

# Müllerian mimicry: an examination of Fisher's theory of gradual evolutionary change

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In 1927, Fisher suggested that Müllerian mimicry evolution could be gradual and driven by predator generalization. A competing possibility is the so-called two-step hypothesis, entailing that Müllerian mimicry evolves through major mutational leaps of a less-protected species towards a better-protected, which sets the stage for coevolutionary fine-tuning of mimicry. At present, this hypothesis seems to be more widely accepted than Fisher's suggestion. We conducted individual-based simulations of communities with predators and two prey types to assess the possibility of Fisher's process leading to a common prey appearance. We found that Fisher's process worked for initially relatively similar appearances. Moreover, by introducing a predator spectrum consisting of several predator types with different ranges of generalization, we found that gradual evolution towards mimicry occurred also for large initial differences in prey appearance. We suggest that Fisher's process together with a predator spectrum is a realistic alternative to the two-step hypothesis and, furthermore, it has fewer problems with purifying selection. We also examined the factors influencing gradual evolution towards mimicry and found that not only the relative benefits from mimicry but also the mutational schemes of the prey types matter.

**Keywords:** Müllerian mimicry; two-step hypothesis; predator spectrum; advergence; coevolution

## 1. INTRODUCTION

Warning colouration, also called aposematic colouration, can be used by prey to signal unprofitability to a potential predator (Rettenmeyer 1970; Ruxton *et al.* 2004). Predators may have an inherited aversion towards aposematic prey (Shuler & Hesse 1985; Gamberale & Tullberg 1998), or may learn to recognize them as unprofitable by sampling the prey population. During this sampling process, avoidance learning takes place, in which the predator learns to associate the characteristic appearance of the prey with its unprofitability (Gittleman & Harvey 1980). Other species with appearances similar to an aposematic species can profit from the similarity, as the attack probability for the similar prey type can also be reduced, by predators generalizing over prey appearances. This benefit of looking similar can result in evolution towards increased similarity and the establishment of mimicry. Bates (1862) introduced the theory of so-called Batesian mimicry, which entails the mimicry of aposematic signals by palatable species. Mimicry between unpalatable species on the other hand, is referred to as Müllerian mimicry, and is usually considered to be mutualistic (Benson 1977). The theory was first put forward by Müller (1879) and was based on the assumption that a predator needs a certain number of trials of attacking aposematic prey before learning to totally avoid prey with this appearance. Consequently, if several aposematic species take part in the process of educating predators by looking similar, the attack probability on the individuals of each species will be diluted, increasing the survival per capita.

Currently, there is limited knowledge of the evolutionary path towards Müllerian mimicry, although the most

widely accepted idea seems to be that mimicry evolution is initiated by major mutational leaps of one species towards another. The idea of this kind of unidirectional evolution was introduced by Marshall (1908), and further emphasized by Punnett (1915), who argued for an extreme case of saltational evolution, claiming that a mutation needs to land the mimetic pattern precisely on target for mimicry to be selected for. As a compromise, Nicholson (1927) proposed the two-step hypothesis, entailing that mimicry evolves in two stages. A major mutational leap of a mimic towards a model first establishes approximate similarity and is then followed by gradual evolutionary change. The two-step hypothesis has subsequently become widely accepted (Turner 1984; Sheppard *et al.* 1985; Joron 2003). The argument for the necessity of major mutational leaps to initiate the evolution of Müllerian mimicry rests on an assumption of purifying selection from narrowly generalizing predators: when the initial appearances of the future comimics are far apart in trait space, a small mutation that makes individuals only slightly different from the average appearance of their species will be selected against, as such individuals will not be similar enough to any other protected species to compensate for the loss of protection of their own species.

A contrasting idea has been that mimicry evolution is gradual (Fisher 1927, 1930 pp. 146–169), and driven by predator generalization. Considering a protected species, Fisher took as a starting point that variation is equally frequent in either of two directions around the mean appearance. Deviations in both directions could be expected to lose protection equally, but with another protected species present, variation in the direction towards that appearance might benefit from the increased similarity. Selection thus favours variation in that direction and leads to a slight displacement of the appearance

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gaining maximum survival. We will refer to this displacement as a peak shift. The term peak shift is typically used in animal psychology to describe a bias in generalization around a positive stimulus along a dimension, in the direction away from a negative stimulus (Hanson 1959; Mackintosh 1974), and here we use the same term to denote an analogous bias in avoidance around a negative stimulus in the direction of another negative stimulus. This peak shift could, according to Fisher, initiate gradual evolutionary change, and eventually lead to the establishment of Müllerian mimicry. With some exception (Sheppard *et al.* 1985; Turner 1987), Fisher's suggestion has been ignored in recent thinking about Müllerian mimicry.

The extent to which Müllerian mimicry evolution is saltational or gradual can affect the question of which species mimics another. As a consequence of different degrees of protection of species subject to mimicry evolution, resulting from differences in population density or in unpalatability, they might benefit and thus evolve towards each other to different extent. Consider first gradual evolution of two species, initially distinct in appearance. If both species are equally protected by their aposematic colouration, they might converge onto an intermediate appearance through a coevolutionary process. If unequally protected, the less-protected species will be more strongly selected to change its appearance, which might speed up its rate of evolution, while the better-protected species might evolve more slowly or perhaps not at all. Such an evolutionary process involves a lesser degree of coevolutionary convergence and a larger degree of unilateral evolution, referred to as advergence (Brower & Brower 1972). Thus, if gradual evolution of Müllerian mimicry is possible, the evolutionary path might be characterized either by advergence or coevolutionary convergence, depending on the initial protection of the species involved. However, if the evolutionary process mainly consists of mutational leaps, advergence should dominate in the establishment of Müllerian mimicry. For two unequally protected species, the only possible saltational change is for the less protected to admerge to the better protected.

The purpose of this work is to investigate if gradual evolutionary change is possible, as proposed by Fisher (1927), when the future comimics are subject to purifying selection from narrowly generalizing predators, and to evaluate the effect of gradual change on the issue of coevolutionary convergence versus advergence. As an alternative to the two-step hypothesis, we introduce the idea of a predator spectrum, meaning that several types of predators with different generalization abilities prey upon the future comimics. We suggest that a predator spectrum can favour gradual evolution of Müllerian mimicry. At the start, when the future comimics are distinct in appearance, predators that generalize broadly, for instance more generalistic predator species or more naive individuals, might initiate the process, exerting selection making the prey species gradually approach approximate similarity without suffering strong purifying selection from narrowly generalizing predators. More narrowly generalizing predators might then play a role in fine-tuning mimicry to more accurate similarity. To test these ideas, we have conducted individual-based simulations of prey evolution in communities with two prey species and one or two

predator species. We also examine the gradual evolutionary paths with respect to the degree of advergence as a consequence of unequal protection, taking into account the mutational schemes of the species. Based on our results, we then discuss the relative likelihoods of the two competing hypotheses of mimicry evolution and the factors leading to advergence.

## 2. MODEL DESCRIPTION

In developing the model, we have taken into account previous work on modelling mimicry (e.g. Turner *et al.* 1984; Gavrilets & Hastings 1998; Holmgren & Enquist 1999; Speed & Turner 1999; Sasaki *et al.* 2002; Franks & Noble 2004). In our model, the predators are capable of avoidance learning and generalization and the two prey types can differ in appearance, degree of unpalatability and population size. Predators learn to avoid unpalatable prey through remembering attacks on them, using their experience in encounters with prey similar to those attacked earlier. Surviving prey individuals reproduce at the end of the season and die. Their reproductive success and contribution to the next generation will then only depend on escaping predation. The model was analysed using individual-based Monte Carlo simulations.

The experience of a predator with respect to food choice includes prey appearance, expressed as a one-dimensional property  $x$  (this could, for example, be a signal in the form of colouration) and prey unpalatability  $y$ . We describe the predator's experience as a list of the prey  $(x_i, y_i)$  it has attacked. The probability of the predator attacking a discovered prey with the appearance  $x$ , given its experience, is written as  $q(h)$ , where  $h$  is a variable describing the state of the predator as follows ( $n$  being the number of attacked prey):

$$h(x) = \sum_{i=1}^n g_{\sigma}(x - x_i)y_i. \quad (2.1)$$

We can think of  $h$  as the degree of attack inhibition towards prey with trait  $x$ .

The function  $g_{\sigma}(x - x_i) = \exp[-(x - x_i)^2/2\sigma^2]$  is a Gaussian centred on  $x_i$  with width  $\sigma$  and describes the generalization of the predator in the trait space consisting of all  $x$ -values. The expression (2.1) means that the predator accumulates inhibition for every attack on unpalatable prey. The amount of inhibition towards the appearance  $x$  gained from an attack on a prey individual with  $(x_i, y_i)$  depends on the degree of generalization from the familiar type  $x_i$  and on its unpalatability  $y_i$ . For the attack probability  $q(h)$  we use

$$q(h) = \frac{e^{-s(h-h_0)}}{e^{-s(h-h_0)} + 1}. \quad (2.2)$$

For large positive  $s$ , the function  $q(h)$  has a step-like shape that corresponds to classical Müllerian number-dependent predation, but other shapes may also be used, corresponding to different kinds of avoidance learning. The parameter  $h_0$  is the inflexion point of the curve and  $s$  is a measure of the steepness of  $q(h)$  at this point. In a purely number-dependent case, where  $q(h)$  declines abruptly from 1 to 0, the predator would need to attack  $h_0/y$  of a certain prey type before learning to totally avoid it, that is, reaching attack probability  $q(h)=0$ . More precisely,

the maximum number of attacked prey individuals would be the nearest integer larger than  $h_0/y$ .

The predator–prey community consists of  $N_p$  predators and two prey types  $a$  and  $b$  with fixed unpalatabilities  $y_a$  and  $y_b$  and population sizes  $N_a$  and  $N_b$  at the start of each season. An individual predator independently discovers prey at a rate  $u$  per unit time and prey individual, regardless of prey appearance. The population sizes  $N_a(t)$  or  $N_b(t)$  change after every time a predator attacks prey of either type (attacks are always fatal). The duration  $T$  of a season is divided into small intervals  $\Delta t$  of time. The probabilities  $P_a$  and  $P_b$  of an individual predator discovering prey types  $a$  and  $b$  in a time interval are

$$P_a = u\Delta t N_a(t), \quad (2.3)$$

and

$$P_b = u\Delta t N_b(t). \quad (2.4)$$

By choosing the time interval  $\Delta t$  small enough so that both  $P_a$  and  $P_b$  are considerably smaller than one (e.g. around 0.1 or smaller), we can ignore the possibility of several discoveries during  $\Delta t$ . The probability of no prey being discovered is then

$$P_{\text{none}} = 1 - (P_a + P_b). \quad (2.5)$$

On discovery of a prey individual with appearance  $x$ , the probability of attack is computed by determining the state of the predator according to equation (2.1) and then using equation (2.2). If there is an attack, the event is added to the predator's experience. This is repeated for each predator, after which the next time interval is handled in the same way, until the end of the season.

At the start of a simulation, the prey populations are monomorphic with appearances  $x_a$  and  $x_b$ . Prey individuals reproduce asexually and have a genotype determining their appearance  $x$ . The  $N_a$  and  $N_b$  individuals of the next generation are formed by randomly selecting (with replacement) parents among the survivors from the respective population. Mutations occur with a probability of 0.0005 and mutational increments in  $x$  are drawn from a reflected exponential distribution (cf. Orr 1998) with standard deviation  $\sigma_m$ . Unless specified otherwise, we used the following parameter values in the simulations:  $u=0.04$ ,  $N_p=100$ ,  $N_a=1000$ ,  $N_b=5000$ ,  $\sigma=1.0$ ,  $s=2.0$ ,  $h_0=2.5$ ,  $\sigma_m=0.1$ .

### 3. RESULTS

#### (a) Gradual evolution towards Müllerian mimicry

We assessed the possibility of a gradual evolutionary process towards Müllerian mimicry using two populations  $a$  and  $b$  of prey that were equally unpalatable ( $y_a=y_b=1$ ). The population sizes differed by a factor of five,  $b$  being the larger population. To illustrate the scope for gradual change, mutant fitness at the starting point of different simulations are shown in figures 1 and 2, and the resulting evolutionary trajectories are shown in figure 3.

For a case with fairly similar initial appearances of the two prey types, predator generalization caused the peaks of survival around the resident trait values to be slightly shifted towards each other (figure 1a). The consequence of this peak shift for gradual change can be illustrated by looking at invasion fitness for the two prey populations (figure 2a). Invasion fitness is the per generation rate of

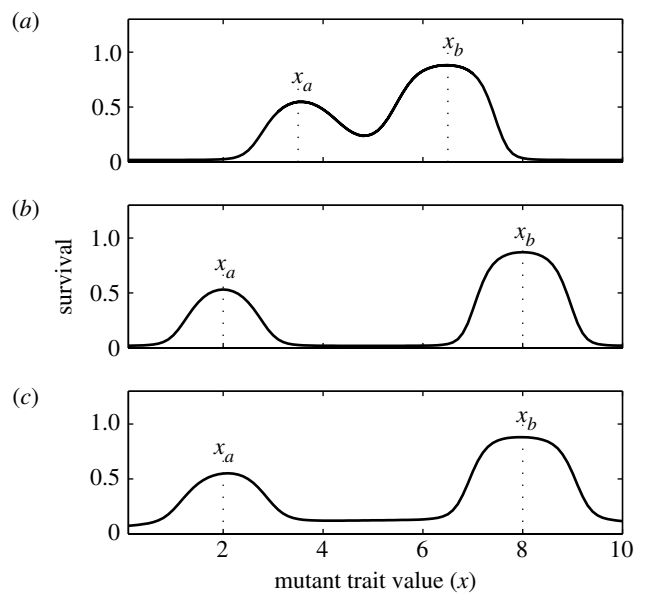


Figure 1. Mutant survival in a situation with two resident prey types, with trait values  $x_a$  and  $x_b$ . The curves give the probability of survival over a season for a single mutant individual with trait value  $x$ . The difference in survival between the two prey types is caused by unequal protection from population sizes ( $N_a=1000$ ,  $N_b=5000$ ). (a) The trait values of the two resident types are relatively close together ( $x_a=3.5$  and  $x_b=6.5$ ). Predator generalization ( $\sigma=1.0$ ) causes the survival peaks around the resident types to be slightly shifted towards each other. (b) When the resident trait values are further apart ( $x_a=2.0$  and  $x_b=8.0$ ), the peak shift is very small, leading to very weak selection for gradual change. A saltational mutation from  $x_a$  to the neighbourhood of  $x_b$  could however invade, corresponding to advergence of type  $a$  towards type  $b$ . (c) With a spectrum of predators, some of which generalize more broadly (for half of the predators we used  $\sigma=1.0$  and for the other half  $\sigma=3.0$ ), there is noticeable peak shift also with initial trait values that are further apart ( $x_a=2.0$ ,  $x_b=8.0$ ).

change of the logarithm of the size of a rare mutant subpopulation (Metz *et al.* 1992), which in our case is given by the logarithm of the ratio mutant survival/resident survival (so that invasion fitness of the resident trait itself will be zero). In figure 2a, the invasion fitness is positive for mutants of type  $a$  in the direction towards type  $b$ , and the same holds for mutants of type  $b$  towards type  $a$ , but over a narrower interval in trait space. This set the stage for a gradual process of mimicry evolution, depicted in figure 3a.

For two prey populations that are more separated in trait space, figure 1b shows that peak shift is quite small, which is seen more clearly from invasion fitness in figure 2b. The consequence, as illustrated by the evolutionary trajectory in figure 3b, was that no evolution towards mimicry occurred, at least not over the time span of our simulation.

We then analysed the influence of a predator spectrum on the evolution of Müllerian mimicry. We used two types of predator with different generalization widths  $\sigma$  and used the same initial prey appearances as in figure 1b. The effect of this predator spectrum was that the survival peaks were slightly shifted towards each other (figure 1c), and the invasion fitness (figure 2c) of mutants of both prey types was positive over wider intervals compared to using only one type of predator. This peak shift was sufficient to

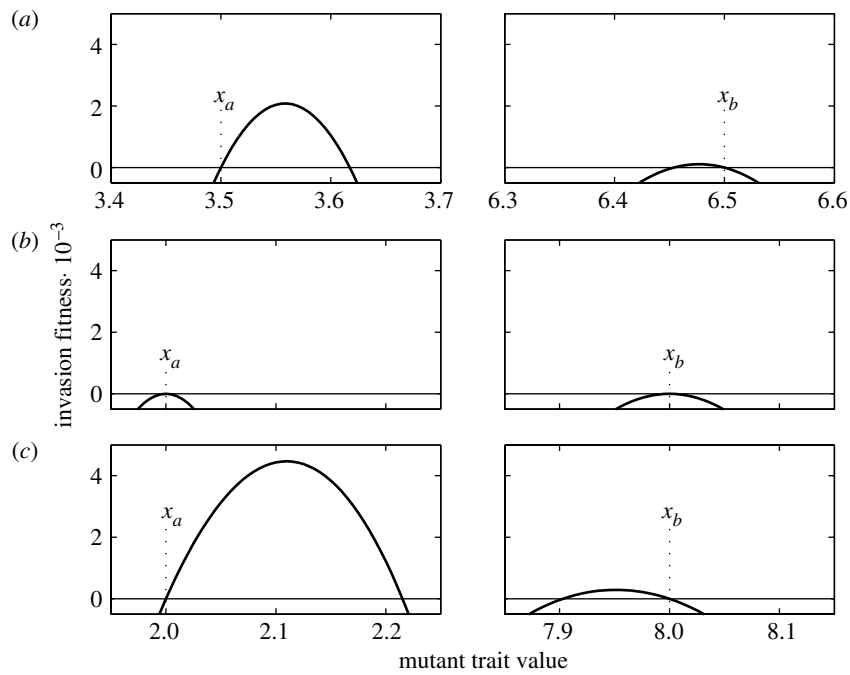


Figure 2. Invasion fitness for the three situations illustrated in figure 1. (a) When resident traits are fairly close to each other ( $x_a=3.5$  and  $x_b=6.5$ ), mutants of type *a* in the interval 3.50–3.62 can invade, while mutants of type *b* can invade in the narrower interval 6.45–6.50. Mutants of type *a* have a maximum invasion fitness of  $2.1 \times 10^{-3}$  at  $x=3.56$ , while mutants of type *b* have a smaller maximum invasion fitness of  $0.2 \times 10^{-3}$ , located at  $x=6.48$ , closer to their resident trait value. (b) When resident traits are further apart ( $x_a=2.0$  and  $x_b=8.0$ ), the intervals where mutants are selected for become very narrow and the positive values of invasion fitness are quite small. (c) A spectrum of predators dramatically increases the widths of the intervals with positive invasion fitness, as well as the maximum values.

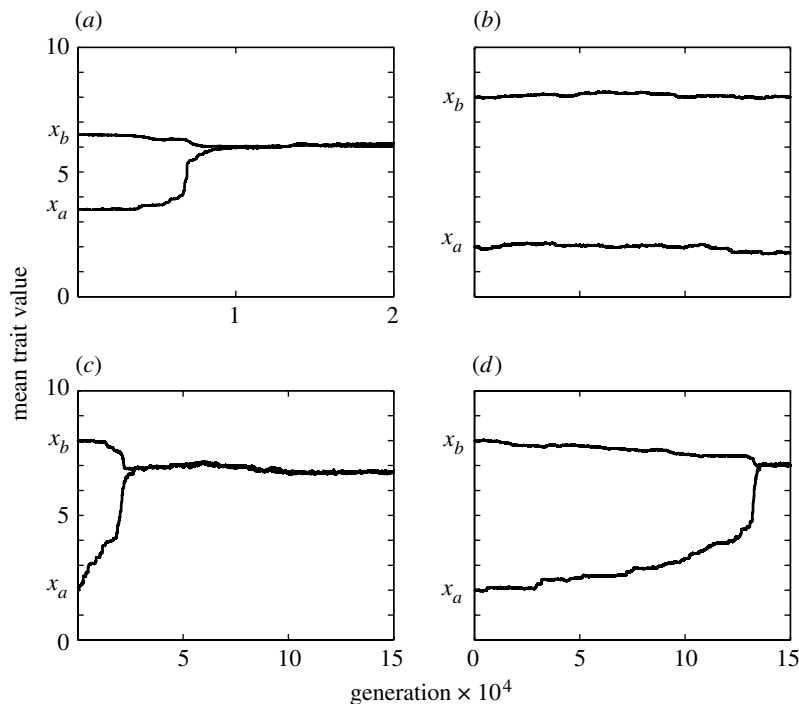


Figure 3. Gradual evolution of prey appearances for the situations illustrated in figures 1 and 2. The trajectories of  $x_a$  and  $x_b$  are average trait values as a function of time for the two prey populations. (a) Fisher's process is possible for  $x_a$  and  $x_b$  sufficiently close in trait space. (b) When the distance between initial traits increases, selection is insufficient to initiate evolution towards mimicry. (c) When a spectrum of predators is used (50% of each type), evolution leads to mimicry also for the initial trait values used in *b*. (d) Mimicry also evolves when a smaller part of the predators (15%) generalize more broadly. Note that the scale of the *x*-axis in (a) differs from those in (b), (c) and (d).

initiate gradual evolution, and the evolutionary trajectory (figure 3c) shows that accurate Müllerian mimicry was attained even for these more distinct initial appearances. Additionally, we tried a case with parameters identical to

those in figure 3c, but with a smaller proportion of broadly generalizing predators (figure 3d), and mimicry evolved also under these conditions. This result suggests that there are conditions under which Müllerian mimicry

could evolve gradually, according to Fisher's (1927) theory.

In our simulations, there was a possibility that mimicry could have been established by saltational evolution, as (though not shown in figure 2) the invasion fitness of mutants of type  $x_a$  increased and became larger than zero close to the resident trait of type  $x_b$ . This means that sufficiently large mutations, besides small ones, could invade. Nevertheless, we observed no such saltational evolutionary change in our simulations for figure 3 (nor in those for figure 4 below), most likely because the required mutations occurred too rarely to influence the evolutionary trajectory. However, using a rectangular distribution of mutational increments with a range large enough to cover the appearances of both prey types resulted in saltational change.

#### (b) Advergence versus coevolutionary convergence

We investigated the degree of advergence, i.e. the extent to which one prey type evolved towards the other, both for different relative population sizes and for different relative unpalatabilities. We defined the degree of advergence of type  $a$  towards type  $b$  as

$$\frac{x_m - (x_a + x_b)/2}{(x_b - x_a)/2},$$

where  $x_m$  is the final appearance when mimicry is attained. The degree of advergence would then be equal to one when the evolutionary approach of type  $a$  towards type  $b$  is total, equal to zero for complete convergence to an intermediate appearance, and equal to minus one for a total approach of type  $b$  towards type  $a$ . We used the same conditions as in figure 1a with respect to initial prey appearances, unpalatabilities and predator generalization. Varying the size of population  $b$  led to a varying degree of advergence. Equal population sizes led to coevolutionary convergence while large differences in population size produced more advergence of the less-protected prey type towards the better-protected prey type (figure 4).

How much advergence a certain difference in population size gives rise to might depend on the size of the mutational increments. Such an effect could be predicted from the invasion fitness in figure 2, where the maximum value of the invasion fitness sets the optimal size of mutations for driving the evolutionary process. To investigate this dependence, we used three different widths of the distribution of mutational increments (same for both prey types),  $\sigma_m = 0.5$ ,  $\sigma_m = 0.1$  and  $\sigma_m = 0.02$ . The broadest width produced the largest degree of advergence (figure 4), while the narrowest width produced least advergence. The explanation might be that the mutational effect sizes drawn from the broadest distribution were more optimal for type  $a$  than for type  $b$ . For type  $b$ , most mutations would be too large to invade, because of purifying selection. The smaller mutations of the other distributions increased the evolutionary potential of type  $b$  relative to type  $a$ , reducing the difference between their rates of evolution. This implies that the degree of advergence, and thus the coevolutionary component of a gradual evolutionary process, not only depends on the relative protection of the prey types (their fitness landscapes in figure 1), but also on their mutational schemes. This applies also when using a predator spectrum. We found a smaller degree of advergence when two types of

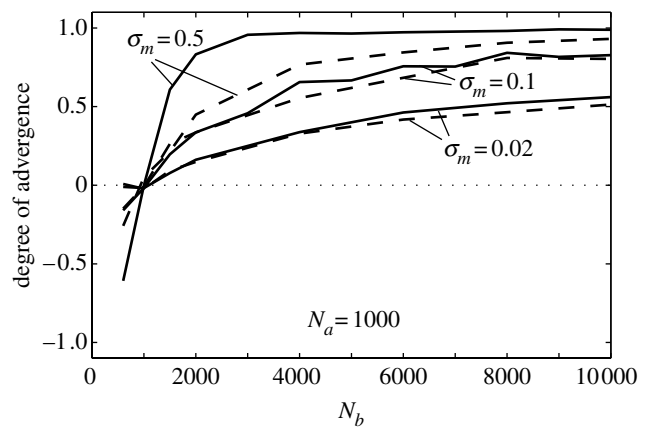


Figure 4. Degree of advergence as a function of relative population size. The population size of type  $a$  was kept constant at 1000 individuals while the population size of type  $b$  was varied. Every point is an average of the degree of advergence of 30 simulations. The curves correspond to different distributions of mutational increments. For all three distributions, the degree of advergence is greater for larger population size differences. The degree of advergence at a given population size difference decreases with decreasing range of mutational size distributions. Using a predator spectrum (dashed lines) further decreases the degree of advergence, in particular for the distribution with  $\sigma_m = 0.5$ .

predators were used in simulations corresponding to the situation in figure 1c, using the same three widths of mutational increment distributions as before (figure 4).

Comparing the effect of relative unpalatability to the effect of relative population size, we found that when one species was twice as common than the other (for equal unpalatabilities) less advergence was produced than when the species was twice as unpalatable as the other (for equal population sizes) when mutation rates were low (0.0005). Increasing mutation rates (to 0.01) erased this difference in resulting advergence between the two kinds of protection. The reason for this phenomenon is probably that for low mutation rates, evolution could be mutation limited (Dieckmann & Law 1996). For unequal population sizes, evolution of a large population may speed up as a larger population produces more mutants, which then could decrease the degree of advergence. For unequal unpalatabilities, an effect of the supply of mutations will not be present, and for higher rates of mutation, the speed of evolution will no longer be constrained by the supply of mutations.

#### 4. DISCUSSION

We found that gradual evolution of Müllerian mimicry according to Fisher's (1927) theory is possible for initially relatively similar prey appearances, and also for more distinct appearances provided there is a predator spectrum. The evolution towards mimicry in our simulations consisted only of small mutations that were favoured by peak shift, while major mutations did not contribute even if there was a possibility for their occurrence. Selection for similarity in appearance was weak at the beginning of the evolutionary process but became stronger as similarity increased. The final adjustments of similarity just before reaching accurate mimicry were fast but still gradual and happened during a few hundred generations. Based on our results, we suggest that gradual evolution under

the influence of a predator spectrum is a quite realistic alternative to the two-step hypothesis, since it is likely that different predators generalize differently, as a consequence of being different species or having different previous experiences, and that several kinds of predators are present as selective agents for a future Müllerian mimicry association. It seems to us that the two-step hypothesis is fraught with greater problems from purifying selection compared to gradual evolution. It is generally thought that accurate mimicry is the result of narrowly generalizing predators, but for the two-step process to succeed in the face of purifying selection from such predators, the first saltational leap must reach close to the appearance of the model, more or less as envisaged by Punnett (1915). This seems rather unlikely, in particular if one takes into account that mimicry occurs in a multi-dimensional trait space. For the two-step hypothesis to be a realistic alternative, the first saltational step should thus occur in the absence of sharply discriminating predators. These predators should then appear later in the process and fine-tune the mimicry. Since predator faunas might well fluctuate over time and space, such a scenario is not impossible. Nevertheless, given that different kinds of predators, some of which generalize fairly broadly, are needed both for the two-step hypothesis and for Fisher's suggestion, the latter seems to have the upper hand. For gradual evolution of Müllerian mimicry, small mutants escape strong purifying selection by being similar in appearance to their own type, so this process works also in the presence of narrowly generalizing predators.

We used a Gaussian-shaped predator generalization function, which has a zero derivative at the central point. This property is essential for Fisher's process to work, since the zero-derivative point in trait space is displaced giving rise to peak shift. Different shapes of generalization functions have been discussed in animal psychology, for instance, a reflected exponential with an abrupt change of the derivative at the central point, and Gaussian, and current empirical knowledge favours Gaussian shapes (Girlanda & Enquist 2003). A generalization function with an abrupt change in the derivative at the central point has been previously used to model mimicry evolution (Franks & Noble 2004), but such a shape prevents Fisher's process from operating as the generalization function lacks the zero-derivative point needed for peak shift. The maximum of this form of generalization function occurs at a point where the derivative changes abruptly from a positive to a negative value, and although these values can be somewhat perturbed by the presence of a nearby generalization peak, there will still be an abrupt change in the derivative at the point, implying that the maximum stays in the same position.

While the two-step hypothesis mainly leads to advergence in Müllerian mimicry, a gradual process admits both advergence and coevolutionary convergence, and the degree of advergence seems to depend on several factors. In our simulations, population size difference was a fairly good predictor of advergence, but according to our results, the degree of advergence is affected not only by initial differences in protection of the species from population size or unpalatability, but also by the evolutionary potential of a population with respect to the production of mutants and the distribution of mutational effect sizes. Small mutations will be selected for, while mutations large

enough to reach beyond the interval where invasion fitness is positive will be subject to purifying selection (figure 2). The degree of advergence will then depend on how well the mutational effect sizes of a species match the distance from the resident trait value to the trait value gaining maximum invasion fitness. In addition, the picture might be further complicated by the fact that when the probability of mutation is small, evolution could be mutation limited. Under mutation limitation, the larger, better-protected population will have a greater evolutionary potential than the smaller, less-protected because it produces more mutations. This could lead to a decrease in the degree of advergence for large population size differences, compared to a situation in which evolution is not mutation limited. A consequence of this possible dependence of evolutionary potential on population size could be that large differences in unpalatability might be a better predictor of advergence than large differences in abundance.

A conclusion from our results could be that coevolutionary change in Müllerian mimicry evolution is fairly common. Nevertheless, approximate advergence through gradual change can occur, but some degree of coevolution should contribute to the process. There is so far no empirical evidence for coevolution in Müllerian mimicry, while there are examples of Müllerian mimicry that seem to have come about through advergence (Mallet 1999). However, the question cannot yet be considered resolved, as advergence could be explained by either gradual or saltational evolutionary change. In addition, there might be other explanations for advergence in Müllerian mimicry systems, such as quasi-Batesian relationships (Speed 1993; Ruxton *et al.* 2004, pp. 164–171) or effects of spatial dynamics and gene flow.

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