

## CHAPTER 16

# Mimicry, Saltational Evolution, and the Crossing of Fitness Valleys

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### 16.1 Introduction

The relative contribution of gradual and saltational change to evolution has been debated ever since Darwin (1859) emphasized gradualism in his theory of evolution by natural selection. The phenomenon of mimicry was an important example in this debate. In mimicry evolution, members of a population or species become similar in appearance to an aposematic model species and thereby gain increased protection from predation. The number of steps in the approach to mimicry could be few or many and their sizes either large or small. In 1915, Punnett published an influential book on mimicry in butterflies, in which he summed up his strong opposition to gradualistic accounts of mimicry evolution. He dismissed previous suggestions by Poulton (e.g. Poulton 1912, 1913) that mimicry could emerge in a sequence of steps, beginning with the appearance of a rough likeness of the would-be mimic to its model, followed by further improvement in resemblance. Punnett's main argument was representative of the thinking of the early Mendelians, who often pointed to a lack of intermediates between existing variants, inferring that the variants had originated as mutants in a single step, as opposed to being molded by natural selection through successive replacements of intermediate forms. As supporting evidence, Punnett used examples of female-limited polymorphic mimicry, for instance the one found in the butterfly *Papilio polytes*, where the developmental switching between female morphs was known to be controlled by a small number of Mendelian factors, later shown to be alleles at an autosomal locus (Clarke and Shepard 1972). Punnett's position was thus a radical

saltationism. In terms of Adaptive Landscapes, if the mimic-to-be resides on one adaptive peak and the model on another, mimicry evolves in a single mutational leap, and the issue of natural selection only enters through the constraint that the peak jumped to should be higher than the starting peak. This would apply both to Müllerian mimicry, where the starting point is an aposematic species, and to Batesian mimicry, where the starting adaptive peak of the palatable mimic-to-be is determined by functions other than aposematism, for instance crypsis or other protective coloration, like flash coloration (Cott 1940; Ruxton et al. 2004), or partner choice.

In response to claims like those by Punnett (1915), and as part of his efforts to unify gradualism and Mendelian genetics, Fisher (1927, 1930) presented a fully gradualistic alternative. He envisaged a genetically variable population of mimics-to-be and proposed that individuals with trait values deviating from the population mean in the direction of the traits of the model species would be slightly favored over deviations in the opposite direction, because of a slightly higher probability of being mistaken for the model by predators. The outcome could be a gradual shifting of the mean trait values in the direction of improved resemblance. It appears that Fisher intended his gradualistic scenario to apply both to Batesian and Müllerian relations, but it gained more attention in the latter case. In terms of (frequency-dependent) Adaptive Landscapes of Müllerian mimicry evolution, Fisher's process would be a gradual shifting of two peaks, until they overlap and, approximately, merge to a single peak.

Fisher's (1927, 1930) proposition was not generally accepted. The strongest opposition came from

Goldschmidt (1945a,b), who ended his examination of the issue by coming to the conclusion that “Punnett’s interpretation of polymorphism by mutation (saltation) agrees better with the facts than Fisher’s neo-Darwinian theory.” Although not subscribing to the saltationism of Punnett and Goldschmidt, even Fisher’s close associates (for instance E. B. Ford and P. H. Sheppard), who were preoccupied with the problem of Batesian mimicry evolution, came to deviate in their views from Fisher’s original proposition (see Turner 1985 for an overview). Instead the so-called two-step process, where a large mutation first achieves approximate similarity to the model, after which smaller changes can improve the likeness, became accepted as describing Batesian mimicry evolution. The idea is often credited to Nicholson (1927), although Poulton (1912) had already suggested it. Over time, the two-step process became accepted also in the context of Müllerian mimicry (Turner 1984; Sheppard et al. 1985). In terms of Adaptive Landscapes, the process entails a mutational leap from the adaptive peak of the mimic-to-be, protected as it is by predator learning of that phenotype, to somewhere on the slope of the higher, more protective peak of the model, thus crossing a fitness valley, followed by a series of modifications climbing the higher peak. Because mimicry often involves several traits, which at least initially can be genetically independent, this first mutational leap is clearly a less demanding assumption than a saltation as argued for by Punnett and Goldschmidt. Even so, the assumption needs to be backed up by arguments or observations making it likely that predators in fact would avoid attacking the first, quite imperfect, mutant mimic.

A different kind of ingredient in explanations of mimicry evolution is that, possibly only in a particular region or period of time, evolutionary forces other than mimicry may modify the appearances of mimics-to-be, fortuitously bringing about sufficient resemblance to a model to start off mimicry evolution. Examples could be selection in relation to mate choice or thermoregulation (Mallet and Singer 1987). Random genetic drift in small populations is another general category of this kind. In aposematism, with learnt attack avoidance by

predators, selection tends to operate on deviations of appearances from the current population mean. The selective peaks could be constrained, and in part formed by the aesthetics of predator learning, to particular regions of phenotypic space, as well as being influenced by selection towards the current mean. If the population mean appearance changes to explore new aesthetic combinations, predator learning need not always act to bring the mean back to a previous value. This implies that the mean may perform a random walk over evolutionary time, exploring parts of the relevant trait space, and possibly different peaks of an Adaptive Landscape, in a shifting balance process (Wright 1977; Mallet and Singer 1987; Coyne et al. 1997; Mallet and Joron 1999; Mallet 2010; see also Chapters 2 and 4–6). This would correspond to a random walk to a new adaptive peak. The phenomenon will be more pronounced in small local populations, and/or in populations with limited predation pressure, where selection towards the current mean will be weakened. The process could be responsible both for mimicry evolution and for the rapid diversification of novel aposematic signals that occurs in many aposematic groups (Mallet and Joron 1999; Mallet 2010).

In the following, we extend this brief review of the history of ideas, outlining some recent work on mimicry evolution. The concept of an Adaptive Landscape will be central in the presentation, in particular the question of how a transition from one adaptive peak to another can come about. The landscapes we consider depict fitness as a function of the phenotypic traits of individuals, rather than as a function of genotype or allele frequencies (see Chapters 1–3, 5, 7, 18 and 19 for expositions and discussions on different types of Adaptive Landscapes). It should be kept in mind that, for aposematism and mimicry, Adaptive Landscapes are strongly density- and frequency-dependent, in the sense that their shapes depend on the traits and population sizes that are present in a prey community (this is also true for many other types of Adaptive Landscapes; see Chapter 7). The reason for the frequency dependence is that predator behavior is influenced by learning and generalization about the properties of the community.

## 16.2 Transitions between adaptive peaks

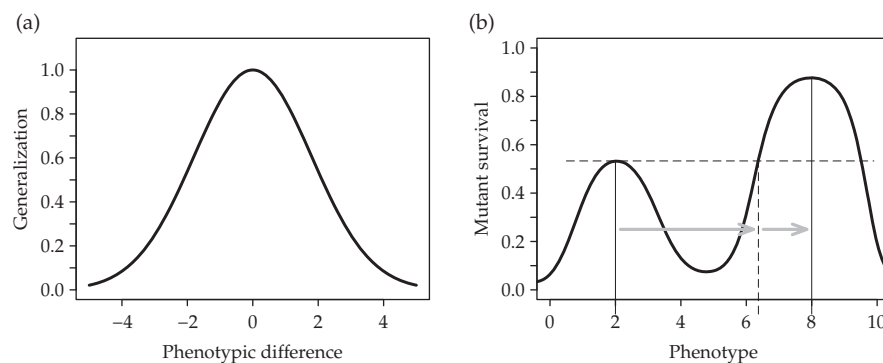
Predators learn about prey, for instance to avoid attacking those with particular appearances if they have been found to be distasteful or otherwise unprofitable in previous attacks. Generalization is another crucial aspect of predator psychology: if a predator encounters prey with a different appearance than previous prey, the reaction to the new prey may be a generalized version of the learnt reaction to similar-looking prey. From assumptions about learning and generalization by predators in a predator–prey community, an Adaptive Landscape of prey survival as a function of phenotype can be defined. Fig. 16.1 shows a generalization function and an Adaptive Landscape for a one-dimensional trait space. It is convenient to conceptualize the landscape as the survival of a prey individual with a mutant phenotype, so that the survival in principle is defined for any point in the trait space, whether or not the point is near the traits of the resident prey populations. The landscape in Fig. 16.1b is computed from an individual-based simulation, using assumptions similar to those in Balogh and Leimar (2005) and Ruxton et al. (2008). Briefly, the assumption about generalization along a one-dimensional stimulus space, illustrated in Fig. 16.1a, is among

the most commonly used and empirically substantiated in animal psychology (Ghirlanda and Enquist 2003). Similarly, the assumptions about predator learning follow broadly accepted ideas of associative learning (Rescorla and Wagner 1972).

Restricting attention to a single trait, a two-step process of Müllerian mimicry evolution is illustrated in Fig. 16.1b. Because large-effect mutations are known to occur, at least for certain traits, for instance for the hue or intensity of pigmentation (Socha and Nemeč 1996), and because large-effect alleles have been found in Müllerian mimicry systems (Joron et al. 2006b; Baxter et al. 2009), it follows that a two-step process involving a single-locus mutation could well produce shifts between adaptive peaks in one-dimensional trait spaces.

## 16.3 Peak shift in multidimensional trait spaces

To gain an appreciation of the possible constraints from predator psychology on the two-step process in a space of complex, multitrait appearances, it is instructive to quote Punnett's (1915, p. 140) remarks on what is required of predators as selective agents in butterfly mimicry, of which birds are believed to be the most important:



**Figure 16.1** Predator generalization function (a) and Adaptive Landscape (b) for Müllerian mimicry evolution in a one-dimensional phenotype space. The generalization function indicates the strength of the tendency of the predator to generalize learning about one prey phenotype to other phenotypes, which depends on the phenotypic difference. The Adaptive Landscape shows the survival over a season of a mutant as a function of its phenotype. The longer gray arrow indicates the size of the mutant change needed to jump from the smaller peak, across the valley and onto the slope of the bigger peak. Further mutant changes (smaller arrow) can then lead to the top of the bigger peak, in accordance with the classical two-step process. There is one resident population of 1000 individuals, each of which has phenotype  $x = 2$  and a bigger resident population of 5000 individuals, each of which has phenotype  $x = 8$ , and the generalization function is a Gaussian with standard deviation 1.8. All individuals are equally distasteful.

In the first place, they must confuse an incipient or 'rough' mimic with a model sufficiently often to give it an advantage over those which have not varied in the direction of the model. In other words, they must be easily taken in. Secondly, they are expected to bring about those marvelously close resemblances that sometimes occur by confusing the exact mimicking pattern with the model, while at the same time eliminating those which vary ever so little from it. In other words, they must be endowed with most remarkably acute powers of discrimination.

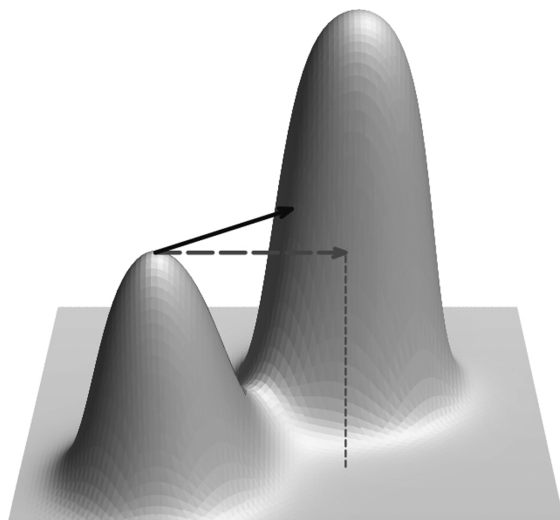
Punnett writes that "we must suppose that it is done by different species," and at least in some cases such a conclusion could be warranted. Fig. 16.2 illustrates the basic problem for mimicry evolution in multidimensional trait spaces, for a case of two genetically independent traits, in the sense of an absence of pleiotropy. For a mutant to reach from the smaller peak to a higher point on the slope of the bigger peak, to initiate a climb up that peak, both traits must mutate (Fig. 16.2), and for the double mutant not to break down through subsequent recombination, the genes for the traits must be linked. These are very severe constraints, and for more than two traits they become prohibitive. One should of course keep in mind the possibility of pleiotropic mutants affecting multiple phenotypic traits. Nevertheless, without further assumptions like pleiotropy, a two-step transition between adaptive peaks that are clearly separated along more than one trait becomes more unlikely the more trait dimensions there are.

**Figure 16.2** Illustration of the difficulty of Müllerian mimicry evolution in multidimensional phenotype spaces. The Adaptive Landscape shows the survival over a season of a mutant as a function of its two-dimensional phenotype. Jumping from the smaller peak, across the valley and onto the slope of the bigger peak requires a simultaneous change in two traits (black arrow). A change in just one trait cannot reach the bigger peak (dashed gray arrow). There is one resident population of 1000 individuals with phenotype at the centre of the smaller peak and another resident population of 5000 individuals with phenotype at the centre of the bigger peak. Predator generalization is given by a bivariate Gaussian with equal standard deviation along each phenotype dimension. All individuals are equally distasteful.

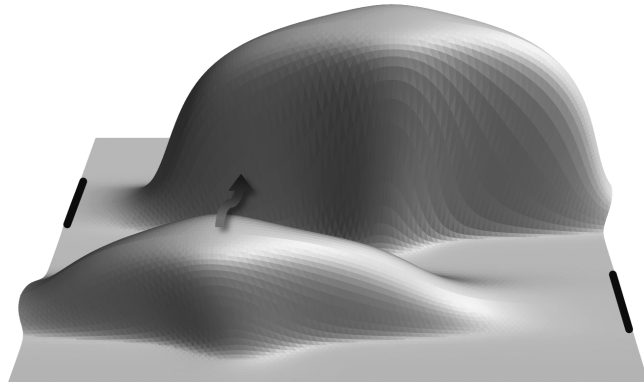
## 16.4 Feature-by-feature saltation

The Adaptive Landscape in Fig. 16.2 is built on an assumption that generalization over a multidimensional stimulus space works essentially in the same way as for a single dimension. This possibility is taken into account in animal psychology, but there are important alternatives, involving other psychological mechanisms, relating to the formation of categories (Pearce 2008). Psychological theories of categorization propose that objects are represented as collections of features. By comparing common and distinctive features, individuals categorize objects as similar or dissimilar (Tversky 1977; Treisman and Gelade 1980). Experiments show that animals often use one or a few features when discriminating among stimuli (Troje et al. 1999; Marsh and MacDonald 2008). There are also studies indicating that such categorization occurs in predators discriminating suitable from unsuitable prey (Schmidt 1958; Aronsson and Gamberale-Stille 2008). A related strategy of similarity judgment is to encode stimuli hierarchically at two levels of detail: category level information is used first to sort stimuli into crude categories, whereupon fine-grain information completes the judgment (Huttenlocher et al. 2000; Crawford et al. 2006).

The two-step process in multidimensional trait spaces would be less constrained if there is sequential or hierarchical stimulus processing by predators, such that first a single feature is used for crude



**Figure 16.3** Müllerian mimicry evolution occurs more readily if one phenotype dimension is used by predators as a feature to categorize prey. The Adaptive Landscape shows the survival over a season of a mutant as a function of its two-dimensional phenotype. The feature dimension runs along the near-far direction of the figure. For mutant traits in two different intervals (shown as black line segments) of the feature dimension, predators classify prey as belonging to two different categories. These categories correspond to the two resident populations: a smaller population of 1000 individuals with phenotype at the centre of the smaller ridge and another resident population of 5000 individual with phenotype at the centre of the bigger ridge. In comparison with the situation in Fig. 16.2, a mutant change in only the feature trait can reach from the top of the smaller ridge, across the fitness valley and onto the slope of the bigger ridge (arrow). From this point, gradual or stepwise changes in each of the two traits can result in a climb to the top of the ridge.



categorization, followed by a comparison of all perceived prey traits (Balogh et al. 2010), or a comparison of additional features. The overall idea is that a trait functions as a feature by aiding the efficient classification of prey (Chittka and Osorio 2007). The initial mutation in the two-step process could then cause prey to acquire a trait that is used by predators as a feature to categorize potential prey as unsuitable. The significance for mimicry evolution is that, if predators have the tendency to generalize broadly between prey types that share a feature, there may be sufficient advantage for new, imperfect mimics. This possibility of a transition between adaptive peaks through an initial single-feature saltation is illustrated in Fig. 16.3. Fine-grained judgments can then favor subsequent improvement of the mimicry (Balogh et al. 2010). More generally, mimicry evolution could be a sequence of feature mutations, combined with gradual adjustment of the mimetic appearance. Given that different species of predators might use different features, or that evolutionary changes in the composition of the prey community could change the categorizations used, the range of evolutionary changes involving feature mutations is expanded. Even so, feature saltations that initiate mimicry evolution from a non-mimetic starting point will have particular significance.

A possible example of a feature is found in *Heliconius*. A number of species in this genus on the West coast of Ecuador have white hindwing fringes,

including *H. erato*, *H. melpomene*, *H. cydno*, *H. sapho*, and *H. sara*. However these five species belong to three very differently patterned Müllerian mimicry rings. Because such white hindwing fringes are virtually absent elsewhere, Sheppard et al. (1985, p. 597) suggested that mimicry of the white hindwing feature allows some generalization by predators, even though much of the rest of the pattern remains very different.

## 16.5 Fisherian peak shifting

We should also examine the applicability of Fisher's (1927, 1930) idea—that mimicry evolution is gradual and driven by occasional predator “mistakes”—to multidimensional trait spaces. 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 would thus favor variation in that direction, which might lead to a gradual change in the mean trait values of the species, in the direction towards each other. A number of aspects of Fisher's proposal have been studied using theoretical modeling (Balogh and Leimar 2005; Franks and Sherratt 2007; Ruxton et al. 2008). A conclusion from these studies is that Fisher's

proposal can work, also in multidimensional trait spaces, if there is wide enough predator generalization, creating a noticeable generalization overlap between the traits of the species already at the start of the process, together with ample amounts of standing genetic variation in prey traits.

The effect of generalization overlap on an Adaptive Landscape can be seen in Fig. 16.1b. The left-hand, smaller peak is asymmetric, so that survival falls off more slowly from its maximum for mutants in the right-hand compared to the left-hand direction (there is a similar but smaller asymmetry of the larger peak). Even though there is a fitness valley between the peaks (Fig. 16.1b), the asymmetric peak shapes promote Fisher's process. Given sufficient genetic variation, the peak positions can approach each other, although when there is initially only a small generalization overlap, the approach will be very slow (Ruxton et al. 2008).

In general, for Müllerian mimicry, the process leads to convergence on a mimetic phenotype in trait space somewhere between the original appearances. However, if one species has higher population density, or is more distasteful than the other, the outcome is that one species (the mimic) approaches the approximately unchanging appearance of the other (the model), which is consistent with a seeming absence of coevolution in empirical examples of Müllerian mimicry (Mallet 1999). This corresponds to an Adaptive Landscape where a smaller, initially more asymmetric peak (Fig. 16.1b) gradually approaches and blends into a bigger, less asymmetric peak, rather than vice versa. In this way peak movement overcomes the fitness valley that was present originally (this is an example of how frequency-dependence changes the shapes of Adaptive Landscapes during mimicry evolution). An interesting property of the process is that it can operate also if only a relatively small proportion of the predator community generalizes broadly (Balogh and Leimar 2005), thus to a degree satisfying Punnett's (1915) requirements mentioned earlier. Even so, if there is little or no generalization overlap to begin with, Fisher's process will not work, or will be too slow to make a difference in comparison with other conceivable weak fitness effects.

## 16.6 Wrightian shifts in aposematic coloration

A basic idea about the adaptive function of aposematic coloration is that there is an advantage to resembling other members of a population, so that aposematism in itself promotes uniformity rather than diversity in coloration. There is nevertheless substantial geographic diversity in aposematic species (Mallet and Joron 1999), as well as a notable diversity among closely related species (Papageorgis 1975). Of the explanations that have been proposed, an important one is that diverging Müllerian mimicry can give rise to geographic variation in appearance, because of geographic variation in model species. However, mimicry alone is unlikely to generate diversity in aposematic coloration over the long term because no novel phenotypes would be produced, while more and more species converge to fewer and fewer Müllerian models (Mallet and Singer 1987; Turner and Mallet 1996; Mallet and Joron 1999; Baxter et al. 2009; Mallet 2010). The shifting balance process (Wright 1977) has been proposed as another general mechanism that could result in geographic variation, such that warning coloration phenotypes come to occupy different adaptive peaks, representing different efficient solutions to the problem of signaling unprofitability to predators (Mallet and Joron 1999; Mallet 2010).

Granted that a shifting balance process could result in an exploration of different adaptive peaks in a trait space of aposematic appearances, the phenomenon could also be of importance for Müllerian mimicry evolution. If different aposematic species diversify over a limited number of adaptive peaks, there is a chance that they occasionally will become similar enough for Müllerian mimicry to evolve. This follows because Fisherian convergence of aposematic phenotypes is likely to happen only if species are already similar enough to be generalized by at least some predators, which would also make the two-step process more likely to occur.

The possible importance of the shifting balance process in setting the stage for mimicry evolution exemplifies the general principle that mimicry is likely to evolve only under restricted circumstances, including restrictions on the starting points from which mimicry is likely to evolve.

For instance, as emphasized by Nicholson (1927), mimicry is more likely to evolve between related species, partly because of an already existing similarity in appearance, but also because of a similarity in the mutants that may be produced. This in effect acts as a developmental genetic constraint on the evolution of mimicry, along the lines of the ideas of Goldschmidt (1945a, 1945b), who suggested that similar saltational genetic pathways would be re-used by model and mimic. In general, if mimicry evolution corresponds to a transition between adaptive peaks, an important prerequisite is a sufficient closeness of the starting positions of the peaks in trait space.

### 16.7 Well-studied cases

A presentation of a few much studied instances of mimicry evolution illustrates the concepts we have discussed. One example concerns the variable burnet moth, *Zygaena ephialtes*, which has a wide distribution in Europe and exhibits geographic variation in coloration. North of the Alps it resembles other zygaenids, including the abundant *Zygaena filipendulae*, which has red forewing spots and red hindwing patches on a black background. The northern variant of *Z. ephialtes* also has a red abdominal band and is referred to as the red peucedanoid form (Turner 1971). In some parts of southern Europe, the species instead occurs as the yellow ephialtoid form. This southern variant of *Z. ephialtes* resembles the co-occurring *Syntomis (Amata) phegea* (Arctiidae), which is black with white wing spots and a yellow abdominal band, and lacks hindwing patches. That *Z. ephialtes* mimics *S. phegea* in this region, and not the other way around, is supported by the fact that *S. phegea* and other *Syntomis* species have white and yellow in their coloration also when they occur alone (without *Z. ephialtes*), whereas *Z. ephialtes* is white and yellow only when it co-occurs with *S. phegea*. In addition, the population densities in the areas of sympatry are much higher for *S. phegea* (Sbordoni et al. 1979). There are also regions in Europe where an intermediate variant of *Z. ephialtes* is found—the red ephialtoid form—which lacks hindwing patches and has white wing spots, apart from two red basal forewing spots, and has a red abdominal band

(Fig. 16.4). The intermediate form occurs either as a local monomorphism or in a polymorphism with one or both of the other two variants (Turner 1971). The difference in appearance between the red peucedanoid form and the intermediate form is determined by a single locus and the difference between the intermediate and the yellow ephialtoid form is determined by another, unlinked locus. This implies that the evolutionary transition between red peucedanoid and yellow ephialtoid (Fig. 16.4) must have involved at least two (and probably more than two) steps. One of these steps might represent a feature saltation, for instance the shift from red to white wing spots, or the shift from red to yellow pigmentation.

The switch from the red peucedanoid form to the yellow ephialtoid form of *Z. ephialtes* has been used in evolutionary genetics to exemplify transitions between two adaptive peaks (Coyne et al. 1997; Gavrillets 1997; Barton et al. 2007). The suggestion is that a transition from the original red peucedanoid form to the intermediate form occurred first, being favored in situations where both the models *Z. filipendulae* and *S. phegea* are present, and was followed by a change from red to yellow of the abdominal band, leading to the yellow ephialtoid form (Fig. 16.4; an illustration of suggested Adaptive Landscapes are found in fig. 24.4 of Barton et al. 2007). The scenario is in agreement with the argument by Sbordoni et al. (1979), to the effect that the intermediate form is favored in situations where *S. phegea* is abundant early in the season but only *Z. filipendulae* is present later in the season.

The transition from the original to the intermediate form of *Z. ephialtes* could be a single feature saltation (Balogh et al. 2010), but reality is likely to be more complex. The difference in appearance between the red peucedanoid and the intermediate form involves changing two different traits: the color of the wing spots and the degree of melanism in the hindwings (Fig. 16.4). The locus controlling these traits seems to be a supergene with two closely linked components (Sbordoni et al. 1979). For the degree of melanism, a number of variably melanic forms occur in certain Mediterranean regions (Hofmann 2003; Hofmann et al. 2009), suggesting that a change in hindwing melanism could have preceded a change from red to white wing



**Figure 16.4** (See also Plate 3.) Burnet moth mimicry. The top row depicts mimetic forms: red peucedanoid (left), red ephialtoid (middle), and yellow ephialtoid (right) of the variable burnet moth *Zygaena ephialtes*. In the bottom row are two models; the six-spot burnet *Zygaena filipendulae* (left) and the nine-spotted moth *Syntomis phegea* (right) are presumed models for the red peucedanoid and the yellow ephialtoid mimetic forms, respectively. The red ephialtoid form might have been an intermediate in an evolutionary transition from red peucedanoid to yellow ephialtoid; the form might have an advantage if both *Z. filipendulae* and *S. phegea* are present. Images derive from photos by Clas-Ove Strandberg of hand painted illustrations in Boisduval (1834) and Hübner (1805), obtained with permission from the Library of the Royal Swedish Academy of Sciences, deposited in Stockholm University Library. Original illustrations are (top left) nr. 8, (top middle) nr. 5, (top right) nr. 6, (bottom left) nr. 10 on Plate 55 of Boisduval (1834), and (bottom right) nr. 100 on Plate 20 of Hübner (1805). Some original species names and identities vary from those in our illustration.

spots in *Z. ephialtes*, in which case the intermediate form would have evolved in two or more steps.

An alternative scenario is that the appearance of hindwing melanism was followed by a transition from red to yellow coloration, and only after this event the white wing spots appeared. In such a case, the red ephialtoid form would have arisen at a later time, perhaps as a consequence of hybridization of red peucedanoid and yellow ephialtoid populations (Hofmann 2003), and would not have been an intermediate step in mimicry evolution. Thus, in the alternative scenario of the evolutionary transition in *Z. ephialtes*, hindwing melanism first appears, possibly for thermoregulatory reasons, setting the stage for an abrupt transition from red to yellow pigmentation (which might be a feature saltation), followed by a whitening of the wing spots (Hofmann 2003).

*Heliconius* butterflies have been extensively studied with respect to geographic variation and Müllerian mimicry (Turner 1971; Mallet and Gilbert 1995). Common colorations are the “rayed” (orange-rayed hind wings) and “postman” (red and yellow bands and bars; Sheppard et al. 1985; Joron et al. 2006a) appearances, and one of these may

be ancestral; (recent molecular data indicate that red forewing bands are ancestral in *H. erato*; Hines et al. 2011) it has been difficult to reconstruct ancestral wing patterns in *Heliconius* because of their rapid diversification (Joron et al. 2006a). A less common *Heliconius* appearance is the “tiger” coloration (orange and yellow stripes and blotches on a black ground; Turner 1971; Sheppard et al. 1985) that involves Müllerian mimicry with Ithomiinae butterflies. The coloration occurs in several species within one, probably monophyletic, group of *Heliconius* species (Beltrán et al. 2007), the so-called silvaniform group, and is probably a derived character. The central orange and black in the “tiger” pattern is a candidate for a feature that predators use in prey categorization. There is considerable variation in the “tiger” coloration of different silvaniform butterflies, a possible result of evolutionary fine-tuning towards more accurate mimicry of different Ithomiinae species. In general, mimicry evolution in *Heliconius* appears to be a complex process, possibly with a strong influence of introgression of wing pattern genes through hybridization between different species (Gilbert 2003). *Heliconius* is a likely



candidate for the operation of a shifting balance process (Mallet 2010), acting to diversify aposematic patterns, and this process perhaps also plays a role in mimicry evolution. Furthermore, two-step scenarios, including instances of feature saltation, could well apply to *Heliconius*, if one takes into account spatial and temporal variation in predator and model communities.

The genetics of mimicry in *Heliconius* has been mapped, and the genomic regions that include mimicry genes have recently been cloned in a number of species. The impressive Müllerian mimicry between multiple, divergent geographic races of *Heliconius erato* and *H. melpomene* are now known to employ major-effect loci from the very same regions of the genome in both species. Surprisingly, the silvaniform *Heliconius numata* also employs one of these same genomic regions to effect switches among phenotypes of a very different “tiger” pattern mimicry of unrelated ithomiine butterflies (Joron et al. 2006b). Not only are major-effect alleles involved, as expected from the saltational two-step model, but also the number of loci developmentally capable of mimicry appear constrained in an almost Goldschmidtian manner (Baxter et al. 2009).

There are also well-studied cases of Batesian mimicry that can illustrate transitions between adaptive peaks. The spectacular polymorphic mimicry in the Mocker Swallowtail butterfly, *Papilio dardanus*, is one example where scenarios of mimicry evolution involving big-effect mutations have been proposed (Clarke and Sheppard 1960; Turner 1984; Nijhout 2003; Clark et al. 2008; Gamberale-Stille et al. 2012). Finally, the feasibility of gradual mimetic evolution has recently been proposed in the context of Batesian coral snake mimicry (Kikuchi and Pfennig 2010), the claim being that, in situations of high model abundance, intermediates between mimics-to-be and accurate mimics are not attacked more frequently than the original appearance, resulting in an Adaptive Landscape without a valley. The suggested explanation is that a highly toxic and abundant model gives rise to wide predator generalization, overlapping the intermediate phenotypes (Kikuchi and Pfennig 2010), turning Batesian mimicry evolution into a straightforward hill-climbing process.

## 16.8 Concluding comments

Mimicry and aposematism are phenomena for which the concept of an Adaptive Landscape has proven helpful. Turner (1984) may have been the first to present heuristic illustrations of adaptive peaks of prey appearance, with evolutionary transitions between peaks. Results of theoretical modeling have also been presented as multipeaked Adaptive Landscapes (e.g. Figs. 16.1–16.3; Leimar et al 1986; Balogh and Leimar 2005; Franks and Sherratt 2007; Ruxton et al. 2008). Furthermore, there are field experiments demonstrating adaptive peaks with valleys between them (Kapan 2001), so for these phenomena the concept has empirical support and goes beyond the role of just an attractive heuristic (see Chapters 2, 3, and 19 for different viewpoints in this discussion).

A reason for the great attention given to mimicry evolution, over a period of more than a century, could be that the nature of the selection acting on multitrait phenotypes—to achieve visual resemblance to a model—is readily understood. Even so, the different elements needed to clarify how mimicry actually evolved in particular cases have proven difficult to come by. A good understanding requires a combination of experimentation on predator psychology, field studies on predator prey communities, and studies on the developmental and evolutionary genetics of mimetic phenotypes, and all of this should be put into a biogeographic and phylogenetic perspective. While there has been recent progress in several of these aspects, not least in the genetics of mimicry in butterflies (e.g. Joron et al. 2006a; Clark et al. 2008; Baxter et al. 2010; Hines et al. 2011; Reed et al. 2011), the magnitude of the task still seems challenging, even in the face of the substantial and ingenious efforts of the students of mimicry. Still, it seems possible that empirically well supported examples of transitions between adaptive peaks soon will emerge from the field.

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## References

- Aronsson, M. and Gamberale-Stille, G. (2008). Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration. *Animal Behaviour*, 75, 417–423.
- Balogh, A. C. V. and Leimar, O. (2005). Müllerian mimicry: an examination of Fisher's theory of gradual evolutionary change. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2269–2275.
- Balogh, A. C. V., Gamberale-Stille, G., Tullberg, B. S. and Leimar, O. (2010). Feature theory and the two-step hypothesis of Müllerian mimicry evolution. *Evolution*, 64, 810–822.
- Barton, N. H., Briggs, D. E. G., Eisen, J. A., Goldstein, D. B. and Patel, N. H. (2007). *Evolution*, Cold Spring Harbor Laboratory Press, Cold Spring Harbor.
- Baxter, S. W., Johnston, S. E. and Jiggins, C. D. (2009). Butterfly speciation and the distribution of gene effect sizes fixed during adaptation. *Heredity*, 102, 57–65.
- Baxter, S. W., Nadeau, N. J., Maroja, L. S., Wilkinson, P., Counterman, B. A., Dawson, A., et al. (2010). Genomic hotspots for adaptation: the population genetics of Müllerian mimicry in the *Heliconius melpomene* clade. *PLoS Genetics*, 6, e1000794.
- Beltrán, M., Jiggins, C. D., Brower, A. V. Z., Bermingham, E. and Mallet, J. (2007). Do pollen feeding, pupal mating and larval gregariousness have a single origin in *Heliconius* butterflies? Inferences from multilocus DNA sequence data. *Biological Journal of the Linnean Society*, 92, 221–239.
- Boisduval, J. A. (1834). *Icones historique des lépidoptères nouveaux ou peu connus*. Tome II. Roret, Paris.
- Chittka, L. and Osorio, D. (2007). Cognitive dimensions of predator responses to imperfect mimicry? *PLoS Biology*, 5, 2754–2758.
- Clarke, C. A. and Sheppard, P. M. (1960). Super-genes and mimicry. *Heredity*, 14, 175–185.
- Clarke, C. A. and Sheppard, P. M. (1972). The genetics of the mimetic butterfly *Papilio polytes* L. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 263, 431–458.
- Clark, R., Brown, S. M., Collins, S. C., Jiggins, C. D., Heckel, D. G. and Vogler, A. P. (2008). Colour pattern specification in the mocker swallowtail *Papilio dardanus*: the transcription factor *invected* is a candidate for the mimicry locus H. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1181–1188.
- Coyne, J. A., Barton, N. H. and Turelli, M. (1997). Perspective: A critique of Sewall Wright's shifting balance theory of evolution. *Evolution*, 51, 643–671.
- Cott, H. B. (1940). *Adaptive coloration in animals*. Methuen, London.
- Crawford, L. E., Huttenlocher, J. and Hedges, L. V. (2006). Within-category feature correlations and Bayesian adjustment strategies. *Psychonomic Bulletin & Review*, 13, 245–250.
- Darwin, C. (1859). *On the origin of species by means of natural selection*, Murray, London.
- Fisher, R. A. (1927). On some objections to mimicry theory; statistical and genetic. *Transactions of the Royal Entomological Society of London*, 75, 269–278.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. A complete variorum edition. Oxford University Press, Oxford.
- Franks D. W. and Sherratt, T. N. (2007). The evolution of multicomponent mimicry. *Journal of Theoretical Biology*, 244, 631–639.
- Gamberale-Stille, G., Balogh, A. C. V., Tullberg, B. S. and Leimar, O. (2012). Feature saltation and the evolution of mimicry. *Evolution*, doi:10.1111/j.1558-5646.2011.01482.x.
- Gavrilets, S. (1997). Evolution and speciation on holey adaptive landscapes. *Trends in Ecology & Evolution*, 12, 307–312.
- Ghirlanda, S. and Enquist, M. (2003). A century of generalisation. *Animal Behaviour*, 66, 15–36.
- Gilbert, L. E. (2003). Adaptive novelty through introgression in *Heliconius* wing patterns: Evidence for a shared genetic "toolbox" from synthetic hybrid zones and a theory of diversification. In C. L. Boggs, W. B. Watt, and P. L. Ehrlich (eds.) *Butterflies: ecology and evolution taking flight*. The University of Chicago Press, Chicago, IL, pp. 281–318.
- Goldschmidt, R. B. (1945a). Mimetic polymorphism, a controversial chapter of Darwinism. *Quarterly Review of Biology*, 20, 147–164.
- Goldschmidt, R. B. (1945b). Mimetic polymorphism, a controversial chapter of Darwinism (concluded). *Quarterly Review of Biology*, 20, 205–230.
- Hines, H. M., Counterman, B. A., Papa, R., de Moura, P. A., Cardoso, M. Z., Linares, M., et al. (2011). Wing patterning gene redefines the mimetic history of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences of the United States of America* 108, 19666–19671.
- Hofmann, A. (2003). *Zygaena (Zygaena) ephialtes* (Linnaeus, 1767) im südlichen Balkan nebst Anmerkungen zur Entstehung von Polymorphismus sowie melanistischer *Zygaena*-Formen im Mittelmeerraum (Lepidoptera:

- Zyganeidae). *Entomologische Zeitschrift*, 113, 50–54; 75–86; 108–120.
- Hofmann, A., Kia-Hofmann, T., Tremewan, W. G. and Turner, J. R. G. (2009). *Zygaena dorycnii* Ochseneheimer, 1808, morph *araratica* Staudinger, 1871 (Lepidoptera: Zygaenidae): its Mendelian genetics, sex ratios, hybridisation and speciation. *Entomologist's Gazette*, 60, 3–23.
- Hübner, J. (1805). *Sammlung europäischer Schmetterlinge*. Band 2. Augsburg.
- Huttenlocher, J., Hedges, L. V. and Vevea, J. L. (2000). Why do categories affect stimulus judgment? *Journal of Experimental Psychology – General*, 129, 220–241.
- Joron, M., Jiggins, C. D., Papanicolaou, A. and McMillan, W. O. (2006a). *Heliconius* wing patterns: an evo-devo model for understanding phenotypic diversity. *Heredity*, 97, 157–167.
- Joron, M., Papa, R., Beltrán, M., Chamberlain, N., Mavárez, J., Baxter, S., et al. (2006b). A conserved supergene locus controls colour pattern diversity in *Heliconius* butterflies. *PLoS Biology*, 4, e303.
- Kapan, D. D. (2001) Three-butterfly system provides a field test of müllerian mimicry. *Nature*, 409, 338–340.
- Kikuchi, D. W. and Pfennig, D. W. (2010). High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1041–1048.
- Leimar, O., Enquist, M. and Sillén-Tullberg, B. (1986). Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *American Naturalist* 128, 469–490.
- Mallet, J. (1999). Causes and consequences of a lack of coevolution in müllerian mimicry. *Evolutionary Ecology*, 13, 777–806.
- Mallet, J. (2010). Shift happens! Shifting balance and the evolution of diversity in warning colour and mimicry. *Ecological Entomology*, 35, 90–104.
- Mallet, J. and Gilbert, L. E. (1995). Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in *Heliconius* butterflies. *Biological Journal of the Linnean Society*, 55, 159–180.
- Mallet, J. and Joron, M. (1999). Evolution of diversity in warning color and mimicry: Polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics*, 30, 201–233.
- Mallet, J. and Singer, M. C. (1987). Individual selection, kin selection, and the shifting balance in the evolution of warning colors: the evidence from butterflies. *Biological Journal of the Linnean Society*, 32, 337–350.
- Marsh, H. L. and MacDonald, S. E. (2008). The use of perceptual features in categorization by orangutans (*Pongo abelli*). *Animal Cognition*, 11, 569–585.
- Nicholson, A. J. (1927). A new theory of mimicry. *Australian Zoologist*, 5, 10–104.
- Nijhout, H. F. (2003). Polymorphic mimicry in *Papilio dardanus*: mosaic dominance, big effects, and origins. *Evolution & Development*, 5, 579–592.
- Papageorgis, C. (1975). Mimicry in neotropical butterflies. *American Scientist*, 63, 522–532.
- Pearce, J. M. (2008). *Animal learning & cognition*, 3rd edn. Psychology Press, Hove.
- Poulton, E. B. (1912). Darwin and Bergson on the interpretation of evolution. *Bedrock*, 1, 48–65.
- Poulton, E. B. (1913). Mimicry, mutation and Mendelism. *Bedrock*, 2, 42–56.
- Punnett, R. C. (1915). *Mimicry in butterflies*, Cambridge University Press, Cambridge.
- Reed, R. D., Papa, R., Martin, A., Hines, H. M., Counterman, B. A., Pardo-Diaz, et al. (2011). *optix* drives the repeated convergent evolution of butterfly wing pattern mimicry. *Science*, 333, 1137–1141.
- Rescorla, R. A. and Wagner, A. R. A. (1972). A theory of Pavlovian conditioning. Variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black and W. F. Prokasy (eds.) *Classical conditioning II: current research and theory*. Appleton-Century-Crofts, New York, pp. 64–99.
- Ruxton, G. D., Sherratt, T. N. and Speed, M. P. (2004). *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*, Oxford University Press, New York.
- Ruxton, G. D., Franks, D. W., Balogh, A. C. V. and Leimar, O. (2008). Evolutionary implications of the form of predator generalization for aposematic signals and mimicry in prey. *Evolution*, 62, 2913–2921.
- Sbordoni, V., Bullini, L., Scarpelli, G., Forestiero, S. and Rampini, M. (1979). Mimicry in the Burnet moth *Zygaena ephialtes*: population studies and evidence of a Batesian-Müllerian situation. *Ecological Entomology*, 4, 83–93.
- Schmidt, R. S. (1958). Behavioural evidence on the evolution of Batesian mimicry. *Animal Behaviour*, 6, 129–138.
- Sheppard, P. M., Turner, J. R. G., Brown, K. S., Benson, W. W. and Singer, M. C. (1985). Genetics and the evolution of Müllerian mimicry in *Heliconius* butterflies. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 308, 433–610.
- Socha, R. and Nemeč, V. (1996). Coloration and pteridine pattern in a new, yolk body mutant of *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *European Journal of Entomology*, 93, 525–534.
- Treisman, A. M. and Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97–136.

- Troje, N. F., Huber, L., Loidolt, M., Aust, U. and Fieder, M. (1999). Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision Research*, 39, 353–366.
- Turner, J. R. G. (1971). Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies. In R. Creed (ed.) *Ecological genetics and evolution*. Blackwell Scientific Publications, Oxford, pp. 224–260.
- Turner, J. R. G. (1984). The palatability spectrum and its consequences. In R. I. Vane-Wright and P. R. Ackery (eds.) *The biology of butterflies*. Academic Press, London, pp. 141–161.
- Turner, J. R. G. (1985). Fisher's evolutionary faith and the challenge of mimicry. *Oxford Surveys in Evolutionary Biology* 2, 159–196.
- Turner, J. R. G., and Mallet, J. L. B. (1996). Did forest islands drive the diversity of warningly coloured butterflies? Biotic drift and the shifting balance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 835–845.
- Tversky, A. (1977). Features of similarity. *Psychological Review*, 84, 327–352.
- Wright, S. (1977.) *Evolution and the Genetics of Populations*. Volume 3. *Experimental Results and Evolutionary Deductions*. University of Chicago Press, Chicago, IL.