

Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in *Heliconius* butterflies

JAMES MALLET

*Galton Laboratory, Department of Genetics and Biometry,
4 Stephenson Way, London NW1 2HE*

AND

LAWRENCE E. GILBERT, Jr.

Department of Zoology University of Texas at Austin, Austin, TX 78712, U.S.A.

Received 1 August 1994; accepted for publication 17 October 1994

In the new world tropics there is an extravagant array of sympatric butterfly mimicry rings. This is puzzling under strictly coevolutionary (Müllerian) mimicry: all unpalatable species should converge as 'co-mimics' to the same pattern. If mimicry has usually evolved in unpalatable species by one-sided (Batesian) evolution, however, it is easy to see that mimicry rings centred on different models could remain distinct. If mimicry rings were also segregated by habitat, a diversity of mimicry rings could be stabilized. In this paper we report correlations between behaviour and mimicry of nine unpalatable *Heliconius* species. It is already known that co-mimics fly in similar habitats, and non-mimics fly in different habitats, although there is much overlap. Contrary to a previous report, we find little difference in flight heights of heliconiine mimicry rings; all species fly from ground level to the canopy. However, co-mimics roost at night in similar habitats and at similar heights above the ground, but in different habitats and at different heights from species in other mimicry rings. *Heliconius* (especially the *erato* taxonomic group) are renowned for roosting gregariously; and co-mimics roost gregariously with each other more often than with non-mimics. Gregarious roosting is therefore common between species, as well as within species. There are thus strong links between mimicry and behavioural ecology in *Heliconius*. The paradoxical correlation between nocturnal roosting and visual mimicry is presumably explained by bird predation at dusk when roosts are forming, or at dawn before they have disbanded. Direct evidence of predation is lacking, but there are high rates of disturbance by birds at these times. These results, together with knowledge of the phylogeny of *Heliconius*, suggest that species from the *melpomene*-group of *Heliconius* have radiated to occupy mimetic niches protected by model species in the *Ithomiinae* and the *erato*-group of *Heliconius*. A variety of sympatric mimicry rings is apparently maintained because key models fail to converge, while more rapidly-evolving unpalatable mimics evolve towards the colour patterns of the models. The maintenance of mimetic diversity would be aided by the habitat and behavioural differences between mimicry rings revealed here, provided that different predators are found in different habitats. This explanation for the maintenance of multiple mimicry rings is more plausible for *Heliconius* mimicry than alternatives based on visual mating constraints, thermal ecology, or camouflage.

ADDITIONAL KEY WORDS:—behavioural ecology – Lepidoptera – Nymphalidae – warning colouration – cryptic coloration – predation – sexual behaviour – gregarious roosting.

CONTENTS

Introduction	160
Aims	162
Material and methods	162
Mimicry and behaviour: observations	163
Mimicry in Corcovado <i>Heliconius</i>	163
Mimicry and flight height relative to the forest canopy	165
Flight height, larval host-plants and mating behaviour	166
Flight height and adult host-plants	167
Mimicry and daytime flight habitat	167
Nocturnal roosting and mimicry	168
Discussion	174
What explains mimetic diversity and its behavioural correlates?	174
Mimetic diversity in <i>Heliconius</i> : a hypothesis	176
Conclusion	177
Acknowledgements	178
References	178

INTRODUCTION

Many tropical butterflies are unpalatable to predators and apparently advertise this fact with warning coloration. These species often belong to mimicry 'rings' (groups of unpalatable species, together with some palatable species, that have converged on the same warning colour pattern). In any one area, there are usually a number of these mimicry rings. The existence of mimicry rings was first explained by Bates (1862), who found that presumably unpalatable Ithomiinae, Danainae and Heliconiinae (he called them danaoid and acraeoid Heliconiidae) and presumably palatable Dismorphiinae often converged in pattern. Bates pointed out that unprotected species would be selected to resemble commoner species protected from predators by nauseous smell or taste: this is now known as Batesian mimicry. It is not widely appreciated today that Bates also used this principle to explain mimicry between pairs of species, both of which were presumed unpalatable. He argued that rare unpalatable species, such as the 'silvaniform' now known as *Heliconius numata* (Heliconiinae), should converge on the patterns of commoner or more highly protected 'model' species, such as *Melinaea* spp. (Ithomiinae); a rare protected species would otherwise be vulnerable to predators that had not experienced its colour pattern. Mimicry which involves unilateral convergence, Batesian mimicry, is today usually thought to apply only to palatable species, and Bates himself muddied the waters by also proposing a Lamarckian explanation of mimicry between pairs of unpalatable ithomiines where both species are common. Later, Müller (1879) showed that both unpalatable species of a mimetic pair of arbitrary relative density could benefit, allowing the potential for coevolutionary mimicry in which both species approach an intermediate pattern. This bidirectional coevolutionary interpretation became known as Müllerian mimicry, although since then most authors have called any mimicry between unpalatable species Müllerian mimicry. Recent authors have defined Batesian vs. Müllerian mimicry in terms of benefits and costs (e.g. Wickler, 1968; Edmunds, 1974; Vane-Wright, 1976; Gilbert, 1983; Turner, 1984): if both mimic and model benefit from mimicry, then the mimicry is Müllerian; if only the mimic benefits by deceitful parasitism of the model's signal to predators, then the mimicry is Batesian. Since the exact mode of evolution is never certain, it is sensible

to continue using definitions of Müllerian vs. Batesian mimicry based on cost, even though many so-called Müllerian mimics may have done what Bates originally proposed—to converge unidirectionally on a model. The existence of bidirectional Müllerian convergence is still in doubt because commoner species would probably lose protection by mimicking rarer species (Turner, 1977, 1984): one of us has concluded that there is only slender evidence for any coevolution in mimicry (Gilbert, 1983).

An obvious corollary of Müllerian mimicry (both coevolutionary and unilateral) is that all unpalatable species in an area should converge on a single abundant and effective warning pattern. This Panglossian hypothesis for mimicry can immediately be rejected. Instead, unpalatable butterflies have massively diversified in colour pattern, as though adaptive radiation has occurred. This reaches a peak in the Heliconiinae, where mimetic radiation has occurred again and again in different lineages (Turner, 1976). Given that there are a number of mimicry rings in any one locality, the habitats or microhabitats of the species within a mimicry ring are expected to be similar for three reasons. (1) A mimic should show itself preferentially to predators that have encountered its model. It should avoid predators that have not encountered the model. (2) Alternatively, if the mimic adapts to a habitat or microhabitat already occupied by a common aposematic model, the mimic should converge on that species. (These arguments are phrased in unilateral, Batesian terms, but similar coevolutionary arguments could be made.) (3) Finally, if colour patterns have important effects on thermal ecology or background matching, model and mimic could share habitat requirements. Different mimicry rings are therefore expected to be separated by habitat, while co-mimics are expected to share habitats.

Correlations between habitat and mimicry have rarely been sought. After preliminary work by Poole (1970), Papageorgis (1975), working in Peru, found that butterflies of different mimicry rings flew at different heights in the rainforest, but stated that different mimetic groups did not fly in different habitats. She believed that the same birds were found at all levels in the forest, and so felt that the butterflies were unlikely to be minimizing overlap with predators trained to other mimicry rings. She found that mimicry rings were distributed in the canopy in the reverse of the order expected on thermal grounds: dark-coloured mimicry rings, which absorb heat faster, were often found higher in the canopy than pale mimicry rings suggesting that thermal ecology was unimportant. She then argued that each mimicry ring was camouflaged against its background, and that disruptive pattern was a microhabitat-limited constraint on the evolution of mimetic patterns. This counterintuitive idea proposes that colour patterns are under dual selection for camouflage and warning coloration. Papageorgis rejected purely mimetic and thermal ecology hypotheses and ignored the possibility that mate choice might explain the origin and maintenance of mimicry rings.

After many years of observing all of the genera and species of heliconiines studied by Papageorgis (1975) in nine tropical American countries we have come to somewhat different conclusions. A major feature absent from Papageorgis' work was any discussion of the function of flight which must constrain the butterflies' behaviour. *Heliconius* search in learned home ranges for larval food plants for oviposition (*Passiflora* spp., Passifloraceae), for

coevolved nectar and pollen sources (*Psiguria* and *Gurania* spp., Cucurbitaceae), for mates, and for roosting sites (Gilbert, 1975; Turner 1983; Mallet, 1986; Murawski & Gilbert, 1986). Contrary to Papageorgis' results, Smiley (1978) and Smiley & Gilbert (personal communication) have found that *Heliconius* butterflies fly in major habitat types that are similar to those of co-mimics, but different from those of non-mimics. We agree with Papageorgis (1975) in one respect: there is often a mimicry ring of small 'transparent' ithomiines that fly near the ground in deep forest. These are not conspicuous, and could possibly have evolved transparency for camouflage as Brown (1973) and Papageorgis (1975) suggest. However, R.I. Vane-Wright (personal communication) points out that there are no equivalent transparent, understory mimicry rings in the Old World tropics, as might be expected if transparency-mimicry was selected for in the understory. Recently, Beccaloni (personal communication) has also obtained data showing that there are flight height differences among ithomiines. However, our casual observations (see also Brown, 1988) suggest that the four mimicry rings involving heliconiines (the 'tiger' mimicry ring, including Ithomiinae and Heliconiinae; the 'red' and the 'blue' mimicry rings of the genus *Heliconius*; and the 'orange' mimicry ring of other heliconiines) overlap in flight height far more than reported by Papageorgis.

AIMS

We were therefore interested in testing the prediction that different mimicry rings should be ecologically segregated by habitat or height. By studying the behavioural ecology of mimetic butterflies, we can approach the question of why there are so many mimicry rings in an area.

MATERIAL AND METHODS

Our study site was in regenerating and primary forest at Estación Sirena, Parque Nacional Corcovado, Peninsula de Osa, on the Pacific coast of Costa Rica. The wet forest habitats near Sirena have been described by Herwitz (1981), and a broad outline of the *Heliconius* community at Sirena has been given by Gilbert (1984, 1991). Larval host-plants (*Passiflora* spp.) for Osa peninsula *Heliconius* have been studied extensively (Benson, 1978; Mallet, 1984; Longino, 1984; Thomas, 1990a,b; Gilbert, 1991). Host-plant information at Corcovado mentioned here is based on over 425 records of individual eggs or larvae, or batches of larvae if gregarious (Mallet, 1984).

To examine the effect of adult food-plants on flight height in *Heliconius* we made observations at large patches of *Psiguria warscewiczii* vines in forest light-gaps. These light-gaps, which were naturally caused by multiple treefalls, contained *Psiguria* flowers at a diversity of heights and most local *Heliconius* species. Observations were made for a total of about 1.5–2 h in each patch during the morning foraging peak of *Heliconius*, making a total of 11 h 10 mins observation in six separate patches between May and September 1981. We recorded the heights of the flowers (Table 1) and the numbers and species of *Heliconius* visitors. In this way we allowed *Heliconius* to array themselves on the *Psiguria* vines. In addition, heights of flower clusters and

TABLE 1. Heights of *Psiguria* flowers used during flight observations

Height (m)	Nos. of flowers	Height (m)	Nos. of flowers
0-0.49	0	7.5-7.99	0
0.5-0.99	4	8.0-8.49	2
1.0-1.49	0	8.5-8.99	4
1.5-1.99	6	9.0-9.49	0
2.0-2.49	8	9.5-9.99	2
2.5-2.99	2	10.0-10.49	2
3.0-3.49	5	10.5-10.99	3
3.5-3.99	7	11.0-11.49	2
4.0-4.49	0	11.5-11.99	3
4.5-4.99	2	12.0-12.49	7
5.0-5.49	2	12.5-12.99	2
5.5-5.99	4	13.0-13.49	2
6.0-6.49	2	Then no flowers until ...	
6.5-6.99	4	21.0-21.49	2
7.0-7.49	6		

visits could be measured exactly, eliminating subjectivity. The results will obviously be site-dependent: the proportion of visits of each species at each height depends on local *Heliconius* species diversity and the flower height diversity. However, there was a fairly even spread of flower heights at which the insects were recorded between 0.5 and 13.5 m (Table 1).

To investigate the possibility that nocturnal roosting behaviour is correlated with mimicry, heights and habitats of *Heliconius* roosting sites were recorded (see also Mallet, 1986). The habitats near the Sirena station at Corcovado were mapped and classified into: (1) low, shrubby second growth, including young tree-falls and storm-damaged areas, (2) tall secondary forest including older tree-falls (often dominated by *Ochroma* and *Cecropia* spp.), and (3) mature primary forest (Mallet 1984: 22). The number of individuals of each species present on each gregarious roost (defined as a group of individuals within a sphere of radius less than 2 m) was recorded. Most individuals could be identified by marks received in the mark-recapture programme (Gilbert, 1984). When an individual was recorded roosting on more than one night the first height measurement only was used in the analysis.

For each individual the total number of other individual roostmates of the same and other species of *Heliconius* were recorded. Gregarious roosts are hard to find; therefore all observations were used. Observations have somewhat different sample sizes because the data for some roosts were not complete. There is an overrepresentation of *H. erato* roosting records because of the greater ease of finding this species and because several other studies on *H. erato* were in progress (Mallet, 1986).

MIMICRY AND BEHAVIOUR: OBSERVATIONS

Mimicry in Corcovado Heliconius

We studied three mimicry rings in the genus *Heliconius* at Sirena (Fig. 1). These *Heliconius* have been tested in Parque Nacional Corcovado and were

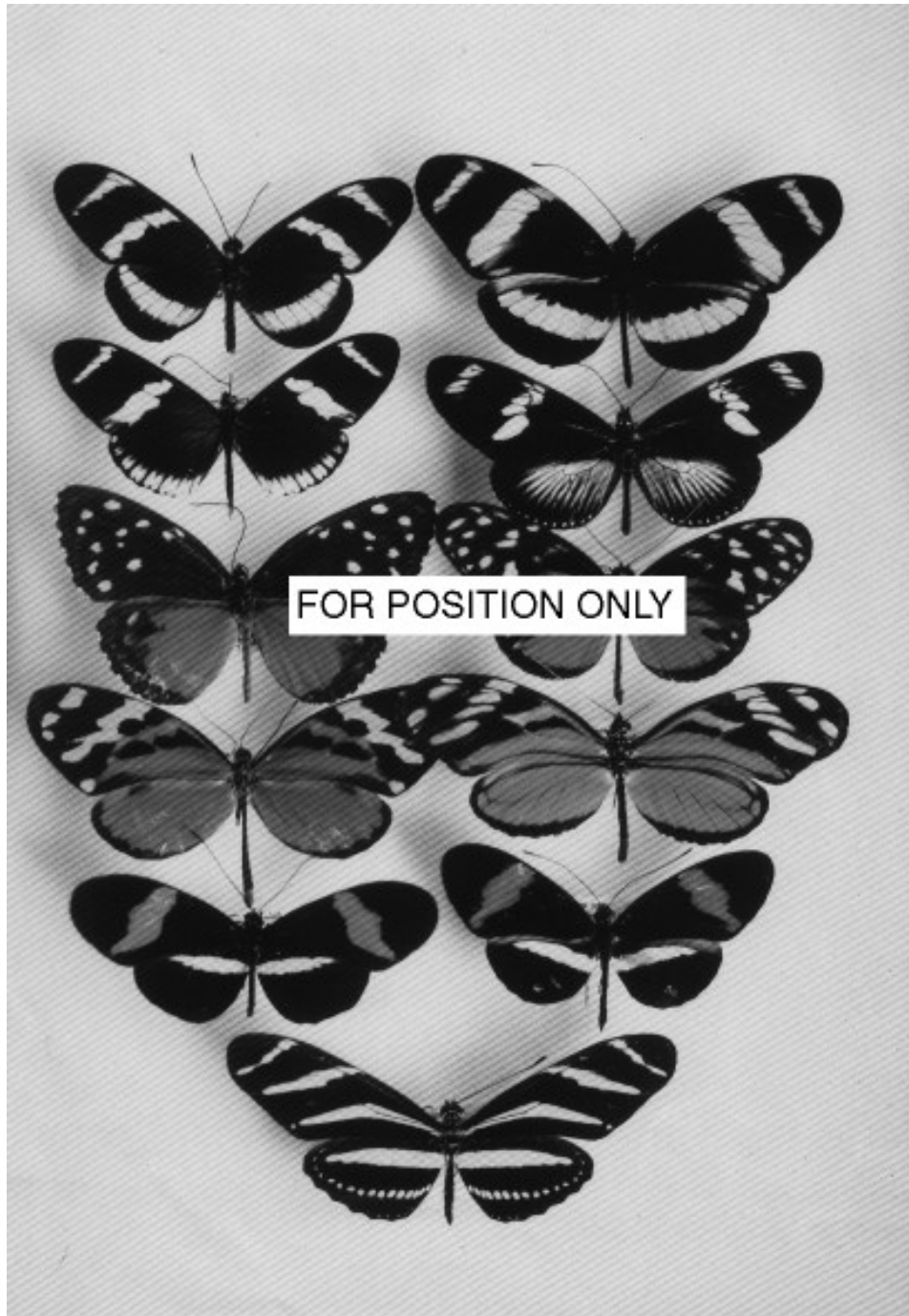


Figure 1. *Heliconius* from Sirena, Corcovado National Park, Costa Rica. Top: *H. hewitsoni*, *H. pacheus* ('yellow' ring). Second row: *H. sara*, *H. doris*-yellow form ('yellow' ring). Third row: *Tithorea tarricina*, *H. hecale* ('tiger' ring). Fourth row: *Melinaea scylax*, *H. ismenius* ('tiger' ring). Fifth row: *H. erato*, *H. melpomene* ('red' mimicry ring). Bottom: *H. charitonia* (non-mimetic).

found to be repellent to caged Jacamars, *Galbula ruficauda* (Chai, 1986). Benson (1972) showed that *H. erato* with altered colour patterns in the Osa Peninsula had shorter adult lives in the field than did controls. Direct and indirect methods of studying selection on colour pattern genes in a set of *Heliconius* hybrid zones in Peru indicate that the selection is greater than 10% against individuals with the non-mimetic colour patterns (Mallet & Barton, 1989; Mallet *et al.*, 1990). These results are good evidence that selection by predators is responsible for maintaining mimicry in *Heliconius*.

The three *Heliconius* mimicry rings at Corcovado are as follows (Fig. 1):

(1) A 'red' mimicry ring consisting of *H. erato* and *H. melpomene*, which corresponds to the 'red' mimicry ring of Papageorgis (1975).

(2) A 'yellow' mimicry ring consisting of the local endemics *H. hewitsoni* and *H. pacheus*; *H. sara* in this region also converges on the pattern of these species. *H. sara* was rare at Sirena, but was common 10 km away in another part of the park, Llorona, where some data were taken. In addition, the usually rare *H. doris* has a locally endemic yellow hindwing-barred form which is convergent to this mimicry ring, though it also has two local non-mimetic forms (blue hindwing barred and red hindwing rayed). This yellow ring closely corresponds to the 'blue' mimicry ring of Papageorgis (1975), which also includes forms of *H. sara* and the 'blue' form of *H. doris*.

(3) A 'tiger' mimicry ring. *H. ismenius* and *H. hecale* both mimic specific members of the ithomiine tiger complex, *Melinaea scylax* and *Tithorea tarricina*, respectively. The mottled patterns of these two 'silvaniform' *Heliconius* are similar and, following tradition (Papageorgis, 1975; Brown, 1988) we have included them in the same mimicry ring. The tiger mimicry ring in the neotropics almost always includes a number of subsidiary rings (Brown 1988); this is also true for the Peruvian fauna studied by Papageorgis (1975). Near Panama City, a few hundred kilometres east of Corcovado, the tiger mimicry rings change, and here *H. ismenius*, *H. hecale*, and a third species, *H. ethilla*, all mimic the same ithomiine, *Melinaea ludovica idae*. So although the mimetic resemblance between *H. ismenius* and *H. hecale* is weak in our study site, it is much stronger in other areas of these species' ranges.

Heliconius charitonia is the only non-mimetic *Heliconius* at Sirena. This species is rare at Corcovado, and probably would be absent if extinctions were not balanced by colonization from areas where it is commoner: cloud forest on the slopes of the central mountains in Costa Rica, and dry forest to the North in Puntarenas and Guanacaste provinces (Gilbert, 1991).

Papageorgis' 'orange' heliconiine ring (*Dryas iulia*, *Dione juno*, *Agraulis vanillae*, *Dryadula phaetusa*, *Eueides aliphera*, *E. lybia*, *E. vivilia*) and 'transparent' ithomiine mimicry rings also occur at Corcovado, but they neither feed on *Psiguria* nor usually roost gregariously, and so were not studied.

Mimicry and flight height relative to the forest canopy

Papageorgis (1975; methods given in Papageorgis, 1974) recorded the height at which mimetic butterflies entered the forest canopy from logged areas. We attempted to obtain comparable results by measuring the flight heights of butterflies entering the forest edge from a grass airstrip at the

Corcovado Park headquarters. We found this method impossible to use, at least at our site. Butterflies flew low across the airstrip (1–3 m in height). Once they reached the opposite side, all heliconiines either remained in low second growth at the edge of the airstrip, or else climbed up to fly through sunny valleys in the forest. They neither entered shaded parts of the forest nor flew over the highest parts of the canopy. By studying the forest edge, Papageorgis claims to have measured flight height where the rate of climb was maximal, which must be both extremely difficult and of dubious value in detecting height segregation. Furthermore, the canopy of primary forest is always so irregular as to make measurement of flight height, even if it were constant, somewhat irrelevant to the microhabitat in which flight occurs. For this reason, we give observations here of the habits of *Heliconius* with respect to larval host-plants, adult food plants, sexual behaviour and gregarious roosting. Food-plants for oviposition and adult feeding, as well as the sites suitable for sexual and social interactions are likely to have a strong influence on where the butterflies fly, and might be expected to show correlations with mimicry.

Flight height, larval host-plants, and mating behaviour

The larvae of the nine species of *Heliconius* mentioned here all feed on new shoots of *Passiflora* (Benson, 1978; Mallet, 1984; Gilbert, 1991). One species, *H. pachinus*, feeds on most Corcovado *Passiflora*, but the rest are either monophagous or feed on a few related species. *Passiflora* is much commoner in second growth and in natural treefall light gaps than in shaded, primary forest; indeed seeds do not germinate unless exposed to strong sunlight (Mallet, 1984). This is true for all species except *P. pittieri*, the host-plant of *H. hewitsoni*, which seems uniformly rare everywhere and does appear to germinate in the understory (Longino, 1984; Mallet, 1984). Female *Heliconius* might be expected to spend much of their time near larval hosts, and we did find higher densities of all *Heliconius* in second growth, especially where larval host-plants were common (Smiley & Gilbert, manuscript in preparation). Only *H. doris* uses shoots of vines in the canopy, which it colonizes in super-gregarious masses of 1000 larvae or more. J. Longino (personal communication) has climbed extensively in the canopy at Corcovado but has never found evidence of herbivory or young stages of other *Heliconius* on the new shoots of canopy vines. These comments also apply to the orange ring; far from being restricted to the forest canopy (Papageorgis, 1975), orange heliconiines spend much of their time near ground level in second growth, where they feed on flowers such as *Lantana* and oviposit on older leaves of low growing *Passiflora* (Benson, 1978).

Heliconius males also visit host-plants, and investigate larvae and pupae on or near their hosts (Gilbert, 1975; 1976; Mallet & Jackson, 1980); in fact, the *erato*-group (including *H. charitonia*, *H. erato*, *H. sara*, *H. hewitsoni*) are known to 'pupal-mate' on their host-plants (Gilbert, 1975; Deinert, Longino & Gilbert, 1994). Males fight for positions on a female pupa the day before eclosion; on the evening before the day of eclosion, the successful male's abdomen penetrates the female pupa near the wingtips, and aligns parallel to the female's under the pupal skin. Upon eclosion the male mates with

the female as she descends from the pupal exuvium (Longino, 1984). Males of the 'melpomene group' (i.e. *H. melpomene*, *H. pachinus*, *H. ismenius*, *H. hecale*), which do not pupal mate, also visit larval hosts, presumably in search of freshly emerged females. Although the larvae of *H. doris* feed on canopy shoots of mature *Passiflora ambigua* lianas, they descend the liana trunk to pupate in the understory in large masses. Males then visit these pupal swarms and mate with newly emerged females near ground level (unpublished observations with J. T. Longino).

Both sexes of adult *Heliconius* are commonly within net range (1–3 m) as indicated by high recapture rates of all species (~50%). We know from mark-recapture study that individuals of all species commute between treefalls or areas of second growth (Mallet, 1986) and can be seen from these sites flying over the forest in sunny valleys of the canopy surface. Only *H. pachinus* and *H. hewitsoni* regularly patrol the shady understory of deep forest, but even these species lay eggs on juvenile *Passiflora* in small light gaps, as well as low in the understory (Benson, 1978; Longino, 1984; Mallet, 1984). Although it is conceivable that we underestimate the amount that *Heliconius* fly in primary forest canopies, all species searched for larval food-plants and for mates within 1–3 m of the ground in second growth, including natural treefalls and openings. For most species of *Heliconius*, new growth of juvenile *Passiflora* is the preferred oviposition site, and it is not therefore surprising that all species overlap at low heights. Larval and sexual ecology of these species demand this overlap.

Flight height and adult host-plants

Heliconius also spend much time near adult food-plants, in Corcovado especially at flowers of the vine *Psiguria warscewiczii* (Cucurbitaceae). *Heliconius* extract amino acids from *Psiguria* pollen (Gilbert, 1972) and this enables them to live long adult lives (up to 6 months, Gilbert, 1975; Dunlap-Pianka, Boggs & Gilbert, 1977). For this reason, adult host-plants are more important to *Heliconius* than to other butterflies (Gilbert, 1975). A visual predator (as modelled by a human) will see greater numbers of *Heliconius* visiting flowers such as those of *Psiguria* than elsewhere. If flight height is stratified, we might expect stratification at large clumps of *Psiguria*, a vine which flowers from near the ground to the tops of subcanopy trees. Observations at large *Psiguria* patches in treefall openings (Fig. 2) make it clear that essentially all *Heliconius* visit *Psiguria* flowers at all available heights. There is little, if any, separation between mimicry rings or between species in their flower visit heights. This lack of difference in flower visit heights backs up our casual observations quantitatively. Because they fly in sun wherever there are adult host-plants, different *Heliconius* have rather similar flight heights.

Mimicry and daytime flight habitat

Significant habitat separation has been found for *Heliconius* mimicry rings in Corcovado and elsewhere in Costa Rica (Smiley, 1978; Smiley & Gilbert, manuscript in preparation). The virtually uniform presence of the yellow mimicry ring on its own in the shady understory of primary forest in

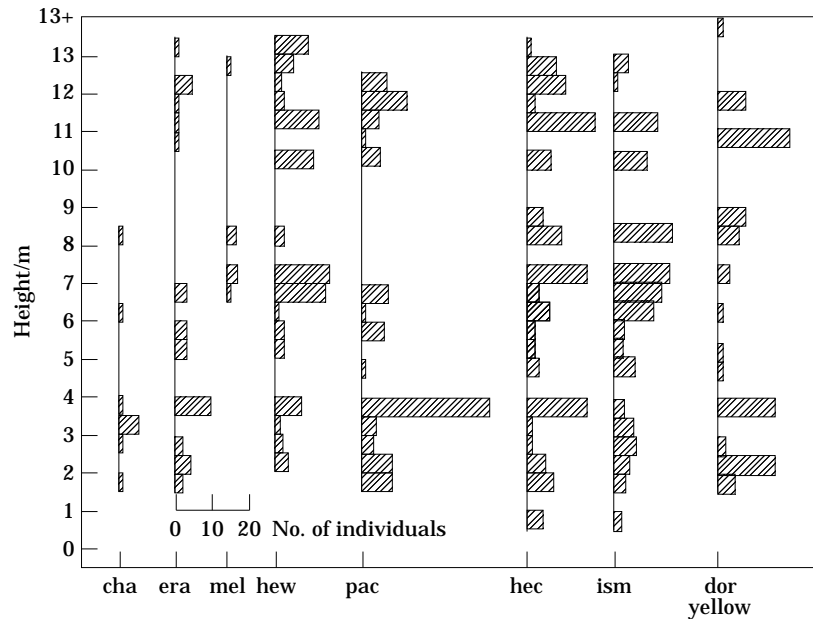


Figure 2. Heights of observed visits to *Psiguria* flowers. Species listed in Fig. 1 are identified here by the first three letters of their species name.

Corcovado (Longino, 1984) is particularly striking. The second growth and light gap areas, however, where *Heliconius* are most abundant, are sites of great overlap for all *Heliconius* mimicry rings, including the yellow ring (for example the Sirena pasture area studied in Gilbert, 1984). Although there are significant differences in habitats between mimicry rings, there is substantial overlap in virtually all sites.

Nocturnal roosting and mimicry

Heliconius are renowned for faithfully returning to gregarious roost sites night after night (Turner, 1971, 1975, 1983; Gilbert, 1975; Brown, 1981; Mallet, 1986). In this section, we explore the potential for correlations between mimicry, roosting habitat, roosting height, and gregarious roosting with members of other species.

Roosting habitat

All *Heliconius* roost on dead twigs or tendrils suspended from mats of dense vegetation or from branches of tall trees. Because they roost away from live plant tissue, they are found in very shady areas either in primary forest or in second growth. Table 2 shows that the habitat in which *Heliconius* roost is different between species ($P \ll 0.001$; some expected values are less than 5, but the very high level of significance is suggestive of real differences between species). There are strong differences between mimicry rings, but also strong differences between species within rings. *H. erato* and *H. melpomene* tend to roost in low second growth and secondary forest, whereas *H. hecale* and *H. ismenius* prefer to roost in taller secondary forest. Species of the

TABLE 2. Habitats in which *Heliconius* roost

species	low second growth	secondary forest	mature forest	total	F*
<i>charitonia</i>	10	1	0	11	1.09
<i>erato</i>	219	156	2	377	1.42
<i>melpomene</i>	30	2	0	32	1.06
<i>hewitsoni</i>	20	19	17	56	1.95
<i>pachinus</i>	23	18	16	57	1.88
<i>sara</i>	4	18	3	25	1.96
<i>doris</i>	1	5	0	6	1.83
<i>ismenius</i>	6	14	0	20	1.70
<i>hecale</i>	7	18	0	25	1.72

*F (species) = $1 \times (\text{proportion in low second growth}) + 2 \times (\text{proportion in tall secondary forest}) + 3 \times (\text{proportion in mature forest})$. See Smiley (1978).

Nested G test on above	G	df	P
(within <i>charitonia</i>)	0	0	!!
within red mimicry ring	19.84	2	<0.001
within yellow mimicry ring	19.03	6	<0.01
within tiger mimicry ring	0.02	2	ns
within mimicry rings	38.89	10	<0.001
between mimicry rings	127.52	6	<<0.001
total heterogeneity between species	166.41	16	<<0.001

yellow ring are virtually alone in their tendency to roost in mature forest, paralleling their diurnal habits, but they roost in other habitats as well. Following Smiley (1978), we define an index 'F', the tendency of a species to be found in primary forest (Table 2).

The order of species along the 'F' dimension does not appear random and seems to be determined in part by mimicry rings. Other orders of species could also conform to a non-interdigitating pattern of mimicry rings like that of Table 2. For example, the order *sara-hewitsoni-pachinus-melpomene-erato-hecale-ismenius* would also be a non-interdigitating order of mimicry rings (ignoring *H. charitonia* and *H. doris*, for which we have few observations, does not affect the outcome of this test). Using simple combinatorial probability, there are in fact 3! orders of mimicry rings possible and 2!3!2! orders of the seven species within three mimicry rings. If species were ordered at random, on the other hand, without regard for mimicry, there would be 7! orders possible. So the probability of obtaining a non-interdigitating order of mimicry rings like the one in Table 2 is $3!2!3!2!/7! = 0.029$, and a null hypothesis of random ordering of species with respect to habitat can be rejected. *H. charitonia* does interdigitate with the red ring, but this does not alter the probability just calculated because the same multiple of interdigitating positions would be included in both numerator and denominator; *H. doris*, lies with the appropriate yellow ring and makes the pattern even more improbable under a random hypothesis.

Roosting height

The heights at which *Heliconius* roost are plotted in Fig. 3; means, standard deviations and overlap values are given in Table 3. *Heliconius erato* and *H.*

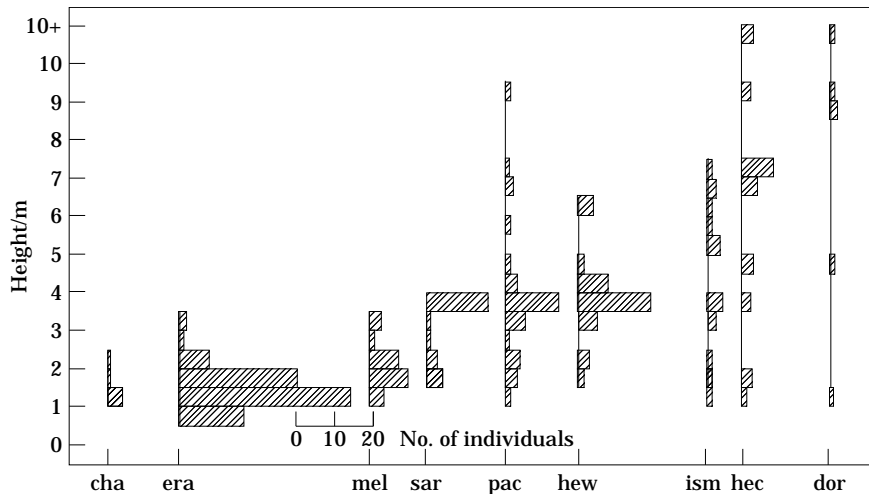


Figure 3. Heights of nocturnal roosting. Abbreviation of species names as in Fig. 2.

melpomene roost low, while three species of the yellow mimicry ring roost higher up. The tiger ring—*H. ismenius* and *H. hecale*—roosts higher still. Although the latter two species are the commonest *Heliconius* at the study site, we have found them roosting only rarely; this is probably because we have missed many individuals roosting high in the canopy, producing a downward bias in data for the tiger ring.

Species differ strongly in roosting height (Kruskal-Wallis test, $H=191.7$ [corrected for ties], 8 d.f., $P \ll 0.001$). Excluding *H. charitonia* and *H. doris* again, the order of the mean height of roosting is dependent on mimicry ring; there are no species whose mean height of roosting interdigitates with the mean heights of roosting of species belonging to other mimicry rings. A non-interdigitating mimetic order like that in Table 3 would by chance occur in the seven species excluding *H. charitonia* and *H. doris* with $P=0.029$ (again using combinatorial probability, see under *Roosting habitat*). The heights at which mimics roost overlap substantially, whereas height overlap between non-mimics is usually less (Table 3). Overlaps in roosting height are quite substantial between the yellow and tiger rings, but this may be in part due to downward bias in data for the higher-roosting tiger ring; *H. charitonia* and the red ring also overlap strongly (Fig. 3, Table 3). On very limited data ($n=6$; Fig. 3), the partial yellow mimic *H. doris* appears to roost higher than other yellow ring species. But although the tiger ring overlaps with the yellow, and *H. charitonia* with the red, the overall lack of interdigitation remains non-random for reasons given in the previous section.

Another way of testing for correlations between roosting height and mimicry is to use the values of overlap from Table 3. The average fraction of range overlap with a mimic (from all relevant cells in Table 3) is 0.58, 2.3-fold greater than overlap with non-mimics. This can be tested by randomly shuffling the species between existing mimicry rings. In only 33 of 1000 randomizations was there a 2.3 times or more overlap between mimics than non-mimics. Thus $P \approx 0.03$ that this association would occur by chance.

As mentioned above, *H. ismenius* and *H. hecale* mimic ithomiines, not

TABLE 3. Overlap in roosting heights of *Heliconius*. Overlap of species X on species Y is expressed as proportion of the height range ($\bar{x} \pm 1$ SD, metres) of species X overlapped by the height range of species Y. Mimetic alliances are shown in boxes

Species (n) X	Y	<i>charitonia</i>	<i>erato</i>	<i>melpomene</i>	<i>sara</i>	<i>pachinus</i>	<i>heavitsoni</i>	<i>doris</i>	<i>ismenius</i>	<i>hecale</i>
$\bar{x} \pm 1$ SD m										
<i>charitonia</i> (6) 1.52 ± 0.39		-	100	62	0	0	0	0	0	0
<i>erato</i> (104) 1.43 ± 0.50		79	-	49	0	0	0	0	0	0
<i>melpomene</i> (26) 1.98 ± 0.55		44	45	-	14	32	0	0	0	0
<i>sara</i> (25) 3.28 ± 0.90		0	0	8	-	100	69	49	88	79
<i>pachinus</i> (37) 3.80 ± 1.62		0	0	11	55	-	59	66	87	82
<i>heavitsoni</i> (41) 3.90 ± 0.96		0	0	0	65	100	-	81	100	100
<i>doris</i> (6) 7.80 ± 4.50		0	0	0	10	24	17	-	33	88
<i>ismenius</i> (17) 4.44 ± 1.84		0	0	0	43	77	52	81	-	96
<i>hecale</i> (26) 6.99 ± 4.23		0	0	0	17	32	23	94	42	-

strictly each other. Why should *H. ismenius* and *H. hecale* roost higher in the canopy than other *Heliconius*? We have very few observations on roosting habitat or height of *Melinaea scylax* and *Tithorea tarricina*, the respective co-mimics of *H. ismenius* and *H. hecale*. We have occasionally seen *Melinaea scylax* perching at dusk on living leaves low in the understory. However, *Melinaea* lays its eggs on canopy epiphytes of *Juanulloa* and *Markea* (Solanaceae) (L. Gilbert & D. J. Harvey, unpublished; Drummond & Brown, 1987). We have never seen *Tithorea tarricina*, the primary model for *H. hecale*, roosting in the evening though we have seen individuals flying high just under the canopy secondary forest soon after sunset. Since we have seen both of these common ithomiines so rarely at dusk, it is almost certain that both normally roost in the canopy. In the early morning, when roost disturbance and therefore predation is likely to be most intense, tiger ithomiines are common in the canopy: we have seen tiger-pattern Ithomiinae and Pericopinae (a subfamily of mimetic arctiine moths) flying at dawn in the canopy from a tower on Barro Colorado Island, Panama.

Intra- and interspecific gregarious roosting

All *Heliconius* at Corcovado sometimes roosted gregariously, but the degree of gregariousness varied between species. This is correlated with phylogeny; 86% of individuals in the *erato*-group species (*charitonia*, *sara*, *erato*, *hewitsoni*) roosted with one or more conspecifics, compared with only 48% of individuals in *melpomene*-group species (Table 4; Mallet, 1986). Only 22% of *erato*-group species roosted with their commonest co-mimic, whereas 46% of *melpomene*-group species roosted with commonest co-mimics: *erato*-group species discriminated strongly in favour of their own species, whereas *melpomene*-group species were about as likely to roost with their commonest co-mimic as with conspecifics. Some individuals of all species roosted solitarily, others roosted with members of other species, and at times gregarious roosts of two or more species were intermingled. Table 4 shows that individual *Heliconius* roosted mostly with members of their own species, but when in mixed roosts, the other species were usually co-mimics. We often found clusters of *H. hewitsoni* mixed with one or two *H. pachinus*, and it is especially striking that individual *H. melpomene* were more often found roosting with their co-mimics *H. erato* than with members of their own species (Table 4; see also photos in Mallet, 1986).

On average, individual *Heliconius* roost next to a co-mimic with probability 0.17, and to a non-mimic with probability 0.06 (averaged over all except diagonal cells in Table 4). Individuals are thus 2.8-fold more likely to roost with mimics than with non-mimics. Shuffling species between mimicry rings gave only 23 examples out of 1000 where mimics roosted together with greater than a 2.8-fold probability ratio. Therefore, $P \approx 0.02$ that mimetic behaviour as extreme as that in Table 4 would occur by chance. While this preferential gregariousness with co-mimics may in part be a consequence of habitat and microhabitat choice, potential roost sites are very common relative to those actually used. *Heliconius* use visual and pheromonal cues to roost gregariously, and 'fanning' interactions between different species are common while roosts are forming in the evening, in the same way that fanning is

TABLE 4. The degree to which *Heliconius* roost together. Numbers of species X roosting with species Y. 'Gregariousness' is given by the proportion of individuals that roosted with other members of their own species (see also Mallet, 1986), 'mimetic roosting' is the proportion roosting with the commonest co-mimic. Mimetic alliances are shown in boxes

Species (n) gregariousness X	mimetic roosting Y	<i>charitonia</i>	<i>erato</i>	<i>melpomene</i>	<i>sara</i>	<i>pachinus</i>	<i>heavitsoni</i>	<i>doris</i>	<i>ismenius</i>	<i>hecale</i>
<i>charitonia</i> (14) 0.86	∞	12	4	3	0	0	0	0	0	0
<i>erato</i> (397) 0.88	0.11	6	350	44	0	14	11	0	3	12
<i>melpomene</i> (33) 0.42	0.61	5	20	14	0	5	0	0	0	6
<i>sara</i> (12) 0.83	0.00	0	0	0	10	0	0	0	0	0
<i>pachinus</i> (57) 0.44	0.39	0	14	3	0	25	22	1	4	3
<i>heavitsoni</i> (54) 0.87	0.54	0	10	0	0	29	47	0	3	1
<i>doris</i> (6) 0.33	0.17	0	0	0	0	1	0	2	0	1
<i>ismenius</i> (14) 0.29	0.21	0	1	0	0	5	1	0	4	3
<i>hecale</i> (29) 0.76	0.62	0	6	4	0	12	2	3	18	22

associated with gregariousness within species (Mallet, 1986). It therefore seems likely that individuals actively select co-mimics as roost-mates.

DISCUSSION

What explains mimetic diversity and its behavioural correlates?

We have found a great deal of overlap between the daytime flight heights of *Heliconius* and other heliconiines with different colour patterns. However, mimicry rings do show habitat differences (Smiley, 1978; Gilbert & Smiley, manuscript in preparation), and in this study we have found strong habitat and height differences between mimicry rings in their nocturnal roosting habitats. Correlations between mimicry, habitat and behaviour cannot be dismissed on the grounds of phylogenetic inertia because members of the two major taxonomic groups of *Heliconius*, the *erato*-group and the *melpomene*-group (Eltringham, 1916; Brown, 1981; Brower, 1994a), are represented in two and three mimicry rings, respectively. These results contrast strongly with those of Papageorgis (1975), who found no differences in habitat between *Heliconius* mimicry rings, but strong segregation in flight height. We cannot explain these differences easily. Some of the discrepancy might be due to differences in the species composition between Peru and Costa Rica, but this does not agree with our own impressions; *Heliconius* overlap strongly in flight height throughout the neotropics. Brown (1988), who did not supply quantitative information, also found much more overlap in flight height between *Heliconius* mimicry rings than Papageorgis, with all groups overlapping between about 2–5 m, and many groups overlapping in the canopy. The exception was the red ring, which according to Brown flies low (1–5 m), though we find them frequently flying high as well (Fig. 2); however even Brown's result contrasts strongly with Papageorgis' opinion; she had the red ring flying only in the canopy. Flight height differences do exist between non-heliconiine mimicry rings: Beccaloni (personal communication) has found that ithomiine mimicry rings are stratified in height.

Paradoxically, the nocturnal roostmates, roosting habitats and roosting heights of *Heliconius* seem from our data to be more strongly influenced by diurnally-visible mimicry than daytime behaviour. Why should a visual pattern that is probably ignored by nocturnal predators affect nocturnal roosting? One possibility is that mimicry is unimportant during the middle of the day, when these poikilothermic butterflies can nimbly dodge predators. Near sunrise or sunset, however, *Heliconius* fly slowly. Presumably at these times of day, the butterflies are not operating at optimal temperatures for flight. After leaving their roosts in the early mornings, *H. erato* spread their wings and bask in the sun nearby; this behaviour also occurs late in the day, or after a cloudy spell. In this position, and on the roost itself, *Heliconius* may be vulnerable to birds that search foliage and chase insects they disturb. Butterflies are presumably less quick to escape from these gleaners at this time of day, as well as being more likely to be attacked because birds tend to forage more heavily at dawn and dusk. In addition, attacks by sallying birds such as Jacamars (*Galbula* spp.) and tyrannid flycatchers may be more common because of slower escape in cooler conditions. Neotropical birds

are known to forage at different heights in the canopy and in different habitats (Terborgh & Weske, 1969; Pearson, 1971; Karr, 1976; Ridgely, 1976). *Heliconius* would certainly reduce the diversity of potential predators by roosting in narrow habitat and height ranges, which could provide selection for habitat and microhabitat divergence between *Heliconius* in different mimicry rings, or reduce selection for convergence between rings in different habitats.

The hypothesis for behavioural mimicry just presented would be more strongly supported if there were evidence for predation on *Heliconius*, especially near roosts. One of us has seen predation at a gregarious roost of *H. charitonia* in Tamaulipas, Mexico (Mallet, 1986). However, similar predation was not seen in Costa Rica, although birds frequently flew near roosts of *H. erato* when the butterflies were still present in the morning. On average, each *H. erato* was disturbed off the roost by a potential predator every third morning (Mallet, 1986). While the birds were never seen to attack the butterflies, they were mainly frugivores or gleaners specializing on slow-moving insects living in rolled leaves; the very high rate of disturbance suggests that there is at least a high potential for predation. There is plenty of evidence for bird attacks in the form of Jacamar and other beakmarks on the wings of *Heliconius*, and from various estimates of selection on mimetic pattern (Benson, 1972; Mallet & Barton, 1989; Mallet *et al.*, 1990).

Another potential explanation for differences in roosting height and habitat is that mimetic patterns differ in their ability to absorb solar radiation. Similar effects are found in many non-mimetic butterflies (Douglas & Grula, 1978; Roland, 1982; Kingsolver, 1988). This was proposed as a possibility, then rejected by Papageorgis (1975). The arrangement of mimicry rings in roosting height seems to support this hypothesis; species possessing the darker colour patterns (in the red and yellow mimicry rings) roost lower than the paler tiger species. (This again contrasts with the pattern found by Papageorgis (1975), who found that the darker blue [similar to Corcovado yellow ring] and red mimicry rings flew higher than the tiger rings.) However, *Heliconius* roost in the shade. In order to bask in the morning, they must all fly to sunny areas. Roost height is therefore unlikely to play much part in the thermal ecology of these species.

We doubt disruptive coloration has anything to do with daytime flight environment of *Heliconius* as reported by Papageorgis. Papageorgis (1975), followed by Endler (1978) and Brown (1988), argued that predators may find it hard to follow *Heliconius* flying against dappled backgrounds; however, this would also be true of almost any object of any colour moving against a contrasty background. *Heliconius*, in our experience, are among the most visible butterflies in flight. Their colour patterns (Fig. 1) suggest that selection has minimized, rather than maximized, any disruptive effect the pattern may have. Garishly coloured spots or bands of red, yellow, or orange are neatly separated from each other and from the edge of the wing by borders of black pigment, sometimes overlaid with iridescent blue. Disruptive patterns are usually thought of as colour patterns that break up outlines, but the bright markings of *Heliconius* are almost always clearly demarcated by dark edges. In any case, if one accepts Papageorgis' data for the distribution of light fleck size at different heights (itself, in our view, dubious), our data

showing red rings are low and tiger rings are high falsifies the notion that fleck size and mimetic pattern are in some way correlated. Camouflage also seems a most unlikely attribute of *Heliconius*; it would be hard to design more conspicuous patterns. These comments apply equally to heliconiines in the orange mimicry ring. Orange heliconiines in flight are visible from far away, and their colours stand out from all rainforest backgrounds.

Mate choice may interfere with the evolution of mimicry: Brower, Brower & Collins (1963) suggest that mimicry may diversify because there is an upper limit to the sexual confusion caused by many species within a mimicry ring, and female-limitation in Batesian mimicry has almost certainly evolved because of sexually selected constraints on male patterns (Turner, 1978). In *Heliconius*, closely related species are often found in separate Müllerian rings (Turner, 1976); speciation is often accompanied by a mimetic switch. In support of this idea, Brown & Benson (1974) found that orange and red rags attract orange tiger pattern *H. numata*, and Mallet *et al.* (1990) used red rags to attract *H. erato* and *melpomene* in the red ring. We recently discovered that white rags are attractive to the black and white *H. cydno* in W. Ecuador. (The yellow and black *H. pachinus* studied here is probably little more than a subspecies of *H. cydno*, itself a 'semispecies' of *H. melpomene* with which it hybridizes regularly in the wild—see below.) These observations suggest that mate choice interacts with mimicry in *Heliconius* colour pattern evolution (see also Swihart, 1967; Silberglied, 1984). However, mate choice alone could not explain the origin of diversity and habitat segregation of mimicry rings, unless one makes the unreasonable assumptions that habitat change requires speciation, *and* that speciation requires a change of colour pattern and colour-related mate choice. During the daytime, *Heliconius* of diverse colour patterns can be seen interacting at floral resources, and males chase members of their own and other species, with apparent disregard for colour pattern. Males of many butterflies approach and even copulate with altered females and simple models (Silberglied, 1984). While mate choice may evolve during mimetic divergence, it is rather unlikely that evolution of mate choice itself drives divergence. It seems rather more likely that mate choice will act as a brake on the evolution of novel mimetic patterns, as in Batesian mimicry (Turner, 1978).

Mimetic diversity in Heliconius: a hypothesis

If mimicry between unpalatable species evolves unilaterally, the development of mimicry rings would depend only on a few key species, the 'models.' Except for *H. doris* which is basal, the *Heliconius* in our study can be divided into two taxonomic groups: a *melpomene*-group and an *erato*-group (Brown, 1981; Brower, 1994a; and see above). The members of the *erato*-group are closely related, but the eggs, larvae and pupae are diverse and can be gregarious or solitary (Brown, 1981). Hybrids between sympatric species have never been found in nature. We have found that roosts of these species are usually rather gregarious, and individuals rarely roost next to co-mimics (Table 4).

Members of the *melpomene*-group are even more closely related than members of the *erato* group (Eltringham, 1916; Brown, 1981). Brower (1994a:

Fig. 6) shows that the mtDNA genealogy of the *melpomene*-group can be explained by 5–8% sequence divergence as compared to 9–19% sequence divergence in the *erato*-group. Morphology of the immature stages of all species is very similar, and all are solitary. F1 and backcross hybrids between *H. ismenius*, *H. pachinus* and *H. melpomene* have been produced in the laboratory (P. Brakefield, personal communication; Nijhout, Wray & Gilbert, 1990), and similar hybrids are regularly found between members of the *melpomene*-group in field collections (Ackery & Smiles, 1976; Brown, 1976). Phylogenies based on mtDNA show that *H. cydno* and *H. pachinus* are nested within *H. melpomene*, making the latter species paraphyletic (Brower, 1994b). This close genetic relationship suggests that the *melpomene*-group species diverged more recently than those within the *erato*-group. Roosts of these species are loose and not as gregarious as those of the *erato*-group (Table 4; Mallet, 1986). They frequently roost as singletons near or in gregarious roosts of *erato*-group comimics (see photos in Mallet, 1986). In the case of tiger species (e.g. *H. hecale*, *H. ismenius*), mimicry is of ithomiine rather than heliconiine models, and the high roosting habit of *H. hecale* and *H. ismenius* likely provides another example of mimetic behaviour in the *melpomene*-group of *Heliconius*. In spite of the recency of their speciation, members of the *melpomene*-group have become enormously diverse in the mimicry rings to which they belong, and, in general, their behaviour has diverged in concert. Therefore, it seems likely that the *erato*-group and ithomiines are models whose colour patterns diverged before those of their *melpomene*-group mimics (see also Bates, 1862: 549–554; Eltringham, 1916; Gilbert, 1983).

A hypothesis for the evolution and maintenance of mimetic diversity is therefore as follows: (1) geographic divergence of warning colours of models leads to the initial evolution of new mimicry rings in parapatry or allopatry (Turner, 1971, 1984; Brown, Sheppard & Turner, 1974; Mallet & Singer, 1987; Mallet, 1993); (2) speciation and possibly habitat divergence of models can allow divergent mimetic patterns to become sympatric; (3) with complete habitat overlap, unilateral Müllerian mimicry should lead to a single mimicry ring in any one area; however, the existence of different abundant mimetic patterns and predators in different habitats/microhabitats can stabilize divergent patterns within any one locality (Fig. 4). This can lead to a lack of convergence of colour patterns over the whole area, and stasis of diverse sympatric mimicry rings.

CONCLUSION

We have uncovered behaviours that reduce overlap between mimicry rings and improve the probability that mimics are found at the same heights and in the same microhabitats. It is likely that co-mimics have similar habits because the diversifying *melpomene*-group species evolved unilaterally towards ithomiines or *erato*-group *Heliconius*, firstly in habitat or microhabitat, and then in colour pattern and behaviour. Mimetic stasis due to the habitat separation that we have found could then prevent a more parsimonious, single local mimicry ring from evolving.

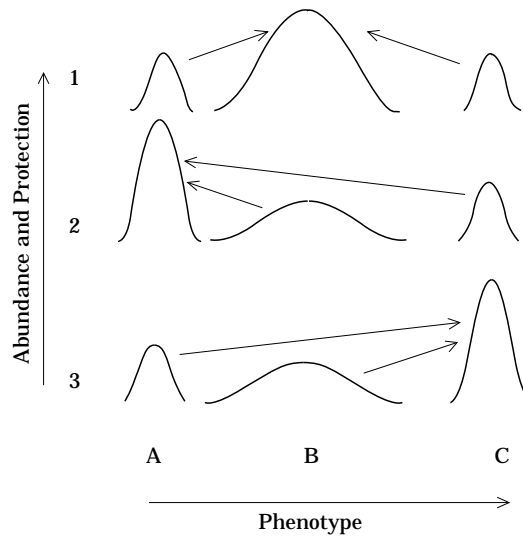


Figure 4. Stability of sympatric mimicry rings. If three different mimicry rings (A, B, C) are distributed among three different microhabitats or habitats (1, 2, 3), and predators are also distributed differentially in these habitats, then different predators would perceive different mimicry rings as dominant. This effect, coupled with unidirectional (non-coevolutionary) evolution of Müllerian mimicry, can stabilize different mimicry rings in different habitats. The protection and abundance afforded by each mimicry ring in each habitat is shown by the area under the curve of protection (see Turner, 1977). Evolution of mimicry within each species, shown by arrows, would be towards the commonest and best protected mimicry ring in that species' favoured habitat, so providing stabilizing selection for a diversity of mimicry rings.

ACKNOWLEDGEMENTS

We are grateful to Janet Burcham and Dave Burton for field assistance. We thank the Servicio de Parques Nacionales and NSF grant no. DEB 79-06033 for supporting our work in Corcovado National Park. We also thank Darlyne and Alex Murawski, Annie Simpson de Gamboa, and Jack Longino for help and encouragement in the field. George Beccaloni, Chris Jiggins, Owen McMillan, Dick Vane-Wright and an anonymous reviewer kindly read the manuscript and advised changes.

REFERENCES

- Ackery PR, Smiles RL. 1976.** An illustrated list of the type-specimens of the Heliconiinae (Lepidoptera: Nymphalidae) in the British Museum (Natural History). *Bulletin of the British Museum (Natural History), Entomology* **32**: 171-214.
- Bates HW. 1862.** Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London* **23**: 495-566.
- Benson WW. 1972.** Nature Selection for Müllerian mimicry in *Heliconius erato* in Costa Rica. *Science* **176**: 936-939.
- Benson WW. 1978.** Resource partitioning in passion vine butterflies. *Evolution* **32**: 493-518.
- Brower AVZ. 1994a.** Phylogeny of *Heliconius* butterflies inferred from mitochondrial DNA sequences (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution* **3**: 159-174.
- Brower AVZ. 1994b.** Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution* **48**: 000-000.
- Brower LP, Brower JVZ, Collins CT. 1963.** Experimental studies of mimicry. 7. Relative palatability and Mullerian mimicry among Neotropical butterflies of the subfamily Heliconiinae. *Zoologica, New York* **48**: 65-84.

- Brown KS. 1973.** *A Portfolio of Neotropical Lepidopterology*. Rio de Janeiro, Brazil: privately published.
- Brown KS. 1976.** An illustrated key to the silvaniform *Heliconius* (Lepidoptera: Nymphalidae) with descriptions of new subspecies. *Transactions of the American Entomological Society* **102**: 373–484.
- Brown KS. 1981.** The biology of *Heliconius* and related genera. *Annual Review of Entomology* **26**: 427–456.
- Brown KS. 1988.** Mimicry, aposematism and crypsis in neotropical Lepidoptera: the importance of dual signals. *Bulletin de la Société Zoologique de France* **113**: 83–101.
- Brown KS, Benson WW. 1974.** Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid.: Nymph.). *Biotropica* **6**: 205–228.
- Brown KS, Sheppard PM, Turner JRG. 1974.** Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proceedings of the Royal Society of London, B* **187**: 369–378.
- Chai P. 1986.** Field observations and feeding experiments on the responses of rufous-tailed jacamars (*Galbula ruficauda*) to free-flying butterflies in a tropical rainforest. *Biological Journal of the Linnean Society* **29**: 166–189.
- Deinert EI, Longino JT, Gilbert LE. 1994.** Mate competition in butterflies. *Nature (London)* **370**: 23–24.
- Douglas MM, Grula JW. 1978.** Thermoregulatory adaptations allowing ecological range expansion by the Pierid butterfly *Nathalis iole* Boisduval. *Evolution* **32**: 776–783.
- Drummond BA, Brown KS. 1987.** Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval food plants. *Annals of the Missouri Botanical Garden* **74**: 341–358.
- Dunlap-Pianka HL, Boggs CL, Gilbert LE. 1977.** Ovarian dynamics in heliconiine butterflies: programmed senescence versus eternal youth. *Science* **197**: 487–490.
- Edmunds M. 1974.** *Defence in Animals*. Harlow, Essex: Longmans.
- Eltringham H. 1916.** On specific and mimetic relationships in the genus *Heliconius*. *Transactions of the Entomological Society of London* **1916**: 101–148.
- Endler JA. 1978.** A predator's view of animal color patterns. *Evolutionary Biology* **11**: 319–364.
- Gilbert LE. 1972.** Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences, USA* **69**: 1403–1407.
- Gilbert LE. 1975.** Ecological consequences of a coevolved mutualism between butterflies and plants. In: Gilbert LE, Raven PR, eds. *Coevolution of Animals and Plants*. Austin, TX: University of Texas Press, 210–240.
- Gilbert LE. 1976.** Postmating female odor in *Heliconius* butterflies: a male-contributed antiaphrodisiac? *Science* **193**: 419–420.
- Gilbert LE. 1983.** Coevolution and mimicry. In: Futuyma DJ, Slatkin M, eds. *Coevolution*. Sunderland, Mass.: Sinauer Associates, 263–281.
- Gilbert LE. 1984.** The biology of butterfly communities. In: Vane-Wright RI, Ackery PR, eds. *The Biology of Butterflies* (Symposia of the Royal Entomological Society of London, 11). London: Academic Press, 41–54.
- Gilbert LE. 1991.** Biodiversity of a Central American *Heliconius* community: pattern, process, and problems. In: Price PW, Lewinsohn TM, Fernandes TW, Benson WW, eds. *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. New York: John Wiley, 403–427.
- Herwitz SR. 1981.** *Regeneration of Selected Tropical Tree Species in Corcovado National Park, Costa Rica*. (Univ. Calif. Publ. Geog. 24.) Los Angeles: Univ. California Press.
- Karr JR. 1976.** Within- and between-habitat avian diversity in African and Neotropical lowland habitats. *Ecological Monographs* **46**: 457–481.
- Kingsolver JG. 1988.** Thermoregulation, flight, and the evolution of wing pattern in pierid butterflies: the topography of adaptive landscapes. *American Zoologist* **28**: 899–912.
- Longino JT. 1984.** *Shoots, parasitoids and ants as forces in the population dynamics of Heliconius hewitsoni in Costa Rica*. Ph.D. Dissertation, University of Texas at Austin.
- Mallet J. 1984.** Population structure and evolution in *Heliconius* butterflies. PhD Dissertation, University of Texas at Austin.
- Mallet J. 1986.** Gregarious roosting and home range in *Heliconius* butterflies. *National Geographic Research* **2**: 198–215.
- Mallet J. 1993.** Speciation, raiation, and color pattern evolution in *Heliconius* butterflies: evidence from hybrid zones. In: Harrison RG, ed. *Hybrid Zones and the Evolutionary Process*. New York: Oxford University Press, 226–260.
- Mallet J, Barton NH. 1989.** Strong natural selection in a warning color hybrid zone. *Evolution* **43**: 421–431.
- Mallet J, Jackson DA. 1980.** The ecology and social behaviour of the Neotropical butterfly *Heliconius xanthocles* Bates in Colombia. *Zoological Journal of the Linnean Society* **70**: 1–13.
- Mallet J, Singer MC. 1987.** Individual selection, kin selection, and the shifting balance in the evolution of warning colours: the evidence from butterflies. *Biological Journal of the Linnean Society* **32**: 337–350.
- Mallet J, Barton N, Lamas G, Santisteban J, Muedas M, Eeley H. 1990.** Estimates of selection and gene flow from measures of cline width and linkage disequilibrium in *Heliconius* hybrid zones. *Genetics* **124**: 921–936.

- Müller F. 1879.** *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London* **1879**: xx–xxix.
- Murawski DA, Gilbert LE. 1986.** Pollen flow in *Psiguria warszewiczii*: a comparison of *Heliconius* butterflies and hummingbirds. *Oecologia (Berlin)* **68**: 161–167.
- Nijhout HF, Wray GA, Gilbert LE. 1990.** An analysis of the phenotypic effects of certain colour pattern genes in *Heliconius* (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society* **40**: 357–372.
- Papageorgis C. 1974.** The adaptive significance of wing coloration of mimetic neotropical butterflies. Ph.D. Dissertation, Princeton University.
- Papageorgis C. 1975.** Mimicry in neotropical butterflies. *American Scientist* **63**: 522–532.
- Pearson DL. 1971.** Vertical stratification of birds in a tropical dry forest. *Condor* **73**: 46–55.
- Poole RW. 1970.** Habitat preferences of some species of a Müllerian-mimicry complex in Northern Venezuela, and their effects on evolution of mimic-wing pattern. *Journal of the New York Entomological Society* **78**: 121–129.
- Ridgely RS. 1976.** *A Guide to the Birds of Panama*. Princeton: Princeton Univ. Press.
- Roland J. 1982.** Melanism and diel activity of alpine *Colias* (Lepidoptera: Pieridae). *Oecologia (Berlin)* **53**: 214–221.
- Silberglied RE. 1984.** Visual communication and sexual selection among butterflies. In: Vane-Wright RI, Ackery PR, eds. *The Biology of Butterflies* (Symposia of the Royal Entomological Society of London, 11). London: Academic Press, 207–223.
- Smiley JT. 1978.** The host plant ecology of *Heliconius* butterflies in Northeastern Costa Rica. Ph.D. Dissertation, University of Texas at Austin.
- Swihart SL. 1967.** Neural adaptations in the visual pathway of certain heliconiine butterflies and related forms to variations in wing coloration. *Zoologica, New York* **52**: 1–14.
- Terborgh J, Weske JS. 1969.** Colonization of secondary habitats by Peruvian birds. *Ecology* **50**: 765–782.
- Thomas CD. 1990a.** Herbivore diets, herbivore colonization, and the escape hypothesis. *Ecology* **71**: 610–615.
- Thomas CD. 1990b.** Fewer species. *Nature (London)* **347**: 237.
- Turner JRG. 1971.** Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies. In: E. R. Creed, ed. *Ecological Genetics and Evolution*. Oxford: Blackwell, 224–260.
- Turner JRG. 1975.** Communal roosting in relation to warning colour in two Heliconiine butterflies (Nymphalidae). *Journal of the Lepidopterists' Society* **29**: 221–226.
- Turner JRG. 1976.** Adaptive radiation and convergence in subdivisions of the butterfly genus *Heliconius* (Lepidoptera: Nymphalidae). *Zoological Journal of the Linnean Society* **58**: 297–308.
- Turner JRG. 1977.** Butterfly mimicry—genetical evolution of an adaptation. *Evolutionary Biology* **10**: 163–206.
- Turner JRG. 1978.** Why male butterflies are non-mimetic: natural selection, sexual selection, group selection, modification and sieving. *Biological Journal of the Linnean Society* **10**: 385–432.
- Turner JRG. 1983.** Mimetic butterflies and punctuated equilibria: some old light on a new paradigm. *Biological Journal of the Linnean Society* **20**: 277–300.
- Turner JRG. 1984.** Mimicry: the palatability spectrum and its consequences. In: Vane-Wright RI, Ackery PR, eds. *The Biology of Butterflies* (Symposia of the Royal Entomological Society of London, 11). London: Academic Press, 141–161.
- Vane-Wright RI. 1976.** A unified classification of mimetic resemblances. *Biological Journal of the Linnean Society* **8**: 25–56.
- Wickler W. 1968.** *Mimicry in Plants and Animals*. New York: McGraw Hill.