Biological Journal of the Linnean Society (1999), *67:* 73–85. With 2 figures

Article ID: bijl.1998.0288, available online at http://www.idealibrary.com on IDEAL®

Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest

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Received 10 March 1998; accepted for publication 10 September 1998

To test whether ithomiine butterfly species within Müllerian mimetic classes are associated in space and time, we sampled a community of ithomiine butterflies at monthly intervals with traps in the canopy and the understory of four forest habitats: primary, higrade, secondary and edge. A species accumulation curve reached an asymptote at 22 species, suggesting that these species have a greater preference for feeding on fruit juices than other ithomiines known to occur at the study site. Species richness and individual abundance showed marked temporal variation, and there were slight differences in the distribution of species richness and individual abundance among the four habitats. The 22 species sampled in this study were not stratified vertically. The five mimetic colour classes of these butterflies were unequally distributed among the four habitats and over the course of the twelve months. There is suggestive evidence that co-mimic species occurred in the same habitats, and strong evidence that they occurred at the same times. Habitat and temporal effects each contributed approximately 10% to the total mimetic class diversity, with the temporal effect being slightly larger than that of habitat. This study demonstrates that Müllerian co-mimic associations can be measured on a much smaller scale than has been done previously.

ADDITIONAL KEY WORDS:—Ithomiinae – Nymphalidae – Müllerian mimicry – habitat association – vertical stratification – species abundance distribution – species randomization – spatial distribution – temporal distribution – habitat destruction.

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0024–4066/99/050073+13 $30.00/0

INTRODUCTION

A remarkable attribute of tropical forest butterfly communities is the pervasivness of interspecific mimicry. Members of the nymphalid subfamily Ithomiinae were postulated to be the original unpalatable models for Batesian and Müllerian mimicry (Bates, 1862; Müller, 1879), and as a result these butterflies are best known for their fundamental role in many neotropical mimicry complexes. These mimicry complexes embrace a wide range of colour patterns and they are typically dominated by an abundance of ithomiine co-mimics (often from different genera and tribes), plus Müllerian and Batesian co-mimics from different families and subfamilies of butterflies (Brown, 1979; Brown & Benson, 1974; Beccaloni, 1997a, b).

The importance of mimicry in neotropical butterfly faunas is evident from the overlapping distributions of co-mimics that have been measured at two spatial scales. The most dramatic examples include the diversity of colour patterns shown by many species and races of ithomiines (and their co-mimics in other groups) that converge across large areas of Central and South America (e.g. Turner, 1977). At this scale when only two species (e.g. *Heliconius erato* and *H. melpomene*) and their multiple co-mimetic colour patterns are mapped over the neotropical region, as done by Sheppard *et al.* (1985), it is difficult to doubt the potent influence of mimicry on the evolution and ecology of tropical butterfly faunas. Secondly, observations at smaller spatial scales testify to the influence of mimicry on butterfly communities. In this case observations from a variety of different sites suggest that sympatric ithomiine mimicry complexes (and some of their co-mimics in other groups) may be separated into vertical strata within forest habitats (Papageorgis, 1975; Burd, 1994; Medina, Robbins & Lamas, 1996; Beccaloni, 1997a). These latter studies essentially conclude that depending on their colour pattern, ithomiine butterflies occupy two strata: those distributed from 1 m or lower, and those distributed above 1 m (see Beccaloni, 1997a for summaries). Consideration of these faunistic and community patterns led directly to the development of conceptual and mathematical models for the evolution of butterfly mimicry (e.g. Moulton, 1909; Punnett, 1915; Fisher, 1958; Brown, 1979; Sheppard *et al.*, 1985; Turner, 1977, 1984, 1987; Turner & Mallet, 1996; Gilbert, 1983; Mallet, 1986a, b; 1993; Mallet & Singer, 1987; Mallet & Barton, 1989).

The implication in all of these studies is that close association of co-mimics is typical in tropical butterfly communities. Although a large and varied literature has shown broad patterns of mimetic associations in butterflies, Mallet & Gilbert (1995) noted that studies that provide a strong quantitative demonstration of co-mimetic association across small spatial scales are rare. Only three studies have attempted to do so: Smiley (1978) showed diurnal habitat limitation in heliconiine mimicry rings, Mallet & Gilbert (1995) showed microhabitat and height associations of co-mimetic *Heliconius* butterflies at nocturnal sleeping aggregations, and Beccaloni (1997a) showed that co-mimetic ithomiine butterflies were vertically stratified into two height intervals. It is therefore likely that a more profound understanding of butterfly mimicry can be achieved through studies that measure quantitatively how co-mimics associate along different habitat dimensions.

This study considers a sample of ithomiine butterflies that were captured during a recent investigation of fruit-feeding nymphalid butterfly diversity (DeVries, Murray & Lande, 1997). The fruit-feeding guild is defined as those species whose adult nutritional requirements are virtually all derived from juices of rotting fruits or plant sap. Although some ithomiine species were collected in fruit traps, ithomiines typically feed on flower nectar, and are thus not strictly part of the fruit-feeding guild. Here we report the spatial and temporal distributions of the ithomiine butterflies trapped by DeVries *et al.* (1997), with particular reference to the distribution of mimetic associations in a small remnant tract of forest. After providing evidence for mimetic assembly on small horizontal and temporal scales, we discuss our results with respect to other studies of mimicry and how tropical forest destruction may influence community structure of mimetic butterflies.

MATERIAL AND METHODS

Study site

This study was conducted within the Jatun Sacha Biological Station and Reserve, Napo Province, eastern Ecuador (01° 04′ S; 77° 36′ W), a reserve that comprises some 1700 hectares at the base of the eastern Andes in the upper Amazon Basin, bounded by the Rio Napo and the Rio Arahuno. The study was confined to a 200 hectare patch of the Jatun Sacha reserve forming a disturbance gradient of four contiguous habitat types: primary forest, secondary forest, higraded forest, and an edge located at the abrupt interface of primary forest and pasture (see DeVries *et al.*, 1997). A broader description of the entire Jatun Sacha reserve can be found in Pearman *et al.* (1995) and Beccaloni (1997b).

Field methods

Within the 200 hectare study area, five replicate sampling sites were established in each of the four habitat types. Each sampling site was fitted with one understory trap and one canopy trap, thus providing a total of ten traps in each habitat—five canopy and five understory. As in the previous study (see DeVries *et al.* 1997) none of the five trap sites were clumped, but haphazardly spread out to approximate a random sampling regime within each habitat. The height of canopy traps varied between *c.* 16–27 m above the ground, but in all cases traps were positioned to sample from within the canopy. Canopy traps were suspended from ropes run over branches of an emergent tree, such that the traps could be raised and lowered from the ground. Understory traps were suspended from low branches such that the bases hung between 1–1.5 m above ground and could be serviced directly.

Traps were baited with locally-obtained bananas which were mashed and mixed well, then fermented for 48 hours in a single reservoir prior to use. On each trapping day bait was placed in a small plastic cup fixed inside each trap, and replenished with fresh bait each subsequent trapping day. Baits were removed from all traps on the afternoon of the seventh trapping day, and the reserve bait was discarded. New bait was made prior to the subsequent sampling interval, and the protocol repeated throughout the study. See DeVries *et al.* (1997) for further details.

As in DeVries *et al.* (1997) this study extended from 16 August 1992 to 26 August 1993, with baited traps maintained for 7 consecutive days every month, except October 1992. During sampling periods all baited traps were serviced daily for 7 days, left empty for 3 weeks, then re-baited and the procedure repeated each sampling period.

Trapped butterflies were stored in individual glassine envelopes bearing all pertinent data, and these specimens were used for subsequent identification and analysis. All butterflies were identified to species and confirmed by specialists working on ithomiines. A list of Ithomiinae from Jatun Sacha is provided by Beccaloni (1997a, b), while a complete inventory of all butterflies from the entire reserve can be found in Murray (in press).

Analyses

To assess the influence of sample size on species richness we used the species accumulation curve (Colwell & Coddington, 1994). A species accumulation curve represents the cumulative number of species as a function of cumulative abundance of individuals in the particular order of collection through time.

Our five classes of mimetic colour patterns follow those of Beccaloni (1997a, b) with the following exceptions. Beccaloni placed *Godyris dircenna* in his 'large yellow transparent' class while *G. zavaleta* was placed in the 'small yellow transparent' class. Consideration of body size and our field observations strongly suggest that these species fit equally well into a single yellow transparent class. Rather than maintain two classes that appear to be homogeneous, for the purposes of this study Beccaloni's two yellow transparent classes were collapsed into a single class termed 'yellow transparent'. Additionally, *Hyalyris coeno* was not placed by Beccaloni into a mimetic class, and thus we omitted our unique specimen of this species from analysis of colour patterns.

Several hypotheses pertinent to understanding spatial and temporal associations of our samples were evaluated using Chi-squared tests. These hypotheses include: the individual and species abundance distributions were equal among habitats and heights, and the abundance of mimetic classes were distributed equally among habitats and months. Note that contrary to widespread views regarding empty cells, Lewontin & Felsenstein (1965) showed by computer simulation of $2 \times n$ contingency tables that Chi-squared statistics are robust to having zero entries and fractional expected values down to 0.5 or substantially lower.

To test for associations between co-mimics in space and time the species within each mimetic class were pooled to construct the net individual abundance distributions of mimetic classes across habitats and months. Chi-squared statistics were then computed to assess the heterogeneity among mimetic class distributions in space and time. However, this alone is not adequate to test the significance of associations among species within mimetic classes because even closely related species often show significant heterogeneity in space and time (e.g. DeVries *et al.*, 1997), which violates a basic assumption of the Chi-squared test. To test the significance of associations of co-mimics in space and time we therefore randomized the 21 species among the five mimetic classes, maintaining the same number of species in each mimetic class as in the actual data in Table 1. For each such randomization the species within mimetic classes were again pooled to construct the net individual abundance

TABLE 1. Ithomiine butterflies captured in traps. Habitat abbreviations are: Pri = primary habitat, Sec = secondary habitat, Hi = higraded habitat, Ed = edge habitat, c = canopy, and u = understory. Sample size: (*N*); Mimicry class (MC) abbreviations (after Beccaloni, 1997a, b, in part) are: C = clear wing, OT = orange-tip, SD = small dark transparent, YT = yellow transparent, T = tiger. Tribal classification (Tribe) abbreviations: NT = new tribe, G = Godyridini, N = Napeogenini, O = Oleriini, I = Ithomiini

	Pri		Sec		Hi		Ed				
Taxon	c	u	c	u	c	u	c	u	*N*	MC	Tribe
Aeria eurimedea negricola (Felder & Felder)	–	–	–	–	–	1	–	–	1	YT	NT
Ceratinia tutia poecila (Bates)	–	–	–	–	–	2	–	–	2	T	D
Godyris dircenna dircenna (Felder & Felder)	–	–	–	1	–	5	–	–	6	YT	G
Godyris zavaleta matronalis (Weymer)	1	4	–	10	1	22	–	2	40	YT	G
Heterosais nephele nephele (Bates)	–	–	–	1	–	4	–	–	5	C	G
Hyalyris coeno norellana (Haensch)	–	–	–	1	–	–	–	–	1	–	N
Hypoleria lavinia chrysodonia (Bates)	–	2	–	1	–	–	–	–	3	OT	G
Hypoleria orolina orolina (Hewitson)	–	4	–	1	–	2	–	–	7	OT	G
Hyposcada anchiala ecuadorina Bryk	–	1	–	3	–	2	–	–	6	T	O
Hyposcada illinissa ida Haensch	–	1	–	5	–	1	–	1	8	SD	O
Hyposcada kena kena (Hewitson)	–	1	–	2	–	–	–	–	3	SD	O
Hypothyris euclea intermedia (Butler)	1	6	1	1	–	3	–	1	13	T	N
Ithomia agnosia agnosia Hewitson	–	–	–	2	–	3	–	16	21	C	I
Ithomia salapia derasa Hewitson	–	–	–	4	–	–	1	8	13	YT	I
Napeogenes inachia avila Haensch	–	1	–	6	1	1	–	1	10	YT	N
Napeogenes sylphis caucayensis Fox & Real	–	1	–	2	–	–	–	1	4	OT	N
Oleria agarista agarista (Felder & Felder)	–	3	–	10	–	11	–	1	25	SD	O
Oleria assimilis assimilis (Haensch)	–	–	–	–	–	4	–	1	5	SD	O
Oleria gunilla lota (Hewitson)	–	–	–	2	–	3	–	7	12	SD	O
Oleria sexmaculata sexmaculata Haensch	–	–	–	2	–	1	–	–	3	SD	O
Pseudoscada florula aureola (Bates)	–	4	–	4	–	–	–	1	9	OT	G
Pseudoscada timna timna (Hewitson)	–	–	–	2	–	2	–	6	10	C	G
Total	2	28	1	60	2	67	1	46	207		

distributions of mimetic classes across habitats and months; we then computed the Chi-squared statistics of heterogeneity among mimetic classes. Species were randomized among mimetic classes 10 000 times to construct empirical sampling distributions of the Chi-squared statistic appropriate for the null hypotheses of no association among co-mimics in space and time. We assessed the significance of associations among co-mimetic species by estimating the probability that the Chi-squared statistic in the randomized data exceeded that for the actual data. Independent randomizations were performed for spatial and temporal tests of association.

To further describe spatial and temporal associations in our sample different measures of total diversity among mimetic classes were partitioned into additive components within and among habitats, and within and among months, as described in Lande (1996) and DeVries *et al.* (1997).

RESULTS

During the 12 sampling periods we trapped 207 individual ithomiine butterflies representing 22 species (Table 1). Of the 22 total species sampled 18 were found in

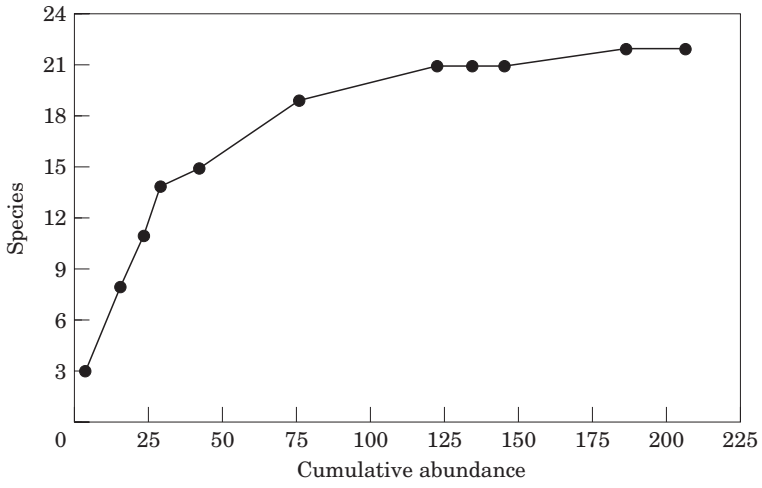

Figure 1. Species accumulation showing total species of ithomiine butterflies versus cumulative individual abundance through time.

the understory only, four species in both canopy and understory, and no species was found in the canopy only. Individual abundances ranged from one to 40 individuals per species, and of the total sample 201 individuals were found in the understory and only six individuals were found in the canopy (Table 1).

Although the total ithomiine richness of Jatun Sacha comprises at least 56 species (Beccaloni, 1997a, b), our species accumulation curve reached an asymptote at 22 species (Fig. 1). The disparity between these observations suggests that the 22 species sampled in this study have a greater preference for feeding on rotting fruit juices than other ithomiine species at Jatun Sacha.

Both species richness and individual abundance varied on a monthly basis over the sampling period. Periods of decline were followed by periods of increase for both measures, including one month (December, 1992) when no individuals were trapped (Fig. 2).

Individual abundance was distributed unequally between canopy and understory; 201 individual butterflies were sampled in the understory, and six individuals were sampled in the canopy. The six individuals found in the canopy belong to four relatively abundant species and are not significantly different from a random sample of the understory species ($\chi^2 = 14.6$, df $= 21$, $P = 0.84$). Therefore the species sampled in this study provide no evidence for vertical stratification.

There were slight differences in the distribution of species richness and individual abundance among the four habitats. Second growth and higrade had more species and greatest individual abundance, followed by edge and primary habitats respectively (Table 2). However, overall individual abundance was unequal among the four habitats ($\chi^2 = 17.0$, df $= 3$, $P < 0.0001$).

A presence-absence comparison showed considerable overlap of species among habitats, and only samples from higrade and second growth habitats contained species unique to them (Table 3).

The five mimetic colour pattern classes were distributed unequally among both habitats and months (Tables 4 and 5). The Chi-squared statistic for habitat heterogeneity among mimetic classes in the original data ($\chi^2 = 75.60$, df $= 12$) was found

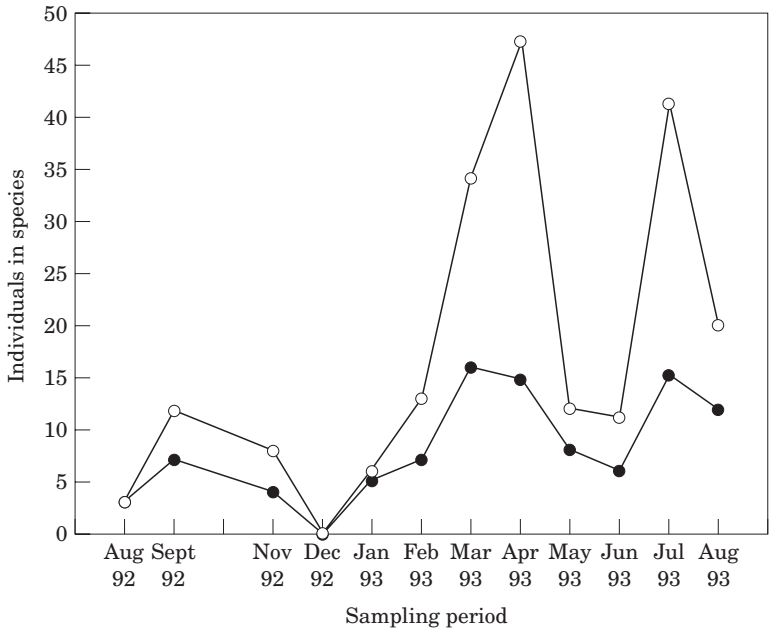

Figure 2. Temporal variation of total ithomiine species (●) and individuals (○) across 12 sampling periods.

Table 2. Distribution of ithomiine species richness and individual abundance partitioned by vertical position and habitats. All species trapped in the canopy were found in the understory of the same habitat

	Canopy		Understory	
Habitat	Richness	Abundance	Richness	Abundance
Primary	2	2	11	28
Secondary	1	1	19	60
Higrade	2	2	16	67
Edge	1	1	12	46

Table 3. Distribution of the species overlap among four habitats (out of 22 total species). Numbers in bold are species unique to a particular habitat. Numbers in parentheses are total species in each habitat

	Edge	Higrade	Secondary	Primary
Primary (11)	7	7	11	**0**
Secondary (19)	10	12	**1**	
Higrade (16)	9	**2**		
Edge (12)	**0**			

by the species randomization test to be marginally significant ($P = 0.056 \pm 0.002$). The Chi-squared statistic for temporal heterogeneity among mimetic classes in the original data ($\chi^2 = 78.51$, df $= 40$) was found by the species randomization test to be significant ($P = 0.019 \pm 0.001$).

Table 4. Abundance distributions of mimetic classes among habitats. Note that the unique individual of *Hyalyris coeno* has been omitted from this analysis. Abbreviations for mimetic classes are: C = clear wing, OT = orange-tip, SD = small dark transparent, YT = yellow transparent, and T = tiger

	Habitats				
Mimetic Class	Primary	Secondary	Higrade	Edge	Total
C	0	5	9	22	36
OT	11	8	2	2	23
SD	5	21	20	10	56
YT	6	21	31	12	70
T	8	5	7	1	21
Total	30	60	69	47	206

Table 5. Abundance distributions of mimetic classes among months. The month intervals follow the sequence established in Figure 2, but as the total individual abundance was zero in December 1992, this month was omitted from the analysis. Also the unique individual of *Hyalyris coeno* was omitted from this analysis. Abbreviations for mimetic classes are: C = clear wing, OT = orange-tip, SD = small dark transparent, YT = yellow transparent, and T = tiger

	Sampling Interval											
	Aug 92	Sept 92	Nov 92	Jan 93	Feb 93	Mar 93	Apr 93	May 93	Jun 93	Jul 93	Aug 93	Total
C	0	0	1	3	2	5	9	5	4	4	3	36
OT	1	5	2	1	0	5	1	0	2	2	4	23
SD	1	6	0	0	3	8	14	2	0	11	11	56
YT	1	1	2	2	8	11	18	3	5	18	1	70
T	0	0	3	0	0	5	4	2	0	6	1	21
Total	3	12	8	6	13	34	46	12	11	41	20	206

Table 6. Partition of ithomiine mimetic class diversity in space and time

Diversity Measure	Total	Among habitats	Among months
Class richness	5	0.146	0.534
Shannon–Wiener	1.503	0.168	0.214
Simpson	0.757	0.059	0.073

These randomization tests provide suggestive evidence that co-mimetic ithomiine species occur in the same habitats, and strong evidence that co-mimetic species occur at the same times.

Partitioning the total diversity among mimetic classes into spatial and temporal components (Table 6) indicates that habitat and temporal effects each contributed roughly 10% to the total mimetic class diversity assessed by the Shannon–Wiener and Simpson measures, with the temporal effect being slightly larger than that of habitat. The relatively low component of mimetic class richness among habitats is due to the fact that all but one habitat (primary) contained all mimetic classes (Table 6).

DISCUSSION

Due to their ease of sampling ithomiine butterflies have been used as focal taxa to estimate total butterfly richness in neotropical sites (Beccaloni & Gaston, 1995). In contrast to our species accumulation curve which reached an asymptote of 22 species (representing 13 genera and 6 tribes) before the end of the study (Fig. 1), Beccaloni (1997a) sampled 56 species (representing 24 genera and 10 tribes) at Jatun Sacha using hand nets. Of the fauna known to occur at Jatun Sacha (see Beccaloni, 1997a, b) we sampled no representatives of the genera *Tithorea*, *Methona*, *Melinaea*, *Thyridia*, *Scada*, *Forbestra*, *Mechanitis*, *Callithomia*, *Dircenna*, *Ceratiscada*, or *Pteronymia*, and only 3 of 6 *Oleria* species, 2 of 6 *Napeogenes* species, 1 of 6 *Hypothyris* species, 2 of 4 *Hypoleria* species, and 2 of 4 *Ithomia* species. Our samples therefore testify to the existence of differential attraction to rotting fruits among ithomiine species, an aspect of ithomiine biology that has not been investigated previously.

Temporal changes in individual abundance and species richness of ithomiines across the 12 month sampling period (Fig. 2) reflect those measured in a simultaneous study on fruit-feeding nymphalids (see DeVries *et al.*, 1997). Both ithomiines and fruit-feeding nymphalids showed a marked decrease in abundance and richness during the driest month (December), and a subsequent increase after February when the rainy season began.

As we found for fruit-feeding nymphalids at Jatun Sacha (DeVries *et al.*, 1997), there was considerable overlap among the four habitats with respect to ithomiine species richness (Tables 1 and 2). However, overall species abundance distributions differed significantly among habitats (Tables 1 and 2).

Finding no evidence among the species in our sample for differential vertical distribution (Tables 1 and 2) is seemingly at variance with previous work on ithomiine butterflies (e.g. Medina *et al.*, 1996; Beccaloni, 1997a). However, it is important to note that our study involved only a subset of the ithomiine community that fed on rotting fruits, but provided no information on the vertical distribution of species in free flight, flower feeding, or during oviposition—observations that are typically gathered with hand nets and/or binoculars (e.g. Beccaloni, 1997a).

The tiger-striped mimetic classes of ithomiines have been suggested to occur in the vertical stratum above 1 m (Medina *et al.*, 1996; Beccaloni 1997a). However, we sampled no species of the 'high-flying' ithomiines of the 'yellow-bar tiger' or 'orange-black tiger' colour classes (*sensu* Beccaloni, 1997a) despite the presence of our canopy traps. These two colour patterns constitute important, often polymorphic, and abundant ithomiine mimicry complexes at Jatun Sacha (and elsewhere), and include members of the genera *Melinaea* (tribe: Melinaeini), *Mechanitis, Forbestra* (tribe Mechanitini), plus some species in the genera *Napeogenes*, *Hypothyris* (tribe: Napeogenini), and *Callithomia* (tribe: Dircennini). Although we cannot eliminate phylogenetic effects, in combination with the observations of Beccaloni (1997a), our study does suggest that ithomiine species attracted to fruits are found in lower strata of the forest, and that differential fruit-feeding by ithomiines may be correlated with colour pattern.

Beccaloni (1997a) postulated that stratification in female ithomiine species results directly from the vertical distributions of specific host plants, and that males of these species are stratified indirectly due to mate seeking behaviour. As suggested for other groups of butterflies (Papageorgis, 1975; DeVries, 1988), Beccaloni also postulated that microhabitat-dependent selection on ithomiine colour patterns by predators might lead to co-mimicry evolving within the same vertical stratum by

preventing convergence among species in different strata, and that mimicry patterns may be further segregated by vegetation types. Although none of these studies provide explicit details on particular predators that could select for butterfly species with different colour patterns within different strata, habitat partitioning in both vertical and horizontal dimensions by neotropical avian communities is well documented. For example, Munn (1985) demonstrated that canopy and understory avifaunas are composed of distinct multi-species flocks, and the core of each of these flocks is composed of 5–10 insectivorous bird species. Although no study has shown differential predation on butterflies among microhabitats *per se*, the high degree of prey specialization in neotropical insectivorous birds (Snow, 1976; Rosenberg, 1990), and their distinct microhabitat preferences (Munn, 1985; Greenberg & Gradwohl, 1986; Cannaday, 1997) argues that insectivorous birds indeed may select for mimetic colour pattern in butterflies at the level of microhabitat in both horizontal and vertical dimensions. Clearly these suggestive observations are worthy of future investigation.

Documentation of the overlapping geographical distributions of Müllerian co-mimics on scales ranging from tens to thousands of kilometers attests to the strength of mimicry in forming large scale patterns in butterfly communities (see summaries in Ackery & Vane-Wright, 1984; Brown, 1979; Mallet, 1986a, b; Sheppard *et al.*, 1985; Turner, 1977, 1981, 1984, 1987; Turner & Mallet, 1996). Although ithomiine and heliconiine co-mimics have been suggested to show habitat associations at particular sites (e.g. Poole, 1970; Papageorgis, 1975; Brown, 1979; Burd, 1994; Mallet & Gilbert, 1995; Medina, Robbins & Lamas, 1996; Beccaloni, 1997a, b and summaries therein), studies that provide quantitative analyses of how co-mimetic association occurs within particular habitats or vegetation types on small geographic scales are exceedingly rare.

The randomization tests used here provide the first quantitative demonstration that co-mimetic ithomiine species associate in space and time within a forest where multiple habitat types are contiguous across merely hundreds of meters. In concert with Mallet & Gilbert's (1995) work on *Heliconius* our observations establish that the effect of mimicry on patterns of butterfly community assemblages can be measured at a much smaller scale than has been shown previously. Our study not only illustrates specific statistical methods for evaluating the effects of mimicry on small geographical and temporal scales, but also provides strong motivation for asking whether co-mimetic butterfly species are associated in space and time at other sites.

We found that habitat and temporal effects each explained about 10% of the total mimetic class diversity in our samples (Table 6). Although these effects are not large, in view of the fact that individual avian predators may have limited home ranges and can learn colour patterns (e.g. Greenberg & Gradwohl, 1986; Chai, 1986, 1996) the spatial and temporal effects observed here are likely to be sufficient to promote substantial coevolution among species in Müllerian mimicry complexes because small selective effects maintained over long timespans can produce major evolutionary changes (Wright, 1931; Haldane, 1932; Fisher, 1958; Lande, 1976). Our study suggests not only that particular butterfly mimicry rings have restricted habitats and flight times on small spatial and temporal scales, but implies that particular predators selecting for the evolution of these mimicry complexes may also show similar spatial and temporal patterns. Taking such observations into consideration may provide further insights into how butterfly mimicry complexes evolve (e.g. Turner & Mallet, 1996).

The implication that mimicry is important to the organization of butterfly communities suggests that habitat destruction may have a dramatic impact on community structure through species loss of plants, insects and vertebrate predators that are fundamental to the evolution and dynamics of mimicry. As the evolution of butterfly mimicry complexes is based on the interaction among multiple species and their predators (Fisher, 1958; Gilbert, 1983; Turner & Mallet, 1996) and disturbance of tropical forests is known to have profound effects on the spatial and temporal structure of communities (Cannaday, 1997; DeVries *et al.*, 1997, and unpublished), these observations suggest that disturbance may strongly affect the evolution of mimetic associations within particular habitats.

Historically the consideration of mimicry, and butterfly mimicry in particular, has stimulated major conceptual advances for understanding evolution by natural selection (e.g. Fisher, 1958). However, surprisingly few studies have quantitatively assessed the associations among species affecting the evolution of complex mimicry systems under natural conditions. This study sets the stage for future work on small-scale spatial and temporal factors that may influence the organization of mimicry complexes in habitats under varying regimes of disturbance.

ACKNOWLEDGEMENTS

We acknowledge the help of David Neill and Alejandro Suarez for facilitating our field work, and for sharing their knowledge of the Jatun Sacha reserve, and George Beccaloni and Gerardo Lamas for assisting in ithomiine determinations. For comments and discussion on earlier drafts of this manuscript we thank George Beccaloni, Chris Dove, Brad Hawkins, James Mallet, Carla M. Penz, Sue Ratner, Thomas Walla and an anonymous reviewer. Portions of this study were supported by the Fundacion Jatun Sacha, the Peace Corps, the Stanford Center for Conservation Biology, and by the National Science Foundation (grant DEB-9225127 to R. L.). DeVries gratefully acknowledges the support of the Museum of Comparative Zoology, Harvard University, the National Geographic Society, the MacArthur Foundation and the Guggenheim Foundation. This study is dedicated to the evolutionary work of Horace Silver, Hank Mobley, Philly Jo Jones, Paul Chambers and Blue Mitchell.

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