
WHY ARE BLACK AND WHITE AND RED ALL OVER?†
**An Overview of the Biology of the *Heliconiini* (Lepidoptera:
Nymphalidae)**

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† Taken from the classical English Joke “What’s black and white and red [read] all over?
(The traditional answer being “A newspaper.”)

ABSTRACT

Heliconiini are a tribe of largely Neotropical butterflies whose key innovation is the ability to ingest and process cyanogens from plants of the family Passifloraceae. They are unpalatable to predators and have distinctive warning colour patterns. Some species in the group are widespread, whereas others are highly range restricted. The combination of unpalatability and a feeding ecology specialised to Passifloraceae and success in predator evasion has enabled the group to expand geographically in the Neotropics. Adaptive radiation has occurred as Heliconiini have specialised to different ecological regions in the Neotropics. Various groups of the tribe have radiated through Müllerian (mutualistic) mimicry processes. Conservation of range-restricted species is important not only for that species but for the mimetic ring and evolutionary processes they support.

KEY WORDS: diversity, *Heliconiini*, lepidoptera, mimicry, neotropics, radiation processes

INTRODUCTION

Among the insects, butterflies have traditionally been one of the groups most studied by taxonomists (OWEN, 1971). The Heliconiinae Swainson (1822), a subfamily of Nymphalidae (Lepidoptera: Papilionoidea), represent one of the best-known groups; for example, pioneering studies in mimicry, e.g. by Bates & Muller, were based upon studies of the tribe Heliconiini (TURNER, 1976; SMART, 1991; THOMPSON, 1994) making the group of special interest to radiation (MALLET, 1999; TURNER & MALLET, 1996). The tribe Heliconiini of the Heliconiinae are characterised by a narrow (oblong-shaped) wing, with distinctive patterns, usually black combined with other bright colours (yellow, white, orange and red). Heliconiini are typically 60 – 100 mm in adult phase body length and, amongst the Lepidoptera, are remarkably uniform in body size (SMART, 1991).

The genetics and phylogeny of Heliconiini have been subject to various analyses and proposed models (see EMSLEY, 1964; EMSLEY, 1965; BROWN, 1979 and others summarised in BROWN, 1979) and the biogeography of the group (summarised in PENZ & PEGGIE, 2003) is well-known (BROWN, 1987). Systematic analysis of the evolution of mimicry in *Heliconius*, since ELTRIGHAM (1916) has been considered as a "model that provides an opportunity to develop an integrative theory of biodiversity" (GILBERT, 1987). Heliconians are well-suited to outdoor insectaries and glasshouses and thus are fit candidates for genetic and physiological experimentation. This has permitted the accumulation of enough genetic information to give a considered understanding of the evolution of Müllerian mimicry (EMSLEY, 1964; PENZ & PEGGIE, 2003; BROWN, 1987; MACDOUGAL & STAMP, 1998; PAPAGEORGIS, 1975 and other references cited in BROWN, 1981).

The Heliconiinae, has recently been expanded following recent higher-level taxonomic changes. According to most recent authors' treatments (e.g. PENZ & PEGGIE, 2003) Heliconiini consists of BROWN (1987) genera (Figs. 1 and 2) with approximately 70 species recognised (BROWN, 1981; HARVEY, 1991; GILBERT, 1984; D'ABRERA, 1984; D'ABRERA, 2001), although new taxa continue to be described, even in recent years (e.g. SALAZAR, 1998).

It has relatively recently been proposed that the subfamily Heliconiinae be enlarged to include various other groups traditionally treated as separate families or subfamilies, such as the Acraeidae and Argynnidae (HARVEY, 1991). Following this approach, Heliconiinae has been organized in four tribes: Heliconiini, Acraeini, Vagrantini and Argynnini (PENZ & PEGGIE, 2003; HARVEY, 1991). The Heliconiini refers to the Neotropical Heliconids together with the old world genus *Cethosia* (PENZ & PEGGIE, 2003; BROWN, 1981; PENZ, 1999).

PATTERNS OF DIVERSITY IN HELICONIINI

Latitudinal and longitudinal patterns of diversity

With the exception of *Cethosia*, whose position within the Heliconiini is controversial (see further below and PENZ & PEGGIE, 2003; BROWN, 1981), Heliconiini are found almost exclusively in the Neotropics, although some species range into the southern Nearctic region. Butterflies are highly dependent upon temperature and sunlight for survival. Heliconiini do not extend in range into the cooler south of South America, nor the north of North America (BROWN, 1981; D'ABRERA, 2001) and the range of this group appears to have been restricted from expansion to other areas, such as the northern Nearctic and the Palearctic due to the cooler temperatures which prevail in such zones (VELEZ & SALAZAR, 1991).

One of the most important factors in butterfly population distribution is the abundance of nutritional resources and primarily food plants. In the Neotropics, such resources are concentrated at low elevation equatorial latitudes and regions of high rainfall, such as Andean foothills adjacent to the Amazon basin and Chocó, where diversity is expected to be highest, as has been revealed in studies of other groups such as birds (MALLET, 1999; BROWN, 1987). Recent papers have been show that the number of coexisting species per genus increases towards tropical latitudes (GILBERT, 1987).

Altitudinal patterns of diversity

Relatively little work has yet been invested into studies of Heliconiini along altitudinal gradients. However, data from Colombia, Venezuela and Brazil suggests that the greatest concentration of Heliconiini species is found at lowest tropical elevations (200–1200 m), whereas cooler higher elevation habitat (above 1200 m) contains lower species diversity (BROWN, 1981; ARIAS & HUERTAS, 2001; BROWN & FERNANDEZ, 1984).

The concentration of Heliconiini at foothill elevations reflects the increased vegetational, topographic and topoclimatic diversity which exists at such elevations in the Neotropics. Furthermore, it is likely that ninety-five percent of the last 2 million years have been appreciably cooler than today, with former lowland zone climatic conditions now reflecting those presently existing in Andean foothills. Water has also probably always been abundant in such forest ecosystems (BROWN, 1987). Such zones, for example on the slopes of the Andes in Colombia and Ecuador, are also regions in which lowland and highland zones, each of which have different species compliments, come together (ARIAS & HUERTAS, 2001). Such regions are of further accentuated interest in that hybridisation is facilitated, perhaps leading to the evolution of further specialised and elevation-specific range-restricted species (see e.g. VARGAS & SALAZAR, 2002).

Refuges and hot spots

Heliconian endemic regions have been considered as four principal groups: (i) transandean (western Colombia, northern Venezuela, Trinidad & Tobago and Central America, and extreme northwestern Peru, 16 range-restricted species); (ii) Andean (mountains of Colombia, Ecuador, Peru, Venezuela and Chile, 8); (iii) Amazonian (Amazonian basin of Brazil, Colombia and Venezuela and the Guyanas, 17); and (iv) Atlantic (Atlantic region of Brazil, 4) (BROWN, 1987) (Fig. 3). The highest concentrations of localised centres of endemism are found in the northern Andean foothill regions of Ecuador and Colombia. Endemic centres have subsequently been further defined as referring to particular Pleistocene

refuges (13,000–20,000 years ago), in which it is considered that such forms evolved when populations were isolated during the Pleistocene ice age (BROWN, 1981).

Phyletic diversification

The phylogeny of the Heliconiini has been subject to detailed study over recent years. Studies were first based in adult characters (e.g. BROWN, 1981), and have recently been combined with studies of early stages (e.g. BROWN, 1981; PENZ, 1999). The use of mitochondrial DNA (mtDNA) is relatively new in such studies, although some phylogenies have been compiled incorporating such data (BROWER, 1997; BELTRAN *et al.*, 2002). Features as wing colour patterns (ANKEN, 1996) and male genitalia (STEKOL'NIKOV, 1976) are the most reliable characters for the identification of species, and are features which show the most measurable biometrical diversity in adult phases, although polymorphism is fairly common in *Heliconius* and its allies and complicates such analyses (MALLET, 1999).

Heliconiini is hypothesised first to have become distinguished from other Nymphalidae during the Oligocene and Eocene periods of the Tertiary era. Most Heliconiini genera arose between the Oligocene and Pliocene, and most modern day species, particularly *Heliconius* into which detailed studies have been made, are thought to have been distinguished in refuges during the Pleistocene (BROWN, 1987; VELEZ & SALAZAR, 1991; KASSAROV, 2000). However, studies of Lepidoptera evolution are complicated by the lack of a good fossil record, due to the group's soft wings and general structure. Just three "*weak impression*" specimens of adult butterflies exist, meaning that they represent very little (0.05%) of known insect fossils (BROWN, 1987; VELEZ & SALAZAR, 1991).

Key innovations

The key innovations of Lepidopterans are well-developed olfactory senses in larval stages; and modifications to the mouthparts in adult phase (SMART, 1991; PENZ & KRENN, 2000) (Box 1).

Amongst the Lepidoptera, probably the most important key innovations demonstrated by the Heliconiini, compared to other closely related groups such as Acraeini, Vagrantini and Argynnini are unpalatability (tested by several authors, see MALLET, 1999) and strong distinctive colour patterns in adult phase wings. Their unpalatability is a selection advantage leading to reduced levels of predation, and bright colour patterns enable them to indicate this to potential predators. Some *Heliconius* species are "flash disruptive" fliers, which dazzle with bright colours, then move suddenly when bright colours are hidden to evade predators (SMART, 1991; MALLET, 1999; BROWN, 1981).

Heliconiini larvae are largely dependent upon secondary plant metabolites from the Passifloraceae family (cyanogenetic glycosides) (BROWN, 1987; BROWN & FERNANDEZ, 1984) from which they derive chemicals for the synthesis of defensive glycosides (linamarin and lotaustralin) which make them unpalatable to predators (BROWN & FRANCINI, 1990; NAHRSTEDT & DAVIS, 1985; KASSAROV, 2000).

Diversity within the Heliconiini

The precise number of species in each genus of Heliconiini has been subject to different treatment by various authors. The Heliconiini tribe, however, have been fairly settled over the past few decades (THOMPSON, 1994; BROWN, 1981), traditionally consisting of 10 genera, plus *Cethosia*. Brown (1981) set out the following number of species for each Neotropical genus: *Philaetheria* (3 species); *Podotricha* (2); *Dione* (3); *Agraulis* (1), *Dryadula* (1); *Dryas* (1); *Eueides* (12); *Neruda* (3); *Laparus* (1); and *Heliconius* (TURNER, 1977).

Heliconius is by far the most diverse genus, containing significantly more species than all other groups combined. Adaptive characters which define this group include: (i) mimicry in both larvae and adult phases common; (ii) pupa usually sited on plant stems; (iii) geographical distribution of each species typically restricted to a particular mountain range or lowland eco-region (with the exception of widespread *H. sara* and *H. melpomene*); (iv) predominantly forest habitats (with exception of generalists *H. charitonia*; *H. hermathena* and *H. ricini*); (v) adults demonstrate social behaviour in almost all species; (vi) polymorphism (regional variation); and (vii) sexual unimorphism (except dimorphic *H. nattereri*; *H. numata*; *H. etilla*; *H. charitonia*; *H. hecalesia*; and *H. demeter*) (characters based on data set out in BROWN, 1981; such data also used as base for phylogenies in PENZ & PEGGIE, 2003). These key features of the genus *Heliconius* have promoted adaptive radiation in this genus through speciation processes which are encouraged by the existence of range-restricted forms, forest habitats, sexual unimorphism, i.e. restriction to Pleistocene refuges, mimicry and hybridisation.

Agraulis, *Dryadula* and *Dryas* are monotypic genera, the species of which are commonly found in human-altered habitats and forest clearings, and which specialise in Passifloraceae crop fields (e.g. passion fruit), some of which species are regarded as pests (e.g. *Agraulis vanillae* of *Passiflora edulis* - BROWN & FERNANDEZ, 1984). These taxa probably increased in geographical distribution in evolutionarily recent time following human habitat alteration, from wild ancestors specialised to ancestors of such crop species, and as such, may not yet be fully radiated.

Ecology and habitat

The majority of the Heliconiini inhabit the lower to middle storeys of shady, humid forests in the Neotropics. The Heliconiini tribe includes within it species which are generalists and specialists, forest and non-forest subspecies (sometimes within single species), highland and lowland species, migrants and residents, pollen extractors and scavengers. Species' populations are regulated and selected by predation, competition, parasitism (by fungus, wasps and flies) at any life stage, larval (KASSAROV, 2000) or adult resources, social interaction and other environmental variables (BROWN, 1987; D'ABRERA, 1984; VELEZ & SALAZAR, 1991). Major predators for Lepidoptera in the Neotropics are birds (mostly Tyrannidae), mantids, mammalia (e.g. *Calicebus*), reptilia (e.g. *Phenacosaurus*) and wasps (e.g. *Polistes*), which are warned from predation of Heliconiini by its bright coloration (VELEZ & SALAZAR, 1991).

Most Heliconiini species are largely solitary, although when abundant food resources exist (e.g. on mammal urine), many individuals often congregate to feed (*pers. obs.*). Adults of most species are relatively slow and lazy fliers, a feature which maximises exposure of warning colours during flight, and a feature not commonly found in non-toxic, non-coloured butterflies many of which move quickly and suddenly or use other strategies to avoid predators (SMART, 1991).

DISCUSSION OF RADIATION PROCESSES

Adaptive radiation

Adaptive radiation refers to "a more or less simultaneous divergence of numerous lines from much the same adaptive type into different, also diverging adaptive zones" (SCHULUTER, 2000).

The key innovative feature of the first Heliconiini was the ability to ingest cyanogens from ancestors of the Passifloraceae without being poisoned, combined with the ability to re-synthesise those chemicals into unpalatable body fluids (BROWN & FRANCINI, 1990; NAHRSTEDT & DAVIS, 1985). The attainment of bright colour patterns was selected for due to its advantage in predator evasion. Initial geographical expansion of the Heliconiini would have been restricted to the range of ancestors of modern-day Passifloraceae. The first Heliconiini to expand geographically would have been extremely successful in multiplying and spreading due to their unpalatability and success against predators. Heliconiini species which specialise on certain Passifloraceae species will have been limited in geographical expansion to the range of their host.

Mimicry

Many colour patterns in butterflies have some survival value or adaptive significance, as each pattern has been moulded, modified and perfected by a long process of natural selection (SMART, 1991). In Heliconiini, as with many other groups, these attributes play a fundamental role for each species in predator evasion and courtship rituals. Heliconiini, however, differ from certain other groups in that mimicry is a key feature of their radiation (SMART, 1991; MALLETT, 1999).

Studies in colour pattern mimicry in *Heliconius* genera have shown that mimicry can be an important process in speciation and adaptive radiation (JIGGINS *et al.*, 2001). Mimetism exists wasps, fishes, and coral snakes as well as in butterflies (MALLETT, 1999). Two common forms of mimicry exist: (i) Batesian mimicry, where a palatable mimic evolves the morphology of an unpalatable model; and (ii) Müllerian mimicry where an unpalatable mimic evolves the morphology of an unpalatable model. Quasi-Batesian mimicry may exist between two unpalatable species, one of which is significantly more unpalatable than the other. Within *Heliconius*, mimicry has not been shown to be different from Müllerian (MALLETT, 1999; SPEED, 1999). Müllerian mimicry has been shown to be a result of unilateral advergence, rather than mutual convergence, i.e. a model and mimic taxon exist between each pair, rather than both acting as model and mimic with respect to one another (MALLETT, 1999). Examples of Müllerian mimetic pairs include *H. cydno* & *H. eleuchia* and *H. erato* & *H. melpomene* (CONSTANTINO & SALAZAR, 1998). Heliconiini species are also sometimes subject to Batesian mimicry by palatable Lepidoptera species. Today's species are derived from "chasing" evolutionary processes, whereby deviations from the morphology of the mimic are of positive selection value of the Heliconid, whereas the mimic is selected towards any such modifications in the Heliconid. Where several non-palatable and palatable forms are involved in the same mimetic ring, the attainment of a particular colour pattern in adult phase is a result of a complicated, multi-variate evolutionary process.

There are hypothesised to be two evolutionary stages to the evolution of mimetic species. Firstly, major genes produce a fairly close resemblance to a model in one step, either through naturally-occurring variation, or following a mutation. Following the initial attainment of a general semblance, natural selection favours those individuals most close in their mimicry (MALLETT, 1989). Mimics are able to radiate throughout the range of their model, and further mimics may evolve over time to mimic other closely-related model species or different subspecies amongst the same group.

An important example of Müllerian mimicry is that of *H. erato* and *H. melpomene* throughout their ranges in Central and South America. Both forms are characterised by a

large number of wing colour patterns in adult phase restricted to different biogeographical regions. Both forms vary greatly throughout their range, but remarkably, at any single locality where both are present, resemble one another extremely closely. Such similarities have been demonstrated not to have been caused by hybridisation, or by retention of ancestral features, and the two species, although very similar in appearance, are structurally distinct (TURNER & MALLEY, 1996). *H. erato* is typically over twice as abundant as *H. melpomene*, and penetrates into dryer, more disturbed and more marginal habitats than *H. melpomene* (MALLEY, 1999). Mathematical analysis based on this data has shown that *H. erato* is the model of these Müllerian mimics, and more specialist *H. melpomene*, the mimic (MALLEY, 1993). Colour patterns in both species change dramatically and simultaneously even over short distances at boundaries between colour forms. Mimicry in each pair of races or polymorphisms has thus taken place independently towards different adaptive peaks for colour combinations, according to the different ecological and evolutionary pressures in each such region (MALLEY, 1999). This drives and accelerates speciation processes. However, the species level treatment of Heliconiini taxa is controversial.

Mimetic process are also affected by relative diversity and relative palatability of the forms involved. The most common form in any region will typically act as the model. As resources differ between regions, so do the selective pressures on each species, meaning that between the same mimetic pair, it is feasible that a different species may act as model or mimic in different regions, further accentuating regional morphological diversity (although examples to date in the literature do not stand up to analysis - MALLEY, 1999).

Differences between patterns are driven by aspects of the physical environment, especially light distribution and structure (EMSLEY, 1964; PAPAGEORGIS, 1975) and by biotic selection on populations in refuges during glacial periods (BROWN, 1987; TURNER, 1977). Müllerian mimicry further promotes sexual monomorphism, as predators may not recognise, or may require more experience to recognise, and avoid a two patterns as opposed to one (MALLEY, 1999), which monomorphism in turn facilitates mimicry processes.

It has been shown that mimetic colour patterns are also important in mate recognition. Assortative mating contributes to speciation because post-mating isolation between some species of *Heliconius* is incomplete. In inter-racial hybrid zones, intermediate colour patterns are unlikely to be recognised as distasteful by predators, generating strong disruptive selection (JIGGINS *et al.*, 2001).

Hybrid sterility and mate selection

Studies have shown that hybrid sterility is also of relevance to parapatric speciation mechanisms which drive adaptive radiation in the Heliconiini, as female hybrids are largely

sterile. In some areas of overlap, hybridisation can be up to 50% (MALLET, 2003). Geographical variations in coloration and pattern in *Heliconius* are further accentuated by mate selection. Any hybrid offspring of two *Heliconius* of different colour patterns have much decreased fitness value as their atypical adult phase patterns are less frequently recognised by predators, leading to a lower survival rate. Predation thus acts strongly against the promulgation of hybrid lines, and mate choice of non-similar individuals by *Heliconius* is strongly selected against. Studies have shown further that such hybrids do not show significantly reduced egg hatch or larval survival rates, highlighting the role of sexual selection against hybridisation in speciation (MCMILLAN *et al.*, 1997).

Although colour patterns are an extremely important attribute and selection criterion against predation, their role in sexual choice is considered to be very limited in the Heliconiini. Butterflies have good vision, and can attract other *Heliconius* from distances of 20 m or more (MALLET *et al.*, 1990). However, mimetic pairs, despite such great similarities in morphology, do not appear to mate or attempt to mate with one another. Rather, it is considered the case that differences in chemical signals, such as pheromones or cuticular hydrocarbons are the most important distinguishing features for mate selection as well male visual search (VANE-WRIGHT & BOPPRÉ, 1993). In Heliconiini, males are chosen by females (MALLET, 2003). However, mating choice alone cannot lead to speciation without other factors promoting different selection pressures in separate regions. Mating choice and hybrid sterility, combined with different ecological pressures, which drive diversification of warning colours, thus appears to be the mechanism through which the differentiation of species and adaptive radiation has occurred in the most successful Heliconiini genus, *Heliconius*.

The derivation of modern day Heliconiini

Adaptive radiation of ancestral Heliconiini to modern-day forms is a result of the processes described above, which in some groups may have been accelerated by repeated cycles of glaciation during the quaternary, which acted as a “species pump” to isolate regional populations and which may have accelerated regional differentiation between Müllerian mimic pairs (TURNER, 1976).

CONCLUSIONS

Future Research

Amongst the butterflies, Heliconiini are one of the best known groups. This is due to their colourful nature, large size and ease of field capture which has led to much attention by early collectors and taxonomists. The work of Brown in particular has meant that the

ecology and life stages of most species are now relatively well-known. Such data has formed the basis of adaptive radiation studies. However, data is still lacking from various of the more remote and rare range-restricted forms, particularly of the genus *Heliconius*, from of Colombia and Brazil to which access is complicated by geographical or political factors, and the ecology and early life phases of which remain little known. Remote regions of the Amazon basin, the Colombian Chocó and isolated mountains of Colombia, Peru and the Brazilian Atlantic forest have still not yet been subject to sufficient study for us to know all about Heliconiini distribution. Such data would improve our understanding of adaptive radiation in the group.

Further DNA studies would also be of importance in refining proposed phylogenies which remain largely based upon morphological and ecological characteristics, and which studies would confirm adaptive radiation theories. The relation between *Cethosia* and other members of the group in particular should be considered together with genetic data to better understand the origins and radiation of the group. Due to the large number of different proposed phylogenies, consensus between experts as to the higher level organisation of the Heliconiini would be helpful.

Mallet has suggested that more research is required into the issue of whether Quasi-Batesian mimetism, which remains only theoretical, may have occurred during adaptive radiation of Heliconiini (MALLET, 1999).

Conservation

Certain members of the Heliconiini are of low conservation concern, being widespread species of human-modified areas. Others, particularly certain members of the genus *Heliconius*, are forest-dependant and can be restricted to narrow ranges, which, together with deforestation pressure, mean that various may be considered threatened with extinction due to habitat loss (BROWN, 1994). Further, certain species, including *H. melpomene* and *H. sara* form mimetic rings with other species and are considered very primitive forms, are considered to contain ancestral alleles which may reveal much about the origins of the group and the Nymphalidae in general.

The Heliconiini, however, are of most importance to conservation in that they show us that it is not just threatened species and subspecies which demand conservation attention: but also the processes which give rise to such taxa. The conservation of a non-palatable model species of a mimetic ring is of accentuated importance in that such a non-palatable species promotes the survival of the palatable and less-palatable species forming part of that ring. The extinction of the non-palatable model would therefore have far reaching

consequences to other members of the ring, such as increased predation, which may lead to the extinction or reduction in population of other members of the ring. However, most importantly of all, the extinction of the non-palatable model species would not only end the species itself, and possibly certain other ring species, but would lead to the extinction of the millennia-old speciation and co-evolution processes which it drives.

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