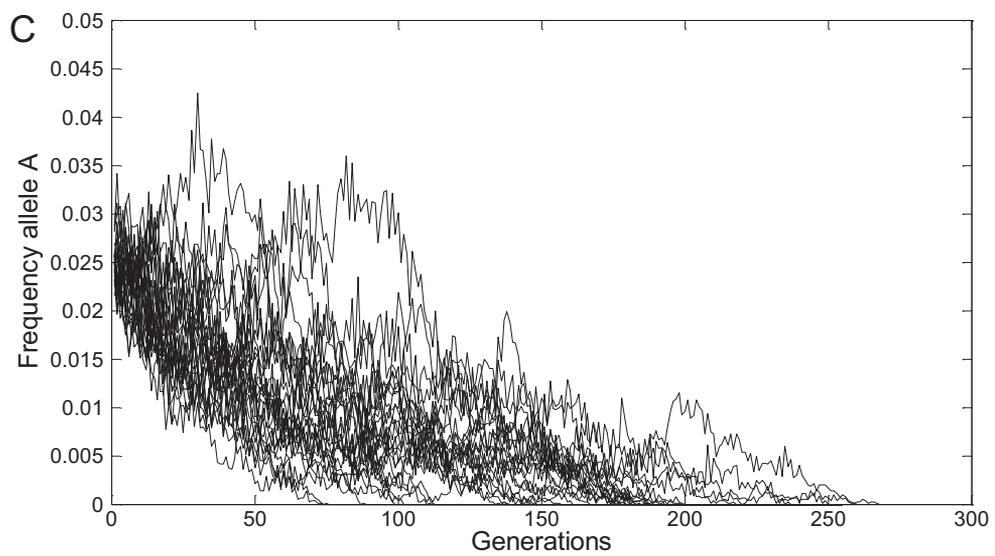
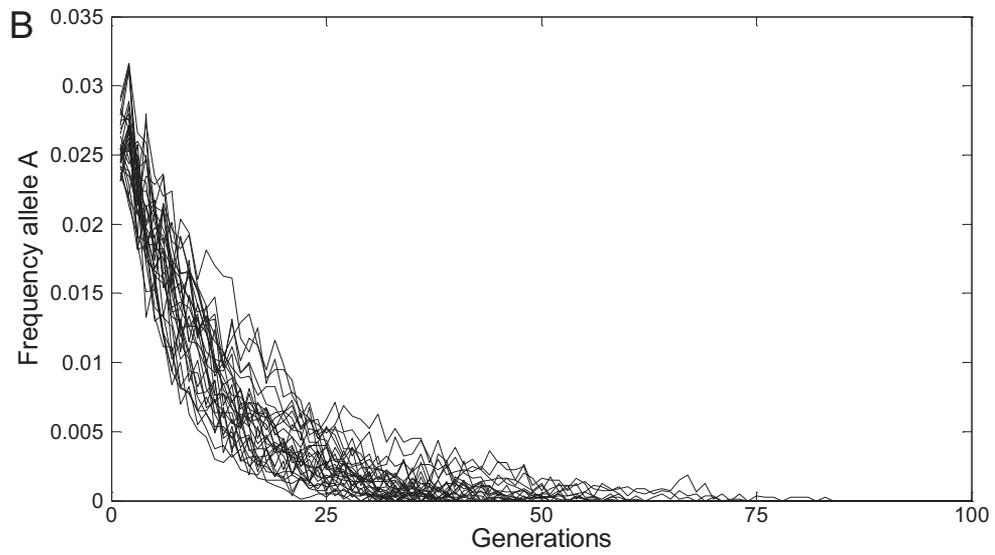
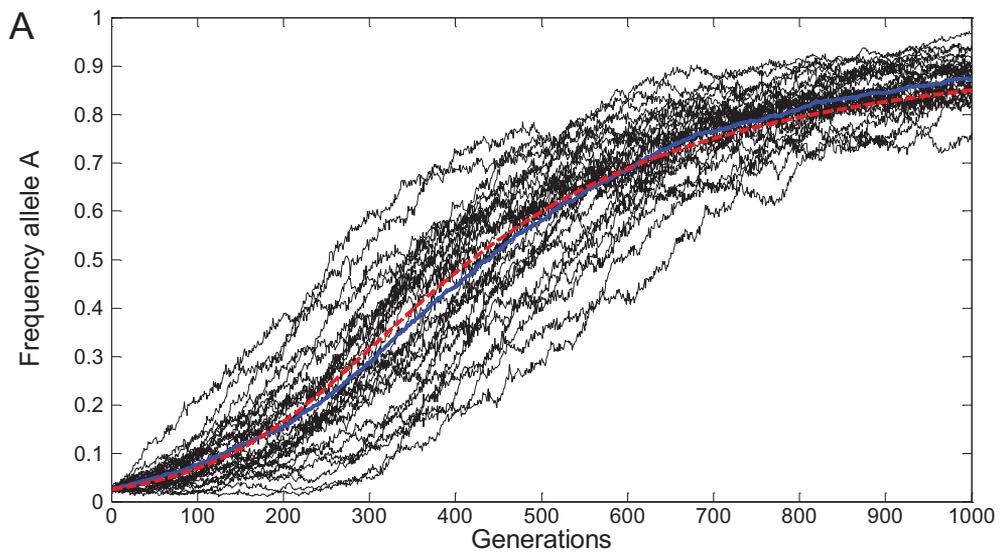
where ψ_i is the absolute fertility of a female mated with a male type i (x, y), also taking into account the order of mating (first, second, etc.). Equation (4) implicitly assumes that no density regulation occurs in each breeding site (i.e., hard selection; Christiansen 1975), and, therefore, offspring production increases with n_i .

After offspring production, population size is kept constant by randomly sampling female and male offspring to replace mature males and model females of the previous generation. Female offspring are the new observer females, and former observer females are the new model females. Simulation programs were implemented in the Matlab algebra environment (ver. 7; MathWorks 2005) together with the collection of tools supplied by the Statistics Toolbox. The routines to run these analyses are made available in the supplementary material, available online.

Analytical Considerations

Our main aim is to see whether an initially rare favorable phenotype can invade the population in spite of (i) female innate preference for the most common male type and (ii) strong positive frequency-dependent bias triggered by naive females copying model females mostly mating with common males. As we already know from previous theoretical work (Kirkpatrick and Dugatkin 1994; Agrawal 2001), this frequency-dependent bias cannot be easily overcome by a fitter phenotype when copying involves only positive public information. We offer some analytical insights on the numerical model and discuss what could be considered reasonable parameter values in the simulations.

Figure 2: Evolutionary fate of a fitter dominant allele A introduced at a frequency of 0.025 at generation t_0 . Males carrying this allele have phenotype x and a higher courtship vigor than y males ($c_x = 5, c_y = 4$) and also produce more offspring regardless of females’ phenotype ($n_x = 70, n_y = 50$; see eq. [4]). For each scenario, 30 independent runs were achieved, and each trajectory is plotted as a black line. A plots the null model with no copying. The blue solid line is the average change in allele frequency, and the dashed red line is the expected change from equation (6) with $h = 0$ and $s = 0.03$. B introduces female copying with only positive public information. C introduces female copying with both positive public information and negative public information. Other parameter values in the model were $N_m = N_{mf} = N_{of} = 2,000$ flies at each generation, mature females mated $m = 2$ as an average, innate preferences $\text{pm}_x = 0.4$ and $\text{pm}_y = 0.6$, $\alpha = 2$ in equation (1), $k = 0.1$ in equation (2), and patch size $\lambda = 5$. Furthermore, we assumed the weight given to negative public information in equation (2) to be $w = 1/3$ (see text for details).



In our model, an increase in fitness of a phenotype (say, x) is brought about by a higher male mating competitive ability ($c_x > c_y$) and/or a higher fertility of females mating with x males ($\psi_x > \psi_y$). From equation (3), we see that the probability of copulation equals female receptivity times female preference. With no copying, a neutral equilibrium is obtained when

$$\exp\left[\alpha \times \text{tfm} \times \left(\frac{1}{c_y} - \frac{1}{c_x}\right)\right] = \frac{\text{pm}_y}{\text{pm}_x}. \quad (5)$$

Because we assume that females have a higher innate preference for the most common male ($\text{pm}_y > \text{pm}_x$), this equality can be attained only if $c_x > c_y$ and $\alpha \times \text{tfm} \geq 1$ (i.e., females mate more than once). This is why remating is an important ingredient in the model, as it is also true for the majority of insects (Arnqvist and Nilsson 2000). For instance, if we assume $\text{pm}_y = 0.6$ ($\text{pm}_x = 0.4$) the question is, what values should tfm and α realistically take for the courtship vigor of male x to prevail over the biased female innate preference? By “realistically” we mean that c_x should not be much higher than c_y . This is because if two male types are very dissimilar, so that mate assessment is cushy, copying should rarely be observed (Dugatkin and Godin 1993; Dugatkin 1996*b*; Witte and Ryan 1998).

Suppose that naive females cannot easily discriminate between male types, where one has at least 80% courtship vigor relative to the other type (e.g., $c_x = 5$ and $c_y = 4$; see Dugatkin 1996*b*). From equations (1) and (5), we see that the absolute female remating receptivity drops but the relative receptivity toward the fittest x male raises with increasing α (fig. 1). Therefore, in our model a male phenotype that moderately increases courtship vigor is unlikely to invade the population unless female remating receptivity substantially drops after the first mating.

Regarding fertility selection in equation (4) and assuming that both males are equal ($c_x = c_y$), a very high female remating incidence (i.e., a low α in eq. [1] and a large tfm in eq. [4]) could help spread a novel and favorable phenotype ($\psi_x > \psi_y$). This is because the likelihood of having offspring sired by x males increases when females can remate many times. However, we will argue in the discussion that mate choice copying is unlikely to be observed in this scenario.

To sum up, we feel compelled to restrict the parameter

space in our model to situations where female innate preference for the common male is 60% and courtship vigor of the common male is at least 80% relative to the fitter mutant phenotype. Therefore, parameter values used in our range of simulations (assuming x is the mutant phenotype) are $\text{pm}_x = 0.4$, $\text{pm}_y = 0.6$, $c_x = 5$, $c_y = 4$, $2 \leq \alpha \leq 4$ in equation (1), and females can mate up to three times in a patch. We also used two patch sizes ($\lambda = 5, 10$) as the parameter values of the Poisson distribution to obtain the average number of mating pairs per patch. This fits with the conclusion that fewer than 20 individuals usually contribute gametes to a breeding site (Santos et al. 1989; Santos 1997*b*).

Simulations also consider the situation where males have equal condition ($c_x = c_y$) because females can also perform copying in this scenario (Mery et al. 2009). We assume $k = 0.1$ in equation (2). Higher values of k would substantially decrease the likelihood that the novel trait spreads in the population, but we think it is unrealistic to have a strongly biased mate choice preference unless females choose between two very contrasting male types (e.g., poor- and good-condition males; Mery et al. 2009) or between males from two different species (ethological sexual isolation; Coyne et al. 2005).

Numerical Results

Invasion of Dominant A Allele

In the first series of simulations, we took x as the rare phenotype and introduced allele A at an initial frequency $f(A) = 1 - (0.95)^{1/2} = 0.0253$; that is, the frequency of x at t_0 was 0.05. Assuming $c_x > c_y$ and that females that mate with x males have a higher absolute fertility than females that mate with the common and innately preferred y males (i.e., $\psi_x > \psi_y$ in eq. [4]), we followed the fate of allele A under three different scenarios: (i) observer females do not copy the mate choices made by model females, (ii) observer females acquire only positive public information, and (iii) observer females acquire both positive and negative public information. The results are shown in figure 2. As expected, allele A quickly invaded the population with no copying (fig. 2*A*). The effective selection that explains its increase in frequency can be roughly approached by assuming random mating and relative fitnesses of ge-

Figure 3: Evolutionary fate of a fitter dominant allele A introduced at a frequency of 0.025 at generation t_0 . Males carrying this allele have phenotype x and a higher courtship vigor than y males ($c_x = 5$, $c_y = 4$) and also produce more offspring regardless of females' phenotype ($n_x = 70$, $n_y = 50$; see eq. [4]). For each scenario, 30 independent runs were achieved, and each trajectory is plotted as a black line. *A* plots the null model with no copying. The blue solid line is the average change in allele frequency, and the dashed red line is the expected change from equation (6) with $h = 0$ and $s = 0.011$. *B* introduces female copying with only positive public information. *C* introduces female copying with both positive public information and negative public information. Other parameter values in the model were as in figure 2, with the exception that patch size here was $\lambda = 10$.

notypes AA , Aa , and aa to be 1 , $1 - hs$, and $1 - s$, respectively, where s is a positive constant and $0 \leq h \leq 1$ is the degree of dominance. By using the standard nonlinear recursion equation to obtain the gene frequency in the next generation (Crow and Kimura 1979),

$$q' = \frac{q - hspq - sq^2}{1 - 2hspq - sq^2}, \quad (6)$$

where q is the frequency of allele a at generation t and q' is its frequency at generation $t + 1$, a nearly perfect visual fit between the observed average change in allele frequencies from the 30 independent runs in figure 2A, and the expected change from equation (6) is achieved when $h = 0$ and $s = 0.03$ —not a very strong effective selection, indeed. Parenthetically, note that in the simulations we have assumed that the total number of (mature) males equals the number of model females ($N_m = N_{mf} = 2,000$), which means that at each generation there are two times more females than males. This is because we are dealing here with female mate choice copying, and immature males do not participate in matings. Ignoring these males in the simulations has a negligible effect on the numerical results: if immature males were to replace mature males in the next generation, this would cause only a minor time lag in the evolution of allele frequencies.

Also as expected, the fittest allele A went quickly extinct in all 30 independent runs when observer females acquired only positive public information (fig. 2B). This was expected because of the strong positive frequency-dependent bias favoring the most common male type y , as it has been shown by Kirkpatrick and Dugatkin (1994). The interesting situation, however, is when both positive public information and negative public information are considered, according to the standard definition of mate choice copying (Pruett-Jones 1992). Allele A increased in frequency and approached fixation in 37% of the simulations (11 out of 30 runs) and went to extinction in 60% (18 out of 30; fig. 2C). This is a striking result because it shows that positive and negative public information can eventually cancel each other out so that a fitter phenotype can invade the population even though the effective selection is not very strong.

From our previous analytical considerations (see fig. 1), it is intuitively obvious that increasing α in equation (1), that is, decreasing the receptivity of females for a second ($t_{fm} = 1$) and a third ($t_{fm} = 2$) mating, would result in a higher fitness advantage of the rare x males when $c_x > c_y$. This is precisely what we have observed using $\alpha = 4$ and the same parameter values as in figure 2. All 30 independent simulations showed that allele A invaded the population when observer females acquired both positive public information and negative public information. How-

ever, this allele went extinct whenever observer females gained positive public information only (results not shown).

Next, we investigated the role of patch size by increasing the parameter of the Poisson distribution to obtain the number of flies per patch from $\lambda = 5$ used in figure 2 to $\lambda = 10$. The results are shown in figure 3. Some quantitative differences with the previous outcomes are clear. First, the strength of effective selection is lower (cf. figs. 2A, 3A): with no copying a good visual fit between the observed average change in allele frequencies and the expected change from equation (6) is now achieved when $h = 0$ and $s = 0.011$. Second, the fittest allele A always went extinct with copying, even when both positive public information and negative public information were considered (cf. figs. 2C, 3C).

The impact of patch size on the effective selection of fitter allele A likely arises from the variance in allele frequencies across patches due to the random sampling of mature females and males. If the number of inseminated females in a patch is relatively small, the frequency of heterozygous offspring will exceed the Hardy-Weinberg expectations by a proportion $1/2N^*$ assuming random mating, where N^* is the effective number of parents (Robertson 1965). The impact of nonrandom mating is more difficult to predict, but whenever there is a chance difference in allele frequency between males and females, a consistent excess of heterozygotes in the progeny will be observed. This heterozygous excess will be higher with $\lambda = 5$ than with $\lambda = 10$ because the effective number of parents is lower in the first case, other things being equal. As we assume that allele A is dominant and that females mating with x males are more fertile, the relative higher excess of heterozygotes with $\lambda = 5$ makes selection more efficient.

In a second series of simulations and taking x as the rare phenotype as before, we assumed both males' phenotypes to have an equal male competitive ability ($c_x = c_y$) and introduced only fertility selection ($\psi_x > \psi_y$). The numerical results were as expected from our previous simulations (fig. 2), namely, allele A could only invade the population in the copying scenario assuming that fertility differences were (unreasonably) large. With $n_x = 70$, $n_y = 50$ in equation (4), allele A always went to extinction when only positive public information was assumed (cf. figs. 2B, 4A) and remained at low frequency in some simulations when both positive public information and negative public information were included (cf. figs. 2C, 4B).

Invasion of Recessive a Allele

We repeated some simulations but now considering the recessive allele a as the fitter one. This allele was introduced at an initial frequency $f(a) = 0.0253$; that is, the frequency

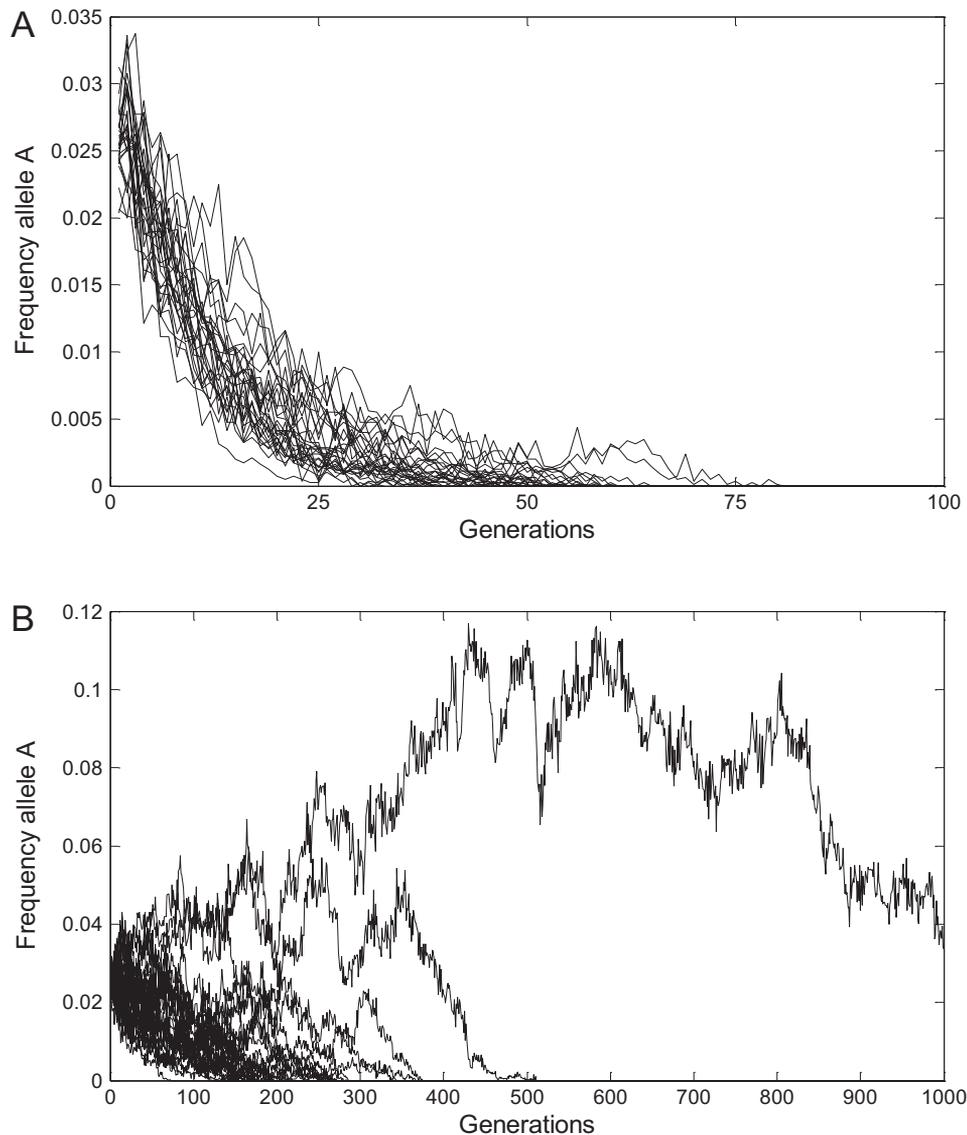
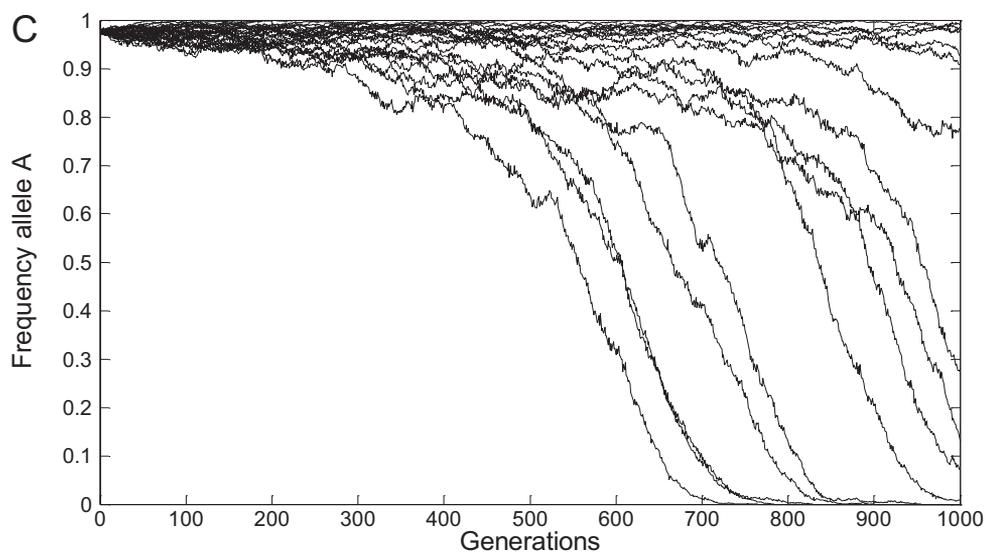
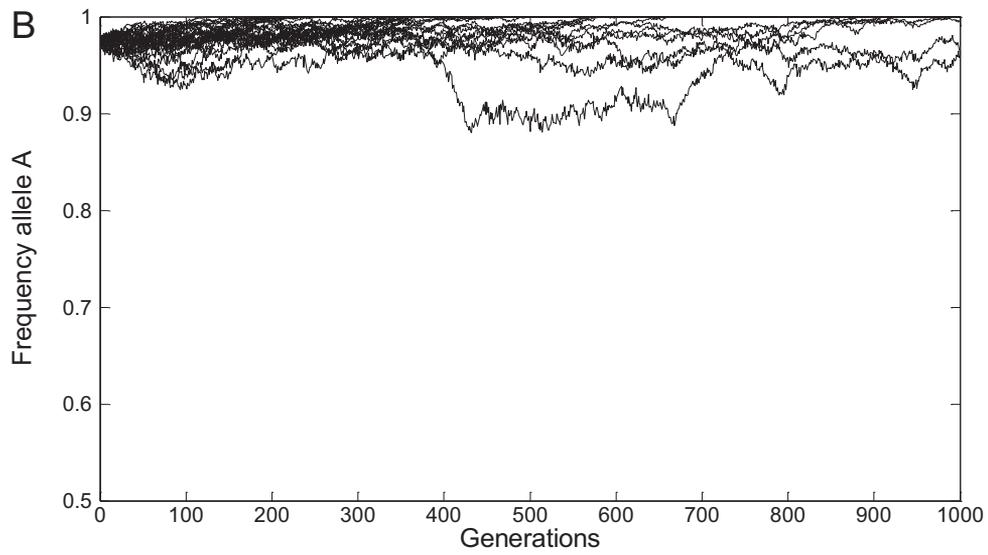
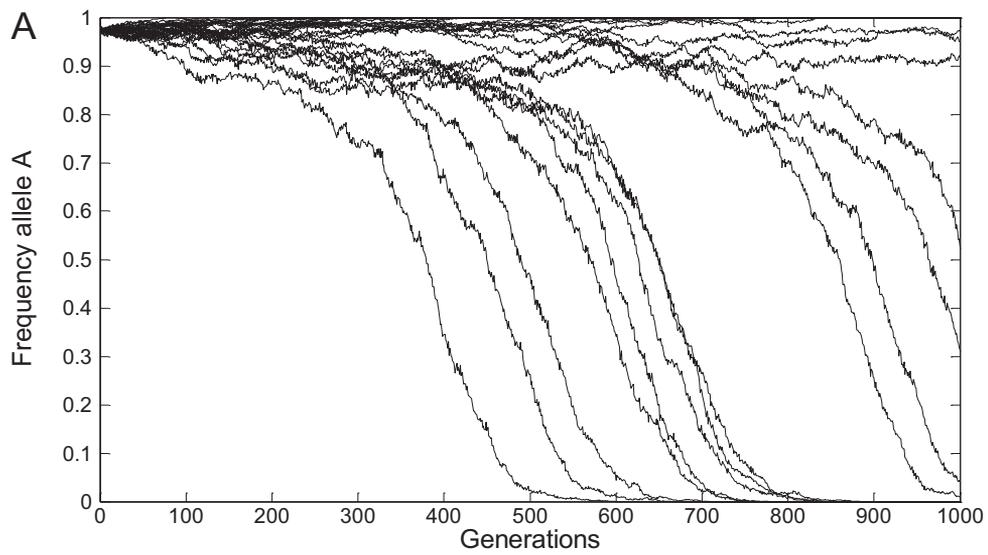


Figure 4: Evolutionary fate of a fitter dominant allele A introduced at a frequency of 0.025 at generation t_0 . Males carrying this allele have the same courtship vigor as common males in the population ($c_x = c_y = 4$) but produce more offspring regardless of females' phenotype ($n_x = 70$, $n_y = 50$; see eq. [4]). For each scenario, 30 independent runs were achieved, and each trajectory is plotted as a black line. *A* assumes female copying with only positive public information. *B* introduces female copying with both positive public information and negative public information. Other parameter values in the model were as in figure 2.

of y flies at t_0 was 6.4×10^{-4} . We now assume $c_x < c_y$, and that females that mate with y males have a higher absolute fertility than females that mate with the common and innately preferred x males ($\psi_x < \psi_y$ in eq. [4]). In this scenario, we will obviously expect a Haldane's sieve, that is, a bias against the establishment of the recessive a beneficial mutation (Haldane 1924, 1927). As before, we followed the fate of allele A under three different scenarios: (i) observer females do not copy the mate choices made

by model females, (ii) observer females acquire only positive public information, and (iii) observer females acquire both positive public information and negative public information. The results are shown in figure 5, assuming $\alpha = 4$ in equation (1) and patch size $\lambda = 5$.

With no copying, allele a went to extinction or remained drifting at low frequency in 18 out of 30 simulation runs and reached fixation, or was on its way to reach it, in 12 (40%) runs (fig. 5A). With only positive public infor-



mation, the allele was generally lost, although it remained drifting in a few runs (fig. 5B). However, when both positive public information and negative public information were considered, the allele was fixed or on its way to fixation in 9 (30%) runs. These results are qualitatively similar to those obtained when dominant allele *A* was considered fittest, but there are some quantitative differences regarding the parameter values used in the simulations. Assuming a lower female remating receptivity (i.e., $\alpha = 2$), allele *a* tended to go extinct or remained drifting: the allele was fixed, or on its way to fixation, in only 6 out of 30 runs with no copying (results not shown). Similarly, increasing patch size to $\lambda = 10$ considerably weakened the effective selection, with allele *a* going to fixation in only 5 (17%) runs with no copying (results not shown).

To sum up, these numerical results show that introducing negative public information in mate choice copying may lessen to some extent the strong positive frequency-dependent selection bias (Kirkpatrick and Dugatkin 1994). An initially rare and fitter allele can eventually invade, depending on the parameter values and model assumptions. We do not tout our model and numerical results as any more than an attempt at explaining why copying might not be maladaptive in the long run after all. In what follows, however, we will argue that copying is unlikely to be a widespread social phenomenon in highly polyandrous species.

Discussion

We have studied the evolutionary fate of a fitter phenotype introduced at a low frequency in a population where immature observer females copy the mate choice decisions made by model females. We considered the situation where individuals use spatially divided and ephemeral resources and a mating system mainly driven by males in pursuit of receptive females for copulation. Following the standard definition of mate choice copying (Pruett-Jones 1992), we considered both positive public information and negative public information gained by observer females as essential ingredients in the model. The numerical results clearly demonstrate that negative public information may override previous conclusions under some circumstances. Unlike copying using positive information only (as in Kirkpatrick and Dugatkin 1994; Laland 1994), copying based

on both positive public information and negative public information eases the spread of a novel (fitter) trait. This reopens the question of the role of public information in sexual selection: when compared with the independent mate choice strategy (no-copying scenario), mate choice copying seems to have a more conservative role in the evolution of male traits, by reducing the strength and direction of selection. A fitter and rare phenotype will invade a population when positive and negative information about the most common phenotype somehow cancel each other out or when the negative information prevails. Only under these conditions does the positive information about the rare phenotype seem able to spread in the population, though the selection is never as strong as under the noncopying scenario.

An interesting interplay among female receptivity, male competitive ability (courtship vigor), remating incidence, and patch size in relation to the evolutionary fate of a fitter allele crops up in the simulations. In a population where naive females copy (based on positive and negative information), it appears that for a rare but fitter male allele to spread, it is important that it has a higher competitive ability than noncarrier common males (cf. figs. 2C, 4B). In this case, a lower female receptivity for mating multiple times (i.e., a high value of α in eq. [1]) helps because it elicits a stronger male-male competition and favors traits that increase male competitive ability (Markow 2002). Conversely, a very high incidence of remating (a low value of α and a large t_{fm} in eq. [4]) could produce mixed outcomes. On the one hand, it makes the effective selection for male mating success weak because female receptivity remains high and approximately the same toward both male types. On the other hand, the likelihood of having offspring sired by the fittest male phenotype increases when females can remate many times. However, it is difficult to figure out the benefits of mate choice copying for a female that can promiscuously remate during its entire lifetime.

If we embrace Bateman's principle (Bateman 1948; Roughgarden 2009, p. 240) that female fitness is independent of the number of mates beyond one because fertility is seldom likely to be limited by sperm production, mate choice is then seen as a vital decision for a female. We know, however, that Bateman's principle is just plain wrong in several species where male gamete production

Figure 5: Evolutionary fate of allele *A* when a fitter recessive allele *a* is introduced at a frequency of 0.025 at generation t_0 . Males carrying this recessive allele have phenotype *y* and a higher courtship vigor than *x* males ($c_x = 4$, $c_y = 5$) and also produce more offspring regardless of females' phenotype ($n_x = 50$, $n_y = 70$; see eq. [4]). For each scenario, 30 independent runs were achieved, and each trajectory is plotted as a black line. *A* plots the null model with no copying. *B* introduces female copying with only positive public information. *C* introduces female copying with both positive public information and negative public information. Other parameter values in the model were as in figure 2, with the exception of innate preferences $pm_x = 0.6$ and $pm_y = 0.4$ and $\alpha = 4$ in equation (1).

can limit potential productivity (Markow et al. 2012; see also Gowaty et al. 2010). In *Drosophila nanoptera* and *Drosophila hydei*, for example, males transfer 81 and 126 sperm per copulation, respectively. This is in contrast with *Drosophila melanogaster*—the species Bateman (1948) worked with—where males transfer 4,600 sperm (Markow 1996, table vii; Markow and O’Grady 2005, p. 196), and with *Drosophila pseudoobscura*, where males transfer more than 25,000 sperm (Snook et al. 1994). The former two species remate several times during 2-h observation periods, whereas the mating latency in *D. melanogaster* is about 5 days (Markow 1996; Markow et al. 2012).

Interestingly, mate choice copying has been demonstrated in *D. melanogaster* (Mery et al. 2009), whereas Auld et al. (2009) failed to demonstrate mate choice copying in another fruit fly from the *melanogaster* species group *Drosophila serrata* (Markow and O’Grady 2005). This is interesting because *D. serrata* has one of the highest incidences of remating in *Drosophila* as assessed by paternity analysis using microsatellite loci, with an estimated number of mates per female around 9–11 (Frentiu and Chenoweth 2008). Taken together, these considerations raise an important caveat to researchers testing the mate choice copying paradigm: the presence or absence of copying might simply mirror the mating system of a species. Besides, mate choice copying is within the paradigm of sexual selection at the precopulatory level, but in many polyandrous species, postcopulatory sexual selection—sperm competition (Parker 1970; Simmons 2005) and/or cryptic female choice occurring inside the reproductive tract (Eberhard 1996; Pitnick and Brown 2000)—might be even more powerful (Snook and Hosken 2004). We hypothesize that a high incidence of female remating significantly weakens any selection for mate choice copying. To put it bluntly, the cost of a wrong mating decision by a highly promiscuous female is likely to be negligible. This can be tested using the information given by Markow (1996, table ix), who subdivided several *Drosophila* species in four categories according to their remating incidence. The A group includes species with the highest remating incidence and the D group with the lowest—*D. melanogaster*, which performs copying (Mery et al. 2009), is in group C. Our prediction is that copying may be widespread in species belonging to groups C and D and absent in those binned in groups A and B (including *D. hydei* and *D. nanoptera*).

To conclude, the present numerical results show that introducing negative public information in mate choice copying may lessen to some extent the strong positive frequency-dependent selection bias (Kirkpatrick and Dugatkin 1994) in patchy habitats. An initially rare and fitter allele can eventually invade, depending on the parameter values and model assumptions. Our results should be primarily considered a proof of concept and help us place in

proper perspective discussions concerning short-term and long-term costs and benefits of female mate choice copying in natural populations. In the end, whether there is copying in a particular species is an interesting question open to empirical research. We suggest that observing mate choice copying in those species with a high remating incidence is unlikely because selection for copying is probably weak.

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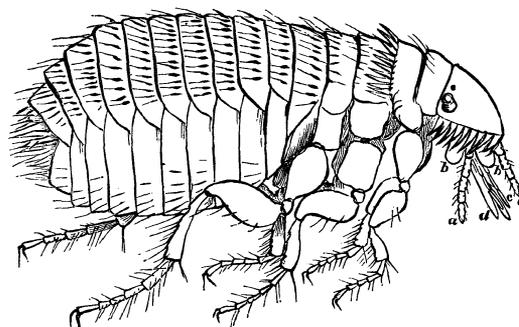
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"The Flea is also a wingless fly [...]. In its adult condition the flea combines the characters of the Diptera, with certain features of the grasshoppers and cockroaches (Orthoptera), and the bugs (Hemiptera). The body of the human flea [...] greatly magnified; a, antennae; b, maxillae, and their palpi; c, d, mandibles; the latter, with the labium, which is not shown in the figure, forming the acute beak) is much compressed, and there are minute wing-pads, instead of wings, present in some species." From "A Chapter on Flies (Concluded)" by A. S. Packard Jr. (*The American Naturalist*, 1869, 2:638–644).