

Gilbert, L. W. (1983) Coevolution and mimicry. In *Coevolution*, Futuyma, D. J. & M. Slatkin, editors. Sinauer Associates Inc., Sunderland, MA.

to eat that and bury the harder-to-open seed for a meal when times are harder.

In all of these cases, generalizations are easy, but not very useful for specific cases. We desperately need case history studies before more specific generalizations are possible, yet in most parts of the world, the case histories are no longer possible. It is very difficult to even attempt to understand fruiting patterns of berries and nuts in the eastern United States, for example, without consideration of passenger pigeons.

#### IN CLOSING

The interaction of seed dispersers and plants is so rich in relevant detail and so idiosyncratic from one system to the next that it may appear so chaotic as to be uninteresting to study. But generalizations are possible: fruits containing seeds dispersed by small birds are *usually* red—and the proportion that are not is an interesting geographically varying trait of habitats. But the subject has been so thoroughly ignored, and the natural arena so thoroughly muddied, that we don't need a massive infusion of theory and generalizations but rather a massive infusion of detailed case studies of how things really work. There must be at least 100 papers on pollination biology for every one in seed dispersal biology. We don't even know if dispersers choose blemished fruit over perfect fruit.

The interaction between plants and their seed disperser coterie should be of special interest to evolutionists for the simple reason that much of the phenotype is spread out in the field to count and measure. When a mutation alters a leaf's temperature regime by 0.2 degree by increasing marginal crenulations, you know that change has many effects on the rest of the plant, but the changes are hidden in microscopic molecules, enzyme rates, and other parts of nature that cost billions to look at. When a mutation alters the color of a fruit from red to orange, the mutant's new seed shadow and disperser coterie is laid out for all to observe.

## COEVOLUTION AND MIMICRY

*Lawrence E. Gilbert*

#### INTRODUCTION

R. A. Fisher called mimicry theory "the greatest post-Darwinian application of natural selection." In his classic synthesis of Darwinian theory, Mendelian genetics, and mathematics, Fisher (1930) devoted an entire chapter to mimicry. Indeed, from A. R. Wallace (1889) to Ford (1971) to current evolution textbooks, the subject of mimicry has been given extensive attention, if not entire chapters.

There are several reasons for the continuing interest by evolutionary biologists in the subject of mimicry. First, mimetic traits of an organism include structures, patterns of color, behaviors, or other phenotypic attributes that set that organism apart from its close taxonomic relatives while promoting its resemblance to a more distantly related taxon. Thus, nonmimetic relatives provide an idea of the primitive phenotype, and the model phenotype is the standard toward which the mimetic species evolves by natural selection. Second, many mimetic species display both intra- and interpopulation variation with respect to mimetic attributes, and for some cases, the genetic basis of that variation is established. Finally, mimetic species are generally parasites of previously evolved systems of communication between other ("host") species, so that "host-parasite" coevolution is one possible consequence of mimicry.

This chapter concerns both the circumstances that might lead to detectable coevolution between organisms involved in mimicry systems and the extent to which mimicry itself might result from coevolution. Throughout this chapter the term *coevolution* is used in a restricted, microevolutionary sense, namely, evolution that occurs in populations of at least two species as the result of reciprocal selective influence that each has on the other. I am therefore using the narrowest definition described by the editors (see Chapter 1).

## A BRIEF SYNOPSIS OF MIMICRY THEORY

The theory of mimicry was first developed by the great naturalist H. W. Bates (1862) as a means of explaining remarkable resemblances between certain South American butterfly species belonging to different families (Figure 1). According to Bates' friend Ralph Meldola, the theory occurred to Bates only after he was back in England working with his collections. He was struck by the geographical correlation of color pattern changes within entire sets of butterfly species that he had collected in the Amazon Basin. Having just read Darwin's *Origin of Species*, Bates proposed that edible species had evolved by natural selection to resemble warningly colored, noxious species and that predators such as birds were the likely selective agents.

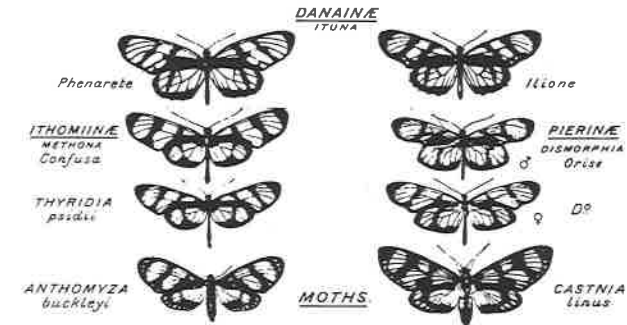
Some twenty years after Bates' landmark contribution, another of the great nineteenth century naturalists, Fritz Müller (1879), identified another form of protective convergence, namely, that between different distasteful species. In this form of convergence, each species has different warning patterns initially but converges on the same pattern under selection from predators. Using a simple mathematical model, Müller argued that two warningly colored species in the same area should converge on a common appearance because such cooperative education of predators would require fewer deaths for each species. He proposed that mutants of species A bearing slight resemblances to species B would benefit from the umbrella of predator protection resulting from past predator experience in testing individuals of B and would have a selective advantage over pure A genotypes. Likewise, mutants of B that resemble A should be selected over pure B by the reciprocal argument. Müller proposed that the final mimetic pattern would be determined by the relative abundances of A and B, such that the rarer species should converge on the pattern of the common species faster than the common one converges on the rare pattern.

There is a vast literature on classical Batesian and Müllerian mimicry, most of which is concerned with butterflies and other insects. Reviews or monographs on this subject have appeared in practically each decade of the last 100 years. Those by Carpenter and Ford (1933), Brower (1963), Rettenmeyer (1970), Turner (1977), Rothschild (1979), and Vane-Wright (1980) are thoughtful analyses that also provide an index to the background literature dealing mainly with the Bates-Müller theory. A few highlights follow.

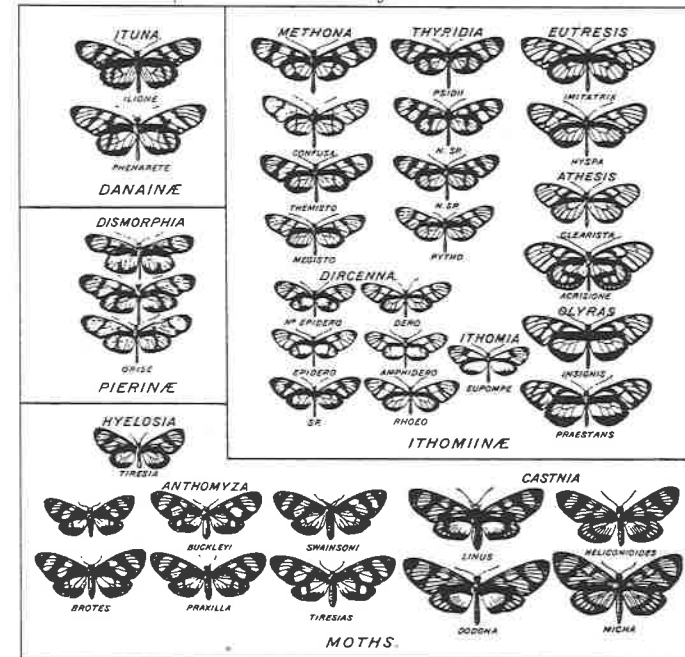
The geographical correlation in color pattern between model and mimic species, first noted by Bates and illustrated by Moulton (1909), has been further documented from a genetic perspective by Sheppard (1962) and Turner (1971). The potential for birds to act as selective agents on prey color pattern was given credibility by Swynnerton (Carpenter, 1942) and experimentally verified for captive birds by Brower (1958) and for wild birds by Jeffords et al. (1979). The genetics

Poulton.

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1. Group as described by H W Bates in 1861.



2. Group as known in 1897. EDWIN WILSON, CAMBRIDGE

RESEMBLANCES IN TROPICAL AMERICAN LEPIDOPTERA.

FIGURE 1. A plate from an early review of mimicry by E. B. Poulton. Bates was concerned with the resemblance between presumed edible pierid *Dismorphia* and the ithomiine *Methona*. Müller's theory was based on observations of the danine *Ituna* and the ithomiine *Thyridia*, both of which are distasteful. Neither Bates nor Müller had the modern view of systematics reflected in Poulton's arrangement of the plate.

of mimetic variation, which developed as a field of interest immediately after the rediscovery of Mendel's work, culminated in the classic work of Sheppard, Clarke, and their associates (see Turner, 1977). The unpalatability to vertebrates assumed for model species by most students of mimicry has now been demonstrated for a few species such as the monarch butterfly (Brower and Glazier, 1975). It frequently results from the storage of host plant-derived chemicals (references in Rothschild, 1979). Ecological studies of model and mimic populations of burnet moths (Sbordoni et al., 1979) have verified Müller's assertion that the rare species of a distasteful pair should converge on the more common, and in this case, less noxious, species.

In addition to these contributions to the Bates-Müller tradition, other lines of biological research have revealed significant new categories of mimetic relationships in nature. Of particular interest are forms of mimicry not involving a predator as the selective agent. Many such examples emerged from the kinds of ethological studies pioneered by Tinbergen and Lorenz. Wickler (1968) reviews the entire subject of mimicry from this fresh perspective and develops a general theoretical framework that includes Batesian mimicry as a special case.

In Wickler's scheme, mimicry evolves only in the context of well-established communication systems, wherein organisms that send signals as well as organisms that receive and react to those signals have a strong mutual interest in clear, unambiguous transfer of messages. Both the unpalatable insect and its potential attacker benefit from a clearly transmitted warning signal. The insect does not sustain life-threatening damage; the predator does not waste time and energy in pursuit of unsuitable prey. Wickler defines mimicry as the sending of fake signals by a third organism, which derives some advantage (such as predator protection) in the deception of the signal receiver.

Late last century, Poulton (1898) pointed out that Müllerian mimicry probably should not be regarded as true mimicry. Wickler would agree because such convergence of warning signals does not involve deceit. Or does it? Another important feature of Wickler's theory is that phenotypic traits should only be categorized relative to the signal receiver. For example, a mantid that resembles a flower is an aggressive mimic from the standpoint of insects that are attracted to the imitated flower, but cryptic (imitation of nonsignals) to an insectivorous bird. Likewise, it must be true that as the degree of unpalatability is variable within and among species of Müllerian complexes (Brower et al., 1963), some predators will treat the entire set as unacceptable whereas others, possibly specialists on noxious insects, will find part of the same complex edible and will lead us to view the system as Batesian mimicry. There are other reasons to treat Batesian and Müllerian mimicry as a continuum (Sbordoni et al., 1979, and references therein) that involves relative palatability and relative abundances—aspects of the problem largely anticipated by Müller himself.

## COEVOLUTION AND MIMICRY

The Batesian-Müllerian gradient is a special version of the parasitism-commensalism-mutualism continuum well known in ecology. It is generally thought that relationships that begin as parasite-host relationships may evolve toward commensal or mutualistic relationships. For example, the relationship between pollinating insects and higher plants most likely began with insects as parasites of plant reproduction, and became mutualistic as plants and insects coevolved toward the specialized pollination systems of today. The tricky problem is how a parasite-host coevolutionary race becomes coevolved mutualism. We would expect Batesian models either not to evolve as mimicry evolves (in the case of a rare, and/or somewhat distasteful, *commensal* mimic) or to evolve away from the mimetic pattern (as with a common, edible, *parasitic* mimic). In the case of Müllerian models, either no coevolution occurs (with rare, and/or slightly less noxious, *commensal* mimic/comodel) or two warningly colored species coevolve toward an intermediate pattern (equally abundant, equally distasteful, Müllerian mimics). These relationships are shown in Figure 2.

From these simple considerations it is clear that coevolution need not result from the evolution of Batesian mimicry nor be the mechanism by which Müllerian species come to possess similar patterns. But, by the same token, certain instances of mimicry almost certainly involve coevolution and thus provide an unusual opportunity for developing direct evidence for the study and documentation of this elusive process.

## MÜLLERIAN MIMICRY AS EVIDENCE FOR COEVOLVED MUTUALISM

Coevolution is more likely to occur under circumstances of tight ecological association between species, as in host-specific parasitism. It is most likely to be detected if extensive comparative knowledge of the morphology, behavior, and genetics of the higher taxa involved can be used to establish a basis for picking out the reciprocally evolved traits of each species in a coevolving pair. For example, Janzen's (1966) study of obligately associated species of ant *Acacia* and *Pseudomyrmex* ants revealed numerous morphological and behavioral attributes of both the ant and the *Acacia* which, on the one hand, set them apart from congeners not participating in such mutualism, and on the other, are best explained as a consequence of a coevolutionary interaction.

Many Müllerian associates, although not involved in such a tight ecological linkage as *Pseudomyrmex* and *Acacia*, do appear to have evolved away from close relatives with respect to those attributes that function in the cooperative warning and education of predators. But as Müller anticipated and Figure 2 restates, strong coevolved mutualism is only expected where the mimics have similar abundance. Müller's comment on this point is, in my opinion, the first quantitative statement of coevolution: "If two or even several distasteful species are equally common, resemblance brings them a nearly equal advantage, and each step which the other takes in this direction is preserved by natural selection" (Müller, 1879, p. xxviii).

F. A. Dixey (1897, 1909) elaborated Müller's concept of mutual convergence—he called it diaposematism—based upon his studies of pierid butterflies. The Dixey papers touched off a debate that, in retrospect, appears to be a case of both sides being partly correct. Marshall (1908) argued against the possibility of diaposematism or coevolution. He reasoned that a rare species should converge on a common species, but the common species would not itself evolve toward the rare pattern because relatively few predators would have encountered and learned the pattern of the rare species. Therefore, mutants of the common species that resemble the rare form would have lower fitness than the standard individuals.

Modern experimental evidence from natural populations does support the notion that major alteration of a warning pattern results in significantly higher attack rates by birds. Benson (1972) blacked out the forewing red patch of wild *Heliconius erato* and established a control group visually identical to unaltered specimens (red, black forewing; yellow, black hindwing). He detected increased wing damage by birds and shorter longevity in the altered individuals. I have already mentioned other field studies that show convergence of rare species or the phenotype of the common species in distasteful moths (Sbordoni et al., 1979). Had these results been available in 1908, Marshall would have used them to support his case against coevolved Müllerian associations.

Fisher's (1927, 1930) analysis of this problem introduced a concept akin to what today would be called "punctuated equilibria" (for a discussion of this interpretation see Turner, 1977; 1981). Put briefly and simply, Fisher identified two classes of genes defined by the nature and degree of their impact on the phenotype: (1) Major genes, mutations of which cause major alterations of phenotype. (2) Modifier genes, mutations of which cause slighter alterations in color and pattern components and which account for gradual evolution of phenotype in the time period between major genetic changes.

Fisher's theory would predict that coevolution would occur between two distinct aposematic species only after a major gene mutation in the rare species has produced a phenotype that, though not

exact, can be confused with the common species. Once rough resemblance is achieved (evolving unidirectionally as Marshall would have predicted), minor coevolved modifications of both species would lead to a more perfect resemblance, as Müller and Dixey had suggested.

The controversy over Müllerian convergence led to some very creative thinking (especially by R. A. Fisher, the influence of which is

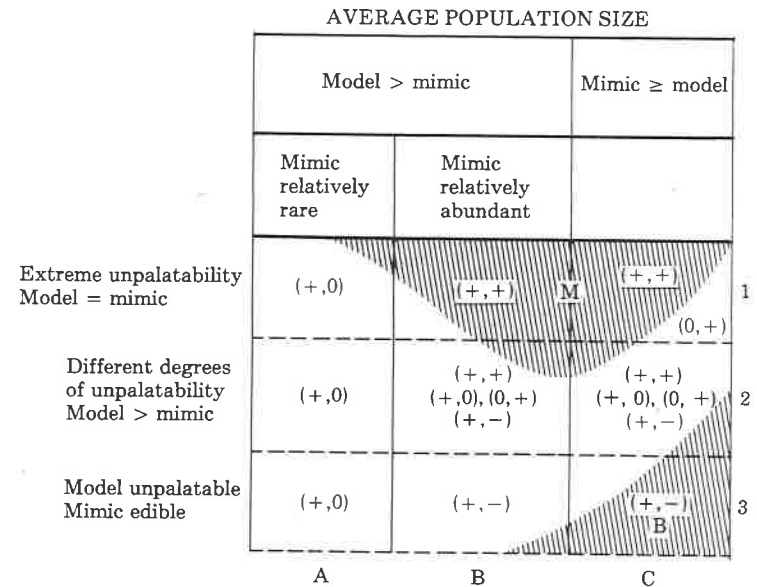


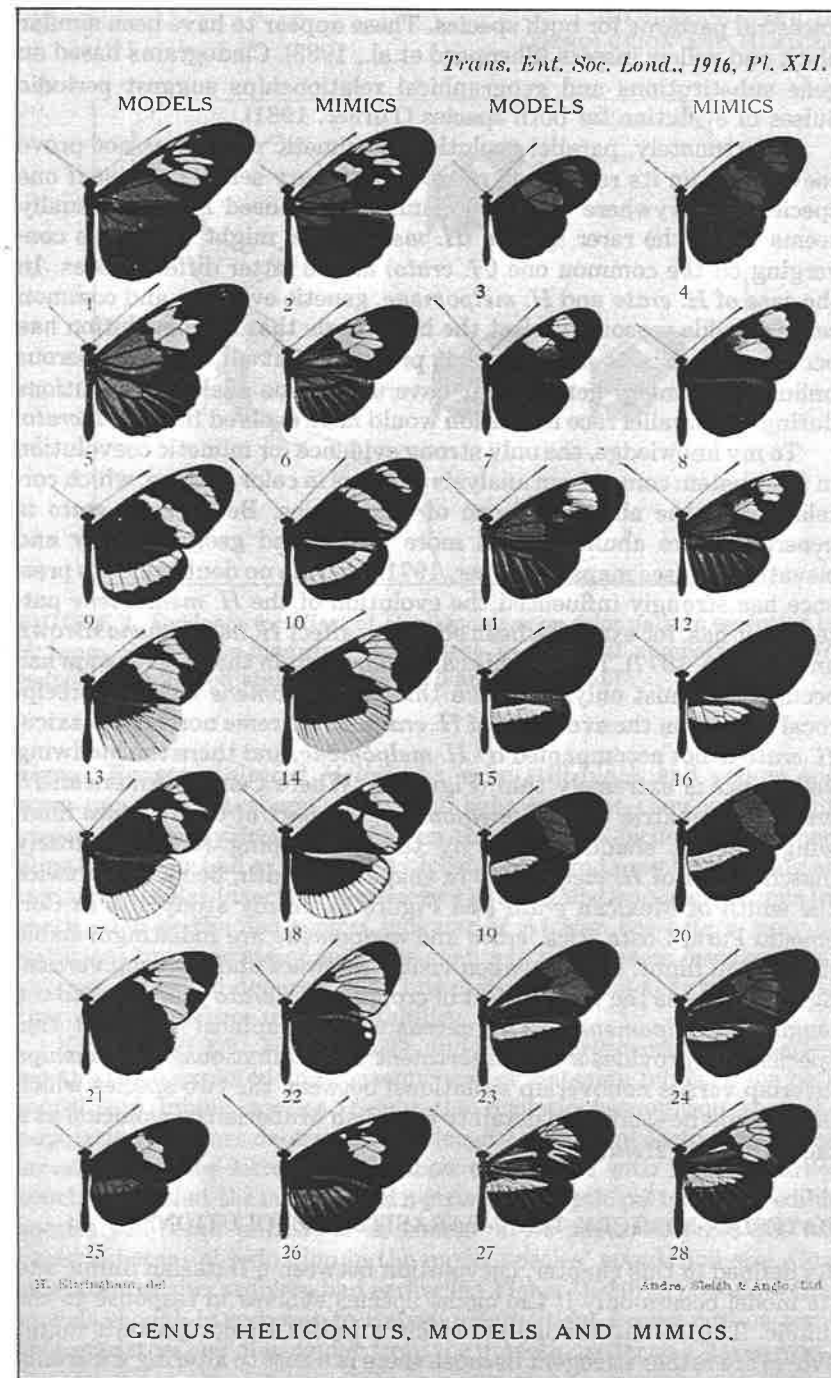
FIGURE 2. Ecological interactions and coevolution in Batesian-Müllerian mimicry. Hypothesized interaction between gradients of palatability (rows), relative abundance of model and mimic species (columns), and net ecological interaction coefficients between mimic and model (shown as negative, positive, or zero in parentheses in cells of chart) are related to potential for coevolution (hatched zone of table). The entry (+, -) means that the relationship has a positive impact on the mimic but a negative impact on the model. Cells 2B and 2C show that the net effect of mimicry is basically uncertain without more knowledge of relative palatability (measured in terms of the most significant natural predators) and more precise population data. Depending upon variables such as toxicity of local host plants, local population sizes of each species through time, and seasonal effects on predator palatability thresholds, a given pair of mimetic species might occupy many cells of this chart through both ecological and evolutionary time. (M = zone of likely Müllerian coevolution; B = zone of likely Batesian coevolution.)

seen in the work of Ford, Sheppard, Turner, and others. The debate was, and is, more complex than my distillation would lead one to believe. Commonness and rarity are often treated as species phenotypes rather than ecological variables. Müllerian coevolution seems much more likely if the two species in question periodically switch rank in terms of numerical dominance, a circumstance that undoubtedly occurs within many Müllerian associations through time and space.

The best documented example of Müllerian convergence is the extensive parallel race formation of the neotropical *Heliconius erato*, *Heliconius melpomene*, and other members of the *H. erato* and *H. melpomene* groups (Figure 3). In Müller's day, too little was known of the taxonomic affinities within *Heliconius* for anyone to seriously suspect that such remarkable convergence reflected anything more than very close taxonomic affinities. But as careful biogeographical and morphological information on the genus developed it became clear that *H. erato* and *H. melpomene* represented distinctive radiations within the genus, and Eltringham (1916) presented what amounts to a modern view of the relationships between these species. We now know of extensive differences between these species groups of *Heliconius*. *H. erato* and its relatives have distinctive pupal and male clasper morphology. They often mate on pupae, and females are monogamous. They are generally associated with the *Plectostemma* subgenus of *Passiflora* (passionvines) as larvae (Gilbert, 1976; Benson et al., 1976; Brown, 1981). *H. melpomene* and its relatives have standard butterfly courtship, females mate repeatedly, and morphology and host relations are generally distinct from *H. erato* (see previous references).

*H. erato* and *H. melpomene* have been the subjects of extensive genetic and biogeographical analyses during the past 25 years. Highly distinctive races of these two species (Figure 3) are closely correlated in space (Turner, 1971) but a sample of genes not involved in color pattern determination is not differentiated geographically (Turner, 1979). Variation in a half dozen or so major genes and a host of minor modifying loci, most unlinked, account for the racial differentiation of each species (Sheppard et al., 1981). Thanks to the extent and quality of these data, it has been possible to demonstrate the parallel evolution of races in *H. erato* and *H. melpomene*. On the assumption that recessive alleles at a locus are replaced by dominant alleles and thus define ancestral color pattern components, it has been possible to construct

FIGURE 3. Parallel races in the genus *Heliconius* according to Eltringham (1916). *H. erato* (3, 7, 11, 15, 23, 25, 27) are matched against sympatric races of *H. melpomene* (4, 8, 12, 16, 24, 26, 28). Races of *H. erato* relative *sapho* (9, 13, 17, 21) are matched against sympatric varieties of *H. melpomene* relative *cydno* (10, 14, 18, 22). In one case, the mimic of *H. erato* is considered to be a *cydno* (19, 20). (This figure is reproduced in color on the cover.)





ancestral patterns for both species. These appear to have been similar black and yellow insects (Sheppard et al., 1983). Cladograms based on gene substitutions and geographical relationships suggest periodic pulses of evolution for both species (Turner, 1981).

Unfortunately, parallel evolution of mimetic races does not prove coevolution (in its reciprocal, microevolutionary sense) because if one species is everywhere the more common, as indeed *H. erato* usually seems to be, the rarer species (*H. melpomene*) might be always converging on the common one (*H. erato*) as the latter differentiates. In the case of *H. erato* and *H. melpomene*, genetic evidence and common sense provide reason to reject the hypothesis that no coevolution has occurred, that is, it is simply not probable that all of the numerous unlinked "mimicry genes" that have undergone allelic substitutions during the parallel race formation would have evolved first in *H. erato*.

To my knowledge, the only strong evidence for mimetic coevolution in this system comes from analysis of clines in color pattern, which correlate with the absence of one of the species. Because *H. erato* is generally more abundant and more widespread geographically and elevationally (see maps in Turner, 1971), there is no doubt that its presence has strongly influenced the evolution of the *H. melpomene* pattern as it has, for example, been shown to affect *H. hermathena* (Brown and Benson, 1977). Thus in this case, to be certain that coevolution has occurred, it must only be shown that *H. melpomene* has some reciprocal impact on the evolution of *H. erato*. In extreme northern Mexico, *H. erato* is not accompanied by *H. melpomene*, and there the hindwing yellow bar is extremely thin (Figure 4). Where Central American *H. erato* is sympatric with *H. melpomene*, the part of the *H. erato* hindwing bar not shadowed out by the overlapping forewing closely matches that of *H. melpomene* in shape and width, being about twice the width of Mexican *erato* (see Figure 5). In my study site in Corcovado Park, Costa Rica, *erato* and *melpomene* are indistinguishable not only in flight, but also when visiting flowers under strong vertical light, which has the visual effect of cropping the *erato* yellow bar to the length of *melpomene*'s. The extensive geographical range of this species pair provides a rich assortment of distributional relationships (overlap versus nonoverlap situations) between the two species which now should be studied in detail to establish Müllerian coevolution as a fact of life for *Heliconius*.

#### BATESIAN MIMICRY: HOST-PARASITE COEVOLUTION?

As defined in this chapter, coevolution between a Batesian mimic and its model occurs only if the model species evolves in response to the mimic. The conditions under which a model's color pattern might evolve are rather stringent because there is a cost to altering a warning

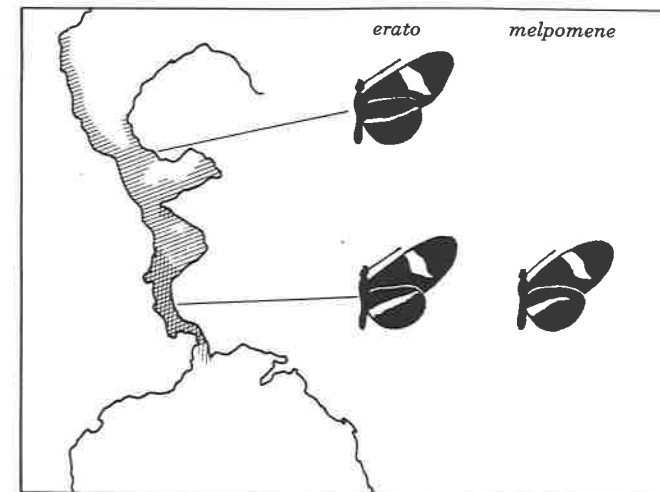


FIGURE 4. Evidence for effect of *H. melpomene* on color pattern evolution in *H. erato*. *H. erato*'s hindwing bar widens in zones of sympatry with *H. melpomene* (stippled area). (See Figure 5 and its legend.)

signal. Benson's altered *Heliconius* were still black and yellow and were unaltered in shape and flight behavior, yet they suffered increased mortality from birds. Even though most birds might generalize from their bad experience with bright-colored prey by ignoring all remotely similar insects, a few species of specialists on conspicuous insects, such as the neotropical jacamar or African bee eaters, may be sufficient to act as major selective agents in this system, because their success in feeding depends upon fine distinctions between similar prey that differ in degree of unpalatability.

Nicholson (1927), Fisher (1930), and later Charlesworth and Charlesworth (1975) explored the consequences of Batesian mimicry for both model and mimic species. Using the realistic assumption that the population sizes are determined by density-dependent factors acting on larval stages, the latter authors show (consistent with Fisher's earlier conclusions) that the evolution of a gene for mimetic pattern in an edible species will result in little or no change in its population size but will cause substantial reduction in the model species' population size. Consideration of this problem had earlier led Fisher (1930) to postulate that models should, in response to Batesian parasitism, evolve new patterns that predators can distinguish from the mimetic patterns. Charlesworth

	E1				
E1	Mexico N = 7 X = 1.21 sd = 0.24				
		E2			
E2	**	C.R. Atlantic N = 8 X = 1.80 sd = 0.35			
			E3		
E3	**	*	C.R. Mt. Cent. N = 7 X = 2.24 sd = .25		
				E4	
E4	***	**	**	C.R. Pacific N = 9 X = 2.73 sd = .32	
					M4
M4				N.S.	C.R. Pacific N = 9 X = 2.92 sd = .22
					M3
M3		*		N.S.	C.R. Atlantic N = 6 X = 2.65 sd = .30

FIGURE 5. Preliminary analysis of variation in width of hindwing bar in *H. erato*. In the chart, E1, E2, E3 and E4 represent four geographically separate samples of *H. erato* and M3 and M4 represent *H. melpomene* sympatric with E2 and E4. The diagonal cells give location, sample size, mean bar width (in mm), and standard deviation for each sample. Asterisks in the cells of the chart indicate probability from one-way ANOVA, that differences are due to chance (\*,  $p < 0.01$ ; \*\*,  $p < 0.001$ ; \*\*\*,  $p < 0.0001$ ). Thus, all *H. erato* samples are different, with a continuous increase in bar width from Mexico to the Pacific side of Costa Rica, at which point there is no significant difference between *H. erato* and *H. melpomene* bar width (hatched cell, M4/E4). Note that Atlantic side *H. erato* differ significantly from sympatric *H. melpomene* (hatched cell, M3/E2). Thus, gene flow from the north may be preventing accurate mimicry in the Atlantic lowlands, whereas mountains protect the Pacific lowland *H. erato* populations from this influence.

and Charlesworth (1975) disagree: "However, a new form of the model will lose the protection from which all members of the model species share, through the fact that the predator learns best to avoid the form of the model which is most common, so that the model species may well be unable to evolve a new pattern, despite the evolution of mimicry in another species living in the same area."

Are we then to conclude that Batesian mimicry involves only convergence by edible parasitic species toward the predator warning signals of a distasteful model or host species and that coevolution, *sensu stricto*, does not occur in Batesian systems? As tempting as this conclusion appears to be, it would be made in ignorance of the evolutionary options that are available to the model in nature.

Simple theories of coevolution necessarily consider evolution in parallel traits of model and mimic, such as the components of color pattern visible at a distance. However, a model's evolutionary response to "mimic pressure" could take the form of behavioral avoidance of mimics in time or space, or the development of nonvisual signals (such as bad-tasting wings or strong odors) and the addition of subtle pattern elements (such as the white thoracic spots of monarch butterflies) that would improve predator ability to distinguish model from mimic (after capture but before killing prey). Such traits should vary within an aposematic, distasteful species between geographically separate populations exposed to different degrees of Batesian parasitism. However, much more study of natural predators that are important as selective agents will be needed before we will be able to adequately understand the coevolutionary options of Batesian models.

Returning to the possibility of coevolutionary changes in model patterns resulting from the evolution of Batesian mimicry, it should be pointed out that not all mutant patterns of the model species would necessarily have lower fitness than the original type. Most authors have ignored the possibility that a model species might escape a Batesian mimic by switching to another sympatric mimicry system containing more comodels and fewer edible Batesian mimics. As with the standard argument for the evolution of Batesian mimicry itself, this mechanism works only if the initial mutation has a major effect on the model's phenotype in the direction of its new Müllerian model.

One of the frequently recited principles of mimicry is that distasteful, warningly colored species should be monomorphic for aposematic traits. Yet we know of several polymorphic, yet distasteful, butterflies, including African *Acraea encedon* (Owen and Chanter, 1968) and American *Heliconius ethilla* (Turner, 1968) and *H. numata* (Brown and Benson, 1974). Brown and Benson hypothesize that *H. numata* has a Batesian relationship to more numerous and more distasteful ithomiine butterflies and argue that color pattern switch genes have evolved in *H. numata* in the context of temporal and spatial patchiness of different ithomiine species. But why are there so many patterns to copy among the ithomiines (Papageorgis, 1975)?

One case of polymorphism in a distasteful model appears to be con-



sistent with a coevolutionary escape hypothesis. D. A. S. Smith (1979) sampled the African danaid *Danaus (Limnas) chrysippus* and its Batesian mimic *Hypolimnna misippus* for 11 months near Dar es Salaam, Tanzania. Four major morphs of *D. chrysippus* are paralleled closely by four morphs of *H. misippus* (see Smith, 1973). Smith recorded bird beak marks on the two most common forms of *D. chrysippus* to determine whether different levels of predator pressure were experienced by different morphs of *D. chrysippus* in relation to the abundance of corresponding mimetic morphs of *H. misippus* (see Figure 6).

As classical theory would have predicted, the *D. chrysippus* morph most frequently attacked by birds had the larger following of mimics. *D. chrysippus* form *aegyptius* showed a more significant incidence of bird damage than did *D. chrysippus* form *dorippus* (12.7% to 6.0%; D. A. S. Smith, 1979). During that period (1974–1975) *D. chrysippus* form *aegyptius* was 5 times as abundant as its mimic *H. misippus* form *misippus*, whereas *D. chrysippus* form *dorippus* was 32–41 times as abundant as its mimic *H. misippus* form *inaria* (D. A. S. Smith, 1976, Table 2). *D. chrysippus* form *dorippus* also participates in a large Müllerian complex containing several distasteful *Acraea* and relatively few Batesian mimics.

Genetic evidence is consistent with the idea that *D. chrysippus* form *dorippus* evolved from *D. chrysippus* form *aegyptius*. The latter

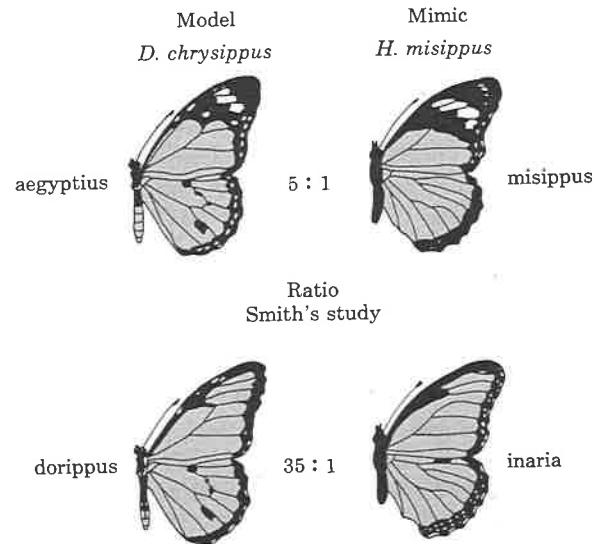


FIGURE 6. Smith's illustration of parallel polymorphic forms of *D. chrysippus* and Batesian mimic *H. misippus* in Tanzania.

is converted to *dorippus* by a dominant allele at the *C* locus (Smith, 1975). So, if the East African populations of *D. chrysippus* are composed mainly of toxic individuals, the evidence is in general support of the idea that was put forward by Owen and Chanter (1968) that genetic polymorphism in this species results from an overloading of Batesian mimics. However, it should be emphasized that evolutionary escape from Batesian mimics is but one of several possible explanations for the polymorphism in *D. chrysippus* (Smith, 1980). It should also be pointed out that in some areas of West Africa, *D. chrysippus* populations consist of a majority of individuals that are edible because they feed on non-toxic hosts (Brower et al., 1975). Thus until African *D. chrysippus* is better studied, any explanation for its polymorphic status must be tentative.

#### MIMETIC COEVOLUTION IN NON-BATESIAN SYSTEMS

This chapter has focused on the classic forms of mimicry in butterflies because it is here that the most extensive taxonomic, geographical, and genetic information exists. However, it is in other forms of mimicry that coevolution is more likely to be a constantly ongoing process. In cases of intraspecific mimicry such as egg mimicry by male cichlid *Haplochromis burtoni* (Wickler, 1968), wherein a mimetic egg on the male's anal fin organizes oral insemination in this mouth breeder, coevolution between morphology and behavior of the sexes seems certain. But putting aside the special case of intragenomic coevolution, there remain many cases where coevolution is made likely by the nature of relations between signal-sending and signal-receiving species.

In the case of cleaner wrasses (*Labroides*), whose colors and behaviors elicit passive behavior in larger predaceous fish, strong mutual benefits prevent dissolution of the relationship under the pressure of mimicry by the saber-toothed blennies (*Aspidontus*), which parasitize rather than clean the larger fish (Wickler, 1968). The highly specific and obligate nature of this mutualism, coupled with the predaceous abilities of the signal receiver, promotes coevolved mimicry. Apparently, regular removal of ectoparasites by cleaner fish is crucial to the survival of many larger marine fish. The relationship between the cleaner wrasse and its "host" involves communication of cleaner status both through color pattern and ritualized dances by the wrasse. The entry of mimics into this system has apparently created selective pressures that favor improved visual discrimination by the "cleaned fishes" and, at the same time, select strongly for a more complex or sophisticated mode of signaling by the cleaner.

Other mimicry systems, within which ongoing coevolution is virtually certain, also possess the elements of strong mutualism coupled with signal receivers that have intimate relationships with model and mimic. The most striking cases are those in which signal senders and receivers are either juveniles and adults or males and females of the same species. Reproduction, sex, and death are the stakes in this most obligate and specific of signal transfers. Mimetic eggs or young of brood parasitic birds (Payne, 1977), false courtship signals in male-eating female fireflies (Lloyd, 1965), mimetic floral signals (Wiens, 1978), and dummy butterfly eggs on passionvines (Williams and Gilbert, 1981) can all be included in this category.

The case of plants mimicking insect eggs illustrates the indirect and tortuous sequence of coevolutionary events that culminated in this mimicry between trophic levels. The first steps that must be considered involve the evolution by ancestral Passifloraceae of allelochemicals in response to a diffuse background of herbivores. According to one view (Gilbert, 1971), each advance in chemical defense would have eliminated all but those herbivores able to evolve counter defense. This process would lead to specialization on Passifloraceae by a few insect groups. Once the fauna using Passifloraceae had been reduced to a few types such as heliconiine butterflies, it is hypothesized that successful advances in herbivore defense would have been increasingly aimed toward heliconiine and other specialists and would have been less chemical in nature because those insects are in the business, as it were, of circumventing the chemical defenses of Passifloraceae.

Mechanical defenses such as hooked trichomes represent the type of specialized nonchemical defense that would appear to be most likely to arise after the plant fauna had been reduced during diffuse coevolution (Gilbert, 1971). Egg mimics also represent a mechanical device, but one that manipulates the behavior of ovipositing insects.

Explaining why a butterfly would avoid mimetic eggs further emphasizes the complex web of relationships that must be understood in order to trace the probable course of coevolution. It appears that relatively recently the genus *Heliconius* arose from other heliconiines and underwent spectacular adaptive radiation (Brown, 1981). Two steps seem to have been involved. One of these is the expanded reproductive life span and the increased adult investment in reproductive effort allowed by the habit of feeding on the pollen of certain curcubit vines (Gilbert, 1975). The second innovation of ancestral *Heliconius* was their specialization on the very youngest shoots of *Passiflora* and other Passifloraceae (Benson et al., 1976). Both of these evolutionary developments set the stage for further selection favoring sophisticated foraging behavior by adult *Heliconius* (Gilbert, 1975), one aspect of which is the careful choice of oviposition site by females. Because the larvae exist on small parcels of suitable host, the likelihood of larval

crowding and competition is high, and aggressive, cannibalistic larvae have evolved among many of the *Heliconius*. Females ignoring the presence of eggs already on shoots risk leaving no offspring.

In contrast to most other heliconiines that lay relatively inconspicuous eggs, *Heliconius* lay bright yellow eggs, the color of which constitutes a signal used by many species in the genus. This signal would have both an intra- and an interspecific function, because *Heliconius* species often share *Passiflora* species. Several species appear to respond strongly to the presence of eggs on the host plant and the role of egg color has been implicated by experiments on discrimination by ovipositing females of *H. cydno* (Williams and Gilbert, 1981).

When the butterflies evolved discrimination against ovipositing near previous eggs, the way was open for the coevolution of egg mimics by the *Passiflora*. Based on current taxonomic and geographical occurrence of the trait, the evolution of egg mimicry seems dynamic and ongoing. Only approximately 2% of the more than 500 species of *Passiflora* are known to possess these structures. Also, several independent origins of the trait are evidenced by the use of different structures (nectaries, stipules, buds) to form the fake egg and by the independent occurrence of egg mimicry in several subgenera. Furthermore, the occurrence of the trait is geographically variable among populations of the same or closely related species (Williams and Gilbert, 1981). Shapiro's (1981) discovery of a similar phenomenon in crucifer hosts of pierids in California suggests that such mimicry may be widespread.

The coevolutionary responses by *Heliconius* to evolving egg mimicry in *Passiflora* are not yet identified, but careful study of species whose geographically separate populations are differentially exposed to egg mimicry by their host plants should provide some clues.

In both documented cases (Williams and Gilbert, 1981; Shapiro, 1981), egg mimicry has apparently evolved in the absence of conspicuous demographic impact by the butterflies on the plants. Thus, the arguments that butterflies are minor components of plant faunas and therefore are not likely to select for plant defensive traits are similar to arguments against the role of birds as selective agents in butterfly mimicry (on the grounds that most mortality occurs to eggs and larvae).

These and other "Wicklerian" mimicry systems constitute many spectacular cases of mimicry that are, no doubt, dynamically coevolving systems deserving of the detailed attention that has been given to Batesian and Müllerian systems. It is tempting to propose egg mimicry in plants as a model case for intertrophic level coevolution.

It should now be clear that systems of Batesian or Müllerian mimicry do not, given our present knowledge, provide many unambiguous examples of coevolution, in the strict sense of the word. This is in part because much past research has been overly occupied with proving facets of mimicry theory that, thanks to a vast amount of systematic, genetic, geographical, and natural historical data, have been virtually certain for most of this century. Given limited resources and a possible time limit on the survival of intact natural ecosystems, it is now time to begin using mimicry systems as probes for more general ecological and evolutionary problems (see Vane-Wright, 1980) rather than working to convince the last skeptic that mimicry exists.

We should also not stall too long on the questions of whether coevolution occurs or how pervasive it is. Rather, we should soon proceed with testing predictions of an emerging theory of coevolution as best we can. Mimicry systems will prove valuable in part because sets of species involved in mimicry will have a much greater likelihood of having coevolved with respect to particular attributes than similar sets of nonmimetic relatives. Mimetic groups can therefore be compared to nonmimetic relatives to answer such questions as the impact of coevolution on rates of differentiation in particular parts of the genome, as well as on other micro- and macroevolutionary phenomena.

Evolutionary theory and its corollary—mimicry theory—were spawned in the minds of nineteenth century biologists who had the good fortune to observe and study tropical faunas and floras. We now view tropical rain forests as the most species-rich, highly organized, and perhaps most energetically dynamic ecosystems on our planet. Such forests are characterized by an overwhelming variety of mimicry systems and other coevolving subsystems (Gilbert, 1980). Practically every diurnally active and conspicuous arthropod participates in some form of mimicry, and the obvious cases are just a hint of what might be found using sensitive assays of auditory, visual, and chemical signals being sent, received, and imitated in the system. Mimicry *reduces* the apparent phenotypic variety in a system by increasing the similarity of unrelated species, but it *increases* the phenotypic diversity among closely related species that segregate ecologically by habitat and by mimicry complex (see Gilbert, 1983; Gilbert and Smiley, 1978). Polymorphic mimicry and the differentiation of mimetic races increases within- and between-habitat diversity, respectively.

In any ecosystem, exchanges within and between trophic levels of food webs usually are based on interacting pairs of individuals. Likewise, the persistence of populations within the system involves courtship, mating, oviposition, brood care, pollination, and other key behavioral interactions (involving communication) between individual or-

ganisms. Building on Wickler's theory (i.e., mimicry of communication signals), we can view the incidence of mimicry as a rough index to the degree of specificity of behavioral interaction in an ecosystem. The incidence of mimicry should thus reflect the long-term mildness and predictability of the climate within which a particular ecological system has been evolved. This is because mimicry often represents a parasitic specialization on small parcels of materials and energy being exchanged in the system, the constant and predictable availability of which is mandatory for the evolution and persistence of the mimicry.

It could be argued that the apparent increase in mimetic relationships in tropical rain forest is a trivial outcome of the fact that such habitats possess more species. However, I suggest that involvement in mimicry may account for the local persistence of many rare species (Gilbert, 1982) so that mimicry actually promotes local species richness. Indeed, when our knowledge of the geographical incidence of mimicry within taxonomic groups of organisms is more complete (along the lines of Hespenheide, 1973b), we may find evidence that this phenomenon correlates with the general importance of deterministic relationships between species and with the likelihood of community coevolution. Mimicry is possibly the most compelling evidence that community patterns are more than random noise.