Did forest islands drive the diversity of warningly coloured butterflies? Biotic drift and the shifting balance

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SUMMARY

Species of the South American butterfly genus *Heliconius* have undergone remarkably wide racial divergence in their patterns, and most of the resulting races are muellerian mimics. As warning coloration normally imposes stabilizing selection on the pattern, this divergence is much in need of explanation. Two models have been suggested. Brown, Sheppard and Turner proposed that the divergence results from 'mimetic capture', the switching of patterns between adaptive peaks generated by changes in the overall composition of the local biota ('biotic drift') and hence of the mimicry rings to which each species belongs; these changes have in turn been generated by long term patterns of species extinction in island refuges as biota became progressively isolated and contiguous during contraction and expansion of the rain forest during the Pleistocene. An alternative model, proposed by Mallet, is that truly novel colour patterns became established by mutation and random drift, then spreading to become predominant in local areas; subsequently the novel patterns spread over wide areas by the migration of clines. Under this application of Wright's shifting balance model, refuges are not necessary for divergence, and muellerian mimicry evolves after divergence rather than being the driving force for race formation. Although our respective models appear diametrically opposed, the hypotheses are difficult to distinguish and there are broad areas of agreement; in both models there is an initial stochastic event, followed by natural selection for mimicry, and both will operate either in parapatry or allopatry. The diversity of warning patterns is better explained by the shifting balance model, but there are alternative selectionist explanations such as sexual selection.

1. THE PROBLEM

According to Stephen Hawking 'God does throw dice'. Our question will be 'When are the dice thrown?' It has been customary to think of Wright's shifting balance as a stochastic theory of evolution and Fisherian natural selection as deterministic; contrariwise both R. A. Fisher and S. Wright believed in fundamental stochasticity (Turner 1987*a*, 1992). We propose a different dichotomy: that divergence can take place as an adaptive response either to stochastic changes in the genetic structure of the population, or to stochastic changes in the biotic environment, or of

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course, both. We will explore this through the spectacular evolutionary divergence of the colour patterns of South American butterflies, particularly *Heliconius*.

2. THE FACTS

Geographical variation in South American long-winged butterflies (*Heliconius*, ithomiines and others) is among the most striking examples of evolutionary radiation. 'In tropical South America, a numerous series of 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). The geographical diversity of colour patterns, coupled with the close similarity of colour patterns between species within any one area led to Bates' (1862) theory of mimicry. Turner (1976) showed that there has been a pattern of convergent evolution within the Heliconiini, such that individual clades have radiated into many of the mimetic patterns, and each of these patterns in turn is shared by members of separate clades. This pattern of divergence and convergence within the genus is repeated as a pattern of divergence and convergence between races within species: it is a fair conjecture that this racial divergence/convergence is what underlies the pattern at the higher taxonomic level. The most spectacular example is the now well-known parallelism of the mutual muellerian mimics *Heliconius melpomene* and *Heliconius erato*, which each have around thirty identifiable races and around fifteen distinct colour patterns. Each race and pattern of *Heliconius erato* is sympatric with a closely similar-looking and presumably mimetic race of *Heliconius melpomene* (there is one exception) (figure 1). The rampant geographical diversification within these species demands an explanation. Predators' memories ensure that warning patterns are subject to strong frequency-dependent and stabilizing selection: rare patterns are at a disadvantage and a new pattern will be favoured only once it has evolved to a high frequency, selection usually favouring the commoner and best recognized form (e.g. Mallet & Singer 1987; M. P. Speed & J. R. G. Turner, unpublished data). A similar problem arises with the origin of warning colour itself: a rare pattern may gain little advantage of its own, and may sacrifice fitness by being conspicuous compared with the original cryptic pattern. There are difficulties in explaining how warning colours evolve from a low frequency within a population (Fisher 1930; Turner 1971*a*; Harvey & Greenwood 1978) without resorting to a group selectionist argument that aposematism is 'an adaptation involving only a small sacrifice of life' (Poulton 1890). Thus there are three related evolutionary puzzles: the origin of warning colour itself, the origin of new warning colours from old, and the divergence of existing warning patterns, as seen in *Heliconius*.

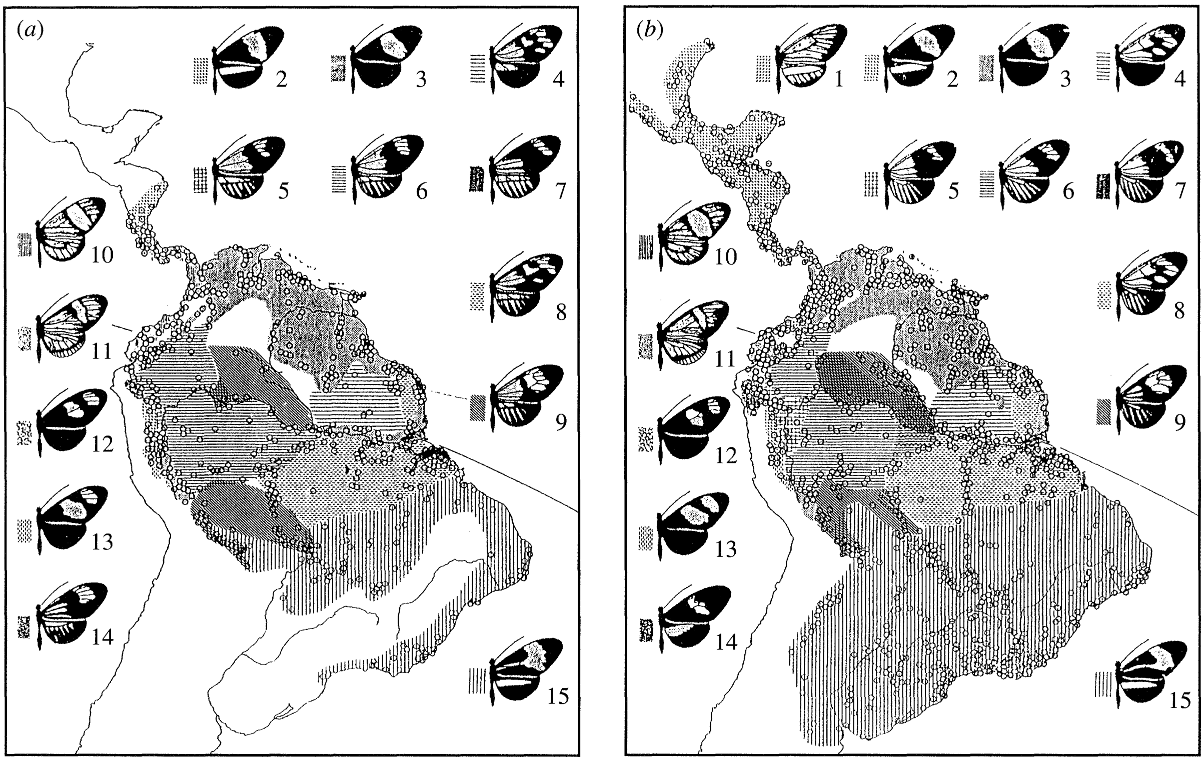

Figure 1. Parallel mimicry and geographical variation between *Heliconius melpomene* and *Heliconius erato*. From Sheppard *et al.* (1985). (*a*) Geographical variation of *Heliconius melpomene*. Circles are collection points, grouped into quadrants of 30 min of latitude and longitude; hybrid zones between races are narrow and are not shown; some races showing only minor differences are not distinguished. (*b*) Geographical variation of *Heliconius erato*, the parallel comimic of *Heliconius melpomene*. Symbols as in (*a*).

3. THE BIOTIC DRIFT MODEL

The Brown–Sheppard–Turner model (Brown *et al.* 1974; Turner 1983, 1984*a*; Sheppard *et al.* 1985) assumes that the conversion of the butterflies from one mimetic pattern to another is brought about by natural selection, with no contribution from random genetic drift. The stochastic element occurs at the level of the composition of the ecological community. Because species are usually distributed patchily, as now adumbrated in the 'metapopulation model' (Gilpin & Hanski 1991), any small (or indeed large) isolated part of a 'continent' of species contains at any one time only a stochastic subsample of the species which might be present: thus the islets of the Gulf of Finland have sharply differentiated floras as a result of more or less random accidents in their colonization history (Halkka *et al.* 1975). The species composition of the flora and fauna undergoes 'biotic drift' ('faunal' and 'floral' drift are alternatives). The classic case of mammals on the mountaintops that contain the fragments of a previously continuous moist forest now split by the arid conditions of the Great Basin (Brown 1971) shows what happens during biotic drift (figure 2). Although it is clear that some islands have a greater loss of species than others, and that some species have a higher probability of extinction than others, so that the pattern is 'disorderly extinction' (Turner 1977*a*, 1984*b*) rather than 'random extinction', there is a large stochastic element.

It follows that the form which natural selection takes, for all the constituent species, will differ from island to island or patch to patch. This introduces a strong stochastic element into the process of adaptation itself.

It is suggested that the patterns of warningly coloured butterflies evolve primarily by 'ring switching' (Turner 1976*b*; also see Turner 1977*b*, 1984*a*, *c*, *passim*, Sheppard *et al.* 1985). Natural selection favours the convergence of the patterns of warningly coloured butterflies onto a common pattern, so that they all become muellerian mimics: such an assemblage is called a 'mimicry ring'. In the tropics it is normal for around six such rings to coexist within one life-form (bees, long-winged butterflies), indicating that something prevents total convergence. This barrier is held to be the considerable differences between the patterns of the rings, such that the cognitive generalization of predators never confuses one ring with another; probably this is enhanced by microhabitat differences between both mimicry rings (Beccaloni 1995; Mallet & Gilbert 1995) and the predatory birds. There is thus an 'adaptive valley' between the rings which can be crossed only when suitable major mutations arise which allow a shift between adaptive peaks. Individual species are likely to cross the valley, and thus 'switch rings' or undergo 'mimetic capture' if the patterns of two rings are sufficiently alike that a mutation in a species in one ring produces a passable resemblance to the pattern of the other ring. The resemblance does not have to be perfect, only sufficiently good to confuse enough of the predators enough of the time; higher levels of mimetic resemblance are achieved later through gradual convergent evolution.

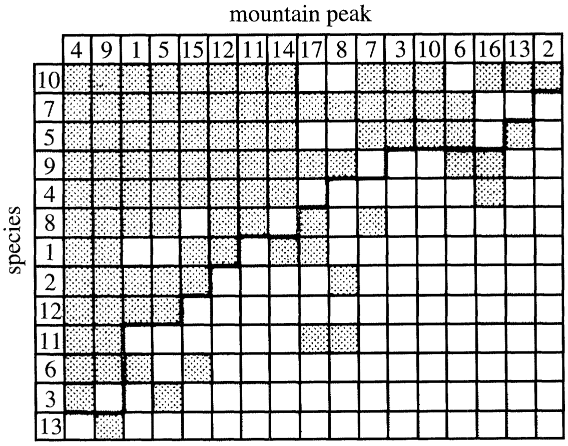

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Figure 2. Biotic drift or disorderly extinction of the boreal mammal fauna of the Great Basin (western U.S.A.) following its fragmentation by desert conditions: each mountain peak contains a subset of the total fauna. Shading indicates presence; numbers are mountain peaks or mammal species. After Brown (1981), redrawn by Turner (1977*a*, 1984*b*). See Brown for the names of the peaks and the mammals.

To effect the capture of a species, the capturing ring has to be better protected than the ring from which the capture occurs: better protection arises either from more effective chemical defense, or from being more numerous. Thus capture is expected to be ongoing, with species exchanged between different rings at different times, or even whole rings totally captured, as rings change in their overall abundance, or in their composition: a ring which contains a particularly distasteful species, or which has become more numerous (as a result of containing a few common species or a very large number of species) is the ring that will effect the captures from other rings. As rings change their abundance over time, species will be captured and maybe recaptured, and if rings differ in their capturing power in different geographical areas, the captured species will undergo racial divergence. The theory is thus capable of explaining racial differentiation of the kind seen so spectacularly in *Heliconius melpomene* and *Heliconius erato*.

The Brown–Sheppard–Turner model therefore requires nothing more than changes in the abundance of species in muellerian mimicry rings that last for a sufficient time to enhance mimetic captures, the time involved being the delay before a suitable mutation occurs, and the time taken to substitute one allele for another. But Turner (1982) argued that although the biotic drift model could generate racial divergence in mimetic *Heliconius* purely by ecological fluctuations in continuous forest, the changes were much more likely and possibly larger during periods when the fauna and flora were fragmented into refuges undergoing extensive and long-term biotic drift. Local extinction of species is universal, but in a continuous habitat is likely to be relatively short-term, as the vacated patches of habitat are recolonized from neighbouring populations. In a habitat fragmented into islands, such an extinction is permanent except through infrequent long-distance recolonization, or until the islands coalesce again. In such island refuges, there is stochastic change in the composition of the flora and fauna which is profound and long lasting.

Such changes must surely have considerable effects on evolution. In general, the extinction of species affects the ecology and hence evolution of the remaining species, by removing host plants, predators, parasites or competitors, and leaving open ecological niches that were previously occupied. Specifically the mimicry rings will change their species composition by the loss of individual species, but also their abundance because of the loss of parasites, competitors, host plants etc. Such long-term changes would have great power to generate ring capture and divergent evolution in mimetic butterflies. The theory has therefore been allied with the 'forest refuge model' for evolution in Amazonia (Fox 1949; Turner 1965, 1976*b*; Haffer 1969; Prance 1973; Brown *et al.* 1974; Brown 1979, 1987), which proposes that the patterns of race formation seen in the biota of much of tropical America are to be explained by a model of allopatric race formation on 'island' refuges; the islands being formed by the shrinkage of the now continuous humid forests during the cool dry periods that accompanied the glacial maxima of the Pleistocene.

4. THE SHIFTING BALANCE MODEL

Mallet has suggested an alternative to the biotic drift model: that the evolution and diversification of warning colours in *Heliconius* might constitute a good example of Wright's (1932, 1977) shifting balance theory (Mallet 1986*a*, *b*, 1990, 1993; Mallet & Singer 1987). There are three phases.

1. Phase I: random factors such as mutation, drift, kin-founding, or fluctuations in selection might occasionally cause a novel colour pattern rise to a high frequency in a local population. If by chance this frequency is high enough to exceed the point of unstable equilibrium imposed by the frequency-dependent selection on warningly coloured forms (say around 50% in a species which does not belong to a mimicry ring), this will trigger phase II.
2. Phase II: the new colour pattern being advantageous when common, frequency-dependent selection raises its frequency so that it becomes locally predominant; once it approaches fixation in a local area this leads to phase III.
3. Phase III: the new pattern spreads to other populations at the expense of the older patterns by means of interdemic selection (via population pressure; see Wright 1977) or moving clines (Barton 1979; Mallet & Barton 1989*a*; Mallet 1993).

Phase III of the shifting balance is perhaps its most important feature, because it preserves and amplifies the rare events of phase I and II; this is analogous to natural selection of randomly produced mutations in simple selective processes. Spread by the movement of clines is not the same as the group or interdemic selection proposed by Wright (which may be involved as well), but it has the same effect of spreading novel adaptations that are disfavoured at low frequency, and may indeed be helped by interdemic selection. Once a new form has evolved in a local area whether by drift or by selection, contact with the original form will not lead to swamping: frequency-dependent selection will ensure that the two forms remain apart; selection will produce sharp clines in warning colour pattern between the different forms (Mallet & Barton 1989*a*). In phase III such clines move in favour of better-adapted colour patterns. Thus the cline that forms in this way will be similar to clines formed through selection against heterozygotes, as in chromosomal evolution (Bazykin 1969; Barton 1979), in that the spatial location is not determined by the environment: depending only on predators' labile memories, and not rooted to any environmental gradient, these clines can move. If there are any asymmetries in selection or migration between the two patterns – for instance, if one form is better at warning away predators, or even if there is genetic dominance for one of the patterns – the clines will move at constant velocity in the direction of the fitter or of the dominant form (briefly because at the centre of the cline the allele frequency will be 0.5 but the frequency of the dominant phenotype at 0.75 will be above the unstable equilibrium point; see Mallet 1986*a*, Mallet & Barton 1989*a*).

However, there are many limits to spread. Moving clines will become trapped at a variety of local barriers. Novel, spreading colour patterns may encounter abiotic conditions under which they are no longer advantageous, whereupon their advance will be halted (Haldane 1948; Slatkin 1973; May *et al.* 1975; Endler 1977). Alternatively, the fronts between invading colour patterns may become trapped on regions of low density (Bazykin 1969; Barton 1979; Hewitt 1988), because more individuals flow into the centre of a density trough than flow out from the low population in the centre. Finally, any actual breaks in the distribution (which are equivalent to very strong density troughs) will also stop moving clines. Density trough trapping could explain why so many hybrid zones between colour pattern races are located at the major Amazonian rivers, in low mountain ranges, and at the isthmus of Panamá. The biogeographical results of multiple shifting balances are therefore expected to be a dynamic equilibrium consisting of a patchwork of different colour pattern races within an aposematic species, exactly like that seen in *Heliconius* today.

5. THE EVIDENCE

(*a*) *Genetic architecture*

Crossing experiments have revealed that colour patterns in *Heliconius* are inherited at loci of major effect, coupled with modifiers which perfect mimetic adaptation (Sheppard *et al.* 1985; Mallet 1989). However, because mimicry produces a highly rugged adaptive surface, ring switching requires mutations of relatively large effect to cross the adaptive trough between two mimicry rings (Turner 1977; Sheppard *et al.* 1985). Phase I of the shifting balance works best with mutations of minor selective effect (Barton & Rouhani 1987, 1991, 1992; Whitlock 1995). Apparently, then, the genetic architecture of warning colours in *Heliconius* supports natural selection for mimicry over genetic drift as an initiator of divergence.

(*b*) *Mimetic capture*

In northern Europe the warningly coloured moth *Zygaena ephialtes* shares its pattern with the other members of the genus *Zygaena* (and with some other groups such as the planthopper *Cercopis vulnerata*). It is reasonable to suppose that this pattern constitutes a muellerian mimicry ring, in which most of the species share the pattern by virtue of speciation from a common ancestor. In Europe south of the Alps *Z. ephialtes* takes on the markedly different black and white pattern of the ctenuchid moth *Amata phegea* (and several congeners). This other mimicry ring is abundant only in this area of southern Europe, and seems to occupy much the same area of distribution as the convergent form of *Z. ephialtes*. The change of pattern is brought about largely by an apparent single mutation, and it is a fair inference that the *Amata* mimicry ring has captured *Z. ephialtes* from its ancestral mimicry ring (Bullini *et al.* 1969; Turner 1971*a*; Sbordoni *et al.* 1979).

Similarly in western Africa the danaid butterfly *Tirumala petiverana* belongs to a ring which is black with plentiful white spots. In eastern Africa the other species have a similar pattern with a predominantly yellow colour, but *T. petiverana* takes on a completely independent mahogany and white pattern of its own (with its own batesian mimic). We do not know in this case which pattern is ancestral: the theory of ring capture suggests that the west African pattern is the one that effected the capture, or that if the capture was the other way, the species that did the capturing in east Africa are now extinct.

Brown *et al.* found direct evidence for a capture caught in the act (Brown & Benson 1977; Sheppard *et al.* 1985). *Heliconius hermathena* is confined to isolated colonies in dry, open fields within the Amazonian rain forest. Through almost the whole of its range it has its own distinctive pattern of a red band with yellow bars, resembling none of the mimicry rings which fly with it. But in one small area along the Rio Amazonas it flies with the black and postman race of *H. melpomene* and *H. erato*, which it encounters along the edge where field and forest meet. This postman pattern differs only in lacking the yellow bars and spots of *H. hermathena.* In one of the half dozen locations where *H. hermathena* flies with the postman pattern *H. hermathena* has switched its pattern to quite accurate mimicry of the other two species, simply by losing (almost) the yellow marks. It is likely from Hardy-Weinberg frequencies that the bars are removed by a single mutation.

This case is considered to provide rather strong evidence in support of the theory of ring capture: *H. hermathena* has crossed the gap between two mimicry rings (or been captured by a mimicry ring) only where this gap is narrow enough to be bridged by a single mutation, in this case one that suppresses the extensive yellow bars on the wings. In the remainder of the range of *H. hermathena* its ancestral pattern is very different from that of the black, yellow and red *Heliconius* that fly with it (including further races of *H. melpomene* and *H. erato*), and it can reasonably be supposed that more than one large mutation would be required to convert one pattern to the other.

(*c*) *Biotic drift and mimicry in present-day refuges*

The evidence for disorderly extinction in heliconiines is still equivocal. As with the mammals (figure 2), local extinction is often non-random (Mallet 1993, pp. 252). In two currently isolated forest refuges, the Serra Negra in northeast Brasil (Sheppard *et al.* 1985, pp. 588) and the Serranía de la Macuira, in the Guajira peninsula, Colombia, only *H. erato* remains. *Heliconius erato* is also commonly found, together with *H. melpomene* and one or two other common *Heliconius*, such as *H. sara*, in dry forest and the gallery forest of savannah regions (e.g. in parts of Darién, the Rupununi and coastal savannahs in Guyana, and parts of the Urubamba and Huallaga valleys in Perú). In general, when extinctions happen, it is the rarer species that disappear first, not abundant 'weed' species like *H. erato* and *H. melpomene*. It then becomes extremely difficult to explain the geographical divergence of *H. erato* and *H. melpomene*, whose most noticeable feature is that they mimic each other, by means of mimicry of an entirely different set of species in each refuge. Within the heliconiines, there are not enough different species to explain the observed diversification within each species.

(*d*) *Phases I and II: random drift and local change*

The shifting balance model would be in severe doubt if the conditions for random drift did not occur in *Heliconius* populations: such conditions can be investigated via studies of population structure, which show that $F_{st} \simeq 0.012$–0.025 among allozyme loci in local populations (Silva & Araujo 1994; C. Jiggins *et al.*, unpublished data) and $F_{st} \simeq 0.06$ at colour pattern loci in a hybrid zone (Mallet 1993). A substantial fraction of individuals in a population can be caught, so these values of F_{st} are close to their actual values, rather than depending as is usual on unreliable estimates of gene frequency from much larger populations. Assuming equilibrium between migration and drift, these values imply local effective population sizes of $Nm \simeq$ 4–21. Shifting balances in underdominant chromosomal rearrangements, which have near-identical dynamics to warning colours (Mallet & Barton 1989*a*), are likely to occur when $Nm \simeq 1$ (Barton & Rouhani 1987, 1992), suggesting that *Heliconius* populations are generally too large; however, most studies of population structure are done where samples are easy to find, and will therefore usually underestimate the tendency towards genetic drift in unsampled populations.

It can further be urged against this model that, because of mimicry, the ecological conditions for phases I and II to operate will only very infrequently be met:

the population has to be small for the initial drift of the allele to occur, but if the species is rare, then establishment of a new and by definition non-mimetic pattern (phase II) will be resisted by natural selection imposed by the other species in the mimicry ring, which will strongly favour the old pattern. Thus either: (i) the evolving species has to pass through a very brief bottleneck, with the population expanding to the size where it can first overcome selection imposed by the other species (and second, perhaps, capture them); or (ii) the species has to be in possession of a unique pattern already, that does not belong to a mimicry ring. This could readily happen if the other species in the ring had become extinct, perhaps as a result of the same forces that reduced the population size of the evolving species. This suggests that both biotic and genetic drift will be required, and perhaps produced by the same ecological crisis, to cause a shifting balance.

(*e*) ***Phase III*: *cline movement***

Clines can move relatively quickly in theory (Bazykin 1969; Barton 1979; Mallet & Barton 1989*a*; Johnson *et al.* 1990): in *Heliconius*, potential cline movement speeds can be predicted from selection pressures and migration rates using cline theory, assuming that dominance is the only force causing movement. Estimated speeds range from 50–200 km per century (Mallet 1986*a*; Mallet *et al.* 1990). Barton & Hewitt (1989) have argued that cline movement will mostly be prevented by trivial population structural fluctuations, and that adaptations will spread much faster by simple natural selection or population spread from refuges than by cline movement; this would constitute a major limitation on the effectiveness of the shifting balance. Indeed chromosomal and warning colour clines are often found at partial barriers to gene flow like Amazonian rivers and the tops of mountains (Nichols & Hewitt 1986; Hewitt 1988; Mallet 1993). But clines will only become associated with such major barriers to gene flow if they can overcome slight perturbations in population density elsewhere in their range.

Actual hybrid zones are well known to be mobile: the hooded crow/carrion crow zone is known to have moved tens of kilometres in this century (Perrins 1987). Movement of *Heliconius* hybrid zones would provide good evidence for the possibility of phase III. Some disjunct patterns of *Heliconius* distribution do suggest hybrid zone movement in the past (Lamas 1976; Brown 1979; Mallet 1993). Many other hybrid zones in *Heliconius* are apparently stationary, or are on geographical or environmental barriers from which they are unlikely to move (Turner 1971*b*; Benson 1982; Mallet 1993). The data on cline mobility to date are very weak; the Guiana hybrid zone studied by Turner (1971*b*, 1976*b*) could have moved 50 km in several hundred years without detection because early data is incomplete. The only good historical data of which we know shows major (100 km) changes in the distributions of *Heliconius hecale* and *H. ismenius* races in Panamá where accurate locality data were collected in 1916 (G. Small, personal communication; Mallet 1993). Another butterfly hybrid zone, between *Anartia fatima* and *A. amathea*, has moved about 20 km to the east in Darién in the last two decades (Davies *et al.* 1996).

(*f*) ***Centres of endemism***

Strong evidence for differentiation in refuges has always been a tight correlation between patterns of endemism of different taxa. However, the data for most groups has either not been analysed, or is equivocal. Nelson *et al.* (1990) showed that centres of plant endemism discovered by Prance (1973), and used by him as evidence that Pleistocene refuges caused speciation among Amazonian plants, were also areas from which most collections had been taken. It seems that plant centres of endemism may be merely artefacts of poorly documented distributions.

The distribution of some butterflies is much better known. Brown (1979, 1987) collected an enormous dataset for Heliconiini and the better-known Ithomiinae to find areas with high probabilities for Pleistocene refuges. However, Brown's analysis has a number of problems. Using the data, Brown postulated preliminary areas of endemism. Locally endemic taxa were then assigned to one of these areas. Maps of the taxa assigned to a particular area of endemism were then overlaid to produce a contour map of the endemic region. After correction for hybridization and soil types, the centres of such contour maps were assumed to be areas of high probability for the existence of Pleistocene refuges. There are two inherent circularities in this system. First, some of Brown's earlier papers used refuge theory as a justification for naming weakly differentiated taxa as geographical races in taxonomic revisions; these new taxa were then themselves used in the analysis to identify refuges. Second, the whole analysis depends on the preliminary decisions as to which endemic regions exist where, and on the assignment of taxa to endemic regions. If the races and species that form Brown's dataset were actually distributed randomly, it is easy to see that he could have picked areas with weak, randomly produced peaks of endemism and defined them as endemic regions. Any endemic taxa whose distributions centred on this endemic region would be assigned to that region; other taxa with edges running through that endemic region could be assigned to adjacent endemic regions. The assigned taxa, when overlaid on a map would then produce peaks of endemism near the centre of the endemic region first thought of. Brown's knowledge of the geography and taxa is second to none, and we believe that many of the patterns he has identified may be real; however, his analysis should not be interpreted as an independent statistical test for the existence of non-random peaks in endemism or refuges.

Further, Brown's analysis assumes the distributions of comimics are independent. The geographical races of *Heliconius erato* and *Heliconius melpomene* may have similar patterns of distribution only because the two species are highly mimetic: where one changes its pattern, the other follows. One could even argue that species in different mimicry rings might affect each other in the competition for signalling space, so explaining any correlations between taxa in different rings. We must conclude that there is no clear evidence for refuges from the distribution of centres of endemism, at least without a proper statistical analysis of biogeographical patterns.

(*g*) ***Range edges***

Beven *et al.* (1984) tested the bird data of Haffer (1981) using simulations and cut-out models of bird distribution data randomly thrown onto maps of the Amazon basin to find how concordance between the edges of randomly distributed taxa compared with actual concordance of range edges: the random distributions were no more discordant than the natural bird distributions except that the natural distributions tended to be broken significantly more often at major rivers. Many of the butterflies studied by Brown (1979) also show distribution edges on major rivers or low mountain ranges. Such correlations between range edges unfortunately do not discriminate clearly between the refuge and parapatric models. Whereas the original zone of contact after expansion from a refuge is not expected to be at a barrier, under both theories hybrid contact zones or tension zones would move to such density troughs. No similar studies have been performed on *Heliconius* but we believe the patterns to be similar.

(*h*) ***Fossil evidence of refuges***

Much recent work on the Quaternary of South America could have provided support for the refuge theory. There were indeed major climatic disturbances, and especially drying, associated with the glaciation of temperate regions (Brown 1987*b*; Haffer 1987*b*; Iriondo & Latrubesse 1994). What is unclear is whether these turbulent conditions caused the formation of forest refuges. Pollen studies of cores in the lowlands of Ecuador and Panamá suggest that cooling of the order of 5–7 °C occurred in the late Pleistocene. This cooling may have precluded the use of mountainous regions as refuges by lowland forest taxa, and at the same time may have allowed major *friagems* accompanied by killing frosts to sweep throughout much of the lowland Amazon basin where a number of proposed refuges are sited (Bush *et al.* 1990, 1992; Latrubesse & Ramonell 1994). The existence of the Pantepui refuge in the endemic centre of Guiana shield is similarly in doubt; recent geological studies indicate that peat deposition under humid conditions started only in the Holocene, and there is evidence for arid conditions of the Pantepui region during the last glacial maximum (Schubert *et al.* 1994). Eastern Ecuador is now home to a variety of endemic taxa, particularly *Heliconius* subspecies, thought to have originated in Pleistocene refuges, yet between 10000 and 8000 years ago there was a series of massive eruptions that coated most of the area with volcanic ash whose residue is even now 1.5–4 m thick, which would have had a devastating effect on the biota (Iriondo 1994). These studies show that, although there is plenty of evidence for catastrophic environmental changes, these may have been very destructive to all lowland tropical organisms. Many of the endemic races we now see scattered around Amazonia might have evolved in the last few tens of thousands of years. This is not inconceivable; the island of Marajó is known to have been completely submerged in the Amazon embayment 5000 years ago, yet there are three endemic subspecies of heliconiine and ithomiine butterflies (Brown 1979). In contrast, there are still no examples of forest refuges known to have provided lowland wet forest conditions throughout the late Pleistocene.

(*i*) ***Molecular data***

Molecular phylogenies have the potential to reveal the historical branching processes of populations, races, and species (Avise 1994). However, there are no fixed allozyme differences between *Heliconius* races (Turner *et al.* 1979; Mallet & Barton 1989*b*), and mtDNA genealogies are uncorrelated with racial boundaries (Brower 1994, 1996). There is a major fork in the mtDNA genealogies of both *H. erato* and *H. melpomene* in northeastern Colombia (Brower 1996). However, even this major division does not coincide with a racial boundary. The mtDNA break occurs within the races *H. erato hydara* and *H. melpomene melpomene* respectively. Brower concludes that mitochondrial data provide little evidence either for or against the refuge theory.

Brower (1996) has put forward a 'mitochondrial parsimony' hypothesis, which suggests that disjunct red-barred races on either side of the Andes are independently derived. In contrast Sheppard *et al.* (1985) and Mallet (1993) had proposed that 'colour pattern parsimony' is more likely because the genetics of the similar, although disjunct colour patterns is nearly identical. But colour pattern parsimony is now problematic; if colour patterns evolved only once, the mtDNA divergence, estimated to be 1–2 My old, may be newer than the colour pattern differences; this implies a much older time of divergence for some races than the Quaternary suggested by refuge modelers (Brown 1987*a*). However, it is also possible that the evolution of mtDNA and the nuclear genome have become dissociated; this is known in many other species (Avise 1994). Brower's hypothesis could be tested by sequencing the colour pattern genes themselves. However, the results of this work are unlikely to lead to a resolution of allopatry versus parapatry, or drift versus selection.

(*j*) ***The problem of novelty***

New warning patterns have to arise somehow. The biotic drift model 'under-explains' this novelty of patterns: it can permit only switching between existing patterns, and as it involves extinction, the number of patterns must diminish over time. Ultimately the system will cease to diverge even within species, as more and more patterns become extinct. Mimicry cannot explain novelty. The shifting balance allows novel colour patterns to arise. The transparent ithomiines, the tiger ithomiines and heliconiines, and the *H. erato*/*H. melpomene* patterns are evolutionary novelties found nowhere else than the Neotropics. Many races of *Heliconius erato* and *H. melpomene* indeed do not seem to mimic anything much but each other, and although similar ancestral patterns can be constructed for each species, it is not clear what selective mechanism caused the two species to codiversify in the first place; there are no potential models known for most of the Amazonian races (Mallet 1993). Some of the extra-Amazonian races are apparently ancestral patterns which can plausibly be held to be what these two species evolved from, but although the reconstructed intermediate patterns in the cladogram do all resemble heliconiine patterns which still exist somewhere in South America (Turner 1983, 1984*a*), the explanation reads rather like special pleading. The huge variety and novelty of warning colour patterns is strong evidence for some sort of random initiation of divergence such as shifting balance process. Alternative ways of explaining novelty, which could be invoked by sceptics of the Mallet model are as follows.

(i) *Independent origin from different cryptic patterns*

Although this must occur, and when it happens will undoubtedly generate a new warning pattern, it is rare: aposematism has evolved only about 12 times from the non-aposematic condition in around 18000 species of butterfly (Sillén-Tullberg 1988). This is trivial in comparison to the huge number of times that new aposematic patterns have evolved in already aposematic lineages. In the 55 species of *Heliconius sensu lato*, there are about 400 colour pattern races; within some single species of *Heliconius* there are over 30 colour pattern races (Brown 1979), yet we know of no obviously cryptic pattern. Species which have developed their own chemical defense rarely develop a completely novel warning pattern, but are much more likely to evolve a warning pattern which is a muellerian mimic of an already existing warning pattern. It can further be argued that one of the most popular models for the evolution of warning colour, kin, family or green-beard theory (Turner 1971*a*, 1975; Harvey & Greenwood 1978; Harvey & Paxton 1981; Harvey *et al.* 1982; Hedrick & Levin 1984; Turner *et al.* 1984; Guilford 1988) is a special case of the shifting balance model (Mallet & Singer 1987; Mallet 1993). Kin-founding is unlikely to produce novel warning colours every time the appropriate mutation occurs, even in species which are highly gregarious with their own kin, because it depends in part on the paucity of unrelated individuals in the home ranges of the local predators. *Heliconius* were thought once to be ideal candidates for the evolution of warning colours by kin selection, but detailed studies of their population structure made a deterministic kin-founding model of colour pattern evolution seem unlikely (Turner 1971*c*; Mallet 1986*b*, *c*, 1993).

(ii) *Independent origin from a sexual or other brightly coloured pattern*

Sexual patterns are already brightly coloured and readily pre-adapted to being warning patterns, as are batesian mimics and flash coloration: in contrast with evolution from cryptic patterns, there is no loss from increased conspicuousness and therefore no problem of altruism. Warning colours can therefore evolve by individual selection from a bright pattern evolved while the species was still palatable (Huheey 1961; Mallet & Singer 1987). It is very likely that such patterns evolve into warning signals by a simple process of enhancement.

(iii) *Runaway sexual selection*

Runaway sexual selection could alter an existing warning pattern in an apparently random direction. Sexual selection may seem improbable in view of the conventional wisdom that warningly coloured species are seldom sexually dimorphic. However there are a number of outstanding exceptions (*Euploea* in southeast Asia, *Bematistes* in Africa), and given that sexual selection may lead to cyclic evolution in which one sex develops a divergent pattern which is then 'mimicked' by the other sex (the transvestism model of Vane-Wright 1984), this may be a much under-estimated force in the evolution of warningly coloured butterflies.

(iv) *Selection for crypsis, thermoregulation or other physical aspects of the environment*

There may be selection for crypsis, thermoregulation or other physical aspects of the environment (Bates 1862; Papageorgis 1975; Benson 1982; Endler 1982; but see Mallet 1993). 'Compromise crypsis' consists of a warning pattern not being maximally conspicuous, but remaining camouflaged to some predators some of the time. It is notable for instance that many warningly coloured species are duller on the underside than the upperside, suggesting that they reduce their visibility when resting (batesian mimics by contrast are often fully cryptic on the underside; see Papageorgis 1975; Endler 1988; Turner 1995, figure 7). Papageorgis (1975) suggested that warning patterns were furthermore partly camouflaged even in flight by 'flicker' effects adjusted to light and shade patterns in the rain forest. Contrariwise, a similar situation could also arise because of selection for maximal conspicuousness. Where light is poor, as in the under storey, we expect pale yellow and white patterns, and we find them in the form of *Heliconius cydno*, *H. pachinus*, and the *H. sapho/eleuchia* group. Red and orange patterns are expected in bright conditions, such as in second growth; *H. erato/melpomene* and the tiger *Heliconius* are examples (Mallet & Gilbert 1995). There is also a tendency for melanic forms to be found at higher altitudes in the Andes, perhaps as a result of direct selection for heat absorption where the air is cooler (Mallet 1993).

(v) *Origin from hybrid zones*

A rich diversity of patterns appears in hybrid zones (see e.g. Turner 1971*b*; Mallet 1986*a*, 1993; Mallet *et al.* 1990). Recombinants could generate variation at an elevated level compared with mutation. However, we still have the problem of how these recombinants become abundant enough in a local population to become fixed. A combination of habitat change and genetic drift could cause such a recombinant pattern to become locally predominant.

(vi) *Drive by batesian mimics*

In theory at least, the evolutionary arms race between batesian mimics and their models causes the model species to undergo gradual change in their patterns (Turner 1984*a*, *c*, 1987*b*, 1995): we know of no evidence on this point.

6. CONCLUSIONS

We can summarize the differences between our two models as biotic drift, plus mimetic capture plus allopatry in refuges on the one hand versus genetic drift plus shifting balance and cline movement, plus parapatry without refuges on the other. The biotic drift and shifting balance models therefore initially appear diametrically opposed; but it is less surprising than at first thought that they are so difficult to distinguish. The operational distinction between natural selection and genetic drift as a cause of changing gene frequencies is likewise a very fine one (Hodge 1987; Beatty 1992); Wright (1977, pp. 455) includes random fluctuations of selection in phase I of the shifting balance.

Most of the components of each model are compatible. In both models, some of the extraordinary geographical diversity is initiated by a stochastic event which involves small population sizes and a depauperate bioton: both genetic and biotic drift are likely to be produced by the same ecological crisis, whether this is continual metapopulation turnover or the result of climatic deterioration. While genes drift so do biota. We have argued that the shifting balance itself will require not only genetic drift but some degree of biotic drift into the bargain. We have further argued that the pure biotic drift model does not adequately explain the diversity of patterns, but have suggested that the full conditions for the shifting balance might be met rather seldom: against this, one needs to ask how many times they need to be met in what span of time to generate the existing diversity: the shifting balance is a way of magnifying the outcome of a rare event, and in the span of evolutionary time, even an event of low probability may occur frequently enough.

In both models natural selection is extremely important, and even when a novel pattern has arisen by drift, mimetic capture must be playing a major role in further evolution: in the Amazon basin, ten or so *Heliconius* species have the same rayed pattern, which must represent mimetic capture by one or two of the species of the rest. Likewise, whereas the island mimicry model invokes allopatry, to which the shifting balance model was framed as a parapatric alternative, mimetic capture could perfectly well take place in parapatry (Turner 1982) and genetic drift could occur in allopatry or within quaternary refuges. Although moving hybrid zones form the important phase III of the shifting balance, it is likely that the junction boundaries of races originally formed in refuges by mimetic capture or other means, move in the same way.

If it is hard to disentangle the components of biotic drift and the shifting balance, it will be hard to devise a crucial test to distinguish them. It seems very unlikely that we will find a direct historical record that shows whether genetic or biotic drift actually happened to initiate mimetic divergence. Genetic drift in small populations might leave some trace of reduced genetic diversity in a founder population; however, expansion during phase III will quickly mop up variation from surrounding populations. We suggest that it will be more fruitful to find intermediate cases of divergence, because both hypotheses predict local processes causing divergence occur only transitorily. It would be particularly worthwhile to record the species in many more modern-day refuges and metapopulations, and to find whether they have diverged, because both models imply that initial, perhaps failed divergences should be common. Studies of the dynamics of actual contact zones and invasions would produce evidence for cline movement.

Finally, perhaps it is only a lack of imagination which has led us both to propose random or chaotic causes of an apparently haphazard diversity of colour patterns. Maybe a deterministic explanation has eluded us; but we doubt it!

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