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Altitudinal variation in Ithomiine (Nymphalidae) color patterns

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ABSTRACT

Ithomiine butterflies contain several color complexes that fly at different heights in the forest, presumably in response to light conditions (Papageorgis 1975; Burd 1994). If so, these complexes should also respond to altitude, as light conditions in the forest change attitudinally. A previous study by Haber (1978) showed that color complexes do respond to altitude, but in a way inconsistent with light response. Either the previous study failed to incorporate forest conditions, like openness, which also alter light levels, or ithomiine color complexes are responding to altitude for different reasons, including the possibility that each color complex had a different center-of-origin corresponding with different elevations. We caught butterflies in closed forest conditions along both slopes of the continental divide in Monteverde, Costa Rica at seven different sites along an altitudinal gradient, from 800 m to 1600 m. Two of the three color complexes responded to altitude, but in ways inconsistent with our expected light response. Clearwings, which favor dark conditions, were more abundant at high altitudes while tiger stripe species, favoring strong, direct and sun-fleck light conditions, were only found at lower altitudes on both slopes. Pacific slope forests generally had more open canopies but the patterns were nearly symmetrical on both slopes. Therefore, we conclude that the change was more likely a result of color complexes evolving at different altitudes and secondarily migrating out of these altitudinal bands. Additionally, light and altitude seem to cause a more complicated relationship than expected, probably because of increased cloud cover and epiphytic growth with increased altitude.

RESUMEN

Las mariposas de ithomiine contienen varios patrones de color que vuelan en diferentes alturas, probablemente en respuesta a la luz (Papageorgis 1975; Burd 1994). Si es así estos complejos deben también responder a la altitud, como en las condiciones de luz a través del cambio del bosque a nivel altitudinal. Un estudio anterior de Haber (1978) demostró que los patrones de color responden a la altitud, pero en una manera contraria con respuesta a la luz. Sin embargo, el estudio anterior no pudo incorporar las condiciones del bosque, como transparencia que también alteran los niveles de luz, o los patrones del color del ithomiine están respondiendo a la altitud por diferentes razones, incluyendo la posibilidad de que cada patrón del color tuvo un centro-de-origen diferente correspondiente con diversas elevaciones. Capturamos mariposas en condiciones cerradas del bosque a lo largo de un gradiente altitudinal, a partir el 800 m a el 1600 m. Dos de los tres patrones del color respondieron a la altitud, pero de maneras contraria con nuestra hipótesis de luz prevista. Mariposas de alas de vidrio, se favorecen por las condiciones oscuras, fueron más abundantes en las altas altitudes mientras que las especies de la raya del tigre, las condiciones de luces fuertes, directas y de las moteadas del sol, fueron encontradas solamente en altitudes más bajas en ambas

cuestas. Los bosques del Pacifico de la cuesta tuvieron generalmente más en lo zonas abierto pero los patrones eran casi simétricos en ambos cuestas. Por lo tanto, concluimos que el cambio era más probablemente un resultado de los patrones del color que se desarrollaban en diferentes altitudes y después que emigraban de estas vendas altitudinal. Además, la luz y la altitud parecieron exhibir una relación menos pronunciada que la esperada, probablemente debido a que la cobertura nubosa y crecimiento epífito se incrementa al incrementar la altitud.

INTRODUCTION

Ithomiinae (Nymphalidae) is a common Neotropical butterfly subfamily (DeVries 1987). All ithomiine genera are chemically protected by pyrrolizidine alkaloids (Brown 1981; Masters 1990, 1992), which they sequester from several plant families, including Asteraceae, Boraginaceae, Caesalpinaceae (Fabaceae), and Orchidaceae (Haber 1978). These alkaloids make ithomiines unpalatable to predators (Masters 1990), a fact that is reflected in their aposematic patterning (Bates 1862; Müller 1879). However, ithomiines' first line of predation defense is crypsis, an idea proposed by Papageorgis (1975).

In Costa Rica, ithomiines converge to five major color patterns: clearwing, tigerstripe, black-and-yellow, black-and-rust, and golden-translucent (Papageorgis 1975; Burd 1994; Levitt 1999, Haber 1978). Several genera converge on each of these distinct patterns, and previous studies have shown that each complex flies in one of three different strata in the forest (Papageorgis 1975; Burd 1994; Levitt 1999). Clearwings fly in the understory, black-and-yellow and golden-translucent in the middle stratum, and tiger-stripes and black-and-rust in the upper stratum (Papageorgis 1975). According to Papageorgis, this pattern indicates that these distinct strata are optimal environments for crypsis of the corresponding ithomiine complexes. Clearwings are least visible in the low-light environment of the understory, as their translucent wings have low contrast to the vegetation. Black-and-yellow and golden-translucent, typically brown, gold, yellow and red, have somewhat translucent wings and are most cryptic in the brown, wooddominated conditions and diffuse light of the middle stratum. The tiger-stripes and blackand-rust patterns are most cryptic in the bright, sun fleck-prone upper stratum of the forest.

Light conditions in closed canopy tropical forest also change with altitude (Whitmore 1989). Canopy tree height decreases, the density of large trees decreases, and leaves get smaller (Bruijnzeel and Veneklaas 1998), a trend consistent on both slopes of the continental divide in Costa Rica (Nadkarni et al. 2000). Changes in the composition of the forest equates to changes in the amount and kind of light that gets through the forest canopy (Lee 1987). Integrating the vertical stratification of ithomiine complexes with this trend in light availability over an altitudinal gradient, we predict that changes in altitude should correlate to changes in the relative abundance of ithomiine color complexes there. Higher elevation forests with more direct light coming through the canopy should result in an increased relative abundance of the tiger-stripes and black-and-yellows to remain relatively constant because diffuse light is common to all forest habitats (Endler 1993).

Indeed, ithomiines in Costa Rica appear to respond to altitude (Haber 1978), though not in a way consistent with predicted patterns. Instead, clearwings are more

abundant at higher altitudes on both the Pacific and Atlantic slopes and decrease with elevation, while tiger-stripes and black-and-rust patterns are more abundant at lower altitudes and decrease with increasing altitude (Haber 1978). It is possible that this trend reflects the study sites selected, as changes in forest canopy cover could obscure altitudinal impacts on light.

Alternatively, the pattern of Haber (1978) may be best explained by the center-ofradiation model (Mora 2003), in which the area where species originate contains the highest species richness, and richness declines proportionally to distance from this locus, reflecting the radiation of species from this point (Karlson et al. 2004; Jablonski et al. 2006). Neotropical butterflies may have evolved and eventually speciated on mountain tops during the Pleistocene (Brown 1987). The forest refugia theory (Haffer 1979) postulates that isolated wet "refuges" were created by glacial climate change that dried the lowland Tropics. Thus, separate mountaintops became refuges that reproductively separated many populations, due to allopatric speciation (Haffer 1979). Drawing upon this theory, we predict that ithomiine clearwings may have speciated in such refuges at high elevations, thus accounting for their continued greater abundance at higher altitudes (Haber 1978). Clearwing species subsequently radiated downwards on both slopes, accounting for their decreasing richness with decreasing altitude. Other color complexes may have speciated at lower refuges, and therefore still prefer these altitudes.

The intentions of our study are thus to reevaluate the trends found in previous work using only closed forest sites on both slopes. If ithomiine color complexes respond to light in closed forests, clearwings should become less common at higher altitudes in lighter environments, compared to other, more light-adapted color patterns. If ithomiine complexes are responding to light, ratios of color complexes for a given altitude should differ for a given altitude in a predictable way. If color complexes evolved speciated and secondarily moved out of their preferred altitudinal band, ratios of color complexes should decline with increased distance from the center-of-radiation, but without regard to slope.

MATERIALS AND METHODS

Our study took place over an altitudinal gradient near Monteverde, Costa Rica during the last three weeks of the dry season. We selected collection sites in closed-canopy forest ranging from 800 m elevation on the Atlantic slope to 800 m on the Pacific slope, crossing over the continental divide at 1700 m in the Cordillera de Tilarán. Of importance to our project was that our sites should be lek sites, for three important reasons. When ithomiines lek, the vertical stratification of flight heights is disrupted and all colors complexes occur closer to the forest floor (Haber 1978). This makes the capture of high-flying species possible with a hand net. Additionally, ithomiine leks show great species richness, as individuals of many different species and genera are attracted to these aggregations (DeVries 1987). This increases our ability to accurately describe the species present in closed forest at a given altitude. Lastly, lek sites are not related to host plant availability (Haber 1978). This last characteristic diminishes the risk of a microhabitat bias that could occur if a collection was taken in close proximity to a species' host plant. The lek sites we found were all in closed-canopy forest, within close proximity to a stream or shallow river. We observed that ithomiines only displayed lekking behavior

when the weather was sunny and warm – therefore, we only collected between 10:00 am and 2:00 pm, the warmest hours of the day, and collected on days with full sun whenever possible.

We attempted to collect at least 40 butterflies per site, and used handheld nets (1 and 2 m handle lengths) to do so. Our estimated maximum reach was 5 m in height, however, we observed that the majority of lekking ithomiines flew below 3 m high, well within our range. We identified the butterflies to species using DeVries (1987).

Study Sites

We collected at three different sites on the Atlantic slope. The first site was in the trail network behind Refugio Eladio (Peñas Blancas valley, Bosque Eterno de los Niños), between 800 and 820 m elevation. We found ithomiines lekking in the woods between two streams that connect with the Rio Peñas Blancas. The second Altlantic site was along Sendero Tabacón, a trail below the Estación San Gerardo (Bosque Eterno de los Niños), between 1150 and 1190 m elevation. There were several lek sites along this 2km loop, all near the streams that cross the trail heading down the mountain. The third Altantic site was in the trail network above the Selvatura skywalks, between 1610 and 1640 m elevation. Although we did not observe lekking behavior at this site, we believe that this was due to the poor weather when we visited. During good weather, we would expect to see butterflies lekking in the flat, densely vegetated areas alongside the stream that runs parallel to the main trail at this elevation.

On the Pacific slope, we collected at four different sites. The first site was in the Bajos de San Luis, along the Rio Guacimal just below the confluence of the Quebrada Socorro, between 810 and 820 m elevation on the Mata Family farm. We collected in the forest between the river and the pastures on the hillside. The second site was along the trail to the San Luis waterfall, on the Leitons' property, at between 1160 and 1190 m elevation. The majority of lekking butterflies flew around the forest edge right along the Rio San Luis. The third site was near Monteverde, along the Rio Guacimal below the Bajo del Tigre reserve on the Trostle property, between 1350 and 1370 m elevation. We observed lekking behavior in a flat, depressed area adjacent to a bend in the river. The fourth site was along the Quebrada Máquina, above the Estación Biológica Monteverde, between 1540 and 1590 m elevation. We observed occasional lekking behavior along Sendero Jilguero, which parallels the stream for a stretch.

All seven of our sites were within closed canopy forests, within 100 m of moving water. Closed canopy was an important requirement, as we wanted to avoid possible bias from the butterflies often seen along disturbed forest edges and roadsides, as well as migratory species that can be found in greater abundances in clearings and disturbances (DeVries 1987).

RESULTS

Over the three-week span of our data collection, we captured and identified 342 ithomiines (see Appendix for complete listing) representing 37 of the 61 known Costa Rican species according to DeVries (1987). All species we collected can be found on both slopes, except for six that are unique to the Atlantic slope. We found species from

all five color complexes described by Haber (1978), however due to pattern similarities and rarity of two of the complexes, we merged the black-and-yellow and goldentranslucent color patterns into a single complex called tawny, and the tiger-stripe and black-and-rust color patterns into the tiger-stripe complex. All three mimicry patterns were present in four of the seven sites, two of the patterns in two of the sites, and only one pattern in our high-elevation Atlantic slope site.

Our data showed that the relative abundance and richness of clearwing ithomiines generally increased with elevation, while those of the tiger-stripes generally decreased. The relative abundance and richness of tawny ithomiines varied but showed no clear pattern other than being omnipresent over the study sites (Figures 1 and 2). We defined abundance as the number of individuals of all species within a mimicry complex, and richness as the number of species within a color complex. Abundances were significantly different when considered at each site individually and over all sites. Richnesses, however, were only significantly different for two of the three color complexes and two of the seven sites (see Tables 1a and 1b). The trends we found in relative abundances agree with the results of Haber (1978). Although not statistically supported, the trends in relative richnesses correspond to species elevation data. Using DeVries (1987), we calculated the midpoints of the elevation ranges for all ithomiines in Costa Rica. We then grouped this data by mimicry complex and calculated the mean range midpoint for each complex (Figure 3). These means approximated the elevations of greatest species richness for the corresponding color pattern. In concordance with the trends from our relative species richness data, these means demonstrated that clearwings were most rich on average at higher elevations and tiger-stripes at lower elevations.



Figure 1. Relative abundances of the three mimicry complexes at the seven collection

sites, based on the number of individuals collected. The first three sites are on the Atlantic slope, the other four on the Pacific slope. Elevations of these sites are plotted on the secondary y-axis. The stippled bar corresponding to the Selvatura site represents the fact that the collection size was less than our goal (see discussion).



Figure 2. Relative abundances of the three mimicry complexes at the seven collection sites, based on species richness.

Table 1a. χ^2 tests of mimicry complexes over all seven sites. A p-value of less than
0.05 indicates a significant difference in the number of individuals (first column) or
species (second column) in the given complex. Entries in italics indicate the expected
values for that test fell below 5, violating one of the rules of thumb of the χ^2 test.

Complex	By nu	mber of individu	uals	By number of species			
Clearwing	81.78	d.f. = 6	p < 0.05	13.95	d.f. = 6	p < 0.05	
Tawny	61.52	d.f. = 6	p < 0.05	8.08	d.f. = 6	p > 0.05	
Tiger-stripe	58.67	d.f. = 6	p < 0.05	20.00	d.f. = 6	<i>p</i> < 0.05	

Table 1b. χ^2 tests of each site for all mimicry complexes. A p-value of less than 0.05 indicates a significant difference in the number of individuals (first column) or species (second column) in the three complexes at each site.

	1						
Site	By n	umber of in	dividuals	By number of species			
Refugio Eladio	21.00	d.f. = 2	p < 0.05	0.11	d.f. = 2	p > 0.05	
Estación San Gerardo	32.68	d.f. = 2	p < 0.05	5.83	d.f. = 2	p > 0.05	
Selvatura	26.00	d.f. = 2	p < 0.05	10.00	d.f. = 2	<i>p</i> < 0.05	

Estación Biológica Monteverde	21.14	d.f. = 2	p < 0.05	6.00	d.f. = 2	<i>p</i> < 0.05
Monteverde Community	98.93	d.f. = 2	p < 0.05	2.80	d.f. = 2	p > 0.05
San Luis Waterfall	34.37	d.f. = 2	p < 0.05	1.75	d.f. = 2	p > 0.05
Bajos de San Luis	23.03	d.f. = 2	p < 0.05	0.67	d.f. = 2	p > 0.05





In terms of relative abundance, two sites deviated from these trends. At the Selvatura site (Atlantic slope), we only collected 13 ithomiines, all of which were part of the clearwing mimicry complex. This was perhaps due to the cloudy conditions that day. Although we fell shy of our collection goal at this site, we hesitate to dismiss the data. We have observed butterflies of the tawny complex flying in this environment on non-cloudy days, and we believe that a larger sample size taken on a sunny day would demonstrate proportions similar to that of our high-elevation Pacific slope site, showing the joint presence of the clearwing and tawny complexes with a much higher relative abundance of clearwing individuals.

Another site that deviated significantly from the relative abundance trends we found was the Monteverde community site (Pacific slope). We collected many fewer clearwing individuals than we expected at this site. This site was a large, flat area in closed canopy forest, but with noticeably less understory plant density. We have found the majority of clearwing species in dense understory, where they are better able to take advantage of their cryptic patterning. We suspect that this habitat difference was responsible for the anomaly, especially because the relative richness did not deviate from the trend. Another trend shown by our data was that the Atlantic slope sites (except Selvatura) generally had a higher species richness and diversity of all three color complexes. The trend was apparent in both Margalef (Figure 4) and Shannon-Wiener indices (Figure 5). (We measured species richness using Margalef indices to ensure that the trend was not an artifact of larger sample sizes on the Atlantic slope.) We suspect that the higher species diversity in our Atlantic slope lek sites reflected the timing of our study, which took place at the end of the dry season. Ithomiines migrate from the Pacific slope to the less seasonal Atlantic slope to pass the dry season (Haber 1978), and therefore we would expect to. As evidence of ithomiine butterflies' migratory nature, Sorensen's quantitative indices showed comparable species composition overlap between sites on both the same and opposite sides of the continental divide (Table 2). This indicated that species are not completely isolated to either side of the divide, a result consistent with the fact that migratory butterflies are able to cross the divide. The Sorensen's quantitative indices also showed a significant linear relation ($R^2 = 0.19$; p < 0.05; n = 21) between composition overlap and elevation difference between sites (Figure 6), indicating that two sites of similar elevation, regardless of slope, had more species in common than two sites of dissimilar elevation. Although the species were mobile across the divide, they showed an altitudinal preference on both slopes. This was consistent with our findings of altitudinal trends in color complex abundances.



Figure 4. Species richness in terms of Margalef indices.





Table 2.	Species c	omposition	overlap	between	communities,	in terms	of Sorensen's
quantitativ	ve indices.						

	Refugio Eladio	Estación San Gerardo	Selvatura	Estación Biológica Monteverde	Monteverde Community	San Luis Waterfall	Bajos de San Luis
Refugio		0.15	0.00	0.04	0.03	0.12	0.11
Elaulo							
Estacion			0.29	0.46	0.07	0.52	0.01
San			0.28	0.46	0.07	0.52	0.21
Gerardo							
Selvatura				0.40	0.03	0.07	0.00
Estación							
Biológica					0.08	0.35	0.18
Monteverde							
Monteverde						0.06	0.12
Community						0.06	0.13
San Luis							0.02
Waterfall							0.23
Bajos de							
San Luis							



Figure 6. Species composition overlap (Sorensen's quantitative indices) versus elevation difference between communities. Stippled line represents linear regression.

DISCUSSION

Studies have shown that separate color complexes occupy distinct vertical strata (Burd 1994) in order to utilize light conditions unique to each vertical zone to become more cryptic (Papageorgis 1975). Additionally, in mountainous areas in the Tropics, increasing altitude leads to a general decrease in canopy height and leaf size (Bruijnzeel and Veneklaas 1998), suggesting an increase in the amount of direct sunlight. If there is more available light at higher elevations, and the optimal strata for tiger stripes is the strata of the forest that receives the most light, then tiger-stripes should be the most prevalent complex at higher elevations, and clearwings the least.

Our data exhibit different trends for relative abundances of ithomiine color complexes across an altitudinal gradient, similar to those from Haber (1978). Specifically, clearwings are most abundant at higher altitudes, and decrease in abundance as altitude decreases. The inverse is true of tiger-stripes: they are most abundant at low altitudes and increase in abundance as altitude increases (Figure 1). The same trends are also visible in altitudinal gradients of relative species richness (Figure 2), absolute species richness (Margalef indices, Figure 4), and diversity (Shannon-Wiener indices, Figure 5).

The trends refute our light hypothesis, suggesting that other factors influence available light under the canopy and may have obscured or changed the predicted pattern. Namely, at higher elevations there is increased cloud cover, which in fact decreases

available light in the understory due to a dramatic decrease in the amount of direct light reaching the canopy (Endler 1993). Thus, higher altitude habitats, such as cloud forest, might actually be darker in spite of a shorter canopy. Furthermore, in cloud forest and rain shadow environments, the higher mist and precipitation lead to increased epiphyte growth, possibly compounding the effects of the cloud cover. With more epiphytic growth, not only is there a higher amount of green light transmittance into the understory (Endler 1993) but also there is also more vegetation blocking direct light from passing through the canopy strata. These factors would all lead to a lower light environment at higher elevations, and one in which spectral quality is diminished, equating to a more conducive light environment for the clearwings (Papageorgis 1975; Lee 1987). Interestingly, the majority of butterflies we observed in all environments on cloudy days were clearwings, an observation that helps to support this argument. We believe that our initial light hypothesis was incomplete in its evaluation of forest light conditions – the effects of decreased canopy height and leaf size with increasing elevation are likely offset by increased cloud cover and epiphytic growth. The magnitude of this offset needs to be addressed by light-availability studies.

One interesting result from our data is that the proportion of the tawny complex did not show any consistent pattern with elevation. We suggest that because the tawnies' optimal light environment is diffuse light, they will be ubiquitous through the forest habitats, as we observed diffuse light in all of the forest habitats we visited. This one trend supports our original light hypothesis. Apropos of the light discussion above, cloud cover and epiphytic growth should not significantly alter the presence of diffuse light under the canopy.

Center-of-radiation models also appear to be pertinent in explaining our data. The clearwing complex is most prevalent at higher elevations and decreases in species richness across a descending altitudinal gradient. Such a gradient typically denotes a center-of-radiation, as highest richness is found at the geographical center and decreasing richness at further distances from this point (Karlson et al. 2004). We hypothesize that ithomiine clearwings' center-of-radiation was at higher elevations, perhaps reinforced by light conditions optimal to their cryptic patterning. From this elevation, they radiated down both slopes of the divide.

The same model can be applied to the tiger-stripes. We hypothesize that this complex had a center-of-radiation at a lower altitude, also perhaps due to optimal available light, and radiated up both slopes from the lowlands. Considering the center-of-radiation model, the tawny complex is more complicated due to the lack of a clear richness gradient. The tawnies perhaps originated from a center like the other two patterns, but radiated much further due to the fact that their optimal light conditions (diffuse light) are present in a wide range of forest habitats. This center-of-radiation could also have been much broader in altitudinal range than the other complexes' centers. Alternately, the tawnies might have diverged from the clearwings or the tigers, as the tawny patterning visually falls somewhere between the other two patterns.

In conclusion, we believe that the variance in color pattern proportions over the altitudinal gradient was due to a combination of two factors. First, we suspect different origins-of-radiation for the clearwings and tigers, in regard to the opposing directions of these two complexes' diversity gradients. We also suspect that these speciation events were influenced by the second factor: a gradient of available light conditions. Vertical

stratification experiments have demonstrated that an available light gradient is an important microhabitat determinant for ithomiines. However, the quantity and quality of available light over an altitudinal gradient appears to be more complex than the vertical stratification experiments, possibly influenced by factors such as cloud cover and epiphytic growth. Further studies need to examine the genetics of the mimicry complexes, lending more insight into the radiation models. Additionally, the formulation of a better light hypothesis requires studies of available light over an altitudinal gradient.

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				Site				Mimicry Complex
	Refugio Eladio (n=72)	Estación San Gerardo (n=79)	Selvatura (n=13)	Estación Biológica Monteverde (n=42)	Monteverde Community (n=58)	San Luis Waterfall (n=43)	Bajos de San Luis (n=35)	
Callithomia hezia hezia	1							Tiger-stripe
Dircenna chiriquensis				1				Tawny
Dircenna klugii		1				1	2	Tawny
Dircenna relata	1	1						Tawny
Episcada salvinia		2	1	1				Clearwing
Godyris zavaleta sorites	16							Tawny
Greta andromica lyra		4	1					Clearwing
Greta anette		11	8	8				Clearwing
Greta nero		6	1		1			Clearwing
Greta oto					1		3	Clearwing
Greta polissena umbrana		7		1		1		Clearwing
Hyalyris excelsa decumana	2	1						Tiger-stripe
Hypoleria cassotis	3							Clearwing
Hyposcada virginiana evanides	6					2		Tiger-stripe
Ithomia bolivari	1							Clearwing
Ithomia diasa hippocrenis	2	3						Clearwing
Ithomia heraldica	1	24		12	3	30	7	Tawny
Ithomia patilla	3	1				4	1	Clearwing
Ithomia xenos		1		7				Tawny
Mechanitis ethra lilis							1	Tiger-stripe
Mechanitis lysimnia doryssus	3							Tiger-stripe
Mechanitis menapis saturata	4	1					4	Tiger-stripe
Mechanitis polymnia isthmia							1	Tiger-stripe
Melinaea ethra lilis	1							Tiger-stripe
Napeogenes cranto paedaretus	14							Tawny
Napeogenes tolosa amara	1	1						Tiger-stripe
Oleria rubescens		2				2		Clearwing
Oleria vicina		3	2	10		2		Clearwing
Oleria zelica pagasa	1	1				1		Tawny
Olyras insignis insignis	9							Tawny
Pseudoscada utilla pusio	2	1						Clearwing
Pteronymia artena artena	1	3		1	1			Clearwing
Pteronymia fulvescens					52		2	Tawny
Pteronymia notilla		2					14	Tawny
Pteronymia parva		1						Clearwing
Pteronymia simplex simplex		1		1				Clearwing
Tithoria tarricina pinthias		1						Tiger-stripe

Appendix. Number of individuals of each species collected at each site, and the corresponding mimicry complex.