Individual selection, kin selection, and the shifting balance in the evolution of warning colours: the evidence from butterflies

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It is difficult to imagine how warning colours evolve in unpalatable prey. Firstly, novel warningly coloured variants gain no protection from their colours, since predators have not previously encountered and learnt their colour patterns. This leads to a frequency-dependent disadvantage of a rare variant within a species. Secondly, novel warningly coloured variants may be more conspicuous than non-aposematic prey.

Nevertheless, it is obvious that many palatable butterflies have bright colours used in intraspecific communication and in duping predators. Other palatable butterflies are already warningly coloured. Should such butterflies evolve unpalatability, perhaps because of a host-plant shift, these bright colours would be preadapted to a warning role. Warning colours could then continue to evolve by enhancement of memorable characteristics of these patterns, or by mimicry.

Even within lineages of warningly coloured, unpalatable butterflies, colour patterns have continued to evolve rapidly. This diversity of warning colour patterns could have evolved in a number of ways, including individual and kin selection, and by the shifting balance. Evidence for these mechanisms is discussed, as are the similarities between the evolution of warning colours and more general evolutionary processes, including sexual selection and speciation.

KEY WORDS:—Warning colour – mimicry – supernormal sign stimuli – kin selection – shifting balance – frequency-dependent selection – sexual selection – predation.

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INTRODUCTION

Butterfly wings are not just organs for flying. Their colour patterns are especially important: they are used in thermoregulation (Watt, 1968; Douglas & Grula, 1978; Roland, 1982), intersexual recognition (Magnus, 1963; Silberglied & Taylor, 1973; Silberglied, 1984), and in escaping from or warning away predators (Wallace, 1878; Poulton, 1890; Cott, 1940).

The evolution of warning colours is especially interesting because the question 'why are unpalatable species conspicuous?' does not have a simple answer. Natural selection can maintain warning colours once they have evolved, even though a warningly coloured mutant may be at an initial disadvantage. Alternative warning colours may be effective: in warning colour there is an "adaptive landscape" with more than one fitness peak separated by maladaptive troughs. Such landscapes (Wright, 1932, 1977) are probably common, as in the evolution of reproductive isolation (Barton & Charlesworth, 1984), but the only other concrete genetic example is in chromosomal evolution. However it is hard to imagine alternative homozygous chromosomal rearrangements having different fitnesses (Lande, 1985): in contrast, some warning colours are very likely to be better than others; and to explain how warning colour evolves adaptively, we need to know how populations cross from one adaptive peak to another.

The adaptive nature of warning, or 'aposematic' colour patterns seemed clear a century ago (Wallace, 1867, 1878; Poulton, 1890), but recently it has been debated whether 'individual' natural selection may explain their initial evolution (Turner, 1971, 1984; Harvey & Greenwood, 1978; Wiklund & Järvi, 1982; Harvey, Bull, Pemberton & Paxton, 1982; Sillén-Tullberg & Bryant, 1983; Brower, 1984). Fisher (1930) had earlier suggested a similar problem with the evolution of unpalatability. Previous explanations depend purely on selection to explain the evolution of warning colours. Here we propose that drift, combined with natural selection, may also be important.

Early papers on warning coloration were full of natural history (Bates, 1862; Wallace, 1878), but current discussions are rather theoretical. In this paper we attempt to test the theories using information from nature. While the principles of warning coloration are general, we will concentrate on butterflies, which illustrate most of the important features of colouring in animals (Poulton, 1890).

WHAT IS WARNING COLOUR?

Warning colours (aposematism) are colours and patterns of prey that are adaptive because they signal to predators a potential cost of making an attack. This definition implies: that the prey has some punitive effect (other than the colour pattern itself) which causes negative reinforcement; that predators learn the warning colour pattern, and in doing so cause some deaths or injuries to the prey (in rare cases there is an innate, evolved tendency to avoid very dangerous prey—Rubinoff & Kropach, 1970; Smith, 1975; Schuler & Hesse, 1985); and that a warning pattern is a better signal than a non-warning or cryptic pattern.

A warning colour pattern is unlikely to be negatively reinforcing on its own (Schuler & Hesse, 1985); some colour patterns are used in frightening displays (Poulton, 1890; Blest, 1957; Coppinger, 1969, 1970), but do not signal a true threat. Possibly these frightening eyespots, colours, movements and sounds of

Lepidoptera mimic the predators' own enemies which are negatively reinforcing (Blest, 1957). Batesian mimics themselves, which do not back up their colour patterns with punishment, are falsely aposematic under our definition because a mimetic pattern copies one which issues a truthful threat.

EVIDENCE FOR WARNING COLOURS IN BUTTERFLIES

The detailed analagous resemblances between species we call mimicry are the best evidence for the existence of warning signals. Predators can learn to avoid unpalatable insects on the basis of their colour patterns, and mimicry alone can explain such close convergence (Gilbert, 1983; Brower, 1984; Turner, 1977, 1984). Many mimetic butterflies are brightly coloured or conspicuous, but at least some are merely distinctive: mimetic ithomiine butterflies are highly unpalatable (Brower & Brower, 1964; Chai, 1986) but have relatively subdued mottled brown 'tiger' patterns; others are transparent with brown or black edges. However, in these species the patterns are hardly cryptic as there are white and yellow streaks or spots on the wings and bodies. In contrast to palatable butterflies, these and other unpalatable butterflies have undersides similar to uppersides, so their advertising patterns are not hidden at rest.

The warning colours of unpalatable butterflies are very geographically variable (Bates, 1862, 1879), and novel colour patterns have evolved repeatedly within already aposematic taxa. This is still a puzzle today, because frequency-dependent selection against rare morphs should stabilize warning colour patterns. Warning colours occasionally evolved in the ancestors of subfamilies or tribes of butterflies that become unpalatable, but by far the greatest diversity of warning colour patterns evolved after the acquisition of defences, within genera and species of butterflies such as heliconiines and ithomiines (Brown, Sheppard & Turner, 1974; Brown, 1982; Turner, 1984).

Warning colours occur in palatable as well as unpalatable butterflies. For example, mimicry has been found between apparently palatable rapid-flying African butterflies, among beetles, and between beetles and flies (Van Someren & Jackson, 1959; Lindroth, 1971; Hespenheide, 1973). These examples can be explained if predators avoid species that are difficult to catch. Birds can be taught to avoid artificial prey that suddenly disappear before they can be eaten (Gibson, 1974, 1980). Mimicry within the fast-flying nymphalid genus *Adelpha* (Aiello, 1984), and between *Adelpha, Doxocopa* (Nymphalidae) and *Nymula* (Riodininae) (illustrated by Lewis, 1974) might be explained similarly. Aiello suggests palatable *Adelpha* mimic unpalatable Rubiaceae-feeding species of *Adelpha*; but tested Rubiaceae-feeders are palatable to jacamars, birds that specialize on flying insects (Chai, 1986).

Large edible butterflies in other mimicry rings may be avoided because they have tough cuticles and strong wings, and are difficult to subdue (Van Someren & Jackson, 1959). Mimicry among very small African butterflies, some of which are common, could be explained if these palatable butterflies swamp their predators (Van Someren & Jackson, 1959); rarer butterflies might then gain an advantage by mimicking them. The argument now seems less likely because rarer phenotypes of palatable prey usually gain an advantage (Poulton, 1890; B. Clarke, 1962). Yet mimicry between small palatable species does exist. In the forest understory of the neotropics, there is mimicry between small blue satyrines

(*Chloreuptychia* and *Cepheuptychia* spp.) accompanied by similarly patterned Lycaenidae (especially *Eusalesia* spp.—see Lewis, 1974): there is also a white satyrine mimicry ring (Singer, Ehrlich & Gilbert, 1971). This mimicry could also be explained if the slender benefits of eating these tiny butterflies are outweighed by the costs of pursuit.

Conspicuous and edible species are likely to become profitable prey if they cannot escape rapidly. Most of these palatable warningly coloured species are cryptic on their undersides (Chai, 1986), and rest with wings folded during overcast weather. Such species rely on solar energy to raise their thoracic temperatures for efficient flight and escape. However, unpalatable butterflies such as heliconiines and ithomiines are similarly coloured on their undersides and uppersides, fly more slowly, and are active during cloudy weather.

Although mimicry strongly suggests that colour patterns are used as warning signals, there is only anecdotal evidence that warning colours are easier to learn than non-warning colours (Guilford, 1987). Traditionally, it has been assumed that the bright colours of unpalatable insects are more efficient signals (Wallace, 1867, 1878). Birds seem to learn to avoid conspicuous prey more easily (Gibson, 1974, 1980; Gittleman & Harvey, 1980), and humans use bright colours in warning signs. However unpalatable insects could be brightly coloured for other reasons (Guilford, 1986, 1987).

THE EVOLUTION OF WARNING COLOURS

The problem: predator learning and frequency-dependent selection

The fitness, W_A, of a new, mutant or variant colour morph, A, within an unpleasant prey species is likely to be lower than the fitness of a commoner wild-type morph, a, because predators have not learned to avoid the rare colours. Suppose two patterns are equally conspicuous and memorable (but different in appearance) and exist in a population of constant size controlled by, say, larval resources; then the number killed or molested during predator learning will be equal for the two morphs provided that there are enough of each type to learn (if A are very rare learning may not be completed). The rarer morph, A, will suffer proportionally more attacks due to its lower numbers. If A and a are equally common ($Q = Q^* = 0.5$): the morphs will be attacked in equal proportion. If A increases above Q^*, it will then be the fitter morph (Fig. 1, curve X). The fitness of a morph is therefore frequency-dependent. Both fixation points ($Q = 1$, $Q = 0$) are stable, and there is an unstable polymorphic equilibrium, Q^*. It is easy to see that in order for a new warning colour, A, to evolve, its frequency must increase from $Q \approx 0$ to Q^*, against the force of selection. The same principle causes rare unpalatable species to converge to an abundant model in Müllerian mimicry (Müller, 1879; Turner, 1977; Gilbert, 1983). Polymorphisms for warning colour should not exist. Only if predators find some morphs palatable and positively reinforcing will polymorphisms be stable; and then only if frequency-dependent selection favouring rare edible morphs is stronger than the purging selection on inedible warningly coloured morphs, *and* there is a frequency-independent disadvantage against the inedible morphs (Thompson, 1984; Endler, 1987).

Now suppose A is a warningly coloured variant and a is cryptic. The number
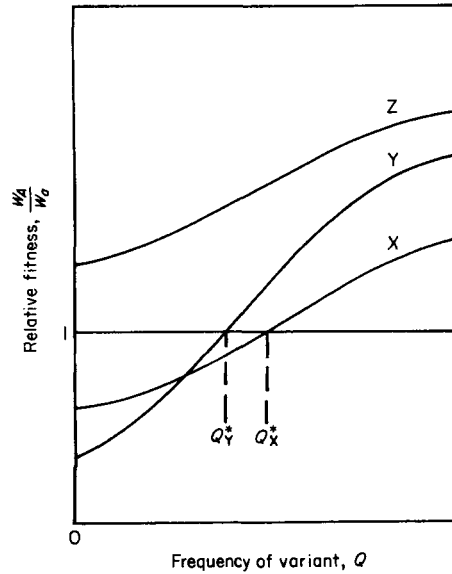
Figure 1. The fitness of a warningly coloured mutant in an unpalatable prey species.

The fitness of a variant morph, A, relative to a wild type, a, is plotted against the frequency, Q, of the variant. Three situations are shown. Curve X illustrates fitness of a warningly coloured variant phenotype A in a prey species with wild-type warning phenotype a. Both phenotypes are assumed to be equally conspicuous, and equally effective at warning away predators, though predators do not confuse the two patterns (generalization between A and a is allowed, but this formulation concerns only that part of the pattern which is not generalized). Curve Y represents a warning coloured variant, A, in a species with a wild-type cryptic phenotype a. A is assumed to be more conspicuous and more easily remembered than a. In curves X and Y, Q^* represents the point at which the fitnesses are equal $(W_A/W_a = 1)$; in curve X, $Q^* = 0.5$. In curve Z, $W_A > W_a$ for all Q. For example, curve Z might represent Müllerian mimicry by A of a second species, relative to a non-mimetic morph a. While these curves are imaginary, they are based on a precise numerical model of the behaviour of predators in the face of different prey phenotypes (Mallet, in prep.). The curves are applicable to small phenotypic differences between A and a, as well as to major colour pattern reorganizations.

of A sampled by a predator memorizing the new morph are by definition lower than the number of a; this causes the critical frequency Q^* to be reduced. However since A is initially rare, even this low number will be a very high proportion of variant morphs—perhaps all of them that are detected. Also, an efficient warning pattern is likely to be more conspicuous than a cryptic pattern. Rarity and conspicuousness both lead to selection against the mutant A when it is rare (Fig. 1, curve Y).

Although most theorists agree that rare morphs of unpalatable species should be at a disadvantage (Müller, 1879; B. Clarke, 1962; Brown et al. 1974; Turner, 1977; Harvey et al. 1982; Leimar, Enquist & Sillén-Tullberg, 1986), there is almost no direct evidence of this. Two field experiments suggest such a disadvantage (Benson, 1972; Mallet & Barton, submitted), but neither measured predation directly. The only tests using unpalatable artificial baits failed to demonstrate selection against rare morphs; in one of these, the rare form was actually favoured (Greenwood, Wood & Batchelor, 1981), perhaps because learning was not completed. Selection against rare forms seems reasonable, but more experiments are needed to test the predictions.

Hypotheses for the evolution of warning colours fall into two classes: (i) *Individual selection* which proposes that $W_A/W_a > 1$ for any Q, so that Q^* is non-existent (Fig. 1, curve Z): preadaptive bright colours, enhancement of existing patterns, and mimicry are three ways in which this could occur. (ii) *Group selection* (in the broad sense of Uyenoyama & Feldman, 1980, and Nunney, 1985), which appeals to population structure to help increase the mutant frequency above Q^*: kin selection and the shifting balance fall into this category.

Individual selection

The hypothesis of Sillén-Tullberg and Bryant

If the greater conspicuousness of warning colour is accompanied by an automatically increased avoidance of the pattern, aposematism might evolve by individual selection: "The avoidance reaction could incorporate learning as well as an initial reluctance to sample the prey" (Sillén-Tullberg & Bryant, 1983). However, the published model (and also that of Engen, Järvi & Wiklund, 1986) does not include the frequency-dependent selection due to predator learning, which is the major problem for the evolution of aposematism discussed above. Sillén-Tullberg & Bryant discuss evidence in support of the possibility of individual selection. First, *aposematic coloration is more easily remembered and associated with distasteful prey than cryptic coloration.* But predators' memories are the basis for the frequency-dependent selection against rare forms. At very low frequencies, a conspicuous mutant will not be remembered however memorable it is because predators nearly always encounter it only once. Increases in memorability can lower the critical frequency Q^* at which the new morph becomes favoured, but increases in conspicuousness will make selection against the new morph more intense at very low frequencies (curve Y *vs.* curve X in Fig. 1).

Secondly, Sillén-Tullberg & Bryant (1983) point out that *predators are reluctant to sample brightly coloured and/or novel prey.* The problem with novelty is that it soon wears off. If the novel variant, A, becomes commoner, it will eventually be tested for edibility (Curio, 1976; Schuler, 1982). The novel mutant will evolve only if it causes enough immediate avoidance to outweigh the disadvantages arising from conspicuousness *and* low frequency: then it is a frightening or mimetic, rather than aposematic, stimulus, and should evolve in palatable as well as unpalatable prey.

A concrete example helps to show that novelty and memorability cannot be very powerful aids to the evolution of warning colours. Sillén-Tullberg (1985) showed that brightly coloured morphs of an unpalatable bug had a sixfold survival advantage over cryptic morphs when offered to birds, though a mixture of novelty and memorability. Now suppose a mutant aposematic bug is born into a population of 100 cryptic bugs living in a bird's territory. To learn the morphs the bird kills six times as many cryptic as aposematic bugs, but since there are 100 times as many cryptic bugs in total, predation will still be $100/6 = 17$ times as great on the aposematic bug. Note that differences in conspicuousness have been omitted; if they were included, predation on the aposematic form would be even heavier. Only if the novel form is extremely

frightening, or the total population size is so low that the predator cannot learn the cryptic form, will the aposematic form increase.

In nature, no colour pattern seems immune to sampling by predators. Beakmarks are common on the wings of brightly-coloured butterflies (Carpenter, 1939, 1941), and the bright colours of fruits have evolved to attract birds (Wallace, 1878). Frightening colour displays in palatable insects are used only as a last resort when crypsis fails and then are accompanied by sudden movements or sounds (Edmunds, 1974). Frightening stimuli may be preadapted to serve as warnings, but do not evolve as warnings in the first place.

Preadaptation

One of the characteristics of butterflies is that they are brightly coloured, and some of the most brightly-coloured butterflies are palatable (Chai, 1986); for example a flying *Morpho* (Morphinae) is visible as a blue flash from several km away. Such bright colours are often sexually dimorphic (e.g. *Morpho*, *Ornithoptera*, *Lycaena*, and *Colias*), and have probably evolved through inter- or intrasexual selection (Darwin, 1871; Wallace, 1878; Turner, 1978; Silberglied, 1984; Vane-Wright, 1984). In these cases, female patterns usually show slight correlations with the patterns of males of their species, as is true of sexually selected traits in other animals (Darwin, 1871). Sexual selection can work against natural selection to favour colours that enhance predation (Darwin, 1871; Poulton, 1890; Endler, 1978; Lande, 1981; Kirkpatrick, 1982). Bright colours are also used by palatable insects to trick predators in a variety of ways: to deflect predator attacks away from vulnerable parts (Poulton, 1890; Carpenter & Ford, 1933; Cott, 1940; Blest, 1957; Wickler, 1968; Robbins, 1981); as 'flash coloration', to confuse predators—brightly coloured insects may seem to disappear on settling (Cott, 1940; Edmunds, 1974; Sheppard, 1975); as a frightening display (Poulton, 1890; Blest, 1957; Coppinger, 1969, 1970); and in deceitful, Batesian mimicry (Bates, 1862). Warning colours advertising various forms of low profitability also exist in palatable species (see above).

These palatable butterflies already use bright colour patterns to signal to each other and to their predators. If such a species becomes unprofitable to predators (perhaps by switching to a larval hostplant rich in unpalatable compounds), the colours are preadapted to serve a warning function: the predator simply uses the same signal patterns in a different way. This has been suggested before by Poulton (1890) for sexually selected colours and by Huheey (1961) for Batesian mimicry.

Enhancement of pre-existing patterns

A prey that has unpleasant memories for a predator will be avoided whatever its colour pattern. Some variants might be *more* reminiscent of the wild-type colour pattern than the wild-type itself—they are "supernormal sign stimuli" (Tinbergen, 1951) of the old pattern. The new pattern could then evolve by exploiting predators' experience of the old pattern. The new pattern will be at an advantage (greater avoidance by experienced predators) which could outweigh a potential disadvantage (greater conspicuousness to the few predators that have not leaned the old pattern). If the new pattern itself has an associated supernormal stimulus which is even more extreme, evolution will continue, provided there are appropriate genetic variations or mutations in colour

pattern, until the pattern reaches a limit of enhancement (see also Leimar *et al.*, 1986, for a similar idea). The evolution of warning colour by this means is a runaway process of signal evolution, first proposed by Fisher (1930) for sexual selection, though there are differences. The predators whose avoidance reactions are causing the evolution of colours usually learn, rather than have genetic predispositions, to avoid prey. Learnt responses of predators enable prey evolution to proceed more rapidly than if it were constrained by genetic change in the predators. (Coevolution between predator and prey may occur where warning colours cause innate avoidance—Rubinoff & Kropach, 1970; Smith, 1975; Schuler & Hesse, 1985.) There is also no genetic correlation between the colours of prey and the avoidance by predators, since the traits are in separate species. In contrast, correlations between female preference and male traits can cause runaway sexual selection on their own, even without supernormal stimuli (Lande, 1981; Kirkpatrick, 1982). Runaway warning colour evolution, which requires supernormal stimuli, is therefore more similar to O'Donald's (1980) interpretation of Fisher's idea, than it is to the models of Lande or Kirkpatrick.

Supernormal stimuli are well known in bird behaviour and are likely to occur in birds' interactions with insect prey. Flash, sexually selected, deflective or frightening markings may be memorable, and accentuation or enlargement of these markings (in both sexes, but especially in females of sexually selected species) could act as enhanced warning signals. Unpalatable arctiid moths use their flash coloured hind wings in aposematic displays (Watson, 1975): these hidden colours need only become expressed on more exposed surfaces to become classically aposematic. Enhancement has occurred in the extra large eyespots of *Taenaris* and *Hyantis* (Morphinae), which are copied by Müllerian and Batesian mimics. These spots are derived from the smaller eyespot deflection markings of palatable satyrines (Parsons, 1984; C. Clarke, F. F. M. Clarke, Collins, Gill & Turner, 1985). *Taenaris* and *Hyantis* probably evolved unpalatability because of a larval host shift from monocotyledons to the Cycadaceae, which are known to contain toxic secondary compounds (Parsons, 1984).

Mimicry is another way in which an advantage due to experienced predators can outweigh the increased conspicuousness of warning colours to inexperienced predators. We are here interested in Müllerian (mutualistic) mimicry, though Batesian mimicry is obviously preadaptive to the evolution of warning colours (Huheey, 1961, and see above).

Conditions for evolution are so broad that Müllerian mimicry is one of the likeliest routes for the evolution of warning colour in unpalatable species, and the existence of an array of mimicry rings prove that this is so. Mimicry can also explain much of the geographic variation within already warningly coloured species. Brown *et al.* (1974) proposed that *Heliconius* were confined to forest refugia during Pleistocene dry spells: random extinction altered mimetic selection pressures and caused racial divergence of the remaining species. However, it would be hard to explain all of the colour pattern *divergence* within species like *Heliconius erato* and *H. melpomene* purely by a theory of *convergence*. The races of these two species mimic each other in every area of the neotropics where they co-occur, and in the Amazon basin are close mimics of other species of *Heliconius*. But outside the Amazonian lowlands *H. erato* and *H. melpomene* have diverged together in directions that are hard to attribute to mimetic pressures. Either a number of now extinct model species caused this colour pattern radiation, or some of the divergence did not involve mimicry.

Group selection

We here consider that *group selection* is selection requiring group structure in order to work (Uyenoyama & Feldman, 1980; Nunney, 1985). *Kin selection* is, under this definition, a subset of group selection where the 'groups' consist of related individuals (Wilson, 1975; Uyenoyama & Feldman, 1980; Nunney, 1985; Slatkin, 1987). 'Gene selectionists' use more restrictive definitions (Dawkins, 1976; Guilford, 1985, 1987).

Kin grouping

Kin grouping can help novel warning colours to evolve in cryptic but unpalatable prey (Turner, 1971; Harvey & Greenwood, 1978; Harvey *et al.*, 1982; Leimar *et al.*, 1986). The evolution of unpalatability itself may require kin selection (Fisher, 1930; Blest, 1963; Benson, 1971; Turner, 1971, 1975; Eshel, 1972; Harvey & Greenwood, 1978) though individual selection is also a strong contender (Brower & Glazier, 1975; Järvi, Sillén-Tullberg & Wiklund, 1981a; Harvey & Paxton, 1981; Wiklund & Järvi, 1982). For warning colours, the basis of the idea is that close kin having the same phenotype can enable the frequency of the new morph to jump to Q^* (see Fig. 1) in a local area, within a single prey generation. Selection will then fix the new warning colour, rather than eliminating it. These models are similar to "kin-founding" models of chromosomal evolution (Bush, Case, Wilson & Patton, 1977; Hedrick & Levin, 1984). For kin selection to work, prey must be closely related within each predator territory (Harvey *et al.*, 1982; Leimar *et al.*, 1986); dispersal of prey between predator territories would undermine the process. For this reason, the model applies best to the evolution of warning colour in groups of gregarious caterpillars laid as eggs by a single female (Harvey *et al.*, 1982), or in asexual, gregarious aphids (Malcolm, 1986).

Harvey *et al.* (1982, 1983), while noting that kin structures occurring before the evolution of warning colour are not necessarily those seen today, cite as evidence for the kin selection hypothesis the existence of a high correlation between gregariousness and aposematism among the caterpillars of British and other butterflies. However, the evidence is not convincing because unpalatable species, which by definition satiate predators rapidly, benefit more from grouping than do palatable species (Turner, 1975, 1984; Treisman, 1975; Järvi, Sillén-Tullberg & Wiklund 1981b; Sillén-Tullberg & Bryant, 1983).

Adult unpalatable and aposematic butterflies that have been studied often disperse rather widely. This is true for Danaidae (Eanes & Koehn, 1979), Ithomiinae (Brown & Neto, 1976), and troidine Papilionidae (Brown, Damman & Feeny, 1981). In contrast, *Heliconius* appeared to have the low rates of dispersal and adult family grouping required for the evolution of warning colour and unpalatability by kin selection (Benson, 1971; Turner, 1971; Harvey & Greenwood, 1978; Harvey *et al.*, 1982). However, recent studies on *H. erato* have thrown even this example into doubt. The longest movements made by *H. erato* are made by newly eclosed adults, and these movements were missed in previous mark-recapture studies (Mallet, 1986a). *Heliconius* roost gregariously, but individuals move between roosting groups, which are neither kin-based nor strictly associated with particular foraging sites (Mallet, 1986b). Genetic evidence from the edges of hybrid zones in *H. erato* and *H. melpomene* shows that rare warning colour morphs do not build up to high frequencies in small local

areas as expected if dispersal were rare, but are instead distributed evenly over distance scales of about 5 km (Mallet, 1986c). It is of course possible that dispersive aposematic butterflies evolved from species that were once kin-grouped in the appropriate way (Harvey *et al.*, 1983), but, at least in the heliconiines, 'ancestral' species are even more dispersive (Benson, 1971). Kin selection (as defined above) is therefore an unlikely mechanism for the deterministic evolution of adult colour patterns, though it may act occasionally in combination with drift.

Shifting balance

Another way in which the frequency of a novel variant can rise above Q^* is by means of genetic drift in a small local population, whereupon selection will tend to fix the new form. Random divergence may then be helped by the runaway process discussed above. Strictly, kin founding models involve drift in that they rely on small numbers of families within a predator territory, so that mutant genes can suddenly increase in frequency after mutation in the germ line of a parent (Benson, 1971). Because drift can happen over more than one generation, the 'group' involved in genetic drift consists of prey within a 'neighbourhood' population size (Wright, 1969), a local panmictic unit which is a product of prey density and dispersal, whereas the group drifting in kin founding consists only of prey in a single predator territory within a single prey generation (Harvey *et al.*, 1982).

Once a local area is nearly fixed for the mutant colour pattern by drift and selection, the problem becomes one of whether this small area can resist swamping by gene flow from the standard forms that surround it (Barton, 1979; Rouhani & Barton, 1986). If the area fixed for the mutant form is sufficiently large, clines will form between the two colour patterns; these clines are stable in width, but, because they do not depend on the environment, are unstable in position (Mallet, 1986c). If the new form has a higher overall fitness, dispersal, or population density than the wild-type, clines will move outwards. Stochastic changes in population structure or selection aross a cline, and even genetic dominance of one of the colour patterns can also cause movement (Barton, 1979; Mallet, 1986c). Clines of warning colour are similar to chromosomal clines (Bazykin, 1969; Barton, 1979): both types are mobile and of stable width. If a cline moves outward, the new form may spread until it covers the entire range of the species, or until it reaches a barrier to dispersal (Barton, 1979).

The local fixation by drift of a novel warning colour pattern, followed by spread behind a moving cline is, like stasipatric chromosomal evolution (White, 1978), an example of Sewall Wright's "shifting balance" model of adaptive peak shift (Wright, 1977; Lande, 1985). In the shifting balance, genetic drift causes local populations to shift to the unstable equilibrium between two adaptive peaks in gene frequency space; selection then pushes the local population up to a higher adaptive peak. The population analogy of individual selection, "interdemic selection" (Wright, 1977) between populations of the new and wild-type morphs, may then preserve and spread a fitter morph once it has evolved. This interdemic selection makes the shifting balance more likely to generate adaptive evolution than has generally been realized.

It is difficult to evaluate this model. Population structure is poorly known in butterflies, and indeed in any organism (Slatkin, 1987). The shifting balance is

intractable mathematically because of the difficulty of modelling realistic, continuous populations (but see Lande, 1985; Rouhani & Barton, 1987). Even if measurements of population structure were available, it would be difficult to know if local populations are small enough to allow drift; especially since the evolution may occur during rare founder flushes. A feature of the shifting balance is that truly novel colour patterns may have evolved: on the other hand, if all warning colours evolved by mimicry, the number of patterns should be progressively reduced.

CONCLUSIONS

In most butterflies, the switch from non-aposematic to aposematic has occurred so long ago that it may be fruitless to speculate how warning colours first arose. But the evolution of novel colours in subspecies of unpalatable butterflies is very common, and is exactly the same theoretical problem (with different parameter values—see Fig. 1). Their speed of evolution suggests that warning colours probably arose very soon after a switch from crypsis became advantageous (comparing the heights of the fitness peaks, *not* the relative fitnesses of rare aposematic variants and commoner cryptic forms).

Because the evolution of warning colours requires a shift between adaptive peaks, warning colour might serve as a model for similar types of evolution where the adaptive value of the transformation is less well understood, as in chromosomal rearrangements. Warning colours and secondary sexual traits may both evolve by runaway processes. Speciation itself also involves a transition between adaptive peaks (Barton & Charlesworth, 1984). Darwin (1863), commenting on Bates' (1862) paper which first demonstrated geographic divergence in the colour patterns of unpalatable, mimetic butterflies, wrote "whilst reading and reflecting on the various facts given in this Memoir, we feel to be as near witnesses, as we can ever hope to be, of the creation of new species on this earth." Darwin's statement remains accurate.

ACKNOWLEDGEMENTS

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