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Mate-choice copying: a fitness-enhancing behavior that evolves by indirect selection

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Supporting Information

Figure S1 – Moore neighborhood applied in the simulations

Figure S2 – Schematic of female and male strings used in simulations

Table S1 – Summary of simulation results for one-to-many horizontal cultural transmission and fixed innate preferences

Abstract

A spatially explicit, individual-based simulation model is used to study the spread of an allele for mate-choice copying (MCC) through horizontal cultural transmission when female innate preferences do or do not coevolve with a male viability-increasing trait. Evolution of MCC is unlikely when innate female preferences coevolve with the trait, as copier females cannot express a higher preference than non-copier females for high-fitness males. However, if a genetic polymorphism for innate preference persists in the population, MCC can evolve by indirect selection through hitchhiking: the copying allele hitchhikes on the male trait. MCC can be an adaptive behavior −i.e., a behavior that increases a population's average fitness relative to populations without MCC−, even though the copying allele itself may be neutral or mildly deleterious.

Key words: mate-choice copying, sexual selection, individual-based simulations, social information, indirect selection.

Introduction

Many animals acquire new patterns of behavior by witnessing what others are doing, a process known as social learning (Heyes and Galef 1996; Galef and Laland 2005). Mate-choice copying (hereafter referred to as MCC) is one form of social learning based on inadvertent social information (also known as public information; Danchin et al. 2004; but see Wagner and Danchin 2010) where mating decisions (usually by females) are influenced by observation of the mating preferences of others (Pruett-Jones 1992; Dugatkin 1996a). The first theoretical models of MCC (Bradbury and Gibson 1983; Bradbury et al. 1985; Losey et al. 1986; Wade and Pruett-Jones 1990; Dugatkin and Hoglund 1995; Stöhr 1998) sought to explain the high variance observed in male mating success in avian leks (Wiley 1991), in which males aggregate and females' survey potential partners for copulation. These models assumed that non-copier females assessed male quality independently (though not flawlessly; Ryan et al. 2007), whereas copier females assessment depended on male mating success. Generally, if sampling costs associated with active mate choice are assumed, models predict that MCC is an advantageous short-cut strategy to identify high quality mates (Pomiankowski 1990).

Despite the initial focus on lekking species, the first experimental evidence for female copying (Dugatkin 1992; Dugatkin and Godin 1992) came from guppies (*Poecilia reticulata*), a species where males actively pursuit mates. Similarly, in the fruit fly *Drosophila melanogaster*, where males display courtship behavior, Mery et al. (2009) showed that females copied mating preferences for arbitrary (in terms of potential mate quality) phenotypic traits. Mery et al. (2009) artificially generated two male phenotypes by dusting flies with green or pink powder. A prospector female witnessed a (e.g.) green male copulating with a model female and secondly a (e.g.) pink male that did not copulate because the model female was nonreceptive. After this double demonstration, two new colored males were presented to the prospector female. Females preferably mated with the male dusted with the color associated with active copulation.

Bayesian decision theory suggests that a female should perform MCC only when her own perception does not indicate much difference between two males (Uehara et al. 2005; see also Brooks 1996; Nordell and Valone 1998). Results from guppies and sailfin mollies show that females rely on personal information when males are substantially different (Dugatkin 1996b; Witte and Ryan 1998), supporting this hypothesis. Contrarily to this, however, Mery et al. (2009) also showed that prospector females used social information even after observing model females mated with poor condition males. In *Drosophila*, juvenile performance is positively correlated between the sexes but adult performance is negatively correlated. Thus, there is no net intersexual correlation for total fitness (Chippindale et al. 2001). Owing to this intersexual conflict, a female choosing to mate with a ‘good’ quality male will produce average adult daughters. It may, thus, be that there are nonadaptive reasons for the expression of MCC behavior in *Drosophila*, and perhaps in other species (Dugatkin and Godin 1993): how and why is this behavior maintained, and why did it evolve?

Indirect mate choice population genetics models provide an alternative approach to the study of evolutionary dynamics and consequences of MCC. A standard example of indirect selection is Fisher’s (1958, pp. 151-152) runaway coevolution, in which (innate) female preference evolves as a correlated response to the selection of male traits, which female preference itself induces, creating a self-sustaining feedback loop. The body of theory that developed around Fisher’s proposal originally assumed that females assess males independently of what other females are doing (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988; but see Bailey and Moore 2012). However, later models that explicitly addressed the coevolution of learned female preferences and male traits have shown that a process akin to Fisherian runaway selection can occur (Kirkpatrick and Dugatkin 1994; Laland 1994; Ihara et al. 2003). Servedio and Kirkpatrick (1996) were the first to address the important question of how MCC can initially arise through indirect selection. They showed that when copier females mate with males that have higher total lifetime fitness, MCC may spread by hitchhiking on the male trait even if the copying gene is mildly deleterious. Once MCC is established, it creates a strong positive frequency-dependent bias that eliminates novel or rare male traits, irrespective of their fitness (Laland 1994; Kirkpatrick and Dugatkin 1994; but see Agrawal 2001). The potentially maladaptive consequences of MCC can be somewhat alleviated by including negative social information (i.e., when females can reverse their choice after having observed a previously attractive male being rejected by another female) in the models (Santos et al. 2014).

Kirkpatrick and Dugatkin (1994) and Servedio and Kirkpatrick (1996) models make different assumptions about female innate preferences. Although there is no genetic variation for preference in either model, Kirkpatrick and Dugatkin (1994) assume females have an innate preference for the more common, unfit males; whereas Servedio and Kirkpatrick (1996) assume both copier and non-copier females are born with an innate preference for high-fitness (combination of natural and sexual selection) males. In Servedio and Kirkpatrick (1996), preference and copying are jointly controlled by a single locus and preference changes only through cultural evolution. Thus, female innate preference is overridden after observing mate-choices of an older female cohort. Yet, there is abundant evidence for genetic variation in female innate preference (Bakker and Pomiankowski 1995; Chenoweth and Blows 2006; Fowler-Finn and Rodríguez 2016), which is a requirement in Fisherian runaway models (Lande 1981; Kirkpatrick 1982; Tomlinson and O'Donald 1996; Kokko et al. 2002; Mead and Arnold 2004). Furthermore, genetic preference can also (co)evolve by indirect selection when natural selection favors a correlated trait that increases other fitness components such as fecundity (Kokko et al. 2003). To include genetic evolution of innate preference in studies of MCC will thus require modeling the evolution of at least three characters/genes: a gene/trait for innate female preference for a given male trait, a gene/trait acting in females that determines whether they rely on inadvertent social information or choose based on innate preference (the 'copying' gene), and the gene/trait of males. The focus of this article is to explore such a scenario numerically using a 'major-gene' approach. We therefore let female innate preferences and copying tendencies coevolve with a male trait, and assume that a female copying tendency is evolutionarily linked to her innate preference. This serves to avoid the criticism that copying and innate preference are independent and go against each other (Vakirtzis 2011). Results are compared to the situation where females vary in fixed innate preferences, rendering coevolution with the male trait impossible, as in Servedio and Kirkpatrick (1996).

Many species exhibit a patchy population structure, with individuals distributed in spatially scattered aggregates (see Santos et al. 2014). We used a discrete, spatially explicit individual-based simulation model where MCC occurs through horizontal cultural transmission (in *Drosophila* and in other taxa learning within a single generation has been documented; Servedio and Dukas 2013, and references therein). Females and males are associated with a location in a two-dimensional lattice and interactions happen locally. That is, female and male local groups are within signaling and receiving distance during courtship and mating activities. The focus is centered on females rather than on males because MCC appears to be more frequent in females (Dugatkin 1996a; Westneat et al. 2000), although MCC by males is also known to happen (Auld and Godin 2015). Furthermore, it is assumed that females learn to copy preference for phenotypic traits (Kirkpatrick and Dugatkin 1994; White and Galef 2000; Agrawal 2001; Swaddle et al. 2005; Mery et al. 2009), which remains to be demonstrated in males (Witte et al. 2015).

Results show that Fisherian sexual selection, where innate female preference coevolves with the male trait, makes the evolution of MCC unlikely. However, the spread of the copying allele by indirect selection can reinforce the invasion of a new, high-fitness male trait once a genetic polymorphism for innate female preference is allowed to persist. This novel finding suggests that under these circumstances, MCC is an adaptive strategy, because it helps the invasion of an overall fitter trait that results in average fitness of MCC populations to be higher than average fitness of populations without MCC.

The Model

Spatial setting and genomes

For the sake of simplicity, we assumed a sexual population of chromosomes (the 'organisms') living in a two-dimensional regular lattice of linear length $L = 30$ with approximately $0.90L^2$ randomly distributed nonempty entries (population size $N \approx 800$ individuals with average 1:1 sex ratio) and periodic boundary conditions (i.e., a torus).

Each chromosome has three sex-limited loci. Locus one $(pref)$ is expressed in females, and codes for a preference gene with two alleles: allele 0 indicates that the female has an innate preference for males with trait x; allele 1 indicates the preference is for males with trait y. The second bi-allele locus (soc) is also expressed in females and codes for a 'social' gene: allele 0 indicates that (non-copier) females will mate according to their innate preference dictated by the allele at locus one $(pref)$; whereas allele 1 specifies that (copier) females rely on socially acquired information that prevails over the fixed genetic preference (see, e.g., Vakirtzis 2011). Neither loci affect female survival or fecundity (but see below). Finally, the third locus $(trait)$ affects male survival and specifies the male trait: type x has allele 0; type y has allele 1.

Life cycle and mating decisions

Generations are discrete and non-overlapping. At the start of each generation, each cell in the lattice is randomly occupied by a female, by a male, or remains empty. The initial population at generation t_0 is seeded with frequencies $p_{pref}^{t_0}$, $p_{soc}^{t_0}$ and $p_{trait}^{t_0}$ for allele 1 at each locus. Only Moore neighborhood sexual interactions are allowed, with eight cells surrounding a central cell on the square lattice (Fig. S1).

At each time step, we pick a random position in the lattice occupied by a virgin (target) female and define its Moore neighborhood. A neighbor male courts the female and she can accept or reject mating based on her preference. Non-copying females rely on their innate preference and always act as demonstrator females. Naïve-copying females (‘observers’) mate and act as demonstrator females only after acquiring social information (see Fig. S2). When the target female is a demonstrator female, she will accept mating if courted by a male whose phenotype matches her innate (non-copier) or learned (copier) preference. If, on the other hand, there is a conflict between the female preference and the male trait, she can eventually mate according to her cost of choice relative to random mating (Pomiankowski 1987). Note that any female might encounter a biased sample of males in her neighborhood, which can result in her choosing non-preferred males. Therefore, female preference (i.e., the sensory and behavioral components that influence females to mate differentially with certain male phenotypes; Heisler et al. 1987) should be distinguished from mate choice (i.e., the outcome of interactions among individuals resulting in the *a posteriori* deviation from random mating; see Appendix S1 − Matting pattern). A choosy female shows unequal preferences and mates with the non-preferred male with probability $p = 1 - \text{'choice cost'}$. Thus, choosiness increases linearly with cost and is maximum when $\text{'choice cost'} = 1$, whereas if $\text{'choice cost'} = 0$ the female shows an equal preference for any male type. We assumed this cost to be the same for copier and non-copier females. We also assumed that females do not incur in viability or fecundity costs for being too discriminant (e.g., $\text{'choice cost'} > 0.5$).

At the end of each time step, the target female can either mate or remain unmated. If she mates, naïve-copying females in the Moore neighborhood imprint on her choice. Two processes of cultural transmission are assumed (Mesoudi 2011, table 3.1): ‘one-to-many’ where the decision taken by the mating female influences all others naïve-copying females in the Moore neighborhood; ‘one-to-one’ where only one randomly chosen naïve-copying female in the Moore neighborhood is influenced. Therefore, like both Kirkpatrick and Dugatkin (1994), and Servedio and Kirkpatrick (1996), we assumed only positive social information. The routine repeats itself through different random sites in the lattice until 85% of females have mated. This decision rule was made for simulation convenience: it allows for a relatively fast cycling through the lattice while at the same time keeping a high proportion of mated females at each generation. The assumption of horizontal cultural transmission, where at the beginning of each generation non-copiers are the only demonstrator females, puts some limitations in the model because the frequency of the copying allele cannot reach 100% (the first ‘social’ female that later acts as a demonstrator female necessarily needs to observe the mate choice of at least one non-copier female). A stop criterion in the algorithm was $p_{soc} \geq 0.95$. Females mate only once, but any male can potentially mate with more than one female.

Offspring generation

After mating, recombination occurs in the diploid stage followed by mutation. With probability r, the crossover operation picks one point m $(m = 1, 2)$ at random from each parental chromosome to form one offspring chromosome by taking all alleles from the first parent up to the crossover point, and all alleles from the second parent beyond the crossover point. All mating pairs produce the same number of progeny, and a new generation starts by randomly allocating the offspring in the lattice (keeping $N \approx 800$). Each haploid individual is assigned to be a female or a male with equal probability. Mutations happen at any locus at rates μ_{pref}, μ_{soc} and μ_{trait}.

Natural selection was incorporated in the form of viability, with selection coefficients $0 \le s_x, s_y < 1$ for a type x (y) male, respectively. Viability selection $1 - s_x$ $(1 - s_y)$ was introduced as hard selection (Christiansen 1975). Namely, we assumed that after migration to a random cell in the grid a male's probability of survival before reproduction equals its viability. We usually assume that common resident males in the population have trait x. Furthermore, we generally assumed that there is no direct fitness cost to the learned preference (so the copying allele is neutral), but we also considered some cases when copier females pay a slight viability cost $1 - s_c$ relative to that of non-copier females (making the copying allele mildly deleterious). This might be a likely scenario because there are costs associated to the capacity of learning (Mery and Kawecki 2003, 2004; Barnard et al. 2006; Burger et al. 2008).

Simulation programs were implemented in MATLAB (ver. R2015a) algebra environment using tools supplied by the Statistics Toolbox. Routines used to run the analyses are provided in the Supporting Information.

Results and Discussion

Case 1: Evolution of MCC with fixed innate preferences

To facilitate comparisons with Servedio and Kirkpatrick (1996), we first suppose that innate female preference does not evolve. To define preference strength in the population we proceeded as follows. Allele 1 at the $pref$ locus starts with frequency $p_{pref}^{t_0}$ (i.e., a fraction $1-p_{pref}^{t_0}$ of non-copier females would favor mating with resident x males) and no mutation $\left(\mu_{pref}=0\right)$. To avoid evolution at this locus when $0<p_{pref}^{t_0}<1$, we reset allele frequencies in each offspring generation by randomly filling this locus with both alleles according to their initial frequencies. This also avoids the building up of linkage disequilibrium with the $pref$ locus.

To check spreading conditions for trait y and the copying allele, extensive computer simulations were performed using a wide range of parameter values for all combinations of innate preference $\left(p_{pref}^{t_0}=0.1, 0.2, \cdots\right)$, selection coefficients against the resident male $\left(s_x=0, 0.05, \cdots\right)$, and cost of choice $\left(\text{'choice cost'}=0.3, 0.5, 0.7\right)$. Table S1 (one-to-many horizontal cultural transmission) and Table S2 (one-to-one horizontal cultural transmission) summarize these results. Conditions for invasion of the copying allele are the same under either cultural transmission rules, but the one-to-one rule results in a lower equilibrium frequency for the copying allele (Fig. S3). In what follows, we focus on results for the one-to-many rule.

The parameter 'choice cost' plays an important role in the evolutionary fate of the copying allele. If female choosiness is weak $\left(\text{'choice cost'}=0.3\right)$ the copying allele never spreads. With intermediate choosiness $\left(\text{'choice cost'}=0.5\right)$ the copying allele may spread if $p_{pref}^{t_0}\leq 0.6$ and natural selection against the resident male x is relatively strong (Fig. 1A). Finally, at strong choosiness $(\text{'choice cost'} = 0.7)$ the copying allele spreads if selection against the resident male x is strong enough and innate preference ranges between $0.3 \leq p_{pref}^{t_0} \leq 0.8$ (Figs. 1B-C). Our model also confirms (not shown) that the copying allele spreads even when there is mild direct selection against it (i.e., $s_c \approx 0.01 - 0.001$; see Servedio and Kirkpatrick 1996). In Tables S1-2 we assumed $r = 0.05$, but increasing the recombination rate does not substantially change the results (not shown).

In those cases where the copying allele spreads, the equilibrium frequency of the copying allele decreases with increases in the frequency of the fixed innate preference for the novel trait (Fig. S3). The behavior of the system (Fig. 1) matches Servedio and Kirkpatrick (1996), that is, the system evolves at two timescales: the trait evolves first, and is followed by a slower evolution of the copying allele. Most importantly, the time lag between timescales varies according to parameter values. When non-copier females tend to prefer resident males x $\left(p_{pref}^{t_0} < 0.5\right)$ the new trait and the copying allele increase in frequency in parallel (Figs. 1A-B), whereas when non-copier females prefer introduced males $\left(p_{pref}^{t_0} > 0.5\right)$ the copying allele spreads only once the new trait has invaded (Fig. 1C). This suggests that MCC might reinforce invasion by a novel trait when natural selection (viability) against resident males opposes sexual selection (innate preference of non-copier females). To verify this, we ran simulations that purposefully avoided the evolution of the copying allele (i.e., $p_{soc}^{t_0} = 0$, $\mu_{soc} = 0$) under those conditions where the allele spread when coevolving with the introduced trait (Table S1). See Figures 2-3 for some numerical examples. As predicted, the equilibrium frequency of the trait $(\hat{p}_{trait})$ was lower without MCC when non-copier females prefer the resident male (c.f. Figs. 2A-C, Figs. 2B-D). On the other hand, there was little change in $\hat{p}_{trait}$ when innate preference of non-copier females tends to favor the novel male trait (c.f. Figs. 3A-C, Figs. 3B-D).

It appears, therefore, that MCC is adaptive (i.e., a strategy that leads the population to a higher relative fitness) because it helps the invasion of an overall fitter trait when innate preference goes against its invasion. Note, however, that the copying allele spreads through indirect selection and does not increase the likelihood of invasion by the new trait. This is the case because copier females copy both types of choices from the non-copiers: the choice of the novel male and the choice of the resident male. It is only the stronger (learned) preference of copier females towards the high-fitness males that increases the equilibrium frequency of the novel trait (Appendix S1).

A potential caveat of the previous conclusion is that the situation could be reversed when innate preference tended to favor a novel trait that has lower viability. For instance, we can envisage a situation where populations are locally adapted to different environments (Kawecki and Ebert 2004) and immigrant males entering a given population have a lower viability, but females might favor mating with these males (Bárbaro et al. 2015). Setting $\text{'choice cost'} = 0.7$, we ran simulations assuming $p_{pref}^{t_0} > 0.5$ with $s_x = 0$ and $s_y > 0$ to see whether coevolution of the copying allele and the ‘invading’ trait could increase equilibrium frequency of the latter. In some situations the copying allele spread to frequency $\hat{p}_{soc} \approx 0.30$, but the equilibrium frequency of the novel trait remained essentially the same with and without MCC (results not shown). Therefore, the former conclusion that MCC is adaptive under some scenarios seems to be sound.

Once established in the population, MCC can cause a strong positive frequency-dependent advantage towards resident males, making it difficult for a fitter male to invade (Kirkpatrick and Dugatkin 1994; but see Agrawal 2001; Santos et al. 2014). We tested this for those conditions in Table S1 where the copying allele spreads, but now assumed different initial frequencies $\left(p_{soc}^{t_0} = 0.2,\ 0.4,\ 0.6,\ 0.8\right)$. Usually, the frequency of the copying allele drops at early generations and then rises in frequency following (and helping; see above) the spread of the new trait (supplementary Fig. S4). Therefore, our results do not support the idea that MCC hampers the establishment of a novel trait in the population. The same result is obtained if the frequency of the copying allele is kept constant through time.

Case 2: Evolution of both MCC and innate preference

A general result from our model is that Fisherian sexual selection, where innate female preference coevolves with the novel male trait, makes the invasion of the copying allele very unlikely (Table S3). This happens because (i) innate preference for the novel trait quickly drops in frequency $\left(p_{pref} \to 0\right)$ making the invasion of the trait more difficult and, hence, the copying allele cannot hitchhike with the new trait allele (Fig. S5); or because (ii) viability selection can overcome the initially strong sexual selection against the novel trait, and its invasion produces a concomitant coevolution of innate preference towards y males $\left(p_{pref} \to 1;\ \text{Appendix S1}\right)$. These findings agree with previous results that assumed fixed preferences: a strong innate preference towards resident males x, or towards the novel trait y, make it very difficult for the copying allele to spread (Tables S1-2; see also Fig. S3).

Concluding Remarks

In the model by Servedio and Kirkpatrick (1996), where female innate preferences do not evolve but are biased towards the high-fitness male trait, the copying allele spreads by hitchhiking with the male trait allele. This raises the question of why we do not observe the spread of the copying allele once the novel trait has invaded and innate preferences are highly biased towards this trait. The reason probably is that the strength of preferences is modelled differently in both cases. Servedio and Kirkpatrick (1996; see also Kirkpatrick and Dugatkin 1994) model preferences by quantifying how much more likely a female is to mate with a given male, and are (in theory) upperly unbounded: copier females replace their innate preference by an effective preference due to the proportion of matings observed (eq. 2 in Servedio and Kirkpatrick 1996), and can express a preference towards the high-fitness trait that is higher than that of non-copier females. In our model, however, preferences are bounded and depend on allele frequencies: when coevolving with the spread of the novel male trait, female innate preference hitchhikes to its maximum frequency $p_{pref} \approx 1$ (barring mutation), and the proportion of mating with high-fitness males is larger for non-copier than copier females (see Appendix S1). Therefore, if MCC evolves by indirect selection we have to add additional assumptions (complications) to our model to understand how genetic variation in female preferences is maintained. An obvious choice is to assume a higher mutation rate at the *pref* locus (i.e., μ_{pref} □ [illegible]) – which does not seem to be very realistic – as this would keep the innate preference towards the novel male trait segregating at intermediate levels (Fig. S6).

In an influential review, Kirkpatrick and Ryan (1991) suggested that there was considerable circumstantial evidence showing that innate preferences evolve because of their direct effects on female fitness rather than the genetic effects on offspring resulting from mate choice. Our assumption that innate preferences do not alter female survival or fecundity and might coevolve with the male traits violates this conclusion. Nevertheless, a recent review by Fowler-Finn and Rodríguez (2016) comprising 43 studies on trait–preference covariance, identified a substantial number of papers (27) that detected such covariance, and presence of genetic variation in innate mate preferences was the main predictor (but see also Greenfield et al. 2014). This suggests that Fisherian sexual selection might be widespread, and also that there might be a long-term balance between the loss of genetic variation and other forces like mutation, migration, and changes in the direction of selection that maintain genetic variation for preference (Bakker and Pomiankowski 1995; Greenfield et al. 2014). This variation is a critical condition for the evolution of MCC in our model.

Along with MCC, two other mechanisms may allow females to change innate mate preferences: sexual imprinting and personal experience (Verzijden et al. 2012). Through sexual imprinting, females acquire a mate preference usually from their father or mother at an early age. Later in life, personal experience allows females to learn from direct evaluation of the male's courtship performance. Both mechanisms may override female innate preference with consequences to sexual selection (Verzijden et al. 2005; Dukas 2013; Servedio and Dukas 2013), but they do not create informational cascades. Informational cascades, the sequential transfer of information in a network of individuals, can only be generated in species where females learn from observing the choices made by others using MCC (Gibson and Höglund, 1992; Giraldeau et al., 2002; Kendal et al., 2005; Rieucau and Giraldeau, 2011). MCC could lead to small or large informational cascades, depending on the proportion of copier females in the population, which is an interesting regulatory system for the population.

In conclusion, if genetic variation in innate preference persists in the population and females do not incur high viability or fecundity costs for being too discriminant, the spread of the copying allele is easier when innate preference is biased towards the low fitness, more abundant resident males. In this case, MCC can be an adaptive behavior even if the copying allele itself is neutral or mildly deleterious.

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Figure legends

Figure 1. Evolutionary fate of the fitter trait (male *y*) when the copying allele can coevolve but innate preference (pref. *y*) remains fixed throughout generations. In all cases the initial frequencies and mutation rates were $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$ (trait *y*), $p_{soc}^{t_0} = 0$ and $\mu_{soc} = 0.001$ (copying allele), and recombination rate $r = 0.05$. *A* plots a sample simulation where 80% of the non-copier females prefer the common unfit resident male *x* (i.e., $p_{pref}^{t_0} = 0.20$, $\mu_{pref} = 0$, $s_x = 0.35$, and $s_y = 0$) and $\text{'choice cost'} = 0.5$. *B* plots a case where $p_{pref}^{t_0} = 0.30$, $\mu_{pref} = 0$, $s_x = 0.30$, $s_y = 0$ and $\text{'choice cost'} = 0.7$. Parameter values in *C* were $p_{pref}^{t_0} = 0.70$, $\mu_{pref} = 0$, $s_x = 0.20$, $s_y = 0$ and $\text{'choice cost'} = 0.7$.

Figure 2. Evolutionary fate of the fitter trait (male *y*) with (panels *A*, *C*) and without (panels *B*, *D*) coevolution of the copying allele when non-copier females have a fixed innate preference (pref. *y*) favoring the common resident male x. In all cases the new trait was introduced with $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$, and recombination rate was

$r = 0.05$. The copying allele was introduced with $p_{soc}^{t_0} = 0$ and allowed to mutate ($\mu_{soc} = 0.001$) or not ($\mu_{soc} = 0$). *A* plots a sample simulation with $\mu_{soc} = 0.001$ where 80% of the non-copier females prefer trait *x* (i.e., $p_{pref}^{t_0} = 0.20$, $\mu_{pref} = 0$, $s_x = 0.30$, and $s_y = 0$) and $\text{'choice cost'} = 0.5$. *B* is the same than *A* but $\mu_{soc} = 0$. Parameter values in *C* were $\mu_{soc} = 0.001$, $p_{pref}^{t_0} = 0.30$, $\mu_{pref} = 0$, $s_x = 0.30$, $s_y = 0$ and $\text{'choice cost'} = 0.7$. *D* is the same than *C* but $\mu_{soc} = 0$.

Figure 3. Evolutionary fate of the fitter trait (male *y*) with (panels *A*, *C*) and without (panels *B*, *D*) coevolution of the copying allele when non-copier females have a fixed innate preference (pref. *y*) favoring the introduced male y. In all cases the new trait was introduced with $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$, and recombination rate was $r = 0.05$. The copying allele was introduced with $p_{soc}^{t_0} = 0$ and allowed to mutate ($\mu_{soc} = 0.001$) or not ($\mu_{soc} = 0$). *A* plots a sample simulation with $\mu_{soc} = 0.001$ where 40% of the non-copier females prefer trait *x* (i.e., $p_{pref}^{t_0} = 0.60$, $\mu_{pref} = 0$, $s_x = 0.15$, and $s_y = 0$) and $\text{'choice cost'} = 0.7$. *B* is the same than *A* but $\mu_{soc} = 0$. Parameter values in *C* were $\mu_{soc} = 0.001$, $p_{pref}^{t_0} = 0.70$, $\mu_{pref} = 0$, $s_x = 0.25$, $s_y = 0$ and $\text{'choice cost'} = 0.7$. *D* is the same than *C* but $\mu_{soc} = 0$.