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

JAMES MALLETT
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.
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 Heliconiidae, 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
BEHAVIOUR AND MIMICRY IN HELICONIUS

Table 1. Heights of Psiguria flowers used during flight observations

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

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
found to be repellant 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. pachinus; 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 sylax and Tithorea tarricina, respectively. The mottled patterns of these two 'sylaniform' 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 junio, Agraulis vanillae, Dryadula phaetusa, Eueides aliphera, E. lybia, E. vibilia) 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 heliconines 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 heliconines 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. hawtsoni 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
BEHAVIOUR AND MIMICRY IN HELICONIUS 169

Table 2. Habitats in which Heliconius roost.

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

*F (species)=1×(proportion in low second growth) + 2×(proportion in tall secondary forest) + 3×(proportion in mature forest). See Smiley (1978).

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.
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 (Kruskall-Wallis test, $H = 191.7$ [corrected for ties], 8 d.f., $P < 0.001$). 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 ithomelines, not...
Table 3. Overlap in roosting heights of Heliconius. Overlap of species X on species Y is expressed as proportion of the height range (±1 SD, metres) of species X overlapped by the height range of species Y. Mimetic alliances are shown in boxes.

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>Y</th>
<th>charitonia</th>
<th>erato</th>
<th>melpomene</th>
<th>sara</th>
<th>pachinus</th>
<th>hecata</th>
<th>doris</th>
<th>simenius</th>
<th>hecule</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x ± 1 SD m</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>charitonia (6)</td>
<td>1.52 ± 0.39</td>
<td>-</td>
<td>100</td>
<td>62</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>erato (104)</td>
<td>1.43 ± 0.30</td>
<td>79</td>
<td>-</td>
<td>49</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>melpomene (26)</td>
<td>1.98 ± 0.35</td>
<td>44</td>
<td>45</td>
<td>-</td>
<td>14</td>
<td>32</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>sara (25)</td>
<td>3.28 ± 0.90</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>-</td>
<td>100</td>
<td>69</td>
<td>49</td>
<td>88</td>
<td>79</td>
</tr>
<tr>
<td>pachinus (37)</td>
<td>3.80 ± 1.62</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>55</td>
<td>-</td>
<td>59</td>
<td>66</td>
<td>87</td>
<td>82</td>
</tr>
<tr>
<td>hecata (41)</td>
<td>3.90 ± 0.96</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>65</td>
<td>100</td>
<td>-</td>
<td>81</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>doris (6)</td>
<td>7.80 ± 1.50</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>24</td>
<td>17</td>
<td>-</td>
<td>33</td>
<td>88</td>
</tr>
<tr>
<td>simenius (17)</td>
<td>4.44 ± 1.84</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>43</td>
<td>77</td>
<td>52</td>
<td>81</td>
<td>-</td>
<td>96</td>
</tr>
<tr>
<td>hecule (26)</td>
<td>6.99 ± 4.23</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>17</td>
<td>32</td>
<td>23</td>
<td>94</td>
<td>42</td>
<td>-</td>
</tr>
</tbody>
</table>
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 Melinae scylax and Tithorea tarricina, the respective co-mimics of H. ismenius and H. hecale. We have occasionally seen Melinae scylax perching at dusk on living leaves low in the understory. However, Melinae lays its eggs on canopy epiphytes of Juanulloa and Marka (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, hawitsoni) 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. hawitsoni 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 = 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.

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>gregariousness</th>
<th>mimetic roosting</th>
<th>charitonia</th>
<th>erato</th>
<th>melpomene</th>
<th>sara</th>
<th>pachius</th>
<th>Hewitsoni</th>
<th>doris</th>
<th>ismenius</th>
<th>lecale</th>
</tr>
</thead>
<tbody>
<tr>
<td>charitonia (14)</td>
<td>0.86</td>
<td>∞</td>
<td>12</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>erato (397)</td>
<td>0.11</td>
<td>6</td>
<td>350</td>
<td>44</td>
<td>0</td>
<td>14</td>
<td>11</td>
<td>0</td>
<td>3</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>melpomene (33)</td>
<td>0.42</td>
<td>5</td>
<td>20</td>
<td>14</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>sara (12)</td>
<td>0.00</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>pachius (57)</td>
<td>0.39</td>
<td>0</td>
<td>14</td>
<td>3</td>
<td>0</td>
<td>25</td>
<td>22</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Hewitsoni (54)</td>
<td>0.54</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>29</td>
<td>47</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>doris (6)</td>
<td>0.17</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>ismenius (14)</td>
<td>0.21</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>lecale (29)</td>
<td>0.29</td>
<td>0</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>12</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>lecale (76)</td>
<td>0.76</td>
<td>0</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>12</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>22</td>
<td></td>
</tr>
</tbody>
</table>
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 Papageorgios (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 Papageorgios (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 Papageorgios. Papageorgios (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 Papageorgios' 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 heliconine 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 Mullerian 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


