Polymorphic mimicry, microhabitat use, and sex-specific behaviour

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Abstract

In order to assess the adaptive importance of microhabitat segregation for the maintenance of mimetic diversity, I explore how flight height varies between the sympatric forms of the polymorphic butterfly Heliconius numata and their respective models in the genus Melinaea. There is no evidence for vertical stratification of mimicry rings in these tiger-patterned butterflies, but males of H. numata tend to fly significantly higher than females and the Melinaea models. This difference in microhabitat preference likely results from females searching for host plants whereas males are patrolling for mates. I then present an extension of Müller’s mimicry model for the case of partial behavioural or spatial segregation of sexes. The analysis suggests that sex-specific behaviours can make mimicry more beneficial, simply by reducing the effective population size participating in mimicry. The interaction between mimicry and sex-specific behaviours may therefore facilitate the evolution of polymorphism via enhanced, fine-scale local adaptation.

Introduction

Müllerian mimicry is the adaptive resemblance of several chemically defended prey that benefit by sending a unique warning signal to predators (Müller, 1879). Contrary to Batesian mimics (edible prey that parasitize the warning signals of nasty models), Müllerian mimics reinforce the efficiency of their own signal; the protection from predation is therefore maximal when all species converge on the same signal. Phenotypic deviants, not recognized as unpalatable by the predators, are selected against (Benson, 1972; Mallet & Barton, 1989; Lindström et al., 1999; Kapan, 2001; but see Rowe et al., 2004), which makes polymorphism and diversification theoretically unlikely (for a review see Joron & Mallet, 1998; see also Jeffords et al., 1979 showing selection against deviant Batesian mimics).

However, there is pervasive diversity in warning signals in nature, found at all taxonomic and geographical scales. Examples include diverging geographic races in Dendrobates frogs (Symula et al., 2001) and Heliconius butterflies (Turner, 1976; Brower, 1996), local coexistence of numerous mimicry rings (Mallet & Gilbert, 1995; Beccaloni, 1997a, b), and even local mimetic polymorphism (Owen et al., 1994). In particular, the butterfly Heliconius numata Cramer (Nymphalidae: Heliconiinae) has up to seven different forms in some localities, each of which is involved in different mimicry rings with large ithomine butterflies (Nymphalidae: Ithomiinae) (Brown & Benson, 1974; Joron et al., 1999; Fig. 1).

Segregation by microhabitat is one likely cause for both the coexistence of Müllerian mimicry rings and the mimetic polymorphism of some species. If there is fine scale spatial heterogeneity in habitat, then any one predator may deal with only a limited set of prey types. Therefore, selection may not favour the resemblance between all prey species, and diversity could be maintained (Brown & Benson, 1974; M. Joron & Y. Iwasa, unpublished data). Empirical studies have provided data suggesting some level of horizontal segregation of butterfly mimicry rings in neotropical forest (Mallet & Gilbert, 1995; DeVries et al., 1999; Joron et al., 1999; Willmott & Mallet, 2004). Vertical segregation, a particular case of microhabitat segregation, has received attention in the study of tropical rainforests in the light

Keywords:

Heliconius;
host search;
Ithomiinae;
Lepidoptera;
mate location;
Melinaea;
microhabitat;
Müllerian mimicry;
Nymphalidae;
polymorphism.

of resource partitioning theory. Some flight height stratification has been found within Neotropical butterfly guilds, albeit with much overlap (Papageorgis, 1975; Burd, 1994; Medina et al., 1996; Beccaloni, 1997b). However, flight-height segregation of colour patterns can also be the consequence of ecological mechanisms other than mimicry, such as host-plant use at similar heights by sister taxa (Beccaloni, 1997b) or intraspecific signalling in different lighting environments (Endler, 1993).

If vertical segregation of predation is a major component of the maintenance of mimetic diversity in one place, taxa radiating in mimicry association should be found at different heights. Polymorphic, mimetic species should have forms flying at the heights of their respective models in the habitat. Heliconius numata, one of the most polymorphic Müllerian mimics with up to seven different morphs belonging to different coexisting tiger-patterned mimicry rings, is therefore an ideal system to test whether flight-height strata represent microecological niches important in the initial stages of mimetic diversification. Here I present data on flight height of the different forms of H. numata and their respective Melinaea co-models. Although I found no evidence for vertical segregation by mimetic pattern, there was a pattern of sex-specific flight height in H. numata probably linked to some aspects of male mate-location and female oviposition behaviours in this forest species. A simple density-dependent model suggests that such niche differences between sexes may facilitate the evolution of Müllerian mimicry and the maintenance of polymorphism by enhancing fine-scale local adaptation.

Materials and methods

Heliconius numata is a butterfly found in the lowland and submontane forests of the Amazon basin. It is polymorphic for so-called ‘tiger patterns’ of orange, yellow and black; each form is a very accurate Müllerian mimic of one or several species in the genus Melinaea (Nymphalidae: Ithomiinae) (Fig. 1). The corresponding mimicry rings also include other butterflies in the Ithomiinae, Danainae, Heliconiinae (Nymphalidae), and Riodininae (Lycaenidae), as well as day-flying tiger moths (Arctiidae: Pericopinae) (Brown & Benson, 1974). Because of the extreme resemblance of H. numata to Melinaea, the mimetic relationship is supposed to be strongest between these two taxa. Spatial variation in the frequency of morphs of these two taxa was shown to be correlated, suggesting strong local selection in H. numata for resemblance to Melinaea (Joron et al., 1999). (For further illustrations and natural history of tiger-patterned mimicry rings involving Heliconius and Ithomiines see Brown & Benson, 1974; Brown, 1976; Beccaloni, 1997a; Joron, 2003.)

Ten sites were sampled in the Amazonian foothills of the Andes in the vicinity of Tarapoto, eastern Peru, in August and September 1997. The area is covered with mostly dry submontane forest (300–1000 m). Most collections were carried out in tall secondary forest with disturbed areas nearby (details in Joron et al., 1999). Butterflies were caught using nets with a 2 m pole, allowing capture up to 4.5 m in height. Although some of the H. numata flying higher could be attracted to red/orange rags waved in the sun, these were excluded from the analysis as attraction may depend on form or sex. Melinaea fly slowly and are easily caught. Using previous measurements taken along the butterfly net (three 60 cm-long pole sections plus a 45 cm-diameter ring), I estimated for each butterfly the flight height before capture (to the nearest 10 cm below 2.5 m, to the nearest 50 cm above). Flight height varies according to rugged terrain and the presence of vegetation. In addition to sex, form, and flight height, two other variables likely to affect flight activity, time and weather, were recorded upon capture. Weather was measured using a subjective

![Fig 1](image-url) Tiger-pattern mimicry rings found near Tarapoto, Eastern Peru. Top row: the five major colour-pattern forms of Melinaea species (Nymphalidae: Ithomiinae). Bottom row: their respective mimetic morphs in the polymorphic species Heliconius numata (Nymphalidae: Heliconiinae). The different forms are made of varying combinations of black, dark orange (grey areas on the figure) and bright yellow (white areas), which give them a strikingly different appearance in flight. By mimetic pair, from left to right: M. marsaeus phasiana and H. n. arcuella; M. m. rileyi and H. n. aurora; M. m. mothone and H. n. bicoloratus; M. menophilus ssp. nov. and H. n. tarapotensis; M. ludovica ludovica and H. n. silvana.
estimate of cloud cover from 1 (low or no cloud cover) to 3 (heavy). Ithomiines were identified by Gerardo Lamas and vouchers were deposited in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru. Heliconius numata forms were identified using Brown (1976). For the analysis, only the five commonest forms (H. n. aurora, silvana, tarapotensis, bicoloratus and arcuella and their respective models; see Fig. 1) were considered.

Nonparametric Kruskall–Wallis tests were applied because the distribution of flight heights deviates from normality (Kolmogorov–Smirnov normality test, P < 0.01). To test for interactions, two-way nonparametric tests could not be applied because of the unbalanced structure of the dataset, so flight-height was square-root-transformed using the link to approximate a normal distribution (Kolmogorov–Smirnov test, P > 0.15). Generalized linear models were applied with sex and form as factors, and time or cloud cover as covariates.

Results

The data show that the different forms of H. numata do not fly at different heights (Kruskall–Wallis test, adjusted for ties: H = 1.18, d.f. = 4, n.s.), nor do they fly at different heights in the different sites (H = 12.90, d.f. = 9 n.s.). Despite the wide variation, however, there is a highly significant difference between sexes (H = 31.56, d.f. = 1, P < 10−6): the 90 males were caught flying at a mean height of 2.30 m, whereas the 35 females were caught at a mean height of 1.09 m (see Table 1; Fig. 2), but no interaction was found between sex and form (F4,112 = 0.75, n.s.; Table 2; Fig. 3a). Time of capture had a significant effect in interaction with sex (Table 2; Fig. 3b) whereas the cloud cover has no significant effect (Table 2). Cloud cover is not independent of time of day, which could explain why the trend of increasing flight height with increasing cloud cover seen on Fig. 3c is not significant in the full model (Table 2).

Ithomiine models, in the genus Melinaea, were caught at a mean height of 1.26 m (Table 1) with no difference between sexes (H = 2.77, d.f. = 1, P = 0.096), colour-patterns (H = 6.53, d.f. = 5, n.s.), or time (F1,49 = 0.01, n.s.). Melinaea flight height was very significantly different from that of male H. numata (H = 37.59, d.f. = 1, P < 10−6), but not different from that of female H. numata (H = 1.65, d.f. = 1, n.s.) (Fig. 2).

An extension to Müller’s model

In view of the consistent flight-height difference between sexes in H. numata, which may be viewed as a different microhabitat use by the two sexes, I implemented an extension of Müller’s (1879) original model of mimicry that includes a measure of microhabitat segregation within the mimic species.

Table 1 Mean and median flight height (in metres) of Heliconius numata and Melinaea spp., as distributed by sex and by colour form.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Mean height</th>
<th>SE</th>
<th>Median</th>
<th>Range</th>
</tr>
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<td>Heliconius numata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>34</td>
<td>1.09</td>
<td>0.11</td>
<td>1</td>
<td>0–2.5</td>
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<td>Males</td>
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<td>2.30</td>
<td>0.10</td>
<td>2</td>
<td>0.2–4.5</td>
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<td>Colour forms*:</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>silvana/illustris</td>
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<td>1.99</td>
<td>0.24</td>
<td>1.65</td>
<td>0.3–3.5</td>
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<tr>
<td>bicoloratus</td>
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<td>2.02</td>
<td>0.17</td>
<td>1.8</td>
<td>0.2–4.5</td>
</tr>
<tr>
<td>arcuella</td>
<td>9</td>
<td>1.88</td>
<td>0.42</td>
<td>1.9</td>
<td>0.3–4.0</td>
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<td>aurora</td>
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<td>1.67</td>
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<td>tarapotensis</td>
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<td>1.99</td>
<td>0.16</td>
<td>1.8</td>
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<td>Melinaea spp.</td>
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<td>Females</td>
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<tr>
<td>Males</td>
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<td>Colour forms*:</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>M. ludovica</td>
<td>1</td>
<td>0.40</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>M. m. mothone</td>
<td>4</td>
<td>1.55</td>
<td>0.32</td>
<td>1.55</td>
<td>0.8–2.3</td>
</tr>
<tr>
<td>M. m. phasiana</td>
<td>14</td>
<td>1.17</td>
<td>0.12</td>
<td>1.2</td>
<td>0.3–2</td>
</tr>
<tr>
<td>M. s. cydon</td>
<td>2</td>
<td>1.10</td>
<td>0.59</td>
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<td>0.5–1.7</td>
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<tr>
<td>M. m. phasiana</td>
<td>9</td>
<td>1.88</td>
<td>0.42</td>
<td>1.9</td>
<td>0.3–4.0</td>
</tr>
</tbody>
</table>

n, total number; SE, standard error of mean.

*Mimicry associations: M. ludovica is a model for H. n. silvana, M. marsaeus mothone for H. n. bicoloratus, M. marsaeus phasiana for H. n. arcuella, M. satevis cydon (and M. marsaeus rileyi, not found here) for H. n. aurora and variants, M. menophilus spp. nov. and M. satevis tarapotensis for H. n. tarapotensis and variants.

In Müller’s (1879) model, \( n_k \) is the number of prey predators kill per unit time in a locality to learn the prey colour pattern; \( M \) is the population size of the model species and \( m \) the total population size of the focal (mimic) species. In the absence of mimicry, the models and the focal species are distinct and predators sample \( n_k \) individuals of each species. If the focal species is
indistinguishable from the model, however, only $m_k = n_k \frac{m}{(m+M)}$ mimics are killed, and Müller (1879) showed that the ultimate benefits of mimicry, defined as the reduction in predation enjoyed by mimicking the models, are then $g = n_k M/(m(m+M))$ (the demonstration is reprinted in Joron & Mallet, 1998).

Here I introduce the parameter $d$ as the proportion of the focal species population that participates in the education of predators in the focal habitat; $d$ can be viewed as a level of habitat segregation of sexes, or as a behavioural sexual diphenism, by which one sex is partly or completely independent of predation by the focal habitat’s predators. $d$ varies between 0.5 and 1 ($d = 1$ in Müller’s equations). In the absence of mimicry, predators sample $n_k$, the individuals of the focal species in the focal habitat ($A$), where $n_{k,A} = n_k$. With mimicry in the focal habitat, the learning predators sample $m_{k,A} = n_k \frac{dm}{(dm+M)}$ mimics per unit time in the focal habitat. The mortality of the proportion of the focal species’ population that has chosen another habitat ($B$) is $n_{k,B}$ whether there is mimicry or not in the focal habitat. The ultimate benefits of mimicry for the focal species are

$$gd = \frac{(n_{k,A} + n_{k,B}) - (m_{k,A} + n_{k,B})}{m} = \frac{n_k M}{m(dm+M)}.$$

Note that the mortality $n_{k,B}$ outside the habitat cancels out in the calculation of $gd$. On the diagram (Fig. 4a), $g$ is the benefit of evolving from I to III, whereas $gd$ is the benefit of evolving from II to IV.

The ratio of $gd$ to $g$ compares the mimetic benefits for a species with habitat segregation $d$, relative to that of a species without habitat segregation ($d = 1$). This ratio, $G$, has a simple expression:

$$G = \frac{gd}{g} = \frac{m+M}{dm+M}.$$

$G$ is plotted on Fig. 4b as a function of the mimic-to-models ratio in the focal habitat, $dm/M$, for different

### Table 2

<table>
<thead>
<tr>
<th>Model</th>
<th>Source</th>
<th>d.f.</th>
<th>Type 3 SS</th>
<th>Mean square</th>
<th>$F$-value</th>
<th>$P$-value</th>
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<td>Sex $\times$ form</td>
<td>Sex</td>
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<td>3.93</td>
<td>3.93</td>
<td>42.84</td>
<td>0.000*</td>
</tr>
<tr>
<td></td>
<td>form</td>
<td>4</td>
<td>0.06</td>
<td>0.02</td>
<td>0.16</td>
<td>0.956</td>
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<tr>
<td></td>
<td>Sex $\times$ form</td>
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<td>0.34</td>
<td>0.09</td>
<td>0.93</td>
<td>0.450</td>
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<tr>
<td></td>
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<td>7.92</td>
<td>0.08</td>
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<tr>
<td>Sex $\times$ time $\times$ clouds</td>
<td>sex</td>
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<td>0.63</td>
<td>0.63</td>
<td>8.00</td>
<td>0.006*</td>
</tr>
<tr>
<td></td>
<td>Time</td>
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<td>0.04</td>
<td>0.04</td>
<td>0.54</td>
<td>0.464</td>
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<tr>
<td></td>
<td>Clouds</td>
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<td>0.01</td>
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<td>0.761</td>
</tr>
<tr>
<td></td>
<td>Sex $\times$ time</td>
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<td>0.41</td>
<td>0.41</td>
<td>5.18</td>
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<td>0.05</td>
<td>0.69</td>
<td>0.410</td>
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<tr>
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<td>0.394</td>
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<td></td>
<td>Sex $\times$ time $\times$ clouds</td>
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<td>0.14</td>
<td>0.14</td>
<td>1.81</td>
<td>0.182</td>
</tr>
<tr>
<td></td>
<td>Error*</td>
<td>89</td>
<td>7.05</td>
<td>0.08</td>
<td></td>
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</tr>
</tbody>
</table>

*Because of the presence of some empty cells, the total number of observations in the sex $\times$ time $\times$ clouds model is a little reduced. *Significant effect, 0.05 level.

![Fig. 3](image-url) Mean flight height of male and female *H. numata* as a function of mimetic form (a), time of capture (b), and cloud cover (c). Measurements are in metres ± standard error. Only time of capture has an effect in interaction with sex (see Table 2).
values of \(d\). As \(d < 1\), species with ecological segregation of the sexes always benefit more from mimicry than species whose sexes have similar ecology.

Sex segregation reduces the local population size of the mimic relative to models in the focal habitat \((A)\). The benefits to the mimic are inversely proportional to the squared mimic-to-model ratio \((\text{Mueller}, 1879)\); therefore, as the mimic’s population is reduced, the benefits of mimicry grow faster than the reduction in the number of individuals that benefit from mimicry, resulting in mimetic benefits being an increasing function of the segregation. The effect can be limited if the sexes are only slightly divergent in ecology, or if the mimic is rare relative to the models, but it can be as high as a 30–50% difference in selection when the mimic is abundant and the sexes well segregated by microhabitat \((\text{Fig. 4b})\). Thus, habitat segregation should generally facilitate the evolution of local mimicry.
Therefore, in the absence of constraints and/or conflicts on colour pattern evolution, we expect species with some degree of habitat segregation to show enhanced local adaptation. Local adaptation results in adaptive spatial variation. In mimicry this is measured, for instance, by a correlation between model and mimic frequencies across localities in a geographic area (see e.g. Joron et al., 1999; Kapan, 2001; Symula et al., 2001).

Discussion

Absence of stratification of tiger mimicry rings

The absence of flight height differences between the different forms of H. numata and its models makes vertical stratification an unlikely explanation for colour-pattern divergence in this species, and for the maintenance of diversity of these mimicry rings. The range of flight-height variation in H. numata is wide compared with the flight height of their Melinaea model, and spans most of the ithomine flight-height strata described by Beccaloni (1997b). Heliconius numata therefore appears as a flight-height generalist within a habitat.

Previous studies on Neotropical butterflies have shown some stratification in flight height (Burd, 1994; Medina et al., 1996; Beccaloni, 1997b) or in roosting height (Mallet & Gilbert, 1995), but we do not know whether this level of segregation causes a selection strong enough to allow for the divergence of mimicry rings. Here, the accurate mimicry of the different forms of H. numata to the different Melinaea species does suggest that predators can discriminate between these patterns, but it is possible that some generalization between all tiger patterns allows several forms to coexist as a result of a somewhat relaxed selection (Mallet & Joron, 1999; Rowe et al., 2004). Nevertheless, variation in form frequency appears to stem from a strong horizontal heterogeneity of mimetic communities (Joron et al., 1999) rather than a vertical segregation of the models (this study). Rather than a strong stratification of mimicry rings, the lack of spatial movement of predators, along with some possible level of microecological specialization in the butterflies across the habitat (Srygley & Chai, 1990b; DeVries et al., 1999; Willmott & Mallet, 2004; Merchán et al., 2005), may thus allow the landscape-scale coexistence of mimicry rings. Therefore, a mosaic of microhabitats is likely to enhance the level of local diversity in mimicry (Mallet & Gilbert, 1995; M. Joron & Y. Iwasa, unpublished data).

It is possible that our measurements omit some aspects of the H. numata life history, such as roosting behaviour. It is indeed suggested that relatives of H. numata roost high in the canopy, despite a very wide range of roosting height measurements (Turner, 1975; Mallet & Gilbert, 1995). Part of the predation might take place at or around such roosting sites where butterflies are rarely observed (Mallet & Gilbert, 1995). However, a scenario for divergence based on roosting segregation requires that colour forms that all fly at the same heights and with considerable variation during the day roost at sharply distinct heights in the canopy during the night. Although this hypothesis is difficult to evaluate in the absence of data for nocturnal behaviour of these butterflies and their predators in the canopy, it does not seem to fit the available data for the tiger-patterned mimicry rings (Turner, 1975; Mallet & Gilbert, 1995). Horizontal heterogeneity of mimicry and gene flow remain more likely causes for the polymorphism in H. numata.

Sex-specific flight height in H. numata

The difference in flight height between male and female H. numata is one of the striking results of this study. Sex-specific flight height has rarely been mentioned in the mimicry literature, although this behavioural dimorphism is easily observed in the field for H. numata. When not feeding at flowers, females are usually found looking for host-plants low in the understory, with a weak wing beat, quite like their Melinaea models. During sunny hours, male H. numata are usually found patrolling their home range (Mallet, 1986; Mallet et al., 1987), searching for mates as well as pollen sources, following a nearly constant route. At any one spot, males may be observed cruising vigorously at mid-elevation, alternating between gliding and flapping sequences, a flight pattern named ‘promenade’ by Brown & Benson (1974). Other Heliconius species such as H. heurippa and H. cydno seem to have a similar behaviour (M. Joron, personal observations; C. Jiggins, J. Mallet, personal communications; see also Gilbert, 1991; Merchán et al., 2005).

Male Heliconius are known to use visual cues to locate potential mates (McMillan et al., 1997; Jiggins et al., 2001; Sweeney et al., 2003), and male H. numata are readily attracted to red or orange rags waved in the sun (Brown & Benson, 1974; M. Joron, personal observations). Besides, female H. numata can mate multiply, and may accept males even when a few months old (Brown & Benson, 1974; M. Joron, personal observations). Therefore, the higher flight of H. numata males may be a mate-locating strategy that allows locating females visually on a wide radius without having to enter the dense lower vegetation. Heliconius numata are found in a wide diversity of habitats, but are especially common in tall secondary forest, where males are seen flying above the shrub layer (>2 m). It may be significant that in H. cydno, also found in tall forest with similar vegetation as H. numata, males also tend to fly high whereas females are found in the understory (Estrada & Jiggins, 2002; Merchán et al., 2005; M. Joron, personal observations).

Contrary to mate-searching males, females may be searching the denser shrub layer, meticulously looking for oviposition plants. Most Heliconius species, including H. ismenius (the sister species to H. numata), oviposit on Passifloraceae plants found in light gaps or in
second-growth understory, and rarely in the canopy (Mallet & Gilbert, 1995, and references therein; J. Longino, personal communication). In the present study, ovipositing *H. numata* females were indeed found around low shoots (mean height 1.10 m, SD = 0.70 m, range 0.2–2.5 m, n = 11). The generally low flight height of female *H. numata* must therefore reflect the preferred height for larval host plants, and a finer-scale, more systematic use of their habitat.

The flight-height variation over the course of the day seems in accordance with the mate search vs. host search dichotomy. The sexual difference in flight height is nonsignificant in the early morning and late afternoon, and peaks in the middle of the day (Fig. 3b). Both sexes typically start the day by looking for pollen and nectar at Palicourea, Psiguria, and other flowers, and males and females seem to have the same floral resources (M. Joron, personal observations; J. Mallet, personal communication; see also Gilbert, 1991; Mallet & Gilbert, 1995, although these studies do not differentiate by sex). By mid-morning males start looking for mates, whereas females start searching for oviposition plants. This appears to be reflected in the general differences in flight height observed in this study. We may hypothesize that the male mate-location cruise requires higher levels of energy, encountered during the hottest hours of the day, as has been found in Pieris rapae (Hirota & Obara, 2000) and in speckled woods Pararge aegeria (van Dyck et al., 1997). By the end of the afternoon, prior to roosting, sexes tend to fly at similar heights again, so the sex-specific flight height most likely reflects the conspicuously different activities of the two sexes during the day.

Sex-specific flight height was apparently not taken into account in previous studies on mimetic stratification. A prediction would be that other forest interior Heliconius species, such as *H. pachinus* studied by Mallet & Gilbert (1995), should show a sex-specific flight height during the day.

### Sex-specific behaviour and mimicry

From the correspondence in flight height between female *H. numata* and *Melinaea* spp. it is tempting to conclude that the mimetic relationship with *Melinaea* is stronger in female than in male *H. numata*, even though *H. numata* is not sexually dimorphic. As behaviour and flight patterns may be used as a recognition cue by predators (Srygley & Ellington, 1999), male and female *H. numata* may not rely equally on mimicry to avoid predation. Ovipositing females tend to have predictable flight-patterns around host-plants and a less agile flight, so they are thought to be subject to overall higher predation rates (Srygley & Chai, 1990a; Ohsaki, 1995; Srygley & Kingsolver, 2000). Mark-recapture studies in various butterfly species consistently show lower recapture rates for females, which may in part be a result of a higher risk of predation (Ehrlich & Gilbert, 1973; Kingsolver, 1996, 1999; Srygley & Kingsolver, 2000). In contrast, males may rely more on escape, agility, and higher activity levels to avoid predation (Turner, 1978; Mallet & Singer, 1987; Turner, 1995; Merchan et al., 2005), which may compensate for the loss in mimetic protection that results from specific mate-location behaviours (as in Batesian mimicry, e.g. Burns, 1966; Ohsaki, 1995). Again, male butterflies are likely to enjoy best agility and reactivity during the hot hours of the middle of the day (Hardy, 1998; Stutt & Willmer, 1998; Hirota & Obara, 2000), which is also when the sexes have the largest difference in flight heights in the present study (Fig. 3b). Stronger reliance on anti-predator signals in one sex leads one to expect a higher stability of mimetic wing patterns in this sex, such as higher pattern symmetry (Forsman & Merilaita, 1999), canalization (M. Linares, personal communication), or stronger dominance relationships between the colour-pattern alleles, which could be relatively easily tested.

Flight height differences between sexes represent most of the variation in the present data, with a scale of segregation comparable with that of previous studies for whole butterfly guilds (e.g. Beccaloni, 1997b). My extension of Müller’s (1879) number-dependent model, to account for partial segregation of the sexes in micro-habitat, suggests that mate search behaviour and different microhabitat use by sexes can interfere with aposematic colours and mimicry (see also, e.g. Forsman & Appelqvist, 1999 for sex-by-colour pattern interactions in grasshopper survival). Indeed, as mimetic benefits are inversely proportional to the relative abundance of the prey species in the local mimetic community (Müller, 1879; Kapan, 2001), the benefit of joining a local mimicry ring is enhanced when predation is uneven between sexes, as opposed to a situation where both sexes have identical ecologies.

Müller’s model therefore suggests that microhabitat differences between sexes will result in higher benefits for close local mimicry in (at least) one sex. In a heterogeneous landscape, any mechanism that makes local adaptation more likely will also make polymorphism more likely if different alleles are beneficial in different places (see Mitter et al., 1979; Hedrick, 1986), and this also holds in the face of positive frequency-dependence as is typical of Müllerian mimicry (Molofsky et al., 2001; M. Joron & Y. Iwasa, unpublished data). *Heliconius numata* show both sexual differences in microhabitat (this study) and heterogeneity in selection at a very small scale (5–10 km; Joron et al., 1999), which is precisely the combination of factors that should favour local adaptation and, with selection-migration balance between neighbouring sites, polymorphism (Mallet & Barton, 1989; Joron et al., 1999; M. Joron & Y. Iwasa, unpublished data). Therefore, the coincidence of sex-specific behaviours and a spatially variable selection may have enhanced local mimicry adaptation and facilitated the evolution of a spectacular mimetic polymorphism in *H. numata*. 

*J. EVOL. BIOL.* 18 (2005) 547–556 © 2005 EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY
More detailed data on the ecology of mimicry is therefore needed to assess the extent of microhabitat segregation within and between mimicry rings (William & Mallet, 2004). Further theoretical investigation could also predict which level of microhabitat selection is necessary to cause a switch in the outcome of local density dependence resulting in local adaptation. Note that, interestingly, the evolution of mimicry is facilitated in species with spatial segregation (Fig. 4a, evolution from II to IV), but this does not mean the evolution of mimicry enhances the ecological divergence of sexes (evolution from III to IV), unless males benefit from a relaxed predation in the alternative microhabitat. In other words, evolving habitat (or behavioural) preferences between sexes may facilitate the subsequent evolution of mimicry, but evolving mimicry first may prevent the evolution of habitat preferences.

The segregation of sexes with respect to predation is found, for instance, if predation on one sex is partly independent of wing colour. This may be the case for species with vigorous male flight such as H. numata. In that case, and in the absence of conflicts between the selection of male and female traits, male colour will follow the selection for mimicry in females, and differences in predation pressures between sexes (Ohsaki, 1995) will not necessarily result in sexual dimorphism; in contrast, microhabitat selection will help local adaptation. This suggests that sexually dimorphic behaviours may foster the evolution of nonsex-limited genetic polymorphism, which has only been investigated theoretically in a handful of studies (Hedrick, 1993, on sex-dependent habitat selection; see also earlier work by Li, 1963; Kidwell et al., 1977), and has received little attention by empiricists despite the wealth of data on sex-dependent habitat selection and behaviour (see Merilaita & Jormalainen, 1997; Forsman & Appelqvist, 1999, and references therein).

The segregation of sexes with respect to predation may also be caused by their partial spatial separation, possibly linked to behavioural differences, as is found for example in lekking species, or if males use specific or localized resources such as mud puddles (e.g. Battus swallowtails) or pyrrolizidine alkaloid plants (Ithomiines). If colour is also a warning signal for the males in their microhabitat, there could be a frequency-dependent barrier against a change of colour in males. Microhabitat segregation might then result in a sexual dimorphism where the local (mimetic) colour only evolves in females, whereas the other sex either retains the ancestral colour, or evolves mimicry to a different model.

Some sexually dimorphic Müllerian mimics have sexes in different mimicry rings: examples include, in the Neotropics, Parides species (Papilionidae) (West, 1994), Godryis zavaleta, several Pteronymia and Hyalyris species (Nymphalidae: Ithomiinae) (D’Abrera, 1984; William & Mallet, 2004), or Heliconius demeter (Brown & Benson, 1975). Such dimorphisms could result from different microhabitat use by the sexes, or from strong behavioural differences. Fine-scale microhabitat segregation of sexes such as that caused by the concentration of male at hilltops leks in Papilio (e.g. Lederhouse & Scriber, 1996), can also be a scenario for sex-limited Batesian mimicry evolution involving lower levels of stabilizing sexual selection on male colours (Turner, 1978; Herrel & Hazel, 1995). Further studies on mate-location strategies may reveal comparable interactions between sex-specific behaviours and colour mimicry, with potential implications ranging from female transvestism (Sherratt, 2001) to speciation (Jiggins et al., 2001; Naisbit et al., 2001).

Acknowledgments

I am grateful to R. Schulte, M. Rodríguez, and G. Lamas for their help with various aspects of field work in Peru, and to C. Jiggins, J. Mallet, M. Linares and two anonymous reviewers for discussions and comments on the manuscript. I thank the Klorane Foundation and the French Ministry of Higher Education and Research for financial support.

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Received 25 May 2004; revised 18 November 2004; accepted 18 November 2004