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OVERVIEW

Shift happens! Shifting balance and the evolution of diversity in warning colour and mimicry

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Abstract. 1. At first sight, it seems most unlikely that *Heliconius* warning colour races have evolved by means of stochastic peak shift or shifting balance.

2. Phase I, random local processes (including genetic drift and idiosyncratic selection), and phase III, interdemic selection are the most controversial phases of the shifting balance. Phase II consists of ordinary natural selection to a new adaptive peak within populations, and is uncontroversial.

3. *Heliconius* have bold patterns of iridescent blue, black, yellow, white, and red. These are clearly warning patterns, and near-perfect Müllerian mimicry has evolved among species, suggesting tight control by natural selection. Field experiments have also demonstrated strong selection (often $s > 0.1$ on single colour pattern loci), and the population structure of *Heliconius* is typically not conducive to phase I. Yet the colour patterns are clearly somewhat independent and incompatible signals of unpalatability.

4. There is empirical evidence in *Heliconius* for both controversial phases. For phase I, occasional and local polymorphisms of colour pattern in a number of species go against the generally expected (and generally observed) monomorphism for Müllerian mimics.

5. For phase III, one of the few colour pattern clines mapped in detail has been observed to move rapidly over a period of 20 years. There are also a number of curious 'leapfrog' geographical disjunctions in colour pattern races. Disjunctions are expected if successful races have spread from the centre of the range (e.g. the Amazonian rayed races) via phase III, in competition with earlier races that are now distributed in scattered places along the periphery of the range.

6. Evidence from the genomes of *Heliconius* may in the near future aid in understanding colour pattern 'supergenes' and to help test for origin and spread via shifting balance.

Key words. Aposematism, evo-devo, *Heliconius,* hybrid zones, kin selection, Lepidoptera, Müllerian mimicry, shifting balance, warning colour chromosomal evolution.

Introduction

The idea of random evolutionary change has a long history. Even Darwin argued that 'mere chance' may sometimes be involved (Darwin, 1859, p. 111). Today it is known that, as well as natural selection, there are many kinds of stochastic effects on evolution, in addition to stochastic mutation (Lenormand *et al*., 2009). Although parallel evolution does occur, it is generally believed that re-running the tape of life would almost always come up with somewhat different results than the actual. The order of origin of mutations, and unpredictable details of the environment in which selection occurs all militate against identical, deterministic outcomes.

One of the most enduring proposals for stochastic influences on evolution is Sewall Wright's idea of 'shifting balance' (Wright, 1932, 1978). The idea combines evolutionary stochasticity and natural selection in an attempt to explain how populations and species may shift between 'adaptive peaks'. Some years ago, I was attracted to the idea that the evolution of warning colour and mimicry races in *Heliconius* might be due to a

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form of the shifting balance (Mallet, 1986). My ideas at this time were undoubtedly naive, and the shifting balance probably seems an odd explanation at first sight, since it is clear that natural selection on *Heliconius* mimicry is extremely strong (Benson, 1972; Mallet & Barton, 1989b; Kapan, 2001; Langham, 2004). How could drift possibly be involved? Since then, the shifting balance has fallen into much greater disrepute. Nonetheless, as I shall show, geographic variation in *Heliconius* warning colour provides a case which, it seems to me, might well be explained by shifting balance, and the *Heliconius* system sidesteps most of the hurdles raised by critics. If it happens here, who is to say it may not be a common means of adaptation in less well understood systems? For the Darwin–Wallace special issue of this journal, I therefore return to this theme, and add arguments based on new empirical data.

The 'shifting balance' theory and its critics

Evolution by natural selection in even a moderately polymorphic species must work with a huge complexity of possible combinations. Based on studies of animal breeding, Wright argued that genetics of multilocus adaptation would be highly epistatic in such a way that many adaptive peaks would be found. The resultant 'adaptive landscape' would be rugged (Wright, 1932). He deduced that it would be almost impossible for natural selection alone, which can only aid climbing local adaptive peaks, ever to attain the fittest global peaks in the multidimensional adaptive space. Populations would get stuck on suboptimal, lower (i.e. less fit) peaks in the landscape.

By analogy with animal breeding, Wright knew that finite populations under selection tend to lose fitness, mainly because rare deleterious alleles become fixed by chance at some loci. However, this inbreeding depression can be reversed by crossing with some of the fittest genotypes from other selected populations. He felt that adaptation could proceed most rapidly under successive shifts in balance, from exploratory stochastic processes, 'genic' selection within populations, to migration, competition, and recombination between genotypes (which he called 'genotypic' or 'intergroup' selection). The recombination and spread of successful peaks would enable peak shifting by the entire metapopulation (Wright, 1980). He therefore intuited that many small, loosely connected demes could explore the available adaptive space, due to stochastic processes, more efficiently than a single, large population. Demes that by chance hit on useful gene combinations would then export their genotypic combinations to other populations, and ultimately to the whole metapopulation, by intergroup selection. In addition, he felt that combinations might form between different successful peaks, resulting in new combinations that were perhaps even more successful than either combining peak alone. In later years, he called the whole process the 'shifting balance' theory of evolution (Wright, 1978). He conceived the process in terms of three phases (Wright, 1982, p. 8):

Phase I: 'extensive local differentiation, with wide stochastic variability in each locality'.

Phase II: 'occasional crossing of a saddle leading to a higher selective peak under mass selection'.

Phase III: 'excess proliferation of, and dispersion from, those local populations in which a peak-shift has occurred, leading to occupation of the superior selective peak by the species as a whole'.

To Wright, this process is a supplement, rather than an alternative to Fisherian mass selection, 'since such selection is involved in all three phases'.

Even the most critical authors agree that shifting balance can cause peak shifts, very likely in combination with Fisherian alternatives. Simulated annealing, or 'Metropolis-coupled Markov chain Monte Carlo' (MCMCMC) methods actually use a similar algorithm for computer optimisation in parameter-rich statistical models, for instance in Bayesian phylogenetic analyses (Huelsenbeck & Ronquist, 2001). Theory shows that shifting balance might well be common in continuous populations provided that neighbourhood population sizes are reasonably small (say 10–30) somewhere within the range of a species (Rouhani & Barton, 1987; Barton & Rouhani, 1991), or in demic metapopulations with $Nm \approx 1$ or less, where $N =$ effective population size of each deme, and $m =$ fraction exchanged with other populations (Barton & Rouhani, 1993). These results show that observed rates of chromosomal evolution, to give just the most concrete example, can readily be explained by stochastic peak shift (Barton & Rouhani, 1987).

The shifting balance has, however, been criticised as being a verbal model lacking rigour, and indeed Sewall Wright himself argued that his theory of evolution explained just about everything from evolutionary progress within species, speciation, punctuated equilibria in the fossil record, and especially macroevolution. A few years ago, the idea was comprehensively attacked (Coyne *et al*., 1997; Gavrilets, 1997). A quick précis of some of the more cogent criticisms is as follows: (1) The shifting balance can be shown to work in theory, but this does not mean that it works more rapidly than selection alone. (2) It is not clear that multilocus adaptive landscapes are really rugged. Peaks in some dimensions may easily be connected via ridges in other dimensions, which potentially allows classical selection to approach global optima without stochasticity. (3) Local population sizes greater than about 10 can make peak shift prohibitively rare. (4) Interpopulation selection as a means of exporting adaptive peaks will typically not be very efficient, and indeed can sometimes lead to establishment of inferior peaks. (5) It would be hard for major adaptations to be assembled by combining adaptive peaks because of likely incompatibilities between them. Finally, (6) although genetic drift, natural selection within populations, and interpopulation selection have all been demonstrated in nature, no system demonstrates all three phases simultaneously. These authors concluded that classical, 'Fisherian' natural selection has not been disproved for any convincing case, and that parsimony therefore leads one to prefer the simpler, one-stage process.

This attack generated considerable discussion between supporters and critics of the shifting balance (Wade & Goodnight, 1998; Peck *et al*., 1998; Coyne *et al*., 2000; Goodnight & Wade, 2000; Peck *et al*., 2000). These criticisms and rebuttals to some extent 'talk past each other'; both sides make good points, and perhaps the most sensible conclusion is to not 'throw the baby out with the bathwater' (Whitlock & Phillips, 2000). In their balanced discussion, Whitlock and Phillips (2000) argue that the adaptive landscape is a useful metaphor, that the shifting balance may be important and is theoretically plausible, but that it is an unsolved empirical question as to how common or necessary stochastic peak shift is. The Coyne *et al.* critique has, on the other hand, had the salutary effect of making one shy away from naive shifting balance models as major explanations for adaptation, unless there is extremely good evidence.

A few exceptions still seem to demand shifting balance or similar stochastic initiating effects in one population which can become later amplified to spread to the entire metapopulation. One of these is polyploidy (see also discussion of underdominant single-chromosome rearrangements below). The first 'neopolyploid' mutant individual in a population is reproductively isolated from its parent species because crosses produce infertile, triploid progeny. As such it is liable to suffer a kind of Allee effect, a minority cytotype disadvantage, due to an absence of its own kind with which to mate (Levin, 1975; Husband, 2000). A neopolyploid individual in a self-compatible lineage can potentially reproduce sexually after mating with itself (i.e. by selfing). However, its fitness inevitably will be reduced compared with the parent species because of the loss of all fitness components normally gained from outcrossing (Levin, 1975; Husband, 2000), and also because neopolyploids almost always suffer from abnormal chromosomal segregation (Ramsey & Schemske, 2002). In the absence of any ecological differences, tetraploids and diploids might both be expected to exclude the other from within their ranges, and there are cases of such patchy mutual exclusion in flowering plants (Burton & Husband, 1999). Yet polyploid speciation is nonetheless reasonably common, causing up to $\approx$31% of all speciation events in ferns and $\approx$15% in flowering plants (Otto & Whitton, 2000; Wood *et al.*, 2009). A likely starter on the route to polyploidy, as with simple chromosomal rearrangement evolution, is local drift: once a polyploid population is established locally, so that the mating disadvantage is lessened, any advantages the new cytotype carries or accumulates may then help it to invade other populations (Hedrick & Levin, 1984; Mallet, 2007).

Stochastic peak shift may also be important in macroevolution. Genome size is thought to be a product of selfish element accumulation in smaller populations of microorganisms. Deleterious excessive DNA synthesis will be too weak a selection pressure to permit junk element purging in populations much smaller than the inverse of the selection pressure. However, the accumulation of junk DNA may also have permitted the possibility of the evolution of multicellularity, due to the freeing up of upstream and intronic regions available and suitable for cis-regulatory elements (Lynch & Conery, 2003). Clearly, this is another stochastic peak-shift-type explanation. As far as I know, this hypothesis is generally accepted by molecular evolutionists (Koonin, 2009), but is hard to evaluate under Coyne and Orr's (1997) parsimony criteria, because we can't easily follow the phase I accumulation of initial mildly deleterious mutations leading to the evolution of multicellularity—it must have happened long before the Cambrian.

In my own view, a major problem with empirical assessment of the shifting balance is that it is hard to find adaptive shifts in 'thousands or tens of thousands of strongly heterallelic loci' (Wright, 1980) when we have little understanding of the genetic architecture of multilocus traits and all the epistatic fitness differentials acting on genotypes at each locus. The problems become more severe the more loci there are. It is hard enough to estimate selection on genotypes of a single, non-epistatic biallelic locus in nature, let alone on thousands of loci. If we could find simplified examples, this may allow us to work up later to more complex systems.

Seeking simpler examples of the shifting balance

Wright framed his argument as a problem in epistatic, multilocus adaptation. However, multiple peaks or evolutionary equilibria exist in much simpler systems. For instance, even a single locus without epistasis may have two adaptive peaks among genotypes: two alleles (say A and a) may be under selection against heterozygotes ('underdominance'), giving two stable equilibria, which are also adaptive peaks, at the fixed gene frequencies $p_A = 0$, 1. There is also an adaptive 'trough' or minimum in mean fitness, with $0 < p_A{*} < 1$, which is also an unstable equilibrium (population genetics textbooks give details). It is unclear how commonly single genes are under such selection (or its converse, heterozygous advantage, for that matter). Chromosomal rearrangements, however, accord with this model, since chromosomal heterozygotes often produce gametes containing deleterious duplications or deletions of genetic material. Peak shift by genetic drift, followed by spread to other populations (Fig. 2), has therefore seemed a plausible scenario to explain the evolution of underdominant chromosomal rearrangements (Lande, 1985; Barton & Rouhani, 1991; Barton & Rouhani, 1993). The evolution of a single chromosomal variant is not everyone's idea of what the shifting balance is (for example, if multilocus inheritance and epistasis is required). Nonetheless, the evolutionary process involving the three phases is similar. If readers prefer, they may use a more general name, such as 'stochastic peak shift', but for the purposes of this article the single locus model of underdominance is considered a form of shifting balance.

Recently, however, even this safe refuge for the shifting balance has been questioned via an ingenious hypothesis that can explain chromosomal rearrangements by purely Fisherian processes. In heterozygote rearrangements such as inversions, mechanical concerns interfere with crossing over, and recombination is reduced, or recombinant chromosomes are selectively lost. Rearrangements can therefore limit the production of successful recombinants, and if they trap locally advantageous pairs of alleles in polymorphic populations subject to gene flow, this 'linkage trapping' can outweigh selection against heterozygotes, which is anyway often weak (Kirkpatrick & Barton, 2006). Whether linkage trapping and local adaptation explains the origins of all chromosomal rearrangements is another matter, but Coyne *et al.*'s (1997) parsimony argument leads one, now, to prefer to explain chromosomal evolution via Fisherian processes (Kirkpatrick & Barton, 2006).

Even if chromosomal underdominance is viewed as a potential example of shifting balance, it still suffers from many of the other problems highlighted by Coyne *et al.* (1997). Although stochastic peak shift, or for that matter, local adaptation trapping, both seem likely, and can be shown in theory, it is difficult to prove that any particular chromosomal morphs actually have the negative heterosis or recombination suppression advantages required. After shifting locally, a chromosomal morph (or novel adaptive peak in general) will never spread deterministically to other populations unless the new rearrangement (or peak) also carries a fitness advantage over the original form (Barton & Rouhani, 1991). We generally know too little about the fitnesses of chromosomal morphs to provide good examples. Thus, it would be nice to find a different simplified genetic system, for which an understanding of fitnesses is sufficiently detailed, and for which we have a clear understanding of selection leading to more than one adaptive peak.

There is such an evolutionary system: warning colour. The evolution of warning colour, or 'aposematism', is normally discussed without much empirical grounding or genetical realism. However, there are good empirical examples. *Heliconius* butterflies, for which genetic basis of warning colour and selection coefficients are known, provide one.

Warning colours as an evolutionary system

The evolution of warning colour has cropped up primarily as a controversial issue in the behavioural ecology literature (Harvey & Greenwood, 1978; Harvey *et al.*, 1982; Ruxton *et al.*, 2004). Insect defence against predators has long been recognised as a potential 'altruism': the bearer of evil taste or a sting may help to teach individual predators that their class of prey is unpalatable, but may risk loss of life or severe impairment as a result of each encounter. This understanding led to one of the earliest propositions of kin selection, whereby self-sacrifice benefits co-inherited copies of altruistic alleles for unpalatability in close relatives (Fisher, 1930, p. 159). Warning colour has sometimes been assumed to be a similar altruism, since by having an effective and learnable signal, an individual may be more conspicuous and is readily attacked (Harvey & Greenwood, 1978). However, warning colour is not really a classic altruism, since when it is common in the general population, individuals would be foolish to lack the signal and instead adopt the aboriginal cryptic coloration, which might be confused with a palatable species. This frequency-dependent selection on warning coloration also leads to Müllerian mimicry among different unpalatable species (Müller, 1879). Another type of mimicry, Batesian, of an unpalatable species by a palatable species need not concern us here (Bates, 1862).

Phylogenetic studies of evolution of warning colour within unpalatable species suggest it is usually ancient as both traits are typically found in large groups. The exact sequence of events in the earliest evolution of these traits within any lineage is probably too mired in history to be understood at all clearly (Mallet & Singer, 1987). However, it is a somewhat surprising fact that aposematic groups appear repeatedly to have evolved novel warning colours and therefore novel Müllerian mimicry rings, again and again in different species, and even among geographic races within single species (Bates, 1862, Eltringham, 1917; Brown & Benson, 1974; Mallet & Joron, 1999) (e.g. in *Heliconius*, Fig. 1). Bates' own reception of Müller's mathematical model of convergent mimicry was perhaps cool for this very reason. He felt that Müller had not explained the most interesting set of facts, about divergence: 'numerous ... gaily-coloured butterflies and moths ... are found all to change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles' (Bates, 1879).

Several features about the evolution of novel warning colours within already warningly coloured species make it particularly tractable. Firstly, it clearly has happened a lot, and also recently in many species' ancestries, as shown by multiple geographic races with different colour patterns in such species. Secondly, it is the same sort of process as the initial evolution of warning colour, but without the added complication of having evolved from a very differently adapted initial state (e.g. crypsis). Thirdly, the switch between warning colours also controls, to some extent, for the level of conspicuousness. If warning colours are to improve via selection, and become more memorable, new warning colours must evolve from old ones with similar, although perhaps not identical conspicuousness. Of course, conspicuousness, as well as other didactically useful features of warning colour may also be enhanced by shifting balance, if the process is effective.

Novel warning colour patterns probably evolve by a variety of mechanisms. Perhaps most likely is individual, Fisherian selection. Here is a list of major possibilities (abstracted from Mallet & Singer, 1987; Mallet & Joron, 1999): (1) *Preadaptation*. Many butterflies are already brightly coloured; they signal to other members of their species for sex or social reasons, or to predators to indicate they are able to escape ('flash coloration'). These often brightly coloured signals are clearly preadapted to act as warning colour on attainment of unpalatability. (2) *Enhancement*. Perceptual systems may often contain a bias which leads to the existence of 'supernormal' stimuli. Predator memory likely encodes some kind of simplified 'caricature' of the real organism, and unpalatable prey, which initially do not match their caricatures, should be selected to exploit the bias and evolve towards a better representation of the caricature, to aid learning. This is especially likely if there is a need to distinct from a contradictory alternative signal (e.g. crypsis) which can push the caricature towards greater exaggeration, a phenomenon known as 'perceptual peak shift', not to be confused with evolutionary peak shift via the shifting balance. Perceptual peak shift has been suggested as likely in the evolution of warning colour (Leimar & Tuomi, 1998), and is related to the idea that unpalatable butterflies evolve to avoid confusion with cryptic, palatable species (Fisher, 1930; Turner, 1984). (3) *Mimicry*. Many unpalatable butterflies in tropical regions belong to Müllerian mimicry rings consisting of several to tens of species. There is a diversity of patterns, but only a few can have initiated

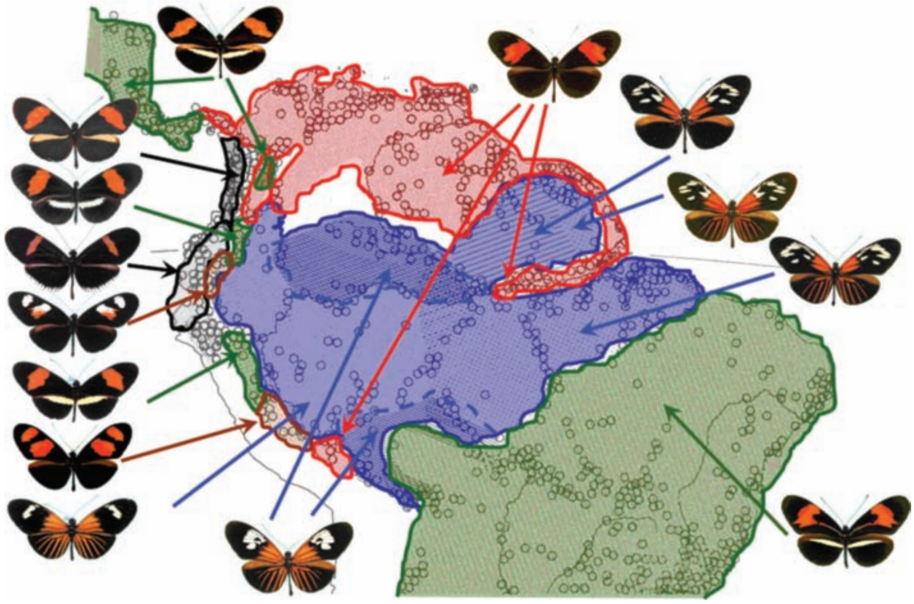

Fig. 1. Simplified distribution of colour patterns in *Heliconius erato*. The major colour pattern races are shown here, somewhat simplified for clarity. All patterns are mimicked accurately by *Heliconius melpomene*. Green racial distributions: 'postman' patterns with red forewing band and yellow hindwing bar. Red distributions: postman pattern without hindwing bar, showing the 'finger' of distribution stretching from the coast up the *varzea* of the lower Amazon. Grey distributions: postman races from West of the Andes in Colombia and Ecuador (these are highly bluish-iridescent above, with a yellow hindwing bar expressed only on the underside (not shown). Brown distributions: 'twin-barred' races from the Eastern Andes in Ecuador and Peru. Blue distributions: 'dennis' and 'dennis-rayed' races from Amazonia. Various named subspecies have been combined. The Andean semispecies *Heliconius* (*e.*) *himera* and *Heliconius* (*e.*) *chestertonii* have both been omitted, as they are not mimicked by *H. melpomene*. (After Sheppard *et al*., 1985.)

novel rings. The rest, which are the majority, are almost certainly copiers. Generalising a little further, it seems likely that when initiating warning colour most lineages exploited existing predator biases for avoidance by evolving as mimics. In summary, these three modes of individual selection seem the most likely and important in the initial evolution of warning colour, soon after unpalatability is acquired (Mallet & Singer, 1987; Mallet & Joron, 1999).

Kin selection and kin founding: phases I and II

Yet some classes of facts about warning colour are not readily explained by individual selection (see below for evidence on *Heliconius*). A second possible mode of evolution of warning colours is an alternative to simple Fisherian selection. By analogy with the evolution of altruism, close relatives may share costs and benefits of novel conspicuous patterns. Harvey and Greenwood (1978) first came up with a version of this idea, and argued that it was a form of kin selection. Later it was termed a 'family model' when examined theoretically (Harvey *et al*., 1982). It is very hard to imagine how a new warning pattern is advantageous when rare. One way to get around this problem is to imagine that a mutant first arises in a small group of prey families whose patterns are typically learnt by the local predators. If the mutation by chance reaches high frequency locally, and if there are few families per locality, it may become locally favoured (Harvey *et al*., 1982). If the new pattern is also better at warning predators, it may thrive better than adjacent cryptic (or differently warning-coloured) prey populations, and spread out.

This idea is almost identical to the 'kin-founding' model of chromosomal evolution (Hedrick & Levin, 1984). Angiosperms generally produce seed which falls nearby. If the parent happens to be a novel rearrangement heterozygote, and there are few other parents locally, offspring of a heterozygous mutant may by chance sometimes form local populations which are enriched for the new rearrangement to the extent that they drift over the unstable equilibrium, p_A*, locally. This may sometimes mitigate the problem of selection against rearrangement heterozygotes. The idea is not a typical kin selection model, as in the evolution of altruistic behaviour in social insects (Hamilton, 1964), which depends only on the genotypes of socially interacting organisms, and not on local population structure. Instead, it can be seen as a form of shifting balance. If the frequency-dependent selection acting on warning colour has a similar adaptive trough and unstable polymorphic equilibrium, the 'family selection' model of Harvey *et al.* is likewise a specialised example of phases I and II of the shifting balance (Fig. 2). It must be emphasised that the 'family' and 'kin-founding' models are not complete models of evolution because they do not explain how new and advantageous local populations spread out to occupy large regions, as in Wright's shifting balance phase III.

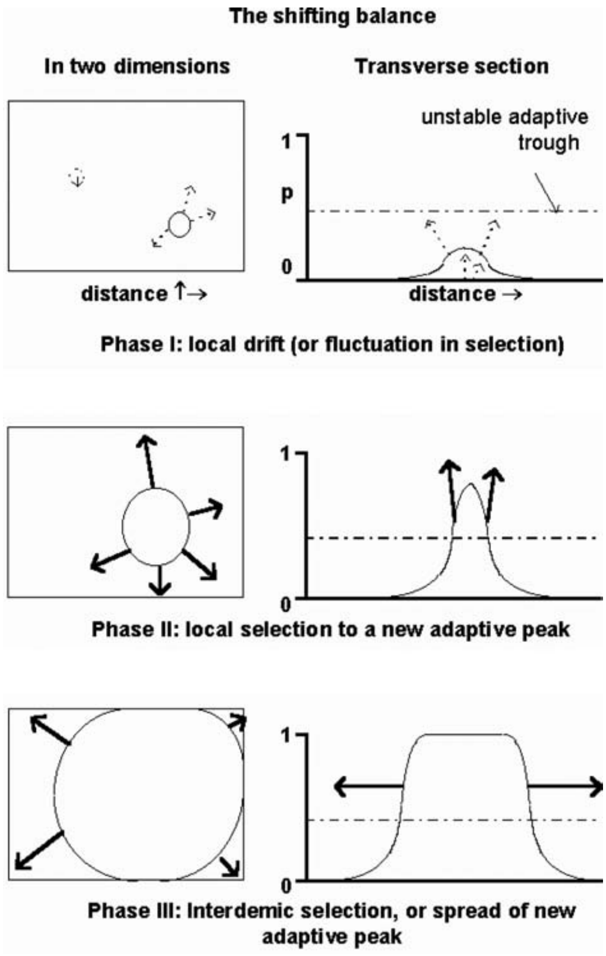

Fig. 2. Spatial evolution under the shifting balance. The diagram shows the three phases of the evolution of a new single-locus adaptive peak, for instance a novel warning colour allele, as a 'bubble' in two dimensions (left), and as a gene frequency versus distance graph (right).

The shape of warning colour frequency dependence

A simple way of modelling warning colour evolution is to treat selection acting on mimicry and warning colour as a form of linear frequency dependence, with the rarer form selected against (Plowright & Owen, 1980; Mallet, 1986; Endler, 1988; Gavrilets & Hastings, 1998). A linearisation of this model, which is accurate for weak selection, leads to a model with dynamics identical to those of heterozygote disadvantage (Mallet & Barton, 1989a); another way of looking at this is that selection against heterozygotes results in a kind of linear frequency-dependent selection on a novel variant.

However, linear frequency dependence ignores the nature of the selection on warning colour. We understand neither precisely how predators remember prey, nor how this might affect selection on genotypes that alter colour pattern, but regardless of cognitive details such as pattern recognition and forgetfulness, if predators are not very stupid the selection is likely to depend more directly on the actual numbers of prey than on their fraction in the population. Once a predator has tried a few unpalatable individuals, it will reduce its attacks on similar patterns to a very low, perhaps zero level. Thus one might expect an approximate, or perhaps asymptotically reached low fixed number of prey to suffer fitness loss in any prey generation regardless of prey population density. These approximately constant costs will be shared out among the entire local prey population. This was the basis of Müller's original mathematical analysis of mimicry among species (Müller, 1879), but it is also the likely basis of selection on warning colour within species (Harvey *et al*., 1982; Joron & Mallet, 1998; Mallet & Joron, 1999; Mallet, 2001a). Alternative assumptions, leading to a predator that kills asymptotically a fraction of prey, whatever their overall density (Speed, 1993; Speed & Turner, 1999), seem to me most unlikely. The predator would have to be extremely stupid not to reduce the fraction attacked on encountering more unpalatable individuals. It is more probable that the asymptotic attack rate is to prey number per unit time, rather than to a fraction of the total population. At the very least, we expect the fraction of attacks to decline as aposeme density increases (Mallet & Joron, 1999). Evidence is hard to come by, but controlled experiments with great tits show that attack rate does indeed

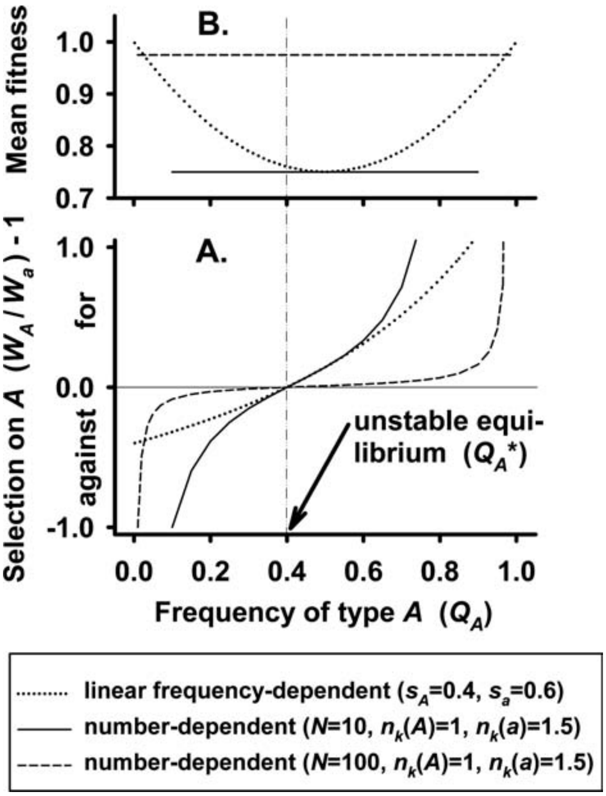

Fig. 3. Warning colour selection on a new colour pattern *A*. Selection for and against a novel pattern phenotype of type *A* under (top to bottom in legend), strong asymmetrical linear frequency-dependent selection, strong number-dependent selection, and weak number-dependent selection. (A) Selection, (B) mean fitness. (After Mallet & Joron, 1999.)

decline with aposeme density (Lindström *et al*., 2001; Mallet, 2001b), agreeing with Müller's intuition.

This 'number-dependent selection' will lead to a highly non-linear kind of frequency-dependent selection on genotypes (Fig. 3). If there are two alleles, each coding for a distinct colour pattern, the shape of the curve for natural selection on each will be approximately hyperbolic. The concatenation of selection on both phenotypes, assuming a constant total number of individuals in the population, leads to highly sigmoid frequency-dependent selection, as in Fig. 3. Many of Wright's ideas about the shifting balance were predicated on the idea that mean fitness is maximised by selection, but in simple Müllerian number-dependent selection, the mean fitness of the population, due to prey deaths, is the same internally across a large frequency spectrum; essentially this means that the adaptive trough for warning colour selection is very broad. Only when a new phenotype is very rare is it strongly counterselected. Although it hasn't been modelled formally, it seems likely that Müllerian number-dependent selection will promote the possibility of kin founding. Provided small populations consisting of a few related families can sometimes be protected from predation (if there are no predator territories locally, for instance), a mutant colour pattern should from time to time be able to drift rapidly to the nearly neutral region surrounding the unstable equilibrium, and thence to a local abundance which favours the new pattern.

Spread of a novel warning colour pattern among populations: phase III

Once the new population is established locally, if it is better at educating predators or has some other bias in its favour, it may spread out via interdemic selection (phase III of the shifting balance, Fig. 2). Any one new warning colour pattern probably evolves and becomes more and more striking and educationally effective by means of gradual adjustment and enhancement, a form of Fisherian individual selection (see above). Yet there are very likely multiple solutions (adaptive peaks) to the problem of signalling unambiguously and memorably to predators, depending on preadaptions and other starting conditions. Phase III of the shifting balance might then sort from among these solutions, leading to more globally successful designs of warning colour.

The key predators of insects selecting for mimicry are vertebrates with colour vision and neural wiring similar to our own. This is why we can appreciate Müllerian mimicry. I therefore propose that the beauty and apparent design of the patterns of warning coloured butterflies to our eyes is generated by successful phase III competition among past patterns for the minds of vertebrates.

Possible ecological explanations for evolution of novel warning colours in *Heliconius*

Nonetheless, applying the parsimony argument of Coyne *et al*. (1997), one's default explanation for the diversity of geographic races of *Heliconius* (Fig. 1) should be individual, Fisherian selection. One idea is that each colour pattern is locally adapted to the environment; this explanation has been brought up as an alternative to the classic 'Pleistocene refuge model' of colour pattern evolution (Benson, 1982; Turner & Mallet, 1996). Benson noted that red forewing band patterns (*H. e. hydara*) were characteristic of open, seasonally dry areas of Northern South America, as well as varzea or flooded forest in the Amazon. There is some distributional evidence for this: an apparently non-random finger of the red forewing banded racial distribution stretches from the North, around the coast of the Guianas, and into the mouth of the Amazon up along both banks for >1000 km as far as Manaus (Fig. 1). It seems likely, indeed, that reds and blacks are selected for maximum detectability in relatively bright, open areas, and that paler colours, such as yellow, orange and white contrast better in darker, closed canopy forests (Turner & Mallet, 1996). Similar effects are known for *Anolis* lizard dewlap colours used in sexual display (Fleishman, 2000). There is also evidence for increasing melanism in *Heliconius* and ithomiine patterns in the Andes, suggestive of the idea that increased need for heat absorption in cooler climates may also play a role (Mallet, 1993). Nonetheless, there appear to be exceptions. Benson himself noted that a red forewing band form of *H. erato*, typical of dry savannas, is characteristic of the Chocó, Western Colombia (Fig. 1). The Chocó, with around 10 000 mm of rain per year, is one of the wettest forested regions on the planet. Benson argued that a more suitable pattern had not yet arisen. In Benson's words: 'I believe that a yellow-banded Amazonian type colour pattern would be better suited to this region' (Benson, 1982). Similarly, while the light environment likely constrains *Anolis* colour patterns in dewlap sexual signalling, it probably does not explain the whole diversity of the dewlap colour patterns (Fleishman, 2000).

Other individual selection ideas, such as those thought to allow evolution of warning colour in general, also appear to fail for *Heliconius*. The colour patterns appear too divergent to be explained by enhancement of another pattern. How could a pattern with orange rays on the hind wing and a yellow forewing band be an enhancement of a pattern with a yellow hindwing bar and a crimson forewing band? Or vice versa (see Fig. 1)? It seems more plausible that these divergent patterns really are on alternative, incompatible adaptive peaks, and this result is confirmed by evidence for strong frequency-dependent visual selection in contact zones between races (see below). Given that so many diverse patterns have evolved within *H. erato*, not all of them can represent preadaptations, either. Individual selection thus fails to explain the existing diversification in any of these ways.

Finally, mimicry. As we have seen, mimicry indeed explains perhaps the majority of colour pattern evolution in *Heliconius*, as well as in other mimicry rings such as those centred around ithomiine butterflies. However, Müllerian mimicry cannot explain divergence in all the species; it explains convergence, but not the initial diversification. One idea is that geographic races of *Heliconius erato* and *H. melpomene* each evolved via mimicry to other species, after stochastic loss, or 'biotic drift', of Müllerian models in Pleistocene refuges (Brown *et al*., 1974; Sheppard *et al*., 1985; Turner & Mallet, 1996). Yet the clearest evidence of mimicry in all these geographic races is that among *H. erato* and *H. melpomene* themselves, as well as a handful of other *Heliconius* species that are close mimics in the Amazon Basin. The rather weak similarities of these two *Heliconius* to pierines, ithomiines, pericopine moths and other potential additional models in each area suggest, on the whole, that the latter are mimics of *Heliconius*, rather than models for *Heliconius* mimicry. The detailed and accurate mimicry between *H. erato* and *H. melpomene*, in particular completely outclasses any mimicry by other species of these two. While mimicry does explain many cases of divergent evolution, there simply are not enough Müllerian models to explain the *ca* 30 colour pattern races in *H. erato* and its co-mimics (Mallet, 1993). Furthermore, because *melpomene* seems to be an 'impressionistic' mimic of *erato*, and because races of *melpomene* evolved more recently, it is most likely that *melpomene*, together with a host of other species in the Amazon Basin, copied *erato*, rather than the other way round (Eltringham, 1917; Mallet, 2001a; Flanagan *et al*., 2004). This leaves the problem of *erato*: how did this species itself diversify, pulling *melpomene*, and its other Amazonian heliconiine mimics, with it?

The shifting balance and *Heliconius* mimicry

The different races of *Heliconius erato* seem, therefore, be alternative solutions to the same problem of effective advertisement—local visual 'fashions' which happen to have become established in different areas. Given Müllerian number dependence, they should then be mutually incompatible, rather than enhancements of one another. We have evidence that this is the case. Between geographic races exist hybrid zones of varying narrowness, and the narrowest zones have the greatest differences in colour pattern, as expected if selection is stronger with more pattern divergence (Mallet *et al*., 1998). Strong selection against foreign colour patterns at low frequency can be demonstrated in nature (Benson, 1971; Mallet & Barton, 1989b; Mallet *et al*., 1990; Kapan, 2001), and wild insectivorous birds such as jacamars possess the relevant pattern memory to effect such strong selection (Langham, 2004).

Selection will also depend on details of the genetics of colour pattern. *Heliconius* work is well advanced in this area as well. Perhaps surprisingly, relatively few loci across the genome of *H. erato* control this great diversity of colour patterns (Sheppard *et al*., 1985; Mallet, 1989; Joron *et al*., 2006). This allows one to genotype hybrid zone butterflies from their phenotypes. These colour patterns are not examples of classic polygenic, quantitative inheritance: instead, very limited regions on a few chromosomes control a great variety of pigment patterns across the wing (e.g. Fig. 4). There is some evidence that such regions may be 'supergenes': different, but tightly linked sites on the chromosome control a number of different pattern elements (e.g. the D^{Ry} locus in *H. erato*, Fig. 4). Very occasionally, recombinants between elements within these supergenes can be observed (Mallet, 1989). Recent molecular work is beginning to pin down these loci to within small regions of the *Heliconius* genome, of order 100 kb or less, and these same regions are re-used in different species, sometimes for very different colour pattern switching (Joron *et al*., 2006; Kronforst *et al*., 2006). Nonetheless, we still have little idea how whole patterns are regulated or can be switched by such small regions of the genome.

The existence of these loci with major effect can be explained in part because mimicry requires a major phenotypic shift so that enhanced fitness of mimics can overcome the loss of fitness due to existing mimicry or warning patterns (Turner, 1984). However, this argument will not explain origination of supergenes in species that are driving diversification of the pattern, in this case *H. erato* (Mallet, 1993). Multiple-element supergenes are not expected to evolve in Müllerian mimicry anyway (Turner, 1984), except in polymorphic mimics such as *Heliconius numata* (Joron *et al*., 2001). Instead it seems likely that relatively few genomic regions are suitable and then recruited for modifying colour pattern (Turner, 1984; Mallet, 1989). Selection on different elements within the supergene may ensure that enhancements of mimicry and warning colour are built up at each region, resulting in the supergenes. Full understanding of the molecular function of *Heliconius* colour pattern loci, and of how they are built up, will have to await further developmental genetic work. For the moment, we assume that mutations at these loci have since their origination had major effects on colour patterns and therefore fitness, even though these effects have likely become enhanced and fine-tuned by further selection within each supergene.

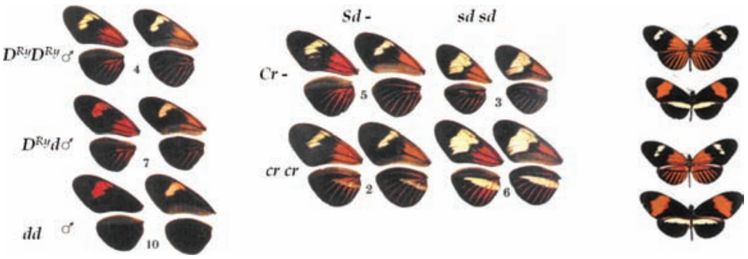

Fig. 4. Genetics of colour pattern in *Heliconius erato*. The three major loci or 'supergenes' involved in switching colour pattern across the Tarapoto hybrid zone in Peru. Left: genotypes at the *D* locus (on a genetic background of *CrCr SdSd*) in the production of red versus yellow forewing band switch and of orange forewing basal patch ('dennis') and hindwing rays. Centre: interaction of *Sd* and *Cr* loci (on a genetic background of $D^{Ry}D^{Ry}$) in the production of yellow hindwing bar and forewing band shape. Right: Pure races of *H. erato* (top) and *Heliconius melpomene* (bottom) that interact in this hybrid zone, showing the mimicry. (After Mallet, 1989.)

Heliconius hybrid zones as examples of phase III of the shifting balance

Purifying frequency-dependent selection can readily produce the kind of flip-flop selection required to maintain a narrow cline in the face of gene flow from either side of a hybrid zone. This has allowed detailed study of one hybrid zone in Peru. Here three major unlinked loci (Fig. 4) are known to affect colour pattern, of which two are dominant. Apart from colour pattern, there are almost no genetic differences across the hybrid zones of either *H. erato* or *H. melpomene* (Nei's $D = 0.003$ and 0.002, based on 32 and 27 enzyme loci run on starch gels, respectively, published here for the first time). In *H. erato*, the shapes of the clines at the two dominant loci, but not the codominant locus, are asymmetrical, as expected if selection is controlled by colour pattern phenotype (Mallet *et al*., 1990, 1998). Based on linear frequency-dependent selection, the maximal selection acting on D^{Ry} is $s \approx 0.33$, and on *Cr* and *Sd*, $s \approx 0.15$ in *H. erato* (recalculated in Mallet *et al*., 1998), giving an overall selection pressure, assuming multiplicative fitnesses, of $s \approx 0.52$. In *H. melpomene*, one might expect selection coefficients by the same predators on the same colour patterns to be similar, and they are: $s \approx 0.25$ per locus on each of four separate colour pattern loci (Mallet *et al*., 1990). Mark release studies on *H. erato* in the hybrid zone confirm very strong selection against foreign colour patterns (Mallet & Barton, 1989b). Given that this Peruvian hybrid zone is between very divergent races, we accordingly expect less selection in less divergent zones. In the Panama hybrid zone, differentiated only by the yellow hindwing bar locus, *Cr* (Mallet, 1986), the colour pattern is therefore expected to be under weaker selection overall, $s \approx 0.15$, if the results from Peru are indicative.

These hybrid zones represent contacts between warning colour adaptive peaks, and therefore we might expect to find the third phase operating. Assuming pure warning colour selection, there are at least four ways in which peaks might spread in this system. First, we might imagine redistribution as a result of population expansion across unoccupied space until a contact zone is formed on confronting another race (Brown *et al*., 1974; Sheppard *et al*., 1985); second, stochastic redistribution is possible (Lande, 1985); third, a race may spread deterministically in a contiguous metapopulation under soft selection (i.e. selection not affecting population density) among genotypes (Mallet, 1986; Mallet & Barton, 1989a); fourth deterministic spread via 'group selection' (Rouhani & Barton, 1993), under hard selection (i.e. selection that does affect population density, and where higher density populations send out more migrants). This fourth possibility is what Wright seems to have intuited as the main cause of his phase III, or interdemic selection. However, the same effect can be achieved by soft selection, in which the population density is regulated tightly, but one pattern wins because of some bias in selection alone. The last two forms of selection can both be regarded as components of phase III, as indeed can biased stochastic spread (Lande, 1985). None of these are, however classical natural selection, because without the spatial population structure, no invasion of the superior morph would occur, even though only the fourth alternative might be termed true group selection.

Because the selection on *Heliconius* colour pattern is not dependent on the physical environment, but, via labile predator memories, more dependent on the frequencies of colour patterns in local populations, the hybrid zone is free to move. In theory, even without any selection or migration bias, movement will occur as a result of genetic dominance alone, or 'dominance drive'(Mallet, 1986; Mallet & Barton, 1989a). In the absence of dominance bias, the speed of advance is expected to be $\approx S/\sqrt{s}$, where S is the selection differential between the two phenotypes (for instance, superiority of one morph at teaching predators), and s is the frequency-dependent selection due to rarity (Barton, 1979). Somewhat to my surprise, hybrid zone movement was indeed found in a *Heliconius erato* hybrid zone in Darién, Panama that I had first sampled in 1982 (Mallet, 1986); the movement can be explained if the zone is under purifying mimicry selection of approximately $s \approx 0.2$. This zone had moved 47 km to the west in the 17 years between samples, suggesting a selective differential or dominance bias of around $S = 0.04$ (Blum, 2002). Curiously, another butterfly hybrid zone in the same area has moved as rapidly, but in precisely the opposite direction. *Anartia fatima* and *A. amathea*, which are non-mimetic, palatable, nymphalid butterflies, meet and form another hybrid zone in Darién. This zone is almost certainly maintained by hybrid inviability, rather than warning colour as in *Heliconius*. Samples taken over 23 years suggest *Anartia* zone movement of about 50 km to the East (Dasmahapatra *et al*., 2002). There has been considerable recent deforestation in Darién, but both the *Anartia* and *Heliconius erato* races occupy second growth habitats, so there is no obvious reason why human-induced habitat change, or change in climate, should affect both species in such opposite ways.

It is expected that some or perhaps most moving hybrid zones will become stuck on population structural boundaries (Coyne *et al*., 1997). However, the confirmation of rapid cline movement in *Heliconius* colour pattern zones, as well as in another butterfly hybrid zone, suggests that deterministic phase III is at least likely under natural situations. Whether the movement in the Panama hybrid zone is a temporary fluctuation or evidence of continued, deterministic spread will have to await further studies, but that hybrid zones like this can move substantial distances does not now seem in doubt. Deterministic cline movement can be effected by biases other than selection (e.g. dominance), so fitness may not always be maximised. Coyne *et al*. (1997: p. 652) argue that phase III therefore will not provide an efficient way of exporting adaptive peaks. However, assuming that other biases are uncorrelated with fitness, such movement will export fitter peaks on average. As with any other kind of selection, it is the average effect, rather than variations around the mean, that is important. Therefore, this does not seem a valid criticism.

Spread from the range centre via phase III also fits with another interesting observation in *Heliconius*—disjunction of certain colour patterns (Fig. 1). The most prominent disjunction involves red forewing band forms with yellow hindwing bars. They are distributed in Central America, patchily in three non-adjacent valleys of the Andes, and also south of the

Amazon Basin in Bolivia, Argentina and Brazil (green distribution areas in Fig. 1). Intermediate regions have other colour patterns. We know from crossing experiments that the same genetic machinery, although somewhat divergent, is employed in the construction of these disjunct patterns (Sheppard *et al*., 1985; Mallet, 1989). The rayed races, on the other hand, form a compact block in the centre, mainly in the Amazon Basin. Another disjunction is given by the 'twin-banded' races from the Eastern slopes of the Andes in central Ecuador and central Peru (brown areas in Fig. 1). One of *erato*'s closest relatives is *Heliconius telesiphe*, which is also twin-barred, suggesting the pattern is plesiomorphic. This is just what one expects if the races with yellow forewing bands and ray patterns had evolved in the centre, and spread out as a recent wave in competition with, and at the expense of, more ancient red forewing and twin-barred band patterns. As they expanded, diversifying into a number of sub-races, the ancestral red-banded patterns would be expected to be found only on the periphery of the distribution. Of course, another possibility is that some or all components of these disjunct colour patterns evolved independently in different locations (Brower, 1996; Jiggins & McMillan, 1997). Perhaps the new developmental genetics work will eventually resolve whether these are parallel evolutionary responses to similar selection pressures, or disjunctions of formerly continuous colour pattern distributions. Until then, we may permit ourselves the luxury of noting that these distributions accord well with those expected if new patterns spread at the expense of old.

Another distribution pattern evident from Fig. 1 is also intriguing: one Guianas yellow forewing band race lacks rays (the northernmost blue area in Fig. 1), probably due to a difference in one element of the D^{Ry} supergene (Mallet, 1989), and this can be seen as an intermediate between the completely rayed races and the red forewing band races which lack them. It is also distributed contiguously between the two races for which it is a genetic intermediate. Similarly, the forms both North-central from the Amazon and South of the Amazon Basin (Bolivia), which have a broad block-like yellow forewing bar extending into the discal cell, are also genetically intermediates (strongly shaded blue areas to the north and south of the Amazon in Fig. 1). The *Sd* allele that determines the broad red forewing band shape in *erato* expresses like this in yellow bands, even in areas where no broad yellow forewing band race exists (Fig. 4). This would be the pattern expected if either new, advantageous pattern alleles arose, one locus at a time, and spread out sequentially, or if hybridisation had led to occasional establishment of new recombinant colour patterns which had spread out to form their own race in intermediate locations. The former explanation seems likely, since different pattern elements are often inherited at separably mutable or recombinable sites within a supergene (Mallet, 1989). Either explanation is again consistent with the kind of sequential, single locus shifting balance suggested here to lead to the colour pattern diversity in *Heliconius*.

Of course, one might argue that the geographic diversity of current warning patterns within *Heliconius* species, as well as the local diversity among species within different mimicry rings, is evidence for the inefficiency of shifting balance-like processes in attaining a single, globally optimal adaptive peak. To some extent this criticism is probably correct whichever side of the argument one takes: even if warning colour does frequently evolve via shifting balance, it seems likely that there are plenty of approximately equivalent adaptive peaks, and that phase III cannot effectively sort between them. Inferior patterns, on the other hand, would still have disappeared long ago from the mix and would be no longer visible. For the criticism to be convincing, one would therefore have to believe that only one or a few warning colour patterns form superior peaks, and that they are generally much better than their next best competitor. To me, this seems unlikely.

One relevant piece of evidence concerns the rates of evolution of these colour patterns. The genus *Melinaea* is a leading member of by far the largest, 'tiger' mimicry ring in the neotropical rainforest (Beccaloni, 1997), and like *Heliconius*, most species have multiple geographic races (Brown, 1979). Many species of ithomiine and heliconiine butterflies mimic *Melinaea* patterns. Judging by a certain impressionism of most other species' colour patterns, it is probably *Melinaea* species that are the prime Müllerian models for the other species' colour patterns (Bates, 1862; Mallet, 2001a) rather than vice versa. Recent molecular studies indicate that a number of full *Melinaea* species, let alone divergently coloured races within each, are indistinguishable genetically, based on mitochondrial and nuclear genetic markers. These results suggest at most $\approx 10^5$ years for the recent species, and maybe $\approx 10^4$ years or less for divergent geographic mimicry colour patterns (Whinnett *et al*., 2005; Dasmahapatra *et al*., in prep.). One possible reason for the existence of geographically diverse patterns that suggests itself is therefore that, instead of the adaptive process being inefficient (and clearly, the mimicry among species shows it is not), warning colour adaptations may be so recent and originating at such a high rate that the system has not had time to reach a steady state equilibrium of a single, globally advantageous pattern.

Population structure and phase I of the shifting balance

Nonetheless, the very strong selection coefficients ($s > 0.1$ per locus) that should be effective in deterministic phase III spread, will also militate against the stochastic shift required by phase I (Coyne *et al*., 1997). While this is indeed a problem for the shifting balance, it has been shown that selection strength only rather weakly affects peak shift probability in continuous two-dimensional metapopulations (Barton & Rouhani, 1987). The reason is that although stochastic peak shift in any single deme becomes more and more unlikely with stronger selection, clines forming around the 'bubble' of the new colour pattern (Fig. 2) will also be much steeper; thus a smaller overall area and smaller overall number of individuals is required to make the shift. In demic population structures with very low migration rates, the need for low population sizes for phase I is much more severe (Barton & Rouhani, 1987).

This is not the only problem for phase I: neighbourhood population sizes must also be reasonably low at least somewhere if genetic drift is to take place readily. Quite to the contrary, there is evidence for rather high long-term effective population sizes in *Heliconius*. Enzyme genes have very high heterozygosities in *H. erato* ($H_e = 0.273$, based on 32 allozyme loci) and *H. melpomene* ($H_e = 0.145$, based on 27 loci) from the Peruvian Amazon, among the highest known values for any organism, as expected if extensive populations across South America had rarely undergone bottlenecks (J. Mallet, unpublished data based on allozymes on starch gels). Differentiation among all populations in the area of the Peruvian hybrid zone above is typically slight ($F_{st} = 0.013$, 0.032, respectively, using the Weir & Cockerham measure, J. Mallet, unpublished data). Similarly low values for allozyme differentiation were obtained in *H. erato phyllis* ($F_{st} = 0.025$) in south-east Brazil (Silva & de Araújo, 1994), *H. erato cyrbia* ($F_{st} = 0.0060$) and *H. himera* ($F_{st} = 0.0003$) in Ecuador (Jiggins *et al*., 1997), and *H. charithonia* ($F_{st} \approx 0.000$) in Florida (Kronforst & Fleming, 2001). Per generation dispersal distances estimated from genetic data in hybrid zones are variously estimated to be in the range 3–10 km (Mallet *et al*., 1990; Blum, 2002). More recently, microsatellite and amplified fragment length polymorphism (AFLP) studies gave somewhat higher F_{st} values, from 0.04 to 0.125 (Kronforst & Gilbert, 2008). Recent molecular data also suggest very high long term effective population sizes, with many nuclear sequence polymorphisms, often ≈1% of nucleotide positions in natural populations (Beltrán *et al*., 2002; Flanagan *et al*., 2004; Bull *et al*., 2006). These newer DNA data tended to have lower sample sizes in terms of numbers of individuals, which may explain the somewhat higher F_{st} values, or these could be a result of scoring differences between the methodologies. In any case, overall there seems little evidence for generally strong population structures of $F_{st} > 0.1$, for example.

Unfortunately, however, the probability of stochastic peak shift cannot easily be assessed from typical studies of population structure. Stochastic peak shift needs to produce a bubble of critical size only once in the entire range of a species (or colour pattern race, see Fig. 2) to initiate deterministic phase III spread; this possibility does not depend strongly on average population structure (Barton & Rouhani, 1991). Samples for the *Heliconius* genetic studies were, for practical reasons, collected where abundant samples could be readily found, rather than from regions where populations were low, and phase I more likely. In spite of this, all of the above population studies show fairly strong local population genetic differentiation with high F_{st} even in Peru where hardly any metapopulation-level genetic differentiation exists overall between geographic races (Nei's $D = 0.003$ in *erato*, see above). So it does not seem improbable that low enough effective population sizes frequently occur somewhere. It is also likely that there are times when there are few predators, and consequently relaxed selection pressures. For example, jacamars in the *Galbula ruficauda* complex probably exert some of the heaviest selection on *Heliconius* (Mallet & Barton, 1989b; Langham, 2004), and yet are absent from some field sites in Peru (Mallet & Barton, 1989b), as well as from the whole of Central Panama (Ridgely & Gwynne, 1992).

Another possibility for causing a peak shift is idiosyncratic or fluctuating selection. If a locus is under positive selection in a local population, linked polymorphisms may 'hitch-hike' with the selected locus, even if neutral or mildly deleterious. Strong positive selection will cause this to happen even if the shifting locus is deleterious at low frequency. Although it can be argued that this effect is not the same as phase I via random drift, selection here primarily acts to reduce effective population size of linked loci, so it is in a sense a drift effect. Pleiotropy may be involved as well as linkage. Colour patterns are certainly affected by the thermal environment (see above) and sexual behaviour in highly visual insects such as *Heliconius*. In *H. cydno* and *H. melpomene*, colour pattern differences have an effect on assortative mating among species (Jiggins *et al*., 2001). Assortative mating also occurs, to a more limited extent, among divergently patterned geographic races of both *melpomene* (Jiggins *et al*., 2004) and *erato* (Estrada & Jiggins, 2008). These effects might sometimes constrain the evolution of novel colour patterns, as well as of Müllerian mimicry. On the other hand, fluctuating natural and/or sexual selection may sometimes drive novel patterns into populations against the predominantly conservative effect of warning colour and Müllerian mimicry.

In conclusion, it seems likely that there are frequent episodes of low population size and relaxed selection pressures or idiosyncratic local episodes of selection that allow peak shifts locally somewhere in the range of *Heliconius* species. Nonetheless, this is not a particularly convincing style of argumentation (see also Barton & Rouhani, 1987). It would be preferable to have direct empirical evidence for phase I.

Empirical evidence for phase I

There is such evidence. Although polymorphisms are prohibited by simple warning colour selection, purifying frequency dependence is sometimes violated, and we see an almost embarrassing amount of polymorphism in natural warning colours. Some examples include the yellow hindwing bar polymorphism of *H. ethilla* on Trinidad (then known incorrectly as *H. numata*) (Turner, 1968), the polymorphism in rays and forewing red patch of *H. timareta* in east Ecuador (Mallet, 2001a), and the polymorphism in *H. cydno* and *H. melpomene*, caused by hybridisation between these two species, presumably some time ago, in one site near San Cristobal, Venezuela (Mavárez *et al*., 2006). Whether these polymorphisms are maintained by selection is unclear, but they all occur in limited regions, and cannot be explained simply by mimicry or warning colour selection. It is possible that the *H. timareta* polymorphism, which cannot easily be explained by past hybridisation, is balanced by some non-visual selection mechanism. These polymorphisms are reminiscent of those found in captive populations of *H. melpomene* found in recreational 'butterfly houses' world-wide. These mixed-ancestry, commercially managed populations, lacking any constraints imposed by natural predators, maintain polymorphisms in which almost no two individuals are alike.

In addition, there are a number of species that are polymorphic mimics of different model species; examples include

Laparus doris (Heliconiinae), which mimics a variety of different *Heliconius*, and in some cases *Parides* species (Papilionidae) (Mallet, 2001a). Perhaps the most impressive polymorphic mimic is *H. numata*, which in the Amazon Basin may be polymorphic for up to eight different morphs, each of which mimics a different *Melinaea* species (Joron *et al*., 2001). Similarly, *H. cydno alithea* in west Ecuador is polymorphic for two major colour patterns that mimic local races of *H. eleuchia* or *H. sapho* (Kapan, 2001). Similar examples are found in Colombia (Linares, 1997). These apparently embarrassing examples of polymorphisms within warningly coloured, unpalatable species are, however, readily explained by spatially varying selection pressures from different Müllerian models, coupled with a suitable 'supergene' genetic architecture that permits single-locus switching (Brown & Benson, 1974; Joron *et al*., 2001; Kapan, 2001; Mallet, 2001a; Joron *et al*., 2006).

Regardless of how they are caused, the existence of these and other local polymorphisms in local populations of *Heliconius*, demonstrate that phase I is not in practice a major hurdle to the evolution of novel colour patterns that may then compete in phase III. Similarly, although chromosomal hybrid zones and partial sterility of heterozygotes are common features demonstrating separate adaptive peaks in chromosomal evolution, the existence of a number of cases of translocation and inversion polymorphisms in natural populations also suggests that phase I may not be as much of a problem in chromosomal evolution as sometimes painted (Coyne *et al*., 1997). Of course, one could argue that most of these would then not be examples of the shifting balance, since selection may not be very strong, or may even temporarily favour such polymorphisms, possibly by hitch-hiking, or genetic 'draft' (Gillespie, 2001). Perhaps so; nonetheless, by deviating from the general norm of warning pattern or chromosomal monomorphism, they go against the general run of selection. Selection, as well as drift, may produce stochastic population exploration of novel adaptive peaks, thereby allowing phase III a chance to operate (Wright, 1932, 1982).

Conclusions

Overall, then, *Heliconius* butterflies provide a system in which the shifting balance can and probably does operate. Returning to the list of critiques extracted from Coyne *et al*. (1997), the *Heliconius* warning colour, mimicry, and geographic system answers most of them:

1 It seems clear, or at least there is a very good argument, that there are real separate peaks in the mimicry/warning colour adaptive landscape. It is almost inconceivable that the different colour pattern races of Fig. 1 are not in some sense different solutions to the same problem. The startling colour patterns, which appear as though designed for beauty to our eye, are known to be learnt by predators and seem likely to have been selected to maximise visibility and predator education. The narrow hybrid zones between them prove they are separate adaptive peaks.

2 The narrow clines and hybrid zones between colour pattern races, and strong selection on known genetic architecture that has been measured for Müllerian mimicry in the group, show that no 'ridges' exist to allow simple, Fisherian transition among peaks.

3 Although the generally high levels of gene flow, strong selection, and high locally effective population sizes in *Heliconius* would apparently militate against peak shifts in colour pattern, it is likely that there are many variations in population density, and frequent enough relaxation of natural selection due to local predator extinctions, for phase I to occur. Indeed, although the general rule is for monomorphism and tight selectional control by purifying warning colour and mimicry selection, some local *Heliconius* populations apparently escape this selective regime and are polymorphic in major colour pattern elements. Phase I therefore has empirical evidence.

4 The argument of Coyne *et al*. (1997), that deterministic interpopulation selection can reduce mean fitness and compromise the shifting balance as a mechanism of adaptation, is not convincing. Some biases, such as 'dominance drive', do produce cline movement and can indeed favour deterministic spread of suboptimal adaptive peaks. However, such biases are unlikely to be correlated with fitness. Given that fitness differences can drive deterministic cline movement in the same way, fitter peaks ought to spread more often than not. In *H. erato* in the Darién, we have an example of a hybrid zone that appears to be trundling along as expected in theory. Thus, phase III also has empirical evidence. Furthermore, the pattern of disjunction of 'leapfrog' peripheral patterns (Fig. 1) resembles that expected if phase III spread of new patterns occurs from the centre, within the Amazon Basin.

5 It is probably true to say that most improvements in warning colour in *Heliconius* cannot be obtained via recombination among adaptive peaks in the manner suggested by Wright, who based an argument about intercrossing among adaptive peaks on analyses of animal breeding, such as short-horn cattle. Instead, we see a geographic pattern expected via sequential accumulation of alleles, within and between 'supergenes', in multiple shifting balances, with intermediate forms often occupying intermediate geographic positions (Fig. 1). However, Wright saw inter-peak recombination mainly as a means to purge inbreeding depression from within local populations. This does seem likely for *Heliconius* colour patterns, which lack strong differences in molecular markers between races. At a still later stage, there is evidence for hybridisation even among species which does allow recombination of mimicry genes among lineages, leading to hybrid speciation and much homoplasy in colour pattern among species (Gilbert, 2003; Mavárez *et al*., 2006; Giraldo *et al*., 2008; Mallet, 2009).

6 In (3) and (4) above, we see that in *Heliconius* butterflies both controversial aspects of the shifting balance, phase I and phase III, are empirically observed, whereas phase II here is merely Fisherian natural selection for mimicry and warning colour conformance, and is uncontroversial. Thus, all three phases are observed in the *Heliconius* colour pattern system: this answers a major criticism of Coyne *et al*. (1997).

Some of the assertions made here are speculative, or supported by still somewhat slender empirical evidence. Future molecular studies could enable tests of the hypothesis that the 'same' colour pattern alleles in different disjunct races have a single origin, as expected if phase III movements caused spread from the centre. More empirical data on phase I and phase III are required. Overall, however, the *Heliconius* work so far support the idea that mimicry colour patterns diversified in part as a result of multiple, stochastic peak shifts, and that incompatible peaks currently compete across clinal boundaries in a dynamic phase III pattern. The idea should at least be borne in mind as an alternative to *deus ex machina* environment forcing, such as biotic drift and Pleistocene (or earlier) refuge theory (Turner & Mallet, 1996). Overall, *Heliconius* provides possibly the most complete system showing that, in addition to individual gene mutations, population-level stochasticity and local experimentation (phase I of the shifting balance) contributes to the raw material of adaptive evolution.

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