

EVOLUTIONARY IMPLICATIONS OF THE FORM OF PREDATOR GENERALIZATION FOR APOSEMATIC SIGNALS AND MIMICRY IN PREY

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Generalization is at the heart of many aspects of behavioral ecology; for foragers it can be seen as an essential feature of learning about potential prey, because natural populations of prey are unlikely to be perfectly homogenous. Aposematic signals are considered to aid predators in learning to avoid a class of defended prey. Predators do this by generalizing between the appearance of prey they have previously sampled and the appearance of prey they subsequently encounter. Mimicry arises when such generalization occurs between individuals of different species. Our aim here is to explore whether the specific shape of the generalization curve can be expected to be important for theoretical predictions relating to the evolution of aposematism and mimicry. We do this by a reanalysis and development of the models provided in two recent papers. We argue that the shape of the generalization curve, in combination with the nature of genetic and phenotypic variation in prey traits, can have evolutionary significance under certain delineated circumstances. We also demonstrate that the process of gradual evolution of Müllerian mimicry proposed by Fisher is particularly efficient in populations with a rich supply of standing genetic variation in mimetic traits.

KEY WORDS: Generalization gradient, Müllerian mimicry, peak shift, warning signals.

Generalization is a commonly reported aspect of animal behavior. By generalization, we mean that if a given behavior is established in response to a certain stimulus, then novel stimuli that are similar to the familiar one will trigger similar behavior. This can be understood as an adaptive strategy for coping with the heterogeneity that is a feature of so many natural stimuli. Generalization is at the heart of many aspects of behavioral ecology; for foragers it can be seen as an essential feature of learning about potential prey, because natural populations of prey are unlikely to be perfectly homogenous (e.g., as a result of size, age, or sex differences between individuals). Here we are particularly interested in con-

sidering the consequences of the shape of the generalization curve (of predator response vs. difference in stimuli, often referred to as a generalization gradient) for the evolution of aposematic signals and signal mimicry. Aposematic signals are considered to aid predators in learning to avoid a class of defended prey. Predators do this by generalizing between the appearance of prey they have previously sampled and the appearance of prey they subsequently encounter. Mimicry arises when such generalization occurs between individuals of different species.

We are interested in generalization curves that show a peaked response, that is to which a specific unique form of stimuli

provides a strongest response, with increasing deviation from that stimulus producing weaker responses. Ghirlanda and Enquist (2003) argue that such generalization behaviors are characteristic of changes in stimulation that involve a rearrangement of a constant total amount of stimulation of the sense organ. Examples they give include variation in tone while keeping the same noise intensity or variation in light wavelength (because total receptor stimulation is approximately constant across wide wavelength ranges in many species). Prey characters to be learned by predators might to a large extent consist of this kind of variation; such changes include colors, shapes, and locations of pattern elements. The two most often suggested alternative mathematical descriptions for symmetrical curves with a peaked shape are Laplacian (reflected exponential) and Gaussian (Normal). Biologically a key difference is that small deviations from the optimal stimulus produce very little change in response under the Gaussian model (a rounded peak) but a dramatic change in response under the Laplacian model (a sharp peak). The shapes also differ at large deviations from the optimal stimulus, where the Gaussian becomes small compared to the heavier tails of the Laplacian shape.

In an extensive study of the available empirical literature on generalization, Ghirlanda and Enquist (2003) found some support for both forms. Specifically, they found that although most of the 223 datasets that they analyzed were better fitted by a Gaussian than a Laplacian, in 25% of cases the Laplacian gave a better fit. In general, the difference in fit between the two forms was rather small. However, the region around the peak, which may be of importance for mimetic evolution, was often poorly sampled in the studies. They also noted that Laplacian fits typically predicted somewhat taller generalization curves than observed, whereas Gaussian fits on average predicted the observed height, and they interpreted this as supporting the Gaussian shape. Even so, both forms seem worthy of consideration. Each alternative can be found in theoretical models of aposematism and mimicry, often with no justification for why one form was favored over the other, and indeed with authors switching between forms within a series of papers without explanation (e.g., Franks and Noble 2003; Franks and Sherratt 2007). It is then of interest to ask what the general consequences are of using one or the other of these shapes of curve as a model to describe how a predator generalizes between prey individuals.

Our aim here is to explore whether the specific form of the generalization curve can be expected to be important for theoretical predictions relating to the evolution of aposematism and mimicry. We do this by a reanalysis and development of the models of the evolution of Müllerian mimicry provided in two recent papers (Balogh and Leimar 2005; Franks and Sherratt 2007). Thus the stimulus we are interested in is the appearance of defended prey individuals, and the behavior is the probability that the preda-

tor will decline to attack an individual of given appearance. We expect a peaked generalization shape to be reasonable, because having had an aversive experience with an individual of given appearance, we expect that the predator will be reluctant to attack subsequent prey of similar appearance, with the probability of passing up the chance to attack prey declining with increasing deviation of appearance of subsequent individuals from the original. Because generalization is intimately connected to stimulus variability, we also examine the influence of the amount of genetic and phenotypic variability in prey traits on our evolutionary predictions.

Comparing Two Forms of Generalization Function

Balogh and Leimar (2005) analyzed a model of the evolution of Müllerian mimicry between two defended species. Specifically, this individual-based model was used to demonstrate the plausibility of the evolution of mimicry arising solely through the accumulation of small changes in appearance. This mechanism is generally attributed to Fisher (1930) and is explicitly driven by predator generalization. The work of Balogh and Leimar (2005) provides an important counter-argument to suggestions that mimicry could only arise if a macromutation arose in one population that caused mutant individuals to immediately look similar to the other species (Turner 1984; Joron 2003).

Balogh and Leimar explain Fisher's mechanism as follows. "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 toward that appearance might benefit from the increased similarity. Selection thus favors variation in that direction and leads to slight displacement of the appearance gaining maximum survival. We refer to this displacement as a peak shift. . . . This peak shift could, according to Fisher, initiate gradual evolutionary change, and eventually lead to the establishment of Müllerian mimicry."

Balogh and Leimar also explain why they use a Gaussian shape for generalization in their model. "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, because the zero-derivative point in trait-space is displaced giving rise to peak shift. A generalization function with an abrupt change in derivative at the center point has been previously used to model mimicry evolution, but such a shape prevents Fisher's process from operating as the generalization function lacks the zero-derivative point needed for peak shift." Thus, they argue that the evolution of Müllerian mimicry of two defended prey types by a process of accumulation of small mutations is

critically dependent on the shape of predator generalization: it can work with a Gaussian shape but not with a Laplacian.

Similar arguments could also be made with regard to the evolution of aposematism versus crypsis. Using a model with Gaussian generalization gradients, Leimar et al. (1986) suggested that generalization peak shift could be a major reason for the evolutionary stability of aposematism. This suggestion has experimental support (e.g., Gamberale and Tullberg 1996), but the theoretical argument rests on the presence of a displacement of the position of the maximum of the peak of a generalization function, which might not occur for a sharply peaked, Laplacian function. The qualitative features of the selective maintenance of warning coloration could thus depend on the shape of generalization functions.

The Model

To study the evolutionary implications of the shapes of generalization functions, we modified the models of Balogh and Leimar (2005) and Franks and Sherratt (2007) to allow for both Laplacian and Gaussian shapes. We also extended these models by allowing more general schemes of inheritance of prey traits, as well as random variation in prey appearance. The model of Franks and Sherratt assumed prey appearance to be a two-dimensional trait (x_1, x_2) , but for simplicity we restrict the model here to one trait dimension (although we note that generalization over multiple stimulus dimensions is a very important issue for mimicry evolution). If each already-experienced stimulus has appearance x_0 and the current prey item has appearance x , then the extent of generalization is given by either a Laplacian,

$$g(x) = \exp\left(-\frac{|x - x_0|}{b}\right), \quad (1)$$

or a Gaussian,

$$g(x) = \exp\left(-\frac{(x - x_0)^2}{2\sigma^2}\right). \quad (2)$$

For the Gaussian, the parameter σ is the width (standard deviation) of the shape, and b is a measure of the width of the Laplacian. We compare the effects of these shapes either when the widths are such that the shapes have equal integrals, which occurs for $b = \sqrt{\pi/2} \sigma$ (see Fig. 2A below for an illustration of the shapes), or when the probability distributions corresponding to the shapes have equal standard deviations, which occurs for $b = \sqrt{1/2} \sigma$. Apart from this, all other assumptions about predator learning and predator-prey interactions over a season are identical to those of Balogh and Leimar (2005) and Franks and Sherratt (2007), including the notation used for parameters and variables in the model (as before, we used $u = 0.04$, $s = 2$, $h_0 = 2.5$ and $y_a = y_b = 1$ in our simulations). Specifically, we used an individual-based model in which predators sample prey and learn,

from experience, whether to attack or avoid them. Appearance of the prey could evolve in response to selection pressure imposed by predation. Two prey species a and b , of population sizes N_a and N_b , were represented with a fixed unprofitability level y and a single-component property x for each individual of each population, expressing their appearances. A community of N_p predators sample the prey and, from their experience, learn which prey to attack or avoid. Predators generalize over their experiences, with the possibility of mistaking different prey of a similar appearance for each other. Predators have perfect memories and do not forget past experiences. However, their memory is wiped clean each season (without this no selection would take place after a couple of seasons when predators have learned to avoid both species entirely). Predators store their experiences as a paired list of each attacked prey's phenotype and unprofitability (x_i, y_i) . This list is used to calculate the probability $q(x)$ of a predator attacking, on encounter, a prey item with appearance x :

$$q(h) = \frac{e^{-s(h-h_0)}}{e^{-s(h-h_0)} + 1}, \quad (3)$$

where h_0 is the inflexion point of the curve and s is a measure of the steepness of the function at that point. Changing values of s allow the model to capture different types of avoidance learning. h is a variable giving the degree of attack inhibition of the predator toward prey with appearance x , given n previous experiences with prey displaying appearances x_i , $i = 1, \dots, n$:

$$h(x) = \sum_{i=1}^n g(x - x_i) y_i \quad (4)$$

The function g is the Gaussian or Laplacian defined above in expressions (1) and (2). In terms of predation, the function represents generalization, where x is the appearance of the currently encountered prey, x_i is the appearance of previously attacked prey ($i = 1, \dots, n$). The expression (4) results in the predators learning and accumulating attack inhibitions or preferences for prey appearances based on their previous experiences

The model was typically run over 150,000 seasons, each divided into multiple time-steps ($1/\Delta t$). In each time-step the probability of each predator coming across a random prey item from each species was $u\Delta t N_a$ for species a and $u\Delta t N_b$ for species b . Predatory attacks are always fatal to prey. After each season, surviving prey are randomly selected to reproduce until a new generation of prey species are created (with population sizes N_a and N_b) to replace the old generation.

Concerning the inheritance of prey traits, we explored different possibilities. Quantitative genetics is often regarded as a reasonably realistic model of the inheritance of continuously varying traits (e.g., Barton and Keightley 2002), particularly traits that are influenced by a large number of loci, which could apply to at least

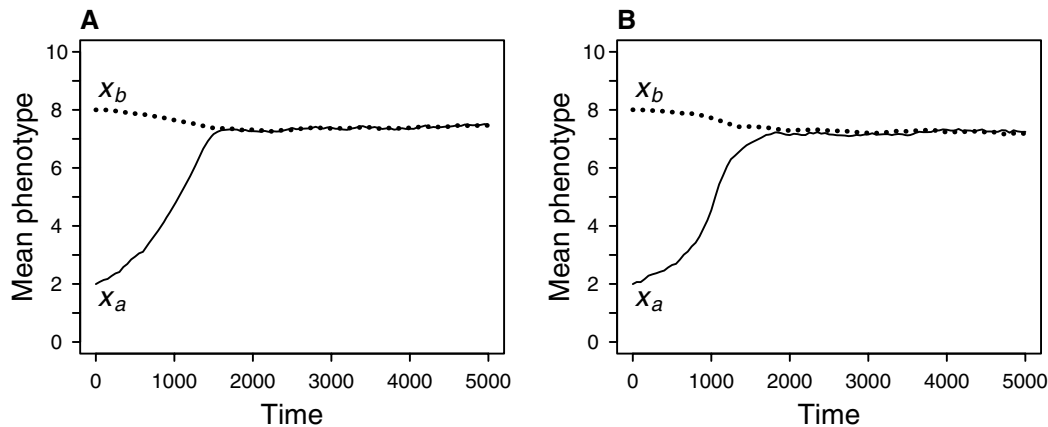


Figure 1. The evolution of the mean prey appearances over time (generations) when predators generalize with a Laplacian (A) or a Gaussian (B) function. In panel (B) the width (standard deviation) of the generalization function is $\sigma = 2$ and in (A) it is $b = \sqrt{\pi/2}\sigma \approx 2.51$. Solid lines represent a species with population size $N_a = 1000$ and dotted lines represent a species with population size $N_b = 5000$. The appearance is a one-dimensional trait with quantitative genetics inheritance, implemented according to the infinitesimal model with within-family variance σ_f^2 , where $\sigma_f = 0.1$. At the start of each simulation the two species have the mean trait values $x_a = 2$ and $x_b = 8$, and there were $N_p = 100$ predators.

certain traits that are involved in mimicry. We used the so-called infinitesimal model (Bulmer 1980; Barton and Keightley 2002), which is an idealization of quantitative genetic inheritance. In the infinitesimal model, the offspring of two parents having traits (breeding values) x_1 and x_2 develop traits that are normally distributed with the mid-parent $(x_1 + x_2)/2$ as mean and a fixed variance σ_f^2 , which is referred to as the within-family variance. As a contrasting possibility, we examined the situation in which prey traits are determined by a single diploid locus with additive allelic effects. Finally, we studied the implications of including a random environmental component into the variation in prey traits.

Results

Because of the stochasticity inherent in our individual-based simulations, we performed several replicates of each simulation and we present representative outcomes in the figures. For quantitative genetics inheritance, our results contrasted rather sharply with the suggestion of Balogh and Leimar (2005), in that we found similar trajectories of gradual evolution toward mimicry for Laplacian (Fig. 1A) and Gaussian (Fig. 1B) generalization functions. From a starting point where the mean traits of the two prey species differed by three times the width σ of the Gaussian generalization function, mimicry became established after approximately 1500 generations. A considerable amount of genetic variation is maintained during the evolutionary process (the standard deviation of the variation in breeding value was around 0.14 in each species for both the Laplacian and the Gaussian case in Fig. 1). This supply of standing genetic variation is the reason for the qualitative similarity between the evolutionary outcomes for the two gen-

eralization shapes. Because predator learning occurs on variable prey populations, the ‘effective predator generalization function’ becomes smoothed out by variation in experience within and between predators, producing roughly similar net selective effects in both cases. The sharp peak of the Laplacian (Fig. 2A) is thus smoothed out, which then allows for peak shift.

In contrast, for single locus determination of prey traits and a low enough rate of mutation, so that evolution approaches mutation limitation, as is often assumed in adaptive dynamics (Dieckmann and Law 1996; Geritz et al. 1998), we found a dramatic difference between evolutionary outcomes for Laplacian (Fig. 3A) and Gaussian (Fig. 3B) generalization functions. As a consequence of the slight peak shift in the Gaussian case (Fig. 2B), mimicry became established after around 10,000 generations, whereas hardly any mimetic evolution occurred for Laplacian generalization. This corresponds to the suggestion by Balogh and Leimar (2005); when there is rather little variation in prey traits within a species, mutants that deviate slightly from the resident appearance, even in the direction of the other species, have lower survival and are selected against in the case of Laplacian generalization (Fig. 2B). If more prey variability is introduced, for instance as a result of random environmental influences, the sharply peaked Laplacian generalization function becomes effectively smoothed out, allowing gradual mimicry evolution in the Laplacian case (Fig. 3C) and decreasing the time until establishment of mimicry somewhat in the Gaussian case (Fig. 3D).

To understand how much prey variability is needed to smooth out the sharp peak of a Laplacian, it is helpful to note that there must be some variation among the handful of prey encountered by an individual predator during avoidance learning, or between the prey encountered by two different predator individuals. Thus, if

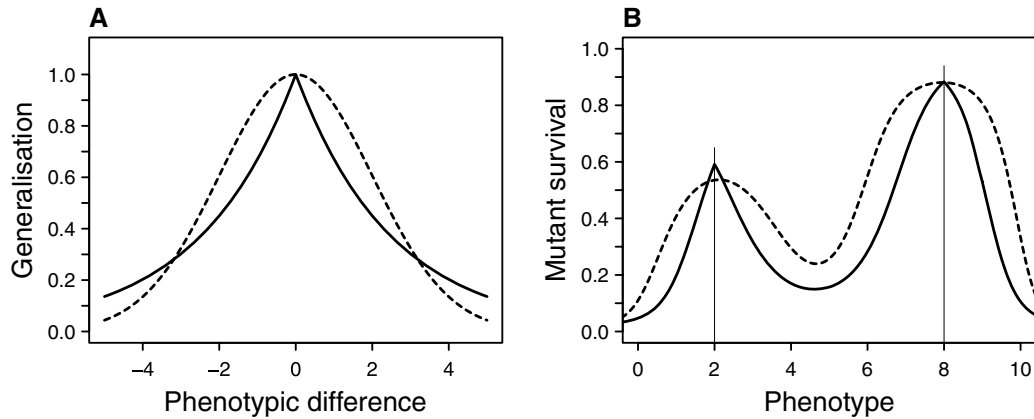


Figure 2. Laplacian and Gaussian generalization functions (A) and the corresponding mutant survival for nearly monomorphic populations (B). The dashed curve in (A) is a Gaussian with width $\sigma = 2$ and the solid curve is a Laplacian with width $b = \sqrt{\pi/2}\sigma \approx 2.51$. The corresponding curves in (B) show survival as a function of trait for a mutant individual in a situation in which there are $N_a = 1000$ individuals with trait $x_a = 2$, $N_b = 5000$ individuals with trait $x_b = 8$ and $N_p = 100$ predators.

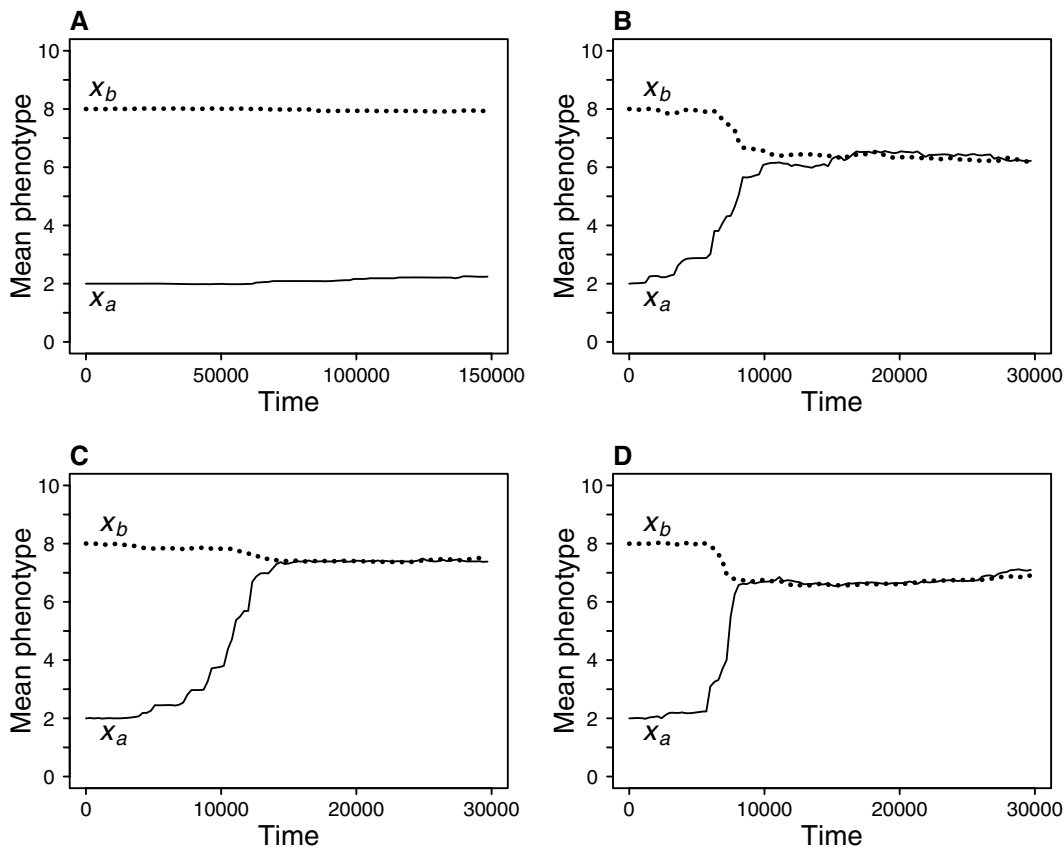


Figure 3. Mutation-limited evolution of the mean prey appearances over time when predators generalize with a Laplacian (A and C) or a Gaussian (B and D) generalization function. The widths of the Gaussian and Laplacian are $\sigma = 2$ and $b = \sqrt{\pi/2}\sigma \approx 2.51$. Solid lines represent a species with population size $N_a = 1000$ and dotted lines represent a species with population size $N_b = 5000$. The appearance is determined by a single diploid locus. The alleles at the locus have additive effects, a mutation rate of 0.0005 per generation, and mutational increments have a Laplacian distribution with a standard deviation $\sigma_m = 0.1$. In (A) and (B) the trait is entirely determined by the additive genetic effects, whereas in (C) and (D) the trait also has a normally distributed environmental component with standard deviation $\sigma_e = 0.2$. Note that the scale on the horizontal axes differs between (A) and the other cases. At the start of each simulation the two species have the mean trait values $x_a = 2$ and $x_b = 8$, and there were $N_p = 100$ predators.

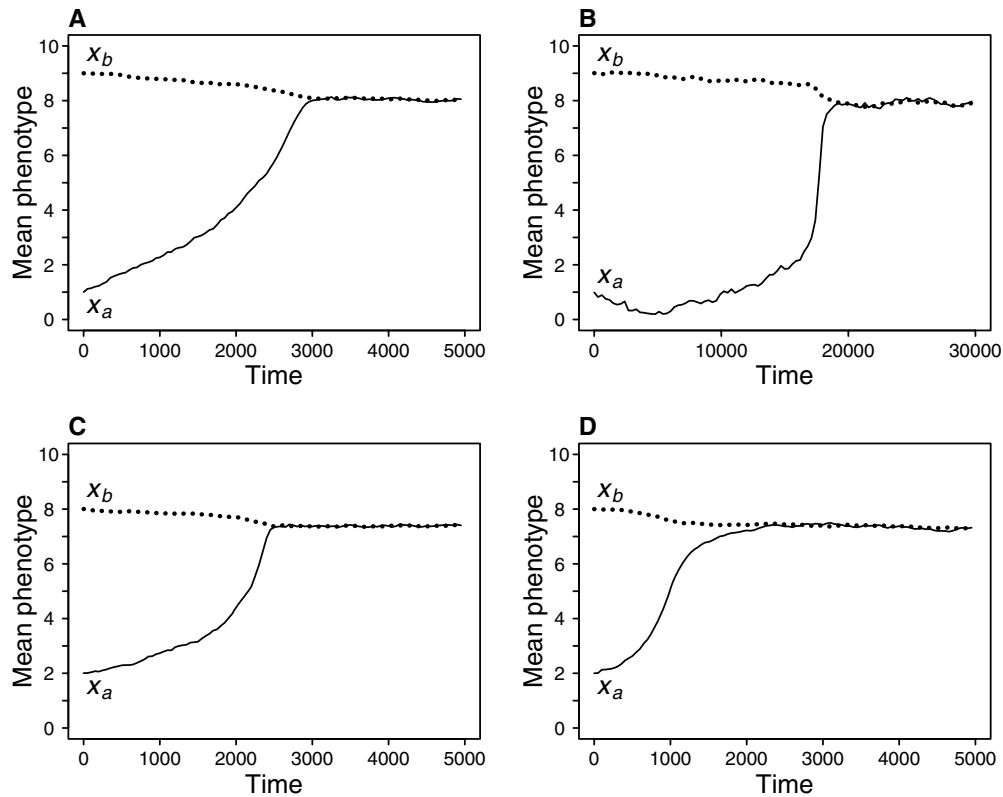


Figure 4. Effects on mimicry evolution of the shape of the tails and of the overall width of generalization functions. In (A) and (B) the generalization functions are the same as in Figure 1A and Figure 1B, respectively (i.e., a Laplacian with width $b \approx 2.51$ in (A) and a Gaussian with width $\sigma = 2$ in (B)), but the initial mean trait values are further apart ($x_a = 1$ and $x_b = 9$), which emphasizes the influence of the shape of generalization functions far away from the central point. Note that the scale on the horizontal axes differs between (A) and (B). In (C) the generalization function is a Laplacian with $b = \sqrt{2} \approx 1.41$ (which is smaller than $b \approx 2.51$ in Fig. 1A) and in (D) it is a Gaussian with $\sigma = 2$ (same as in Fig. 1B), resulting in a standard deviation of 2 for each of the corresponding probability distributions. The initial mean trait values are the same as in Fig. 1 ($x_a = 2$ and $x_b = 8$). As in Figure 1, the appearance is a one-dimensional trait with quantitative genetics inheritance, implemented according to the infinitesimal model with within-family variance σ_f^2 , where $\sigma_f = 0.1$, and solid lines represent a species with population size $N_a = 1000$, dotted lines a species with population size $N_b = 5000$, and there were $N_p = 100$ predators.

an overwhelming majority of the prey have identical appearances, and only a small minority of prey deviate, this will not be enough to smooth out a sharp peak. On the other hand, if most prey differ somewhat from each other, smoothing will occur.

The shape of the tails of a generalization function can also influence mimicry evolution in important ways. As seen in Figure 2A, for large phenotypic differences the Laplacian decreases more slowly toward zero than the Gaussian. As a consequence, the Laplacian has greater potential to promote gradual mimicry evolution for initially more dissimilar phenotypes (Fig. 4A), compared to the Gaussian case (Fig. 4B). For the Gaussian example in Figure 4B, the generalization overlap between the initial populations is too small for a noticeable effect on mimicry evolution. It is only when random genetic drift has moved the mean trait values closer together that generalization bias is strong enough to promote evolution toward mimicry. We found considerable variation between replicate runs for the situation in

Figure 4B, with genetic drift sometimes causing the population mean traits to diverge, preventing mimicry, evolution over periods of 30,000 generations or more.

In general, genetic drift can cause the mean prey appearance to vary over time, and predator generalization has the effect of making drift of the species toward each other somewhat more likely than drift away, leading to the establishment of mimicry with an appreciable probability. However, it might not be realistic to consider evolutionary processes in small populations over many thousands of generations, because these populations are unlikely to persist for such durations.

Instead of comparing Laplacian and Gaussian generalization functions for widths such that the integrals of the shapes are the same, one could compare them for equal standard deviations of the corresponding probability distributions, in which case the Laplacian width is $b \approx 0.707 \sigma$ (instead of $b \approx 1.25 \sigma$). Because of the smaller width, the Laplacian then has a relatively weaker effect

on mimicry evolution in the latter comparison, but the difference need not be very dramatic (Fig. 4C and 4D). It is nevertheless evident that a number of factors interact in their influence on mimicry evolution, among them are the widths and shapes of generalization functions as well as the amount of genetic and phenotypic variation.

Our results modify the prediction of Balogh and Leimar (2005) that a Laplacian generalization function cannot lead to gradual evolution of mimicry. With nearly monomorphic populations and Laplacian generalization, the maximum of mutant survival has a sharp peak at a position that is not influenced by the other species (Fig. 2B). However, mutant survival is affected away from the peak, such that the curve becomes asymmetric with a bias toward values closer to the other species (Fig. 2B). Provided there is a reasonable amount of genetic variation around the species mean, it seems intuitively clear that such asymmetry could allow gradual evolution of prey types toward each other, because the net selective effect of the asymmetric peak is to shift the population distribution in the direction of the bias. The rate of evolution is faster for greater asymmetry, which encourages an advergence of the less protected (less numerous) species toward the better protected (Fig. 1), because the asymmetry is more pronounced for the peak at the position of the less protected species (Fig. 2B). These effects apply to both Laplacian and Gaussian generalization functions, but for the Gaussian form there is also the peak-shift phenomenon discussed by Balogh and Leimar (2005), which permits gradual mimetic evolution even in situations with a limited supply of genetic variation (Fig. 3B).

One can interpret Fisher's original explanation for evolution of Müllerian mimicry as focusing on the issue of asymmetry, rather than on peak shift per se, because he says (1930, p. 154): "Such an argument may, I suggest, be constructed by comparing the fate of any deviation from type A not with the average of that type, but with an equally conspicuous but opposite deviation. . . . Since they are of equal magnitude they will lose (if anything) equally by failing to be recognized as typically A, but if either, or both, are ever mistaken for species B, the greater benefit will certainly be reaped by the variation in the direction of B. Since the whole species may be regarded as made up of such pairs of variations . . . , the net resultant must be a modification in the direction of species B." It seems that Fisher's argument contains an implicit assumption of a considerable amount of standing genetic variation.

Discussion

THE GENERAL EVOLUTIONARY SIGNIFICANCE OF OUR PREDICTIONS

Overall, our analysis supports the key point of Balogh and Leimar (2005) that Fisher's explanation can account for evolution of

Müllerian mimicry through the accumulation of small mutations in appearance. Furthermore, we find that the process is even more general than they suggest and can also occur where predators generalize with a sharp peak, provided there is sufficient variability in prey traits. Our simulations show that a Gaussian functional form promotes gradual evolution of mimicry both for low and for high amounts of genetic variation, because of the peak shifting phenomenon. We also find that the heavier tails of the Laplacian can promote gradual mimicry evolution for appearances that are more dissimilar initially, at least in situations in which there is sufficient genetic variation.

Our investigation of gradual mimicry evolution makes the conceptual point that trait variability can qualitatively influence the predictions delivered by alternative modeling schemes, as exemplified by quantitative genetics (Barton and Keightley 2002) and mutation-limited evolution in adaptive dynamics (Geritz et al. 1998). The merits of these different schemes have been debated (e.g., Barton and Polechova 2005; Dieckmann and Doebeli 2005) and it seems useful to provide cases in which their predictions differ sharply. Gradual mimicry evolution with a Laplacian generalization function and no additional phenotypic variability is one such example, where quantitative genetics predicts evolutionary change but adaptive dynamics does not. This kind of distinction is certainly relevant for modeling, including for the widespread category of ESS models in which evolutionary stability is established by examining the success of rare mutants in an otherwise monomorphic population. The distinction could also be important for real populations, although the phenotypic variability present in many traits would tend to reduce the contrast in predictions between the modeling schemes.

APPLICATION OF OUR PREDICTIONS TO THE EVOLUTION OF APOSEMATISM

We now go on to consider a series of models of the coevolution of defense and appearance in a prey species. These models (presented in Broom et al. 2006, 2007) allow analytic predictions about the effect of aspects of the ecology (such as predator density) on the defense strategy adopted by prey species. Strategy is defined in terms both of their investment in defenses that make them unattractive to predators, and in appearance that can either aid predator learning (aposematism) or reduce detection rates by predators (crypsis). As with the models of mimicry discussed earlier, predator learning and generalization on the basis of previous experiences is at the heart of the selection pressure on prey.

Broom et al. (2006, 2007) provide variants on a model framework, which assume that the generalization function is sharply peaked like the Laplacian. At least one important prediction of the models was critically dependent on this assumption. Specifically, the strategy of an individual was defined by the values given to two continuous variables. One variable described the

appearance of the individual and the other defined the level of investment in defense. In the original model with a Laplacian generalization curve, if there was an ESS involving appearance that was other than that conferring maximum crypsis, then this took the form of a continuum of possibilities. That is, there was a range of values for the appearance variable, where if all of the prey individuals adopted the same value within this range (and a partner value of level of defensive investment) that was an ESS. There was thus an infinite number of alternative ESSs, involving different values for appearance (as long as these values were within the defined range). If the Laplacian function were replaced by a Gaussian function, then this range of ESS values would collapse down to a single point. That is, with the Laplacian function, there is a range of different ESS values to which a population might settle, but with the Gaussian function, only a single point is an ESS.

This difference in model predictions has evolutionary and ecological consequences. Although both alternatives lead to the prediction that local populations should be monomorphic; with the Laplacian function, the model predicts that separate populations might feature different appearances not through ecological differences but just because evolutionary history lead them to settle on different ESSs. In contrast, with a Gaussian function, different populations are predicted to feature individuals of exactly the same appearance, unless there are ecological differences between the situations of the two populations. This difference occurs because for the Laplacian, there is a heavy penalty to be paid for even slight deviations from the resident phenotype, implying very strong purifying selection. Thus, the defining feature of selection is selection for monomorphism. If the population settles on a combination of the two-parameter values that yields slightly sub-optimal fitness, and there is a combination relatively close-by that would yield higher fitness, then the population does not evolve toward the higher-fitness state, because of the strong selection against deviation from the resident phenotype. With a Gaussian generalization curve, very slight deviations from the resident phenotype are not strongly punished, and thus gradual change of the population by the accumulation of small mutations becomes possible. However, as we have shown here, sufficient genetic and phenotypic variability in prey populations would make gradual change a feasible process also for Laplacian generalization.

APPLICATION OF OUR PREDICTIONS TO MÜLLERIAN MIMICRY

Returning to the evolution of Müllerian mimicry, it is clear that the process of gradual change suggested by Fisher can occur, but it is an open question to what extent it is responsible for the evolution of mimicry in nature. As illustrated by our results here, a prerequisite is that there is sufficient interspecific generalization overlap to bias the survival peak around the phenotype of at least

one of the prey species. When comparing the feasibility of gradual evolution with the proposed alternative of a two-step process, in which an initial macromutation achieves approximate similarity followed by a fine-tuning of mimicry, the characteristics of prey evolution and predator generalization in a multidimensional trait space are likely to be crucial. Balogh and Leimar (2005) argued that macromutations that simultaneously achieve similarity in multiple traits are unlikely to occur, and suggested instead that a community of different predators, some of which generalize broadly in trait space, can allow Fisher's process to operate even for initially rather dissimilar species. As a counter-argument, Franks and Sherratt (2007) pointed out that such gradual evolution in a multidimensional trait space presupposes the existence of predators that generalize broadly over all stimulus dimensions, which they suggested is quite unlikely, leaving the two-step process as the more plausible alternative. To properly weigh these arguments against each other, there is need for knowledge both about predator communities and multidimensional generalization, as well as about the number and structure of major genes involved in the evolution of mimicry (e.g., Joron et al. 2007). As illustrated by the difference between pigeons and humans in assessing the similarity of hoverflies and wasps (Dittrich et al. 1993; Bain et al. 2007), there is scope for considerable variation in generalization between groups of species, but it remains to be determined if such phenomena could have played a role in the evolution of Müllerian mimicry. In any case, the form and range of predator generalization is bound to have important implications both for mimicry evolution and for aposematic signaling.

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