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## The evolutionary consequences of mate copying on male traits

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**Abstract** In some species, a female's mating preference can be influenced by the matings she observes. Mate copying occurs when a female alters her mating preference in favor of the type of males she has observed mating with other females. Here I present a model that explores the consequences of mate copying on the evolution of male traits. In contrast to previous work, I show that mate copying can have diverse evolutionary consequences. Mate copying can cause (positive or negative) directional selection on male traits or (positive or negative) frequency-dependent selection on male traits. The type of selection generated by mate copying depends on the details of how females are influenced by the matings that they observe. I discuss my results in relation to previous theoretical work that posits that mate copying can only hamper the spread of novel male traits.

**Keywords** Mate copying · Sexual selection · Gene-culture coevolution

### Introduction

Though females are often assumed to choose their mates independently of one another, evidence is growing that this assumption is not valid for all species (Gibson and Höglund 1992; Brooks 1998). Mate copying occurs when a female alters her mating preference in favor of the type of males she has observed mating with other females. This type of cultural influence on female mating preference has been documented in several species. A variety of studies show that females prefer to mate with males they had observed mating (Dugatkin 1992;

Schlupp and Ryan 1994; Grant and Green 1996; Galef and White 1998). Some studies have even shown that a female's initial preference can be reversed through cultural influence (Dugatkin and Godin 1992; White and Galef 1999). Dugatkin (1996) demonstrated that, in guppies, cultural influence can override weak inherent preferences but not strong inherent preferences. A study on Japanese quail demonstrated that females observing males with novel traits mating successfully prefer other males who have the same novel trait (White and Galef 2000).

Theoretical work shows that the copying behavior itself can evolve through direct (Dugatkin and Höglund 1995; Stohr 1998) or indirect (Servedio and Kirkpatrick 1996) selection. Mate copying has direct benefits to females if it reduces the sampling costs and/or the error rate of mate choice (Dugatkin and Höglund 1995; Stohr 1998). Because females that copy are more likely to mate with males that are attractive to other females, the alleles for copying become genetically associated with attractive male traits. This genetic correlation can allow mate copying to evolve through indirect selection (Servedio and Kirkpatrick 1996). When it exists, mate copying can change the variance in male mating success and can thus be an important part of sexual selection (Wade and Pruett-Jones 1990). Because it can cause gene frequency changes, mate copying represents an interesting interaction between cultural and genetic forces in evolution. Here I show how mate copying can generate different selection pressures on male traits.

Kirkpatrick and Dugatkin (1994) provided the first theoretical insights into the evolutionary effects of mate copying on male traits. They assumed that females are influenced equally by all observations. Because most females observe common male phenotypes mating successfully, cultural experiences tend to bias female preference towards common male phenotypes. Consequently, mate copying causes positive frequency-dependent selection that eliminates novel or rare male traits in their model.

Like Kirkpatrick and Dugatkin (1994), I do not consider the evolution of mate copying itself but rather as-

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sume that mate copying exists and investigate the consequences for the evolution of male traits. However, I make alternative assumptions about how cultural experiences alter female preferences. The primary conceptual difference between my assumptions and those of Kirkpatrick and Dugatkin is that they assume all observations influence females equally whereas I allow different types of observations to have differing degrees of influence. As a result, mate copying can have dramatically different effects than those observed by Kirkpatrick and Dugatkin. Depending on the parameter values, mate copying in my model can cause (positive or negative) directional selection or (positive or negative) frequency-dependent selection. Thus mate copying is capable of (1) causing novel male traits to sweep through the population, even if there is no inherent preference for the novel trait, and (2) maintaining genetic variation for sexually selected male traits.

## The model

For simplicity, I will assume a single male trait. The phenotypic value of this trait in a male is represented by  $z$ . This trait can be rescaled to measure a male's phenotype as the deviation from the population mean,  $\tilde{z} = z - \bar{z}$ . This rescaled measure has the property that males with larger than average values of the trait will have positive values of  $\tilde{z}$ , whereas males with smaller than average values of the trait will have negative values of  $\tilde{z}$ . By definition, common males will have phenotypes that do not differ much from the mean so they will have small values of  $|\tilde{z}|$ . In contrast, rare males will have comparatively large values of  $|\tilde{z}|$ .

### Female preference with cultural influences

I model a female's preference,  $F$ , for a male with a trait value of  $\tilde{z}$  as

$$F = \alpha z + \tilde{z}\Phi[\tilde{z}, \bar{z}_{suc}] + c. \quad (1)$$

The variable  $\alpha$  measures the inherent preference for larger values of the male trait. The term  $\Phi[\tilde{z}, \bar{z}_{suc}]$  measures cultural influence as a function of average male phenotype,  $\bar{z}$ , and the average phenotype of males that a female observes successfully mating,  $\bar{z}_{suc}$ . The third term,  $c$ , is a constant added so that  $F \geq 0$  for all values of  $z$ .

The function measuring cultural influences is:

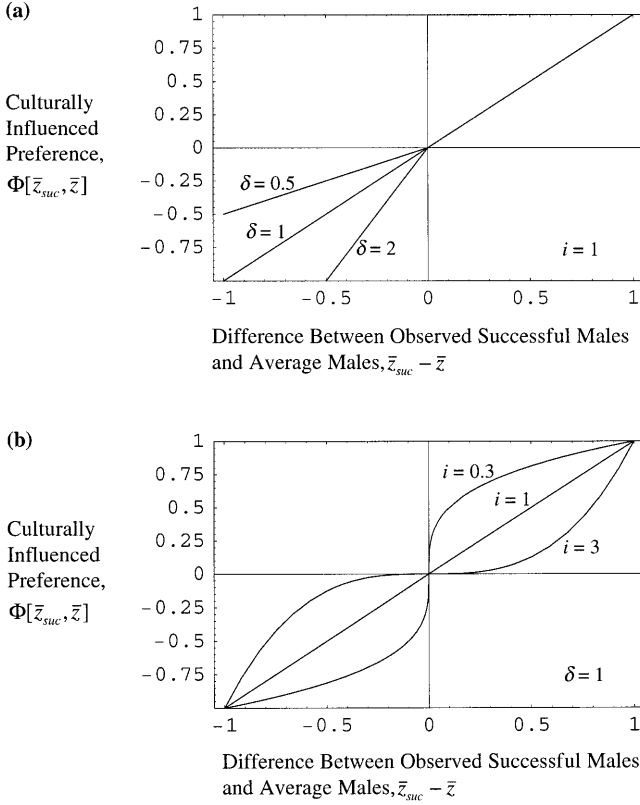
$$\Phi[\tilde{z}, \bar{z}_{suc}] = \begin{cases} (\bar{z}_{suc} - \bar{z})^i & \text{if } (\bar{z}_{suc} - \bar{z}) \geq 0 \\ -\delta|\bar{z} - \bar{z}_{suc}|^i & \text{if } (\bar{z}_{suc} - \bar{z}) < 0 \end{cases} \quad (2)$$

where  $\delta$  is the coefficient of asymmetry and  $i$  is the coefficient of non-linearity (see below). The key element of this function is the difference between the mean phenotype of males that a female observes mating and the mean phenotype of males in general,  $\bar{z}_{suc} - \bar{z}$ . This difference implies that a female is influenced by the males she

observes mating as well as those she observes not mating. When a female observes males of different phenotypes successfully mating in proportion to their frequency in the population (i.e.,  $\bar{z}_{suc} - \bar{z} = 0$ ), her mating preferences are not altered by her social experiences (i.e.,  $\Phi[\tilde{z}, \bar{z}_{suc}] = 0$ ). When a female observes particular male phenotypes mating disproportionately often (i.e.,  $\bar{z}_{suc} - \bar{z} \neq 0$ ), her preference is biased towards these types of males (i.e.,  $\Phi[\tilde{z}, \bar{z}_{suc}] \neq 0$ ). For example, if the male trait of interest is body size, then a female that observes larger-than-average males successfully mating will bias her preferences toward males that are larger than average. A different female in the population might observe a different set of matings in which smaller-than-average males are successful; she will bias her preferences toward smaller-than-average males. The amount of cultural influence generated by a particular set of observations depends on magnitude as well as the sign of this difference ( $\bar{z}_{suc} - \bar{z}$ ). Therefore, a female that observes a rare male phenotype mating is more strongly biased toward this rare phenotype than a female that observes a common male is biased towards the common phenotype. This property of the model incorporates the notion that animals are more strongly affected by experiences involving unusual or unexpected stimuli (e.g., rare male phenotypes) than those involving standard stimuli (e.g., common male phenotypes) (Domjan 1993).

In the cultural influence function above, the variable  $\delta$  measures the asymmetry in importance of observing males with smaller-than-average trait values mate successfully relative to observing males with larger-than-average trait values, holding all else equal. For example, when  $0 \leq \delta < 1$ , a female is less affected by observing smaller than average males mate successfully (i.e.,  $\bar{z}_{suc} - \bar{z} < 0$ ) than another female who observes larger-than-average males mate (i.e.,  $\bar{z}_{suc} - \bar{z} > 0$ ), assuming that the magnitude of the difference is the same in both cases. When  $\delta = 1$ , both females are affected equally (but in opposite ways). When  $\delta > 1$ , the female observing smaller-than-average males mate successfully is more strongly affected. Figure 1a shows a female's preference for males with a larger-than-average trait value as a function of the type of males she observed mating. The preference function is shown for different values of  $\delta$ .

The variable  $i$  in the cultural influence function (Eq. 2) determines non-linearity in the importance of differences,  $\bar{z}_{suc} - \bar{z}$ , of large magnitude relative to differences of small magnitude. When  $0 < i < 1$ , small differences can be almost as important as large differences. When  $i = 1$ , large differences are proportionately more important than small differences. When  $i > 1$ , larger differences are disproportionately more important than small differences. Figure 1b shows a female's preference for males with a larger-than-average trait value as a function of the type of males she observed mating. The preference function is shown for different values of  $i$ .



**Fig. 1a,b** The cultural influence function. The culturally influenced preference (Eq. 2) for the male trait is plotted as a function of the difference between mean phenotype of observed successful males and the mean phenotype of males in general,  $\bar{z}_{suc} - \bar{z}$ . **a** The coefficient of directional asymmetry,  $\delta$ , is varied. Values of  $\delta=0.5$ , 1 and 2 indicate that observing successful males that are smaller than average have less, equal, and more cultural influence, respectively, than observing successful males that are larger than average. In this plot,  $i=1$ . **b** The non-linearity coefficient,  $i$ , is varied. When  $i=1$  there is no non-linearity. A value of  $i=0.3$  or 3 indicates that observations of successful males that are slightly different from the mean, as opposed to much different from the mean, have a disproportionately large or small effect, respectively, on cultural influence. In this plot,  $\delta=1$

### Evolutionary consequences of mate copying on male traits

For simplicity in evaluating the evolutionary effects of mate copying, I assume that variation in the male trait is controlled by a single additive locus. Males with genotypes  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  have phenotypic values of  $z=0$ ,  $0.5$ , and  $1$ , respectively and the frequencies of these three genotypes are  $G_{11}$ ,  $G_{12}$ , and  $G_{22}$ , respectively. Because these alleles are selected in males but not in females, the distribution of these genotypes does not follow Hardy-Weinberg expectations; I used deterministic computer simulations to track the change in frequency of these genotypes. Using these genotype frequencies, the mean phenotype is calculated as:

$$\bar{z} = 0.5G_{12} + G_{22}. \quad (3)$$

I assume that in each generation, a small fraction of initial matings,  $m$ , occur without any cultural influence. These matings are observed and affect the preferences for the remaining matings. The frequency of these initial  $m$  matings that occur with males of genotype  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  is:

$$G_{11}^* = G_{11}c / (c + (0.5G_{12} + G_{22})\alpha), \quad (4)$$

$$G_{12}^* = G_{12}(c + 0.5\alpha) / (c + (0.5G_{12} + G_{22})\alpha), \quad (5)$$

and

$$G_{22}^* = G_{22}(c + \alpha) / (c + (0.5G_{12} + G_{22})\alpha). \quad (6)$$

respectively. (Male mating success of each genotype is calculated based on Eq. 1 with  $\Phi=0$ . The relative mating success of each genotype is equal to the female preference for that genotype divided by the frequency-weighted average preference.) When there is no inherent preference ( $\alpha=0$ ), the initial matings occur at random such that  $G_{11}^*=G_{11}$ ,  $G_{12}^*=G_{12}$ , and  $G_{22}^*=G_{22}$ .

Each female is assumed to observe  $n$  of the initial random matings. Because each female views a different finite sample of all the initial matings, different females will observe different types of males mating successfully. If a female observes  $y_1$ ,  $y_2$ , and  $n-y_1-y_2$  of  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  males mating successfully, then the mean successful male type based on her observations is:

$$\bar{z}_{suc} = (0.5y_2 + (n - y_1 - y_2)) / n. \quad (7)$$

The probability that a female observes  $y_1$ ,  $y_2$ , and  $n-y_1-y_2$  of  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  males mating successfully is given by the trinomial distribution:

$$P[y_1, y_2, n - y_1 - y_2] = \frac{n!}{y_1!y_2!(n - y_1 - y_2)!} (G_{11}^*)^{y_1} (G_{12}^*)^{y_2} (G_{22}^*)^{(n - y_1 - y_2)}. \quad (8)$$

Accounting for the fact that different females observe different samples of the initial  $m$  matings, the average cultural influence is calculated as:

$$\bar{\Phi} = \sum_{y_1=0}^n \sum_{y_2=0}^{n-y_1} \{P[y_1, y_2, n - y_1 - y_2] \Phi[\bar{z}, \bar{z}_{suc}]\}. \quad (9)$$

After these observations, the remaining  $1-m$  matings occur. The mating success of the three male genotypes ( $w_{11}$ ,  $w_{12}$ , and  $w_{22}$ ) is determined by the relative mating preferences of the females, i.e.,:

$$w_{11} = \frac{c + (0 - \bar{z})\bar{\Phi}}{\bar{w}}, \quad (10)$$

$$w_{12} = \frac{c + (0.5 - \bar{z})\bar{\Phi} + 0.5\alpha}{\bar{w}}, \quad (11)$$

and

$$w_{22} = \frac{c + (1 - \bar{z})\bar{\Phi} + \alpha}{\bar{w}}. \quad (12)$$

where  $\bar{w}$  is the average mating success of males:

$$\bar{w} = c + \bar{\Phi}(G_{11}(0 - \bar{z}) + G_{12}(0.5 - \bar{z}) + G_{22}(1 - \bar{z})) + (0.5G_{12} + G_{22})\alpha. \quad (13)$$

Defining  $p=G_{11}+0.5G_{12}$  and  $q=G_{22}+0.5G_{12}$  as the frequencies of the  $A_1$  and  $A_2$  alleles in the current generation, the distribution of genotypes in the next generation is given by:

$$G'_{11} = mp(G_{11}^* + 0.5G_{12}^*) + (1 - m)p(w_{11}G_{11} + 0.5w_{12}G_{12}), \quad (14)$$

$$G'_{12} = m(pG_{22}^* + qG_{11}^* + 0.5G_{12}^*) + (1 - m)(pw_{22}G_{22} + qw_{11}G_{11} + 0.5w_{12}G_{12}), \quad (15)$$

and

$$G'_{22} = mq(G_{22}^* + 0.5G_{12}^*) + (1 - m)q(w_{22}G_{22} + 0.5w_{12}G_{12}). \quad (16)$$

In each of the equations above, the first term results from mate choice in the initial  $m$  matings and the second term results from mate choice in the remaining fraction of matings. The change in the mean phenotype across a generation is given by

$$\begin{aligned} \Delta\bar{z} &= \Delta q = (G'_{22} + 0.5G'_{12}) - (G_{22} + 0.5G_{12}) \\ &= 0.5m(qG_{11}^* + (0.5 + q)G_{12}^* + (1 + q)G_{22}^*) \\ &\quad + 0.5(1 - m)qw_{11}G_{11} \\ &\quad + 0.5((1 - m)(0.5 + q)w_{12} - 1)G_{12} \\ &\quad + (0.5(1 - m)(1 + q)w_{22} - 1)G_{22}. \end{aligned} \quad (17)$$

## Results and discussion

Though there is a growing body of empirical evidence that mate copying occurs in some species, little is known about how females are influenced by their observations. As I show below, the details of cultural influence dramatically affect the evolutionary consequences of mate copying for the evolution of male traits. Here I have assumed that females are influenced by the extent to which the males they observe mating successfully are different from average males in the population,  $\bar{z}_{\text{suc}} - \bar{z}$ . In the model, differences of the same magnitude but of differ-

ent sign can influence females by different amounts. This asymmetry is measured by  $\delta$ . The model also allows the magnitude of the difference,  $\bar{z}_{\text{suc}} - \bar{z}$ , to have a non-linear effect on female preference. This non-linearity is measured by  $i$ .

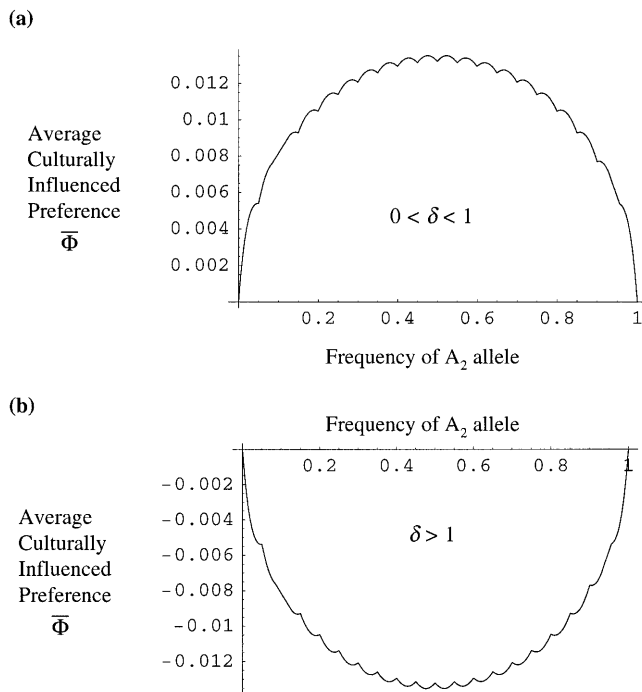
To focus on cultural forces, I first consider the case of no inherent preferences (i.e.,  $\alpha=0$ ). The results of the model are summarized in Table 1. The two variables of the cultural influence function (Eq. 2),  $\delta$  and  $i$ , have qualitatively different effects. Most females will observe common males mate successfully and, if the  $A_2$  allele is initially rare, the value of  $\bar{z}_{\text{suc}} - \bar{z}$  for these females will be small and negative. Nevertheless, some females will observe rare males mate successfully and the value of  $\bar{z}_{\text{suc}} - \bar{z}$  for these females will be large and positive. In determining the average cultural influence (Eq. 9), the frequency of these different observations is weighted by the amount of influence different types of observations have on females (Eq. 2). The distribution of male genotypes determines the frequency of the different observations (Eqs. 4, 5, and 6). The variables  $\delta$  and  $i$  in the cultural influence function (Eq. 2) determine the relative importance of these different observations. The variable  $\delta$  determines the importance of negative differences (i.e.,  $\bar{z}_{\text{suc}} - \bar{z} < 0$ ) relative to positive differences (i.e.,  $\bar{z}_{\text{suc}} - \bar{z} > 0$ ) of equal magnitude. The variable  $i$  determines the importance of small differences relative to large differences. When there is no asymmetry and no non-linearity (i.e.,  $\delta=1$  and  $i=1$ ), most females will be weakly influenced toward mating with common males whereas a small fraction of females will be strongly influenced toward mating with rare males. Under this condition, the net influence is zero and mate copying generates no selection on male traits.

If the observation of larger-than-average males mating has more cultural influence than the observation of smaller-than-average males mating (i.e.,  $0 \leq \delta < 1$ ), mate copying generates positive directional selection for larger male traits. Conversely, if the observation of smaller-than-average males mating has more cultural influence than the observation of larger than average males mating (i.e.,  $\delta > 1$ ), mate copying generates negative directional selection for larger male traits. In Fig. 2, the average cultural influence,  $\bar{\Phi}$ , is plotted as a function of the frequency of the  $A_2$  allele for different values of  $\delta$ .

**Table 1** Summary of results. The selection generated by mate copying depends on how different types of observations influence a female's preference as described by the variables  $\delta$  and  $i$  in the

cultural influence function (Eq. 2). See text for full discussion. The corners of the table are blank because the type of selection depends on the relative values of the two parameters

Coefficient of non-linearity, $i$	Coefficient of directional asymmetry, $\delta$		
	$0 \leq \delta < 1$	$\delta = 1$	$\delta > 1$
$0 < i < 1$		(Positive) frequency-dependent selection	
$i = 1$	Positive directional selection	No selection	Negative directional selection
$i > 1$		(Negative) frequency-dependent selection	



**Fig. 2a,b** The average cultural influence,  $\bar{\Phi}$ , for different values of  $d$ .  $\bar{\Phi}$  is plotted as a function of the frequency of the  $A_2$  allele and is calculated from Eq. 9 with  $c=1$  and assuming the distribution of male genotypes follows Hardy-Weinberg expectations. Although this assumption is not exactly accurate for sexually selected traits, the results of the simulations indicate that this approximation provides qualitatively correct plots. The parameter values used for these plots were  $i=1$  and  $n=10$ . a Negative differences (i.e.,  $\bar{z}_{\text{suc}} - \bar{z} < 0$ ) have less cultural influence than positive differences (i.e.,  $\bar{z}_{\text{suc}} - \bar{z} > 0$ ) of the same magnitude,  $d=0.7$ .  $\bar{\Phi}$  is always positive, indicating that mate copying generates positive directional selection in this case. b Negative differences have more cultural influence than positive differences of the same magnitude,  $d=1.3$ .  $\bar{\Phi}$  is always negative indicating that mate copying generates negative directional selection in this case

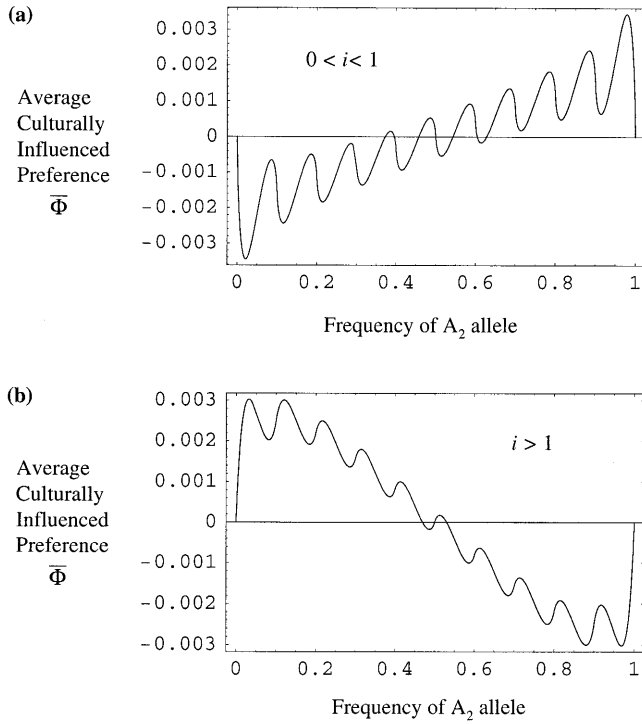
When the observation of successful males that are only slightly different from the mean has almost as much cultural influence as the observation of successful males that are much different than the mean ( $0 < i < 1$ ), mate copying generates selection that is similar to positive frequency-dependent selection. This type of selection occurs because most females are expected to observe successful males of the most common phenotype. By definition, these common males will only differ slightly from the mean phenotype. Because these small differences have almost as much cultural influence as larger differences and because most females observe the common males being successful, there is net selection favoring the common phenotype. The model of Kirkpatrick and Dugatkin (1994) is most analogous to this case. In their model, a female is influenced just as much by observing an average male mate as she is by observing a rare male mate. My model confirms their result that mate copying will generate selection against rare male phenotypes under these conditions.

When the observation of successful males that are only slightly different than the mean has a disproportionately small cultural influence relative to the observation of successful males that are much different than the mean ( $i > 1$ ), mate copying generates selection that is similar to negative frequency-dependent selection. In this case, the females that observe the common males being successful experience very little cultural influence. In contrast, the relatively few females who observe rare males being successful are strongly culturally influenced. These females are responsible for net selection favoring the rare male phenotype.

In Fig. 3, the average cultural influence,  $\bar{\Phi}$ , is plotted as a function of the frequency of the  $A_2$  allele for different values of  $i$ . Positive values of  $\bar{\Phi}$  indicate regions where mate copying generates selection to increase the frequency of the  $A_2$  allele whereas negative values indicate regions where mate copying generates selection to decrease the frequency of the  $A_2$  allele. The shapes of the curves in Fig. 3a, b resemble positive and negative frequency-dependent selection, respectively. Nevertheless, these curves are more complex than simple positive and negative frequency-dependent selection as they cross the  $\bar{\Phi} = 0$  axis multiple times. As a result, there are multiple interior equilibria. Intersections where the slope of the curve is negative represent stable equilibria. Even when  $0 < i < 1$  and mate copying tends to eliminate the rare phenotype (as in simple positive frequency-dependent selection), there can be stable interior equilibrium points (Fig. 3a).

The complex shapes of the curves in Figs. 2 and 3 may result from asymmetries and non-linearities in the preference function. These properties make the average cultural preference dependent on higher moments of the distribution of male phenotypes (e.g., variance, skew) as well as on the mean male phenotype. These higher moments change non-linearly with the mean male phenotype and thus their contribution to the average cultural preference will also change non-linearly.

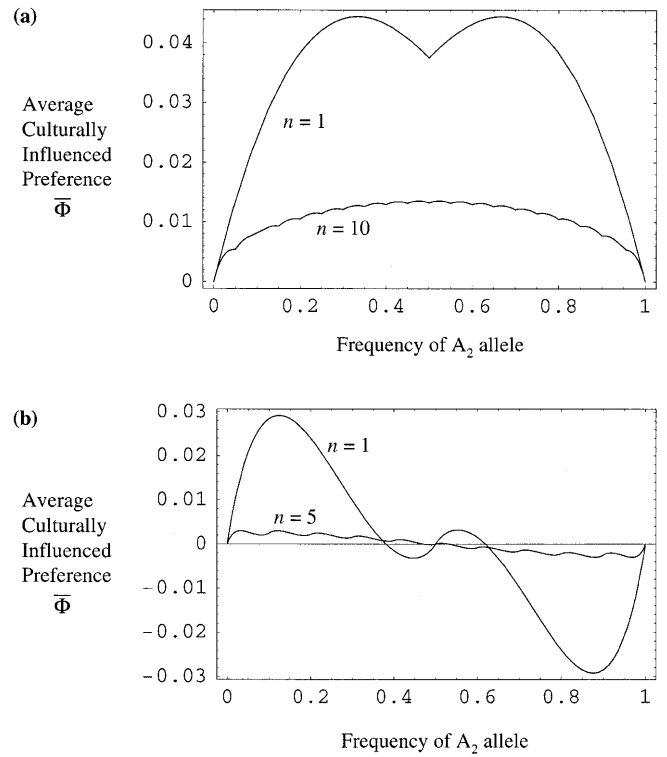
The number of males that a female observes mating,  $n$ , affects the strength of selection (Fig. 4). In contrast to the Kirkpatrick and Dugatkin (1994) model, when females observe fewer matings, selection generated by mate copying becomes stronger in my model. When each female makes only a few observations (low  $n$ ), there will be more variance in what different females observe than if each female were to make many observations (i.e., sampling variance increases as sample size decreases). Consider the extreme case where females see all the initial matings (very large  $n$ ) and have no inherent preference ( $\alpha=0$ ). If the initial matings occur at random, all females observe males mating in proportion to the frequency of male phenotypes. In this case,  $\bar{z}_{\text{suc}} - \bar{z} = 0$  for all females and there is no selection generated by mate copying. The smaller the sample of observations made by each female, the more these samples will differ from the actual mean as well as from each other. As the variance in observations among females increases, cultural influence becomes more capable of generating sexual selection.



**Fig. 3a,b** The average cultural influence,  $\bar{\Phi}$ , for different values of  $\delta$ .  $\bar{\Phi}$  is plotted as a function of the frequency of the  $A_2$  allele and is calculated from Eq. 9 with  $c=1$  and assuming the distribution of male genotypes follows Hardy-Weinberg expectations. Although this assumption is not exactly accurate for sexually selected traits, the results of the simulations indicate that this approximation provides qualitatively correct plots. The parameter values used for these plots are  $d=1$  and  $n=5$ . **a** The observation of successful males that are slightly different from the mean has almost as much cultural influence as the observation of successful males that are much different from the mean,  $\delta=0.9$ . Although the shape of the curve is complex, in general,  $\bar{\Phi}$  is negative when the  $A_2$  allele is rare but positive when the  $A_2$  allele is common. Mate copying generates selection against  $A_2$  when it is rare but selection favoring  $A_2$  when it is common. **b** The observation of successful males that are slightly different from the mean has a disproportionately small amount of cultural influence relative to the observation of successful males that are much different from the mean,  $\delta=1.5$ . In general,  $\bar{\Phi}$  is positive when the  $A_2$  allele is rare but is negative when the  $A_2$  allele is common. Mate copying generates selection favoring  $A_2$  when it is rare but selection against  $A_2$  when it is common

The strength of selection on an entire population generated by mate copying is also affected by  $m$ , the fraction of matings that occur before any cultural influence. When  $m$  is large, most matings occur without any cultural influence and the importance of mate copying is limited because it only affects the remaining fraction of matings,  $1-m$ . Conversely, if  $m$  is small, then most matings will be affected by cultural influence and mate copying can play an important role in the evolution of male traits.

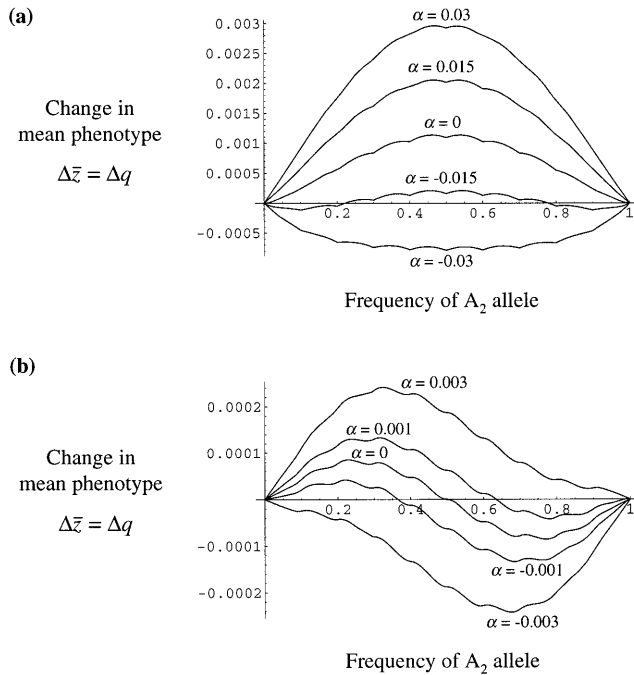
Inherent preference, when it exists, can affect male mating success both indirectly and directly. First, inherent preference indirectly affects net preference by altering culturally influenced preference. Cultural influence



**Fig. 4a,b** The average cultural influence,  $\bar{\Phi}$ , for different values of  $n$ .  $\bar{\Phi}$  is plotted as a function of the frequency of the  $A_2$  allele. Average cultural influence is generally stronger when females observe a smaller number of matings.  $\bar{\Phi}$  is calculated from Eq. 9 with  $c=1$  and assuming the distribution of male genotypes follows Hardy-Weinberg expectations. Although this assumption is not exactly accurate for sexually selected traits, the results of the simulations indicate that this approximation provides qualitatively correct plots. **a**  $\delta=0.7$  and  $i=1$ .  $\bar{\Phi}$  is plotted for  $n=1$  and  $n=10$ . **b**  $\delta=1$  and  $i=0.5$ .  $\bar{\Phi}$  is plotted for  $n=1$  and  $n=5$

is determined by the males that females observe mating. If there is an inherent preference, then the inherently preferred males will be over-represented in these initial matings (i.e., by Eqs. 4, 5, and 6,  $G_{11}^* \neq G_{11}$ ,  $G_{12}^* \neq G_{12}$ , and  $G_{22}^* \neq G_{22}$  if  $\alpha \neq 0$ ). Because cultural influence depends on  $G_{11}^*$ ,  $G_{12}^*$ , and  $G_{22}^*$  (Eqs. 8, 9), inherent preference indirectly affects male mating success through the  $\bar{\Phi}$  term in Eqs. 10, 11, and 12. For example, if there is an inherent preference favoring (disfavoring) the  $A_2$  allele, then this allele will be over- (under-)represented in the successful males of the initial  $m$  matings. The average cultural preference in a population with inherent preference for (against) the  $A_2$  allele will be similar to a population with no inherent preference but with a higher (lower) frequency of the  $A_2$  allele. Thus inherent preference will change the magnitude and possibly the sign (if  $i \neq 1$ ) of average cultural preference.

In addition, inherent preference, by definition, directly affects net female preference (the  $\alpha z$  term in Eq. 1). This effect has direct consequences for male mating success and is the source of the  $\alpha$  terms in Eqs. 10, 11, and 12. Because of these direct and indirect effects, it will be difficult for cultural influences to oppose a strong inher-



**Fig. 5a,b** Culturally influenced preference and inherent preference. The change in the mean phenotype is plotted as function of the frequency of the  $A_2$  allele. Different inherent preference values are shown in combination with different cultural influence functions. Values are plotted from Eq. 17 assuming genotypes follow Hardy-Weinberg expectations and with  $m=0.05$ ,  $n=5$ ,  $c=1$ . **a**  $\delta=0.7$  and  $i=1$ . **b**  $\delta=1$  and  $i=2$

erent preference. Figure 5 shows the change in the frequency of allele  $A_2$  for inherent preferences of varying strength and sign. Inherent preference can change the magnitude and sign of evolution.

Little is known about the details of how females are influenced by their observations of other individuals. My model shows that these details determine the consequences of mate copying for the evolution of male traits. The fundamental empirical issue is whether females are influenced equally by all types of observations or if some types of observations are more influential than others. Experiments could be designed to detect asymmetries and non-linearities in the degree of influence caused by different types of observation. For example, consider tail length in males as the focal trait and assume that average tail length is 10 cm. After allowing naive females to observe a number of males with average tail length, each female would be allowed to view one of five male types mate. The four male types would have tail lengths of 5, 7.5, 12.5, and 15 cm. After this observation, the preference for males with 5- versus 15-cm tails would be measured for each female. Cultural influence would be measured as the extent to which females with an observational experience have different preferences than control females with no observational experience.

Asymmetry occurs if females that observed males with short tails mate are influenced more towards short-

tailed males than females that observed males with long tails [i.e., the magnitude of cultural influence of females who observed 5-cm (or 7.5-cm) tail males mate is significantly different than females that observed 15-cm (or 12.5-cm) tail males]. If females that observed long-tailed males are influenced less than females that observed short-tailed males, then  $0 \leq \delta < 1$ . Alternatively, if females that observed long-tailed males are influenced more than females that observed short-tailed males, then  $\delta > 1$ .

Non-linearity occurs if females that observed the mating of males with tails 2.5 cm greater (less) than average are influenced either significantly more or significantly less than half as much as females that observe males that are 5 cm greater (less) than average. If females that observe the mating of males with tails 2.5 cm greater (less) than average are influenced more than half as much as females that observe males that are 5 cm greater (less) than average, then  $0 \leq i < 1$ . Conversely, if females that observe males mate whose tails are 2.5 cm greater (less) than average are influenced less than half as much as females that observe males that are 5 cm less (greater) than average, then  $i > 1$ .

My model demonstrates that mate copying can have variable effects on the evolution of male traits. Positive and negative directional selection as well as positive and negative frequency-dependent-type selection are all possible outcomes of mate copying. With the appropriate cultural influence function, mate copying can generate directional selection allowing a novel male trait to sweep through the population to fixation, even when there is no inherent preference for this trait. An alternative cultural influence function can cause mate copying to generate selection to favor rare phenotypes and thus maintain variation for male traits. If the observation of successful males that are only slightly different than the mean influences females almost as strongly as the observation of successful mates that are much different from the mean, my results produce similar results to those of Kirkpatrick and Dugatkin (1994) (i.e., selection against rare phenotypes). With regard to sexual imprinting (i.e., biasing mating preference toward phenotypes similar to those of close relatives), previous authors have argued for the importance of asymmetries in the influence transmitted by different types of observations (ten Cate and Bateson 1988; Laland 1994). In general, my model shows that evolutionary effects of mate copying depend on the details of how females are influenced by the males they observe mating. These details can change the strength, direction, and form of selection acting on male traits.

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