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ECOLOGY, NATURAL HISTORY AND BEHAVIOUR OF ITHOMIINE BUTTERFLIES AND THEIR MIMICS IN ECUADOR
(LEPIDOPTERA: NYMPHALIDAE: ITHOMIINAE)

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ABSTRACT.– The ithomiine butterfly species (Nymphalidae: Ithomiinae) which occur at Jatun Sacha Biological Station, Napo Province, Ecuador were found to participate in eight discrete mimicry complexes. These complexes involve a total of 124 insect species: 55 ithomiine species, 34 species which belong to other butterfly families or subfamilies, 34 moth species, and 1 species of damselfly. All species are illustrated and identified, and aspects of their behaviour are discussed. Literature on the chemical defences of the species is reviewed and a study of their ultraviolet reflectance patterns is presented. Data from a mark-release-recapture study show that the majority of individuals in the mimicry complexes studied were ithomiines. Hypotheses to explain polymorphism in Batesian and Müllerian mimics are discussed, in view of the finding that seven species of ithomiines, five other butterfly species, and the single damselfly species were polymorphic at Jatun Sacha.

KEY WORDS: Amazon, Apocynaceae, Arctiidae, Argentina, Batesian mimicry, Boraginaceae, Brazil, Charaxinae, chemical defences, Compositae, Costa Rica, Ctenuchinae, damselflies, Dioptidae, Dircennini, Dismorphiinae, Ennominae, Geometridae, Hedylidae, Heliconiinae, Hesperiidae, Ithomiinae, Jamaica, Lycaenidae, Mechanitini, Mexico, mimicry complexes, moths, Müllerian mimicry, Neotropical, Notodontidae, Nymphalidae, Odonata, Papilionidae, Papilioninae, Pericopinae, Peru, Pieridae, Pierinae, polymorphism, Polythoridae, Pyralidae, Pyrginae, Riodininae, Solanaceae, South America, Spilomelinae, Tithoreini, ultraviolet patterns, unpalatability, Venezuela, Zygoptera.

The Ithomiinae are an exclusively Neotropical subfamily of Nymphalidae, which currently includes some 310 species placed in 52 genera (Brown and Freitas, 1994; G. Lamas, in prep.). Ithomiine butterflies occur in moist forests from sea level up to 3000m (Drummond, 1976) and are found from Mexico (23°N latitude) to Argentina (35°S latitude).

Ithomiines were historically important in the development of the theories of both Batesian (Bates, 1862) and Müllerian (Müller, 1879) mimicry. Bates (1862) believed that ithomiines are unpalatable to predators and that palatable species which belong to other butterfly groups (Batesian mimics) have evolved to resemble them, thus gaining protection by 'deceiving' potential predators. Müller (1879) hypothesised that unrelated unpalatable species may also have converged in colour pattern, thereby reducing the number of different aposematic patterns that predators have to learn to avoid and consequently decreasing overall predation on the co-mimicking species (Müllerian mimics).

Experimental studies have confirmed that adult ithomiines are unpalatable to a variety of potential predators, including several species of birds (Haber, 1978; Brower, 1984; Srygley and Chai, 1990a) and a spider (Brown, 1984). Adults are protected by dehydropyrrolizidine alkaloids (PAs) which they sequester pharmacophagously, largely from the flower nectar of Eupatorieae (Compositae) and the decomposing leaves and stems of Boraginaceae (Brown, 1985). Male ithomiines visit PA sources more frequently than females (Lamas and Pérez, 1981). Females obtain most of their PAs indirectly, via the spermatophore transferred by males during mating (Brown, 1985; 1987). One 'primitive' species, *Tithorea harmonia* (Cramer), has been shown to sequester PAs directly from its larval hostplant *Prestonia acutifolia* Schumann (Apocynaceae) and the adults rarely visit PA sources (Trigo and Brown, 1990). Larvae of the majority of ithomiine species, however, feed on Solanaceae (Drummond and Brown, 1987), a plant family which does not contain PAs. Recently, Freitas *et al.* (1996) have shown that larvae of the ithomiine species *Placidula euryanassa* (Felder & Felder) sequester tropane alkaloids from their solanaceous hostplant *Brugmansia suaveolens* (Wild.) Sweet. These alkaloids are passed through the pupal stage to the adult and there is some evidence that vertebrate predators find them unpalatable.

Classical theory predicts that only one mimicry complex should occur at a locality, since Müllerian mimics (and therefore Batesian mimics) should converge onto the single 'best protected' aposematic pattern present in the area. However, in many regions of the Neotropics, several distinct ithomiine-dominated mimicry complexes occur sympatrically. Beccaloni (1995) has shown that the number of sympatric ithomiine-dominated complexes increases with increasing local species richness of ithomiines. A maximum of about eight complexes are known to occur at sites (in the upper Amazon basin of Ecuador and Peru) with the highest recorded species richness of ithomiines (Beccaloni, 1995).

Ecological studies (reviewed by Beccaloni, 1995) suggest that sympatric mimicry complexes are segregated from each other by microhabitat. Mimicry complexes fly at different heights and in different types of forest. Although there is some overlap between the microhabitat preferences of different complexes, each complex is probably the numerically dominant colour pattern in a particu-


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lar microhabitat. If butterfly predators are also segregated by microhabitat and/or the colour pattern of each complex is adapted to a different microhabitat, then convergence of different complexes over evolutionary time may be prevented. As the complexes in question are dominated by closely related butterfly species (ithomiines), the initial colour pattern divergence of the model species of each complex from a single (ancestral) colour pattern needs to be explained. Beccaloni (1995) argued that divergence of the colour patterns of model species could occur in sympatry, given prior microhabitat segregation of the species together with microhabitat-dependent selection on colour pattern.

Although it is widely assumed that ithomiines numerically dominate the mimicry complexes in which they participate (e.g., Brown, 1988), only a single study (by Poole, 1970) has attempted to quantify this. Poole (1970) found that over 85% of the individuals in the complex he studied in Venezuela were ithomiines; however, he did not present data on the abundances of the individual species involved. In addition, many authors have mentioned the fact that ithomiine-dominated mimicry complexes often occur sympatrically (e.g., Sheppard *et al.*, 1985; Turner, 1984; Brown, 1988), yet few studies have attempted to document the complexes found at a single site. Exceptions are Poole (1970), Papageorgis (1975) and the unpublished thesis work of Drummond (1976).

The present study is an attempt to document the sympatric mimicry complexes which involve ithomiines at one of the richest sites for ithomiine species in the Neotropics (Jatun Sacha Biological Station, Ecuador). All of the species which participate in these complexes are identified (most to species level) and behavioural observations are noted. A study of the ultraviolet (UV) light component of the wing patterns of the species is discussed and data on the abundances of individuals recorded during a mark-release-recapture (MRR) study are presented. Finally, I focus on the presence at Jatun Sacha of several polymorphic species and discuss theories which have been proposed to explain polymorphism in Batesian and Müllerian mimics.

For ease of discussion, I will arbitrarily refer to ithomiines as Müllerian "co-mimics" (of other ithomiine species) and to insects which resemble ithomiines simply as "mimics", as in many cases it is uncertain whether they are unpalatable Müllerian or palatable Batesian mimics.

STUDY SITE AND METHODS

This study was conducted at Jatun Sacha Biological Station, Napo Province, Ecuador, South America. Jatun Sacha is situated at 01° 04'S, 77° 36'W, on the southern bank of the Rio Napo (a tributary of the Amazon) at 450m elevation. The reserve lies 30 km east of the base of the Andes, and the environment is transitional between the lower Andean slopes and the Amazon lowlands. The core of the reserve comprises about 700 hectares of Tropical Wet Forest (Holdridge, 1971), of which 75% is primary and the remainder is secondary regrowth. The terrain is mostly steeply dissected hills crossed by small streams, although there is a small area (100 hectares) on the floodplain of the Rio Napo which is flat and subject to seasonal flooding (Castner, 1990; D. Neill, pers. comm.). Rainfall is fairly evenly distributed throughout the year, although December to the end of January tends to be relatively dry and April to June tends to be very rainy. The average annual precipitation is about 3700mm.

Fieldwork was conducted at Jatun Sacha during the following periods: 5 Sep - 14 Oct 1991; 11 Sep - 7 Nov 1992; and 22 Jan - 15 Feb 1994. A total of 30, 45 and 16 days, respectively, were spent in the field during these periods.

During all three fieldwork periods, I and several helpers (listed in the Acknowledgements) sampled ithomiines and their mimics with butterfly nets from a representative range of the different types of vegetation found in the reserve. The aim was to produce as complete a list as possible of the ithomiine and mimic species present at this site. The nets we used had a diameter of 40cm and a handle 30cm in length, giving a total vertical reach of approximately 2.7m. Sampling efficiency declined increasingly rapidly above about 2m and became virtually non-existent above 2.7m, first because low flying butterflies were easier to observe, and second because of the limited reach of the nets. A very low proportion of the individuals observed flying above 2.7m were, however, captured, by jumping up, climbing onto fallen logs, or waiting for them to descend to within net reach. This sampling bias means that low flying species are probably better recorded than higher flying species. Observations on the behaviour (flight pattern, resting posture, perching position etc.) of the species we collected were recorded.

Several species of mimics observed flying during the day were also attracted to light at night. These, together with other species

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GENERAL LEGEND FOR FIGURES 1-146: "polymorphic" = the species is polymorphic and both sexes have the same mimetic morphs; "♀ polymorphic" = the female is polymorphic and the male is monomorphic (both sexes are mimetic); "♂ not mimetic" = the male has a different colour pattern to the female and is probably not mimetic; "perches under leaves" = individuals were observed to perch under leaves; "at light" = all individuals observed were attracted to light at night; "by day and at light" = observed flying by day and also attracted to light at night.

Fig. 1-36. Mimicry complexes from Jatun Sacha. CLEARWING COMPLEX. **ITHOMIINAE, ITHOMIINI: 1**, *Ithomia agnosia agnosia* Hewitson. **GODYRIDINI: 2**, *Heterosais nephele nephele* (Bates); **3**, *Pseudoscada timna timna* (Hewitson). **LYCAENIDAE, RIODININAE: 4**, *Echenais alector alector* (Butler) ♀ (♂ not mimetic); **5**, *Esthemopsis celina celina* Bates; **6**, *Xynias christalla christalla* Grose-Smith (perches under leaves). **PYRALIDAE, SPILOMELINAE: 7**, *Desmia bajulalis bajulalis* Guenée (perches under leaves); **8**, *Erilusa* nr *leucoplagalis* (Hampson) (by day and at light; perches under leaves); **9**, *Omiodes hypoxantha hypoxantha* (Dognin) (at light); **10**, *Phostria* sp. (at light); **11**, *Phostria euryleucalis euryleucalis* Hampson. **GEOMETRIDAE, ENNOMINAE: 12**, *Emplocia* nr *pallor* (Druce); **13**, *Genussa* sp. (at light); **14**, *Genussa famulata famulata* Felder; **15**, *Nephodia panthea panthea* Druce; **16**, *Penthophlebia radiata radiata* (Felder) (by day and at light). **HEDYLIDAE: 17**, *Macrosoma lucivittata lucivittata* (Walker) ♀ (at light; ♂ lacks white fw spot and is probably not mimetic). **NOTODONTIDAE, DIOPTINAE: 18**, *Dioptis* nr *charila* Druce; **19**, *Euchontha frigida frigida* (Walker) (stridulates loudly when captured); **20**, *Monocreagra pheloides pheloides* Felder ♂; **21**, *Monocreagra pheloides pheloides* Felder ♀; **22**, *Myonia capena capena* (Druce); **23**, *Myonia pales pales* (Druce) (1 specimen ex. pupa - not observed in flight). **ARCTIIDAE, CTENUCHINAE: 24**, *Argyrta* nr *micilia* (Cramer); **25**, *Agyrtidia* nr *uranophila* (Walker); **26**, *Cacostatia* nr *ossa* (Druce); **27**, *Cyanopepla masia masia* (Dognin) (perches under leaves). **PERICOPINAE: 28**, *Hyalurga* sp. 1 (perches under leaves); **29**, *Hyalurga* sp. 2 (at light); **30**, *Hyalurga albovitrea albovitrea* Walker (at light); **31**, *Hyalurga osiba osiba* (Druce); **32**, *Hyalurga rufilinea rufilinea* (Walker) ♂; **33**, *Hyalurga rufilinea rufilinea* (Walker) ♀; **34**, *Hypocrita simulata simulata* (Walker). **ZYGOPTERA, POLYTHORIDAE, POLYTHORINAE: 35**, *Polythore mutata mutata* (McLachlan) ♂; **36**, *Polythore mutata mutata* (McLachlan) ♀ (♀ polymorphic).


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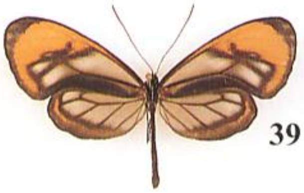
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which resembled them (but which were never observed during the day) were collected whenever possible from around tungsten and fluorescent lights in the reserve buildings and occasionally at a UV lamp hung against a white sheet and sited in the forest.

During fieldwork in 1994 a 16 day MRR study was conducted. The aim of this study was two-fold: first, to quantify the flight heights of ithomiine species and consequently investigate whether mimicry complexes are segregated by flight height; and second, to quantify the abundances of both the ithomiine and mimic species which participate in the mimicry complexes at Jatun Sacha. Only those methods and results relevant to the second part of this study will be given here. Full methods and results of the study on flight heights are given in Beccaloni (in press).

The MRR study was conducted within a 1 hectare plot (permanent study plot "Parcela 5") of primary aliuvial forest on the upper flood plain of the Rio Napo. This plot is surrounded on three sides by secondary regrowth and on one side by pasture. A transect line of nylon string, approximately 595m in length, was strung up through this area in four main loops, in such a way that almost all of the area would be sampled during the study. I and J. Brachi, or J. Brachi and one of several helpers (listed in the Acknowledgements), walked together at a steady pace back-and-forth along the transect continuously for the duration of the sampling period. One of us captured butterflies exclusively, the other both captured butterflies and recorded data into a field notebook. Data were only recorded for those individuals we actually caught. It was rare for there to be so many butterflies present at one time that both of us were required to catch them. Ithomiines and their mimics were sampled within a ca. 2m band on either side of the transect. All mimics were killed and preserved for future identification. Ithomiines, however, were gently removed from the net, identified to species (using if necessary, a set of previously prepared photographic plates illustrating most of the Jatun Sacha ithomiine species), and sexed. They were then marked using a quick drying permanent marker pen and released. Recaptures were recorded, but are not included in the data analysis. The total sampling time was 57 field hours: an average of ca. 3½ hours per day. Whenever possible, sampling was conducted between 9:30AM (0930h) and 1:30PM (1330h).

All specimens collected during fieldwork at Jatun Sacha have been deposited in the collections of The Natural History Museum, London, England, UK or the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.

ITHOMIINE MIMICRY COMPLEXES AT JATUN SACHA

The species involved

During this study 56 ithomiine species (representing 25 genera and 10 tribes) were recorded from Jatun Sacha. However, one of these, *Hyalyris coeno norellana* (Haensch), did not closely resemble any other species observed and it will therefore not be discussed in this paper. A total of 69 insect species were collected which resembled ithomiines. These mimics represent 34 species of butterflies (25 genera, 9 subfamilies and 4 families), 34 species of moths (21 genera, 6 subfamilies and 5 families), and one species of damselfly. Seven species of ithomiines and six species of mimic (5 species of butterflies and the damselfly species) were polymorphic.

Fig. 1-146 illustrate the ithomiine and mimic species (including all mimetic morphs) recorded. The species can be divided into eight discrete mimicry complexes and the specimens illustrated have been grouped accordingly. A mimicry complex is defined here as a group of two or more species which, through a combination of visual appearance and behaviour, resemble each other closely enough that they are frequently confused (at least by the human observer). The aposematic signal transmitted by the members of a complex is perceived by the signal-receiver (i.e., potential predators) to be discrete from other such signals in a habitat (see Vane-Wright, 1976, for an explanation of these terms).

The terminology adopted to describe the complexes is based on a combination of that used by Drummond (1976), Haber (1978), and Brown (1988). The specimens grouped to illustrate each complex (Fig. 1-146) have been arranged in columns from left to right, with ithomiines placed first, followed by other butterflies, then moths and finally Zygoptera. Species are arranged in taxonomic order by family and subfamily, following the arrangement of Harvey (1991) for the Nymphalidae and Scoble (1992) for the other Lepidoptera. Only one sex of each species is illustrated, except in the case of sexually dimorphic species, where both sexes and any mimetic morphs are shown.

It is likely that few (if any) species of ithomiine remain to be recorded from Jatun Sacha, as species accumulation curves for ithomiines are typically steep and rapidly become asymptotic (Beccaloni and Gaston, 1994). However, because most species of mimic are rare (see below), the species encounter rate is low and therefore more species are likely to have gone unrecorded. One possible ithomiine mimic known to have been missed is the female of *Brontiades procas purda* (Evans) (Hesperiidae: Pyrginae). This species is probably a dual sex-limited mimic (i.e., males and females possess different mimetic colour patterns). Two males were collected (they are black and yellow, slow flying, and possibly participate in a non-ithomiine complex dominated by arctiid moths), but the female, which may belong to the Small Dark Transparent Complex (see Fig. 51-65), was not observed.

Fig. 37-65. Mimicry complexes from Jatun Sacha (continued); see general legend on Fig. 1-36. ORANGE-TIP COMPLEX. **ITHOMIINAE, NAPEOGENINI: 37**, *Napeogenes sylphis caucayaensis* Fox & Real. **GODYRIDINI: 38**, *Hypoleria lavinia chrysodonia* (Bates); **39**, *Hypoleria sarepta aureliana* (Bates); **40**, *"Hypoleria" orolina orolina* (Hewitson); **41**, *"Hypoleria" seba oculata* (Haensch); **42**, *Pseudoscada florula aureola* (Bates). **PIERIDAE, DISMORPHIINAE: 43**, *Dismorphia theucharila* f. *erythroe* Bates (polymorphic). **LYCAENIDAE, RIODININAE: 44**, *Ithomeis corena corena* (Felder & Felder); **45**, *Ithomiola cascella cascella* (Hewitson); **46**, *Metacharis regalis regalis* Butler ♀ (♂ not mimetic); **47**, *Pheles heliconides heliconides* (Herrich-Schäffer); **48**, *Stalachtis euterpe latefasciata* Staudinger. **ARCTIIDAE, PERICOPINAE: 49**, *Hyalurga* nr *batesi* (Druce). **ZYGOPTERA, POLYTHORIDAE, POLYTHORINAE: 50**, *Polythore mutata mutata* (McLachlan) ♀ (♀ polymorphic). SMALL DARK TRANSPARENT COMPLEX. **ITHOMIINAE, OLERIINI: 51**, *Hyposcada illinissa ida* Haensch; **52**, *Hyposcada kena kena* (Hewitson); **53**, *Oleria agarista agarista* (Felder & Felder); **54**, *Oleria assimilis assimilis* (Haensch); **55**, *Oleria gunilla lota* (Hewitson); **56**, *Oleria lerda lerda* Haensch; **57**, *Oleria ? sexmaculata sexmaculata* (Haensch); **58**, *Oleria tigilla tigilla* (Weymer). **PIERIDAE, DISMORPHIINAE: 59**, *Dismorphia theucharila* f. *leuconoe* Bates (polymorphic). **NYMPHALIDAE, NYMPHALINAE: 60**, *Eresia clara clara* Bates; **61**, *Eresia plagiata plagiata* (Röber). **LIMENITINAE: 62**, *Vila cacica cacica* Staudinger. **LYCAENIDAE, RIODININAE: 63**, *Mesosemia phelina rubeola* (Stichel); **64**, *Nymphidium minuta minuta* Druce (perches under leaves). **ARCTIIDAE, PERICOPINAE: 65**, *Hyalurga padua padua* (Druce).


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Human and predator perception of mimicry

Although the species discussed in this study were classified as mimetic on the basis of subjective human judgement, many studies have demonstrated that captive predators are unable to separate palatable and unpalatable species which humans perceive to be mimetic (see examples reviewed by Turner, 1977). There is also some evidence that predators assess the degree of resemblance in colour pattern between species in a broadly similar way to the human (Dittrich *et al.*, 1993).

Parallel geographic variation

The existence of parallel geographic variation in colour pattern between different species provides strong evidence that the resemblance between them is a result of mimicry and not chance. This phenomenon was noted by Bates (1879), who observed that ithomiines and similarly patterned but unrelated species "change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles". Many of the species which participate in the mimicry complexes at Jatun Sacha are known to exhibit parallel geographic variation of this kind. Examples of mimics which vary geographically in colour pattern together with various ithomiine species are: *Pterourus zagreus* (Doubleday) (Papilionidae) (see Fig. 6.2 in Tyler, Brown and Wilson, 1994), and *Heliconius numata* (Cramer) (Nymphalidae: Heliconiinae) (see Brown and Benson, 1974). Interestingly, the female of *Metacharis regalis* Butler (Lycaenidae: Riodininae) (Fig. 46) only appears to possess an orange marking on the forewing in areas where its geographical distribution overlaps with that of the Orange-Tip Complex (i.e., the upper Amazon basin). In areas of its range where the Orange-Tip Complex is absent (e.g., parts of Venezuela and Brazil), it lacks the orange marking (pers. observ.) and is presumably not a mimic.

Are the complexes discrete?

Although I and other observers (Drummond, 1976; Haber, 1978; Brown, 1988; J. Brachi, pers. comm.) perceive the colour patterns possessed by the eight mimicry complexes discussed in this study to be discrete aposematic signals, it is possible that predators regard them differently. For example, predators may view these eight patterns as a single "generalisation series" (Ackery and Vane-Wright, 1984). The existence of polymorphism between most of these complexes, however, provides indirect evidence that their natural predators, like humans, perceive the aposematic patterns of these complexes to be discrete. Thus, if we accept that mimetic morphs of a species are adaptive, then their existence can only be explained if the colour pattern of each morph is perceived as a discrete signal by predators. At Jatun Sacha, polymorphism occurs between the Clearwing and Orange-Tip Complexes (i.e., the female of *Polythore mutata* (McLachlan) (Odonata: Polythoridae), Fig. 36 and 50), the Small Dark Transparent and the Orange-Tip Complex (i.e., *Dismorphia theucharila* (Doubleday) (Pieridae: Dismorphiinae), Fig. 43 and 59), and between the Yellow-Bar Tiger, the Orange and Black Tiger, and the Tiger Complexes (e.g., *Heliconius numata*, Fig. 106, 115 and 137). There is, however, no polymorphism between the Small Yellow Transparent Ccomplex and any other complex, or the Large Yellow Transparent Complex and any other.

Fidelity of mimicry between species

Species within a mimicry complex differ in the degree to which they resemble the 'dominant' colour pattern of the complex, i.e., the colour pattern possessed by the majority of the individuals (belonging one or more species) participating in the complex. Although some species (e.g., *Desmia bajulalis* Guenée (Pyralidae), Fig. 7) appear to be relatively 'poor' mimics (to the human observer), only a slight resemblance to noxious prey may be sufficient to deter at least some potential predators from attack. Interestingly, studies have shown (e.g., Brower, Alcock and Brower, 1971; Dittrich *et al.*, 1993) that predators may regard some species which to the human eye appear to be poor mimics, as high fidelity mimics (but see Cuthill and Bennett, 1993).

The fidelity of mimicry between species is a product of both the colour pattern and the behaviour of the species concerned. Thus some species which appear to be relatively poor mimics when seen pinned (e.g., compare *Hypocrita simulata* (Walker) (Arctiidae: Pericopinae), Fig. 34, with *Heterosais nephele* (Bates) (Nymphalidae: Ithomiinae), Fig. 2), are much better mimics when observed alive in their natural habitat. Bates (1862) realised this and remarked when discussing resemblances between species of ithomiine and riodinine butterflies, and dioptine moths, "The imitations may not appear very exact from the figures; but when the insects are seen on the wing in their native woods, they deceive the most experienced eye."

An example of the importance of behaviour in mimicry is the 'mimicry by behavioural illusion' exhibited by the female of *Dysschema jansonis* (Butler) (Arctiidae: Pericopinae), as described by Aiello and Brown (1988). The female of this species is a good mimic of female *Parides* spp. (Papilionidae: Papilioninae) when observed in flight, in spite of differences in the arrangement of the wing pattern elements between it and *Parides* spp. The major difference between *Parides* spp. and *D. jansonis* is that the former have a yellow marking on both the upperside and underside of the forewing, while the latter species has a yellow marking on the underside of the forewing only. This difference is not evident, however, when the species are observed in flight, largely as a result of the high wing-beat frequency of *D. jansonis*.

Fig. 66-94. Mimicry complexes from Jatun Sacha (continued); see general legend on Fig. 1-36. SMALL YELLOW TRANSPARENT COMPLEX. **ITHOMIINAE, MECHANITINI: 66**, *Scada reckia ethica* (Hewitson). **NEW TRIBE: 67**, *Aeria eurimedea negricola* (Felder & Felder). **NAPEOGENINI: 68**, *Napeogenes inachia avila* Haensch. **ITHOMIINI: 69**, *Ithomia amarilla amarilla* Haensch; **70**, *Ithomia salapia* f. *travella* Haensch; **71**, *Ithomia salapia* f. *derasa* Hewitson; **72**, *Ithomia salapia* f. *salapia* Hewitson. **DIRCENNINI: 73**, *Ceratiscada hymen* ssp. n. Lamas; **74**, *Pteronymia vestilla sparsa* Haensch. **GODYRIDINI: 75**, *Godyris zavaleta matronalis* (Weymer) ♂; **76**, *Godyris zavaleta matronalis* (Weymer) ♀. **PIERIDAE, DISMORPHIINAE: 77**, *Moschoneura pinthaeus amelina* (Höpffer); **78**, *Moschoneura pinthaeus ithomia* (Hewitson). **PIERINAE: 79**, *Itaballia demophile demophile* (Linnaeus) ♀ (♂ not mimetic); **80**, *Itaballia pisonis pisonis* (Hewitson) ♀ (♂ not mimetic). **LYCAENIDAE, RIODININAE: 81**, *Hyphilaria nicia nicia* Hübner. LARGE YELLOW TRANSPARENT COMPLEX. **ITHOMIINAE, MECHANITINI: 82**, *Thyridia psidii ino* Felder & Felder. **METHONINI: 83**, *Methona confusa psamathe* Godman & Salvin; **84**, *Methona curvifascia curvifascia* Weymer. **NAPEOGENINI: 85**, *Napeogenes pharo pharo* (Felder & Felder). **DIRCENNINI: 86**, *Callithomia lenea zelie* (Guérin); **87**, *Dircenna loreta loreta* Haensch. **GODYRIDINI: 88**, *Godyris dircenna dircenna* (Felder & Felder). **PIERIDAE, DISMORPHIINAE: 89**, *Patia orise denigrata* (Rosenberg & Talbot). **ARCTIIDAE, PERICOPINAE: 90**, *Dysschema buckleyi buckleyi* (Druce) ♂ (by day and at light; ♀ mimics *Parides* spp. (Papilionidae)); **91**, *Dysschema mosera mosera* (Druce); **92**, *Dysschema* sp. (at light); **93**, *Dysschema grassator grassator* (Hering); **94**, *Dysschema hypoxantha hypoxantha* Hübner (by day and at light).


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Upper- and underside wing patterns

Species with aposematic coloration generally have very similar colour patterns on both the uppersides and undersides of their wings (Kaye, 1914), presumably because predators find a single pattern (i.e., one repeated on both wing surfaces) easier to learn than two patterns (i.e., a different upperside and underside pattern). Only one of the species illustrated in Fig. 1-146 has markedly different upperside and underside wing patterns. This exception is *Consul fabius* (Cramer) (Nymphalidae: Charaxinae) (Fig. 108 and 141), which has an aposematic upperside wing pattern and a cryptic underside pattern which resembles a dead leaf. Interestingly, when *Consul* is observed in flight only the aposematic upperside wing pattern is visible, because the scales on the underside of the wing are translucent and widely spaced, thus allowing the upperside pattern to show through when seen against the light (Kaye, 1922). Some of the other species illustrated exhibit relatively minor pattern differences between the upperside and underside of their wings, the most pronounced being that some species (e.g., the ithomiines *Napeogenes sylphis* (Guerin-Ménéville), Fig. 37, *Hyposcada illinissa* (Hewitson), Fig. 51, *Napeogenes inachia* (Hewitson), Fig. 68, *Methona confusa* Butler, Fig. 83, *Napeogenes achaea* (Hewitson), Fig. 98, and *Mechanitis lysimnia* (Fabricius), Fig. 122) have white spots around the margin of the forewing and/or hindwing on the underside, but not on the upperside. Could these be 'deflection marks' which function to direct the attacks of predators away from the body when these insects are at rest (see Brakefield, 1984)?

Size differences

Differences in size between species which belong to the same mimicry complex are sometimes great (e.g., compare *Pterourus zagreus* (Papilionidae), Fig. 132, with *Phaeochlaena hazara* (Butler) (Notodontidae: Dioptinae), Fig. 146). However, unlike humans, birds and possibly other predators may not use size as an important discriminatory cue (Carpenter and Ford, 1933; Dittrich *et al.*, 1993).

Intraspecific variation

Variation in colour pattern between individuals of an aposematic species is puzzling, as theory predicts that aposematic patterns should be 'stabilised' by strong selection. At Jatun Sacha the following ten species were variable: the ithomiines *Oleria agarista* (Felder & Felder) (Fig. 53), *Hypothyris mamercus* (Hewitson) (Fig. 101), *Hypothyris euclea* (Godart) (Fig. 126), *Callithomia alexirrhoe* Bates (Fig. 103 and 130), *Ceratinia tutia* (Hewitson) (Figs 104 and 131), *Mechanitis mazaeus* Hewitson (Fig. 96, 110 and 123); the dismorphine *Dismorphia theucharila* (Fig. 43 and 59); the heliconiines *Eueides lampeto* Bates (Fig. 114) and *Heliconius numata* (Fig. 106, 115 and 137); and the danainae *Lycorea cleobaea* (Godart) (Fig. 142). Only the 'typical' forms of these species are illustrated. In most cases the degree of variation was relatively minor, such that variants could not be distinguished from the typical form when observed in flight. Variants were rare relative to the typical form of the species, with the exception of *C. alexirrhoe* and *M. mazaeus*, where every individual observed had a slightly different pattern. In the case of six of the above species, every variant individual possessed a slightly different colour pattern, while in contrast, four species (*H. mamercus*, *C. tutia*, *D. theucharila* and *H. numata*) exhibited discontinuous variation. Although the variants of these four species are discrete morphs, they closely resemble other more abundant forms of these species and they appear to belong to the same mimicry complexes as these commoner forms. The morphs in question are as follows: the morph of *H. mamercus* differs from the typical form illustrated in Fig. 101 in that it has yellow marginal spots in the black apical marking of the forewing; *C. tutia* has two morphs both of which are similar to the form illustrated in Fig. 131, except that in one (f. *callichroma* Staudinger) the black hindwing bar is reduced, while in the other the yellow forewing marking is reduced and divided in two; the morph of *D. theucharila* (*i.e.*, f. *melanoe* Bates) is similar to f. *leuconoe* Bates (Fig. 59) but lacks orange on the forewing; the morph of *H. numata* (i.e., f. *euphone* Felder & Felder) is similar to f. *euphrasius* Weymer (Fig. 106) but has a black bar on the hindwing, rather than a large black spot.

Although the reason for variation in the above species is unclear, one possibility is that it is a result of hybridisation between neighbouring parapatric mimetic races of these species (see Mallet, 1993, for a detailed discussion of hybridisation between geographical races of mimetic species). Another possibility is that in the case of polymorphic species, rare variants could be non-adaptive genetic recombinants between different mimetic morphs (e.g., the rare f. *euphone* of *Heliconius numata* may be a recombinant between the mimetic morphs *laura* Neustetter, Fig. 137, and *euphrasius*, Fig. 106).

ULTRAVIOLET PATTERNS OF ITHOMIINES AND MIMICS

Unlike humans, many insects (including Lepidoptera) can see UV-A light (315-400nm) (Silberglied, 1979; Bennett, Cuthill and Norris, 1994; Tovée, 1995). Silberglied (1984) believed that the majority of terrestrial vertebrates cannot see UV, and he postulated that this spectral region may therefore provide a "private channel" for communication among insects. If this were true, then the colour patterns of species which participate in the same mimicry complex may have converged in the 'visible' region

Fig. 95-116. Mimicry complexes from Jatun Sacha (continued); see general legend on Fig. 1-36. YELLOW-BAR TIGER COMPLEX. **ITHOMIINAE, MELINAEINI: 95**, *Melinaea menophilus cocana* Haensch. **MECHANITINI: 96**, *Mechanitis mazaeus fallax* Butler (polymorphic); **97**, *Mechanitis messenoides messenoides* Felder & Felder (polymorphic). **NAPEOGENINI: 98**, *Napeogenes achaea achaea* (Hewitson); **99**, *Napeogenes stella* ssp. n. Brown; **100**, *Hypothyris anastasia honesta* (Weymer) (polymorphic); **101**, *Hypothyris mamercus mamercus* (Hewitson); **102**, *Hypothyris moebiusi moebiusi* (Haensch) (polymorphic). **DIRCENNINI: 103**, *Callithomia alexirrhoe* ssp. n. Lamas (polymorphic); **104**, *Ceratinia tutia poecila* f. *nigronascens* Haensch (polymorphic). **PIERIDAE, PIERINAE: 105**, *Perrhybris pamela amazonica* Fruhstorfer ♀ (♂ not mimetic). **NYMPHALIDAE, HELICONIINAE: 106**, *Heliconius numata* f. *euphrasius* Weymer (polymorphic). **NYMPHALINAE: 107**, *Eresia pelonia* f. *callonia* Staudinger ♀ (♀ polymorphic). **CHARAXINAE: 108**, *Consul fabius aequatorialis* f. *diffusus* Butler (polymorphic). ORANGE AND BLACK TIGER COMPLEX. **ITHOMIINAE, MELINAEINI: 109**, *Melinaea marsaeus mothone* (Hewitson). **MECHANITINI: 110**, *Mechanitis mazaeus mazaeus* Hewitson (polymorphic); **111**, *Mechanitis messenoides deceptus* Butler (polymorphic). **NAPEOGENINI: 112**, *Hypothyris anastasia bicolora* (Haensch) (polymorphic); **113**, *Hypothyris moebiusi unicolora* (Tessmann) (polymorphic). **NYMPHALIDAE, HELICONIINAE: 114**, *Eueides lampeto acacetes* Hewitson; **115**, *Heliconius numata* f. *bicoloratus* Butler (polymorphic). **NYMPHALINAE: 116**, *Eresia pelonia* f. *ithomiola* Salvin ♀ (♀ polymorphic).


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of the spectrum, but diverged in the UV region for the purpose of intra- or inter-specific communication. For example, species which have similar visible patterns could have different 'hidden' UV reflectance patterns, such as those possessed by many otherwise similarly coloured (but probably not mimetic) species belonging to many genera of Lepidoptera (e.g., the Pieridae genera *Colias*, *Gonepteryx* and *Pieris*: for references see Silberglied, 1984). Another possibility is that species which belong to the same complex may have wing markings of the same visible colours, but the markings of each species may reflect different intensities or wavelengths of UV light, and therefore to an organism with UV vision, each species may appear to have the same basic pattern, but with markings of different colours or hues.

An important question, of course, is not only how butterfly species might perceive wing patterns in the UV region of the spectrum, but whether predators can see UV light. Current thinking is that UV vision is probably the rule for birds and many other groups of vertebrate (Bennett, Cuthill and Norris, 1994). While humans only have three types of colour receptor (cones), birds are known to have four (possibly five), including one sensitive to UV (Bennett, Cuthill and Norris, 1994). Birds also possess a system of oil droplets which act as filters to the light entering individual cones and these may alter the number of hues they perceive (ibid.). These anatomical differences suggest that birds may perceive more colours and hues than humans.

If some, or all, of the predators which are responsible for selecting for mimicry between insects have UV vision, then species in a mimicry complex should have converged in both the visible and UV elements of their colour patterns. Studies by Lutz (1933), Crane (1954), and Remington (1973) have shown that Lepidoptera thought to mimic each other usually have similar UV patterns. Remington (1973) found that a few of the putative mimics he examined differed in UV pattern, but unfortunately he did not describe these differences or even list the species he surveyed. No other studies seem to have examined the UV reflectance patterns of mimetic insects.

Methods

Fig. 147-162 represent a preliminary attempt to investigate whether the species I grouped together as belonging to a mimicry complex on the basis of similar visible colour patterns (and similar flight behaviour), differ in their UV patterns. The specimens shown in Fig. 147-162 are the same as those illustrated in Figs 1-146 and they have been arranged in the same way. Specimens were photographed on panchromatic Polaroid film, using a Sinar 5 x 4 camera fitted with an Ilford UV-transmitting filter (transmission range of between ca. 315-385nm, with peak transmission at 350nm). They were illuminated by natural sunlight, which was incident on the plane of the specimens at an angle of ca. 60°. Specimens were photographed against both a 'visible white' UV-reflecting background (Fig. 147-154) and a 'visible black' UV-absorbing background (Fig. 155-162). This was done because some species have wing areas which are transparent or translucent to visible light and it is only possible to judge whether these areas are also transparent or translucent to UV light, if a specimen is viewed against both a UV-reflecting and a UV-absorbing background. For example, a UV transparent specimen on a UV-absorbing background will appear dark in a UV photograph and it will only be possible to determine whether it is UV-transparent or UV-absorbing if it is also seen against a UV-reflecting background.

UV reflectance patterns

Comparison between Fig. 1-146 and Fig. 147-162 shows that the only visible colours which strongly reflect UV light are white and, to a lesser degree, the pale yellow of the wings of the ithomiines *Scada reckia* (Hübner) (Fig. 66), *Ithomia amarilla* Haensch (Fig. 69), *Ithomia salapia* f. *travella* Haensch (Fig. 70), *Ithomia salapia* f. *derasa* Hewitson (Fig. 71), and the riodinine *Hyphilaria nicia* Hübner (Fig. 81), and the hindwing marginal spots of the papilionid *Pterourus zagreus* (Fig. 132) and the charaxine *Consul fabius aequatorialis* (Butler) (Fig. 141). The visible iridescent blue which overlays the visible black on the hindwing of the pericopine *Hypocrita simulata* (Walker) (Fig. 34) also reflects some UV. All other visible colours strongly absorb UV: with black absorbing most strongly, and the orange on the forewings of *Hyalurga* sp. 2 (Arctiidae: Pericopinae) (Fig. 29), *Metacharis regalis* (Lycaenidae: Riodininae) (Fig. 46), and *Pheles heliconides* (Herrich-Schäffer) (Lycaenidae: Riodininae) (Fig. 47), absorbing least strongly. In many cases, wing areas transparent or translucent to visible light are also transparent or translucent to UV light. The 'visibly' transparent or translucent wing areas of some species, however, strongly reflect UV light. This is true for *Ithomiola cascella* (Hewitson) (Lycaenidae: Riodininae) (Fig. 45), all visibly transparent or translucent species which belong to the Small dark transparent complex (Fig. 51-65, 149 and 157), and some species which belong to the Clearwing Complex (Fig. 1-36, 147 and 155).

Similarities and differences between UV and visible wing patterns

In general, most species examined resemble each other as closely in the UV element of their colour patterns as they do in

Fig. 117-146. Mimicry complexes from Jatun Sacha (continued); see general legend on Fig. 1-36. TIGER COMPLEX. **ITHOMIINAE, TITHOREINI: 117**, *Tithorea harmonia hermias* Godman & Salvin. **MELINAEINI: 118**, *Melinaea maelus maeonis* Hewitson; **119**, *Melinaea mnasias abitagua* Brown. **MECHANITINI: 120**, *Forbestra olivencia juntana* (Haensch); **121**, *Forbestra equicola equicoloides* (Godman & Salvin); **122**, *Mechanitis lysimnia elisa* (Guérin); **123**, *Mechanitis mazaeus visenda* Butler (polymorphic); **124**, *Mechanitis polymnia dorissides* Staudinger. **NAPEOGENINI: 125**, *Napeogenes aethra aethra* (Hewitson); **126**, *Hypothyris euclea intermedia* (Butler); **127**, *Hypothyris fluonia berna* (Haensch); **128**, *Hypothyris semifulva satura* (Haensch). **OLERIINI: 129**, *Hyposcada anchiala ecuadorina* Bryk. **DIRCENNINI: 130**, *Callithomia alexirrhoe butes* Godman & Salvin (polymorphic); **131**, *Ceratinia tutia poecila* (Bates) (polymorphic). **PAPILIONIDAE, PAPILIONINAE: 132**, *Pterourus zagreus zagreus* (Doubleday). **PIERIDAE, DISMORPHIINAE: 133**, *Dismorphia amphiona* ssp. n. Lamas. **PIERINAE: 134**, *Charonias eurytele eurytele* (Hewitson). **NYMPHALIDAE, HELICONIINAE: 135**, *Eueides isabella pellucida* Srnka; **136**, *Heliconius hecale quitalena* (Hewitson); **137**, *Heliconius numata* f. *laura* Neustetter (polymorphic). **NYMPHALINAE: 138**, *Eresia eunice eunice* (Hübner); **139**, *Eresia pelonia* f. *pelonia* Hewitson ♂; **140**, *Eresia pelonia* f. *pelonia* Hewitson ♀ (♀ polymorphic). **CHARAXINAE: 141**, *Consul fabius aequatorialis* (Butler) (polymorphic). **DANAINAE: 142**, *Lycorea cleobaea atergatis* Doubleday; **143**, *Lycorea pasinuntia brunnea* Riley. **LYCAENIDAE, RIODININAE: 144**, *Stalachtis calliope calliope* (Linnaeus); **145**, *Themone trivittata trivittata* Lathy. **NOTODONTIDAE, DIOPTINAE: 146**, *Phaeochlaena hazara hazara* (Butler).

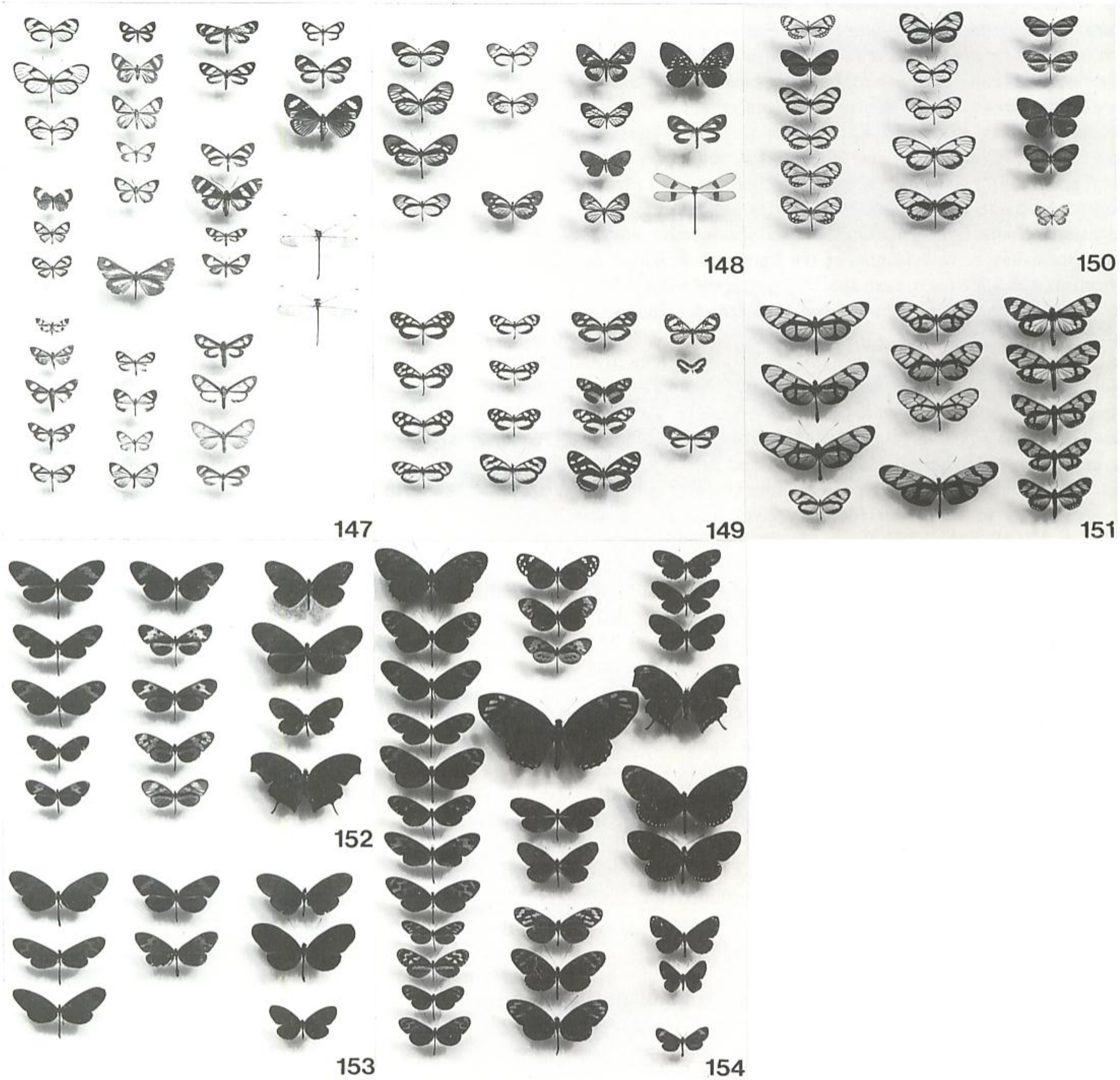

Fig. 147-154. Ultraviolet reflectance patterns of ithomiine and mimic species recorded from Jatun Sacha Biological Station, shown against a UV reflecting background. Specimens are grouped by mimicry complex and are arranged in the same way as in Fig. 1-146. **147**, Clearwing complex (cf. Fig. 1-36); **148**, Orange-tip complex (cf. Fig. 37-50); **149**, Small dark transparent complex (cf. Fig. 51-65); **150**, Small yellow transparent complex (cf. Fig. 66-81); **151**, Large yellow transparent complex (cf. Fig. 82-94); **152**, Yellow-bar tiger complex (cf. Fig. 95-108); **153**, Orange and black tiger complex (cf. Fig. 109-116); **154**, Tiger complex (cf. Fig. 117-146).

the visible element of their patterns, and none of the species have 'hidden' UV patterns. Perhaps the major difference observed between the visible and UV patterns of species thought to belong to the same mimicry complex is that seen between members of the Small Yellow Transparent Complex (Fig. 1-146, 150 and 158). The visible yellow areas of the wings of five of the species in this complex (the ithomiines *Scada reckia*, Fig. 66, *Ithomia amarilla*, Fig. 69, *Ithomia salapia* f. *travella*, Fig. 70, *Ithomia salapia* f. *derasa*, Fig. 71, and the riodinine *Hyphilaria nicia*, Fig. 81) reflect UV, while the corresponding wing areas of the other species either absorb UV or are UV transparent. Thus, although all of the species in this complex reflect a similar visible colour (i.e., yellow), it is plausible that an organism with UV vision may perceive the five species listed above to be of a different colour (UV + visible yellow), from the other species in this complex (which reflect visible yellow only).

It is not clear whether the differences observed between the UV reflectance patterns of species with similar visible patterns are real, or whether they are artifacts of the technique used to examine the UV patterns of the species in this study. For example, although the riodinine *Ithomiola cascella* (Fig. 45) appears to reflect UV more strongly than any other visibly trans-

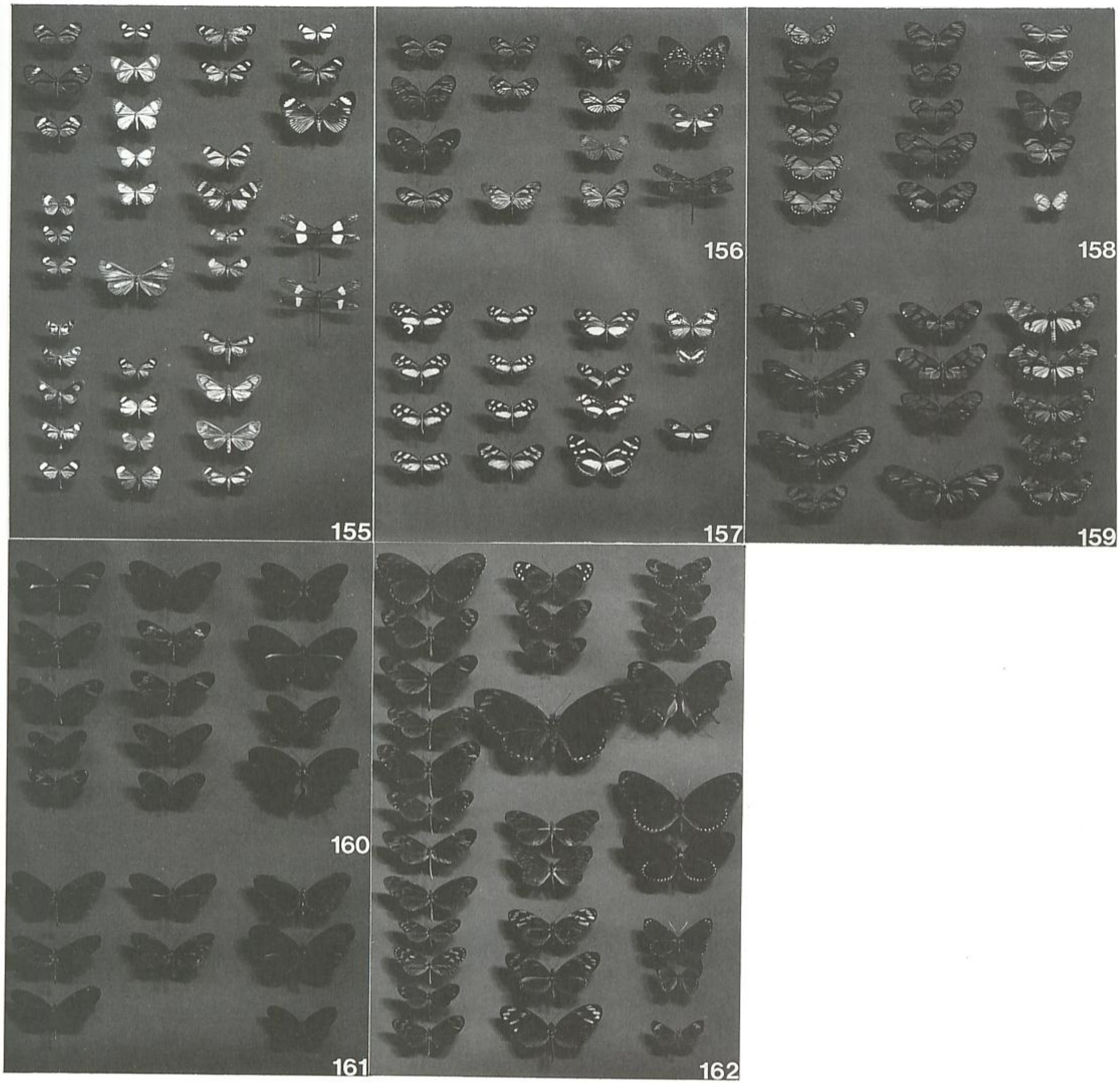

Fig. 155-162. Ultraviolet reflectance patterns of ithomiine and mimic species recorded from Jatun Sacha Biological Station, shown against a UV absorbing background. Specimens are grouped by mimicry complex and are arranged in the same way as in Fig. 1-146. **155**, Clearwing complex (cf. Fig. 1-36); **156**, Orange-tip complex (cf. Fig. 37-50); **157**, Small dark transparent complex (cf. Fig. 51-65); **158**, Small yellow transparent complex (cf. Fig. 66-81); **159**, Large yellow transparent complex (cf. Fig. 82-94); **160**, Yellow-bar tiger complex (cf. Fig. 95-108); **161**, Orange and black tiger complex (cf. Fig. 109-116); **162**, Tiger complex (cf. Fig. 117-146).

parent species in the Orange-Tip Complex (Fig. 37-50, 148 and 156), it is possible that all species in this complex strongly reflect UV when viewed at certain angles (i.e., they may have UV iridescence). An improvement over the method adopted in this study would therefore be to use a video camera fitted with a UV-transmitting filter, so that specimens could be viewed at any angle.

Like the visible spectrum, the UV spectrum is composed of different wavebands which may be perceived as different colours by organisms with UV vision (Brunton and Majerus, 1995). In this study, however, only a relatively narrow range of UV wavelengths were examined (315-385nm). To examine a wider range of wavelengths, specimens could either be photographed using a series of UV-transmitting filters, each with a different peak UV-transmission, or alternatively, the colours of specimens could be measured quantitatively using a spectrometer (e.g., Brunton and Majerus, 1995).

Are differences between the UV patterns of species in the same complex important?

Although differences may exist between the amount of UV light reflected, absorbed, or transmitted (in the case of species with transparent or translucent wings) by the wing patterns of species in a mimicry complex, it is not known whether the natural predators of these insects have UV vision and, if they do, whether they perceive these differences to be important. In many cases the human observer can perceive differences in visible colour or hue between species classified as belonging to the same complex (e.g., compare the ithomiine *Heterosais nephele* (Bates), Fig. 2, with the pericopine *Hypocrita simulata,* Fig. 34). However, these differences are most apparent when the insects are closely examined, and they are less evident (or not evident at all) when the species are observed in flight in their natural habitat. By analogy, even if predators can see colour differences not perceptible to humans between species in a 'human-defined' mimicry complex, it is uncertain whether they would be able to discriminate between these species - at least when they were observed in flight.

The fact that species classified by the human observer as mimetic have converged in the shape and arrangement of the elements of the wing pattern, strongly suggests that predators perceive at least these aspects of the wing pattern in a similar way to the human. If predators and humans perceive the colours or hues of the wing pattern elements of such species differently, however, then they may differ in how they classify these species into mimicry complexes. For example, a human may perceive a group of species with wing patterns comprised of similarly shaped and arranged elements also to have similar colours and therefore hypothesise that they belong to a single mimicry complex, while a predator may perceive the same group of species to be an aggregate of two or more discrete mimicry complexes, each with a different colour. It is possible that this could be the case with the Small Yellow Transparent Complex (Fig. 1-146, 150 and 158): predators may regard the species which reflect UV as a discrete mimicry complex from the species which do not reflect UV (see above). The suggestion that these two groups of species may be perceived by predators as different complexes is supported by the fact that one species, *Ithomia salapia*, has two morphs (*travella*, Fig. 70, and *derasa*, Fig. 71) which reflect UV, and a third morph (*salapia* Hewitson, Fig. 72) which does not. Although the morph *travella* may not be mimetic (it is very rare and may be a recombinant between the commoner *derasa* and *salapia*), it is difficult to account for the existence of the other two morphs unless they are members of discrete complexes. This example is ambiguous, however, as the differences in UV reflection between these morphs and the other species in this complex correspond to differences in the shade of the visible yellow colour of these taxa. Thus if predators were shown to perceive these species as two discrete complexes, it may be on the basis of visible colour alone and the differences in UV reflectance observed between them may be an incidental consequence of the way in which the different visible yellow colours they exhibit are produced.

Only experiments conducted using the natural enemies of these insects will resolve the question of whether predators perceive the mimicry complexes discussed in this study in the same, or in different ways to the human observer.

RELATIVE ABUNDANCE OF ITHOMIINES AND MIMICS

During the 16 day MRR study at Jatun Sacha, 41 ithomiine species (a total of 1361 individuals) and 22 species of mimic (a total of 66 individuals) were captured. Two specimens of the ithomiine *Hyalyris coeno norellana* were recorded, but these are not included in the above figures for the reason stated earlier. A list of the ithomiine species captured and the number of individuals of each recorded is given in Beccaloni (in press), while data on the mimic species sampled are presented in Table 1.

Representatives of all of the eight mimicry complexes illustrated in Fig. 1-146 were collected during the MRR study. Table 2 lists the total numbers of ithomiine and mimic individuals belonging to each complex, while Table 3 lists the single most abundant species in each complex. These data show that ithomiines are the numerically dominant group of insects in the case of all of these complexes, and that the most abundant single species in each complex is an ithomiine. It therefore seems likely that ithomiines are the model species of these complexes. These findings should be regarded with caution, however, as the sample period was short and differential rates of capture between species may have biased the results.

UNPALATABILITY OF ITHOMIINES AND MIMICS

Studies have demonstrated that some ithomiine species have higher average concentrations of PAs in their bodies than other species (Brown, 1985; 1987; Trigo and Brown, 1990). This suggests that some species of ithomiine could be more unpalatable to predators than others and, if this is true, then it is possible that more palatable species of ithomiine may be "quasi-Batesian" mimics (Speed, 1993) of other more unpalatable ithomiine species. Feeding experiments with various species of insectivorous bird (Haber, 1978; Brower, 1984; Srygley and Chai, 1990a) indicate that the degree of unpalatability to potential natural predators may vary between ithomiine species to a degree. However, the amount of variation in unpalatability observed between these species was relatively small and even the least noxious ithomiine species tested were still highly protected. It is therefore likely that all ithomiine species so far tested are 'true' Müllerian mimics and it remains to be shown whether any mildly unpalatable (quasi-Batesian) ithomiine species exist.

Very few of the species of ithomiine mimic found at Jatun Sacha have been experimentally fed to predators or chemically analysed to investigate whether they contain potentially noxious compounds.

The only species of mimic shown to be highly palatable to an insectivorous bird is the charaxine *Consul fabius* (Fig. 108 and 141). Chai (1990) found that 100% of individuals of this species presented to captive rufous-tailed jacamars were eaten.

Contrary to popular belief, some Dismorphiinae may be unpalatable to insectivorous birds, including species of *Dismorphia* (Haber, 1978; Srygley and Chai, 1990a) — the genus which Bates (1862) cited as examples of palatable mimics in his original proposal of Batesian mimicry. The only species of *Dismorphia* found at Jatun Sacha which has been tested is *D. amphiona* (Cramer) (Fig. 133). Srygley and Chai (1990a) found that 57% of individuals presented to the rufous-tailed jacamar were rejected. Feeding experiments using bird predators also indicate that species which belong to the Pierinae genera *Itaballia* and *Perrhybris* may be unpalatable (Haber, 1978, and Srygley and

TABLE 1. Number of individuals of species of ithomiine mimic captured during MRR study at Jatun Sacha Biological Station, Ecuador.

SPECIES OF ITHOMIINE MIMIC	MIMICRY COMPLEX	NUMBER OF INDIVIDUALS		
		♂♂	♀♀	TOTAL (BOTH SEXES)
BUTTERFLIES				
PIERIDAE				
Dismorphiinae				
Dismorphia theucharila f. *erythroe*	Orange-tip	1	-	1
Dismorphia theucharila f. *leuconoe*	Small dark transparent	5	2	7
Moschoneura pinthaeus amelina	Small yellow transparent	7	3	10
Moschoneura pinthaeus ithomia	Small yellow transparent (variant)	1	-	1
NYMPHALIDAE				
Heliconiinae				
Heliconius numata f. *laura*	Tiger	-	3	3
Heliconius numata f. *bicoloratus*	Orange and black tiger	-	1	1
Heliconius numata f. *euphrasius*	Yellow-bar tiger	2	1	3
Nymphalinae				
Eresia eunice eunice	Tiger	1	2	3
Eresia pelonia f. *pelonia*	Tiger	1	-	1
Charaxinae				
Consul fabius aequatorialis f. *diffusus*	Yellow-bar tiger	1	-	1
Danainae				
Lycorea cleobaea atergatis	Tiger	1	2	3
LYCAENIDAE				
Riodininae				
Ithomiola cascella cascella	Orange-tip	1	1	2
Mesosemia phelina rubeola	Small dark transparent	1	1	2
Metacharis regalis regalis	♀: Orange-tip	-	4	4
Nymphidium minuta minuta	Small dark transparent	1	-	1
Stalachtis euterpe latefasciata	Orange-tip	1	-	1
Xynias christalla christalla	Clearwing	-	3	3
MOTHS				
PYRALIDAE				
Spilomelinae				
Desmia bajulalis bajulalis	Clearwing	1	-	1
Erilusa nr. *leucoplagalis*	Clearwing	1	-	1
GEOMETRIDAE				
Ennominae				
Emplocia nr. *pallor*	Clearwing	2	2	4
Nephodia panthea panthea	Clearwing	-	1	1
NOTODONTIDAE				
Dioptinae				
Myonia capena capena	Clearwing	1	-	1
ARCTIIDAE				
Ctenuchinae				
Cyanopepla masia masia	Clearwing	1	-	1
Pericopinae				
Dysschema buckleyi buckleyi	♂: Large yellow transparent	2	-	2
Hyalurga sp. 1	Clearwing	1	-	1
DAMSELFLIES (Odonata)				
POLYTHORIDAE				
Polythorinae				
Polythore mutata mutata	♂ and ♀: Clearwing;	3	3	
	♀: Orange-tip	-	1	7

TABLE 2. Total numbers of ithomiine and mimic individuals of each mimicry complex, captured during MRR study at Jatun Sacha Biological Station, Ecuador.

MIMICRY COMPLEX	NO. ITHOMIINE INDIVIDUALS	NO. MIMIC INDIVIDUALS	TOTAL INDIVIDUALS OF COMPLEX RECORDED	% ITHOMIINES IN COMPLEX
Clearwing	88	19	107	82
Orange-tip	28	9	37	76
Small dark transparent	177	10	187	95
Small yellow transparent	390	11	401	97
Large yellow transparent	38	2	40	95
Yellow-bar tiger	64	4	68	94
Orange and black tiger	23	1	24	96
Tiger	553	10	563	98

TABLE 3. List of the single most abundant species in each mimicry complex, recorded during MRR study at Jatun Sacha Biological Station, Ecuador.

MIMICRY COMPLEX	MOST ABUNDANT SINGLE SPECIES IN COMPLEX (ALL ARE ITHOMIINES)	NUMBER OF INDIVIDUALS RECORDED	PERCENTAGE OF TOTAL INDIVIDUALS (ITHOMIINES PLUS MIMICS) IN COMPLEX
Clearwing	*Ithomia agnosia agnosia*	51	48
Orange-tip	"*Hypoleria*" *orolina orolina*	11	30
Small dark transparent	*Oleria gunilla lota*	112	60
Small yellow transparent	*Godyris zavaleta matronalis*	209	52
Large yellow transparent	*Godyris dircenna dircenna*	15	38
Yellow-bar tiger	*Hypothyris moebiusi moebiusi*	31	46
Orange and black tiger	*Mechanitis messenoides deceptus*	21	88
Tiger	*Hypothyris euclea intermedia*	245	44

Chai, 1990a, respectively), but the species which belong to these genera at Jatun Sacha (Fig. 79-80 and 105) have not been tested.

The data indicating that *Itaballia*, *Perrhybris* and some Dismorphiinae are unpalatable are, however, ambiguous and should be interpreted with caution, as most of the individuals tested in the experiments of Haber (1978) and Srygley and Chai (1990a) appear to have been rejected by the bird predators on the basis of sight rather than taste. As the birds used in these experiments were wild-caught, they probably had previous experience of other undoubtedly unpalatable species (such as ithomiines) which the above mentioned Pieridae resemble, and therefore the Pieridae in question may have been sight-rejected purely because of their resemblance to these unpalatable species. The only evidence for taste-rejection of these Pieridae is in the case of *Perrhybris*: two individuals were apparently taste-rejected by the rufous-tailed jacamar in experiments conducted by Chai (1986).

Most of the mimic species which belong to the Nymphalidae at Jatun Sacha may be unpalatable. Species which belong to the Heliconiinae genera *Eueides* and *Heliconius* are known to contain cyanogenic glycosides (Brown *et al.*, 1991) and all species tested in feeding experiments using bird predators have been shown to be protected (Brower, 1984; Srygley and Chai, 1990a). Srygley (1994) suggested that species of Nymphalinae genus *Eresia* are probably unpalatable, and species of Danainae (including *Lycorea*) are known to sequester PAs pharmacophagously (Brower, 1984) and to be unpalatable to birds (Brower, 1984; Srygley and Chai, 1990a).

Few data are available for the species of mimics not already discussed. Miller (1992) suggests that moths of the Notodontidae subfamily Dioptinae may be unpalatable, although no species have been tested. Many species in the Arctiidae subfamilies Ctenuchinae and Pericopinae are known to sequester PAs pharmacophagously (Brown *et al.*, 1991) and some contain noxious cardenolides; however, none of the species at Jatun Sacha (or even any closely related species found in other areas) has been tested.

Both the Batesian and the rare Müllerian mimics in a mimicry complex are predicted to have converged onto the pattern of the numerically dominant unpalatable species in the complex (e.g., see Turner, 1984). All the mimic species which participate in the complexes discussed in this study are very rare relative to the ithomiine members of these complexes (see Tables 1-3), and it is therefore likely that their colour patterns have evolved to resemble those of the numerically dominant ithomiine species in these complexes.

BEHAVIOUR OF ITHOMIINES AND MIMICS

Flight behaviour

The flight behaviour of the ithomiine and mimic species which participate in the same mimicry complex is usually very similar (pers. observ.). The only species which I did not observe flying naturally were *Myonia pales* (Druce) (Notodontidae: Dioptinae) (Fig. 23), which was obtained from a pupa, and those species of moths which were only collected at light (see legends to Fig. 1-146). The species in all except one of the Jatun Sacha complexes (see below) have a slow 'advertising' flight pattern when undisturbed. When disturbed, however, many of these species exhibit a more rapid and erratic 'escape' flight pattern. The ithomiine *Tithorea harmonia* (Fig. 117), the charaxine *Consul fabius* (Fig. 108 and 141), the pericopine *Hypocrita simulata* (Fig. 34), and the damselfly *Polythore mutata* (Fig. 35-36 and 50) can fly particularly fast when disturbed. All of the species which belong to the Large Yellow Transparent Complex (Fig. 82-94) fly relatively rapidly, even when in undisturbed flight. Studies have shown (Chai and Srygley, 1990; Srygley and Chai, 1990a; Srygley and Chai, 1990b; Srygley, 1994) that flight speed and the degree of palatability to predators are highly correlated in butterflies: palatable butterflies tend to fly fast, while unpalatable species fly more slowly. Interestingly, the ithomiine species with the lowest relative PA concentrations known, *Tithorea harmonia* and *Methona* spp. (Trigo and Brown, 1990), are among the fastest flying species of ithomiine at Jatun Sacha.

Resting posture and perching position

Although the flight behaviour of the species in the same mimicry complex is similar (at least during undisturbed flight), the resting postures of many of the mimic species are very different to their presumed ithomiine models. Like ithomiines, mimics which belong to the Papilionidae, Pieridae and Nymphalidae rest with their wings closed and held vertically. Mimics which belong to the Riodininae, however, rest with their wings open and held flat against the substrate (most of the species at Jatun Sacha), or with the wings held half-open (*Mesosemia phelina* (Felder & Felder) (Lycaenidae: Riodininae), Fig. 63, only). Most of the observed moth mimics, rest with their wings folded over the abdomen, except for *Genussa* spp. (Geometridae: Ennominae) (Fig. 13-14) which rest with their wings open and held flat (the other species of Ennominae were not observed at rest) and *Macrosoma lucivittata* (Walker) (Hedylidae) (Fig. 17) which rests with its wings half open.

Several species of ithomiine mimic also perch in different positions on the substrate to ithomiines. Ithomiines perch on the top surface of leaves, with the single known exception of *Greta diaphana* (Drury) from Jamaica, which perches on the underside of leaves (Brown, 1973). In contrast, two species of Riodininae and four species of moth were observed to perch under leaves (see legends to Fig. 1-146) and other species which belong to these groups may also exhibit this behaviour (not all species were observed at rest).

The observation that many species of ithomiine mimics (including probably all species of Riodininae and moth) have different resting postures (and sometimes also different perching positions) to ithomiines, but that ithomiine and mimic species have similar flight behaviour, suggests that the selection for mimicry between these species must largely take place when they are flying. This hypothesis is further supported by the observations that some mimics (e.g., *Consul fabius*, Fig. 108 and 141) are cryptic when at rest, and that other species (e.g., *Hypocrita simulata*, Fig. 34, and *Polythore mutata* (Odonata), Fig. 35-36 and 50) do not possess colour patterns which accurately resemble those of ithomiines, but are never-the-less convincing mimics when seen in flight (*i.e.,* mimicry is by "behavioural illusion"). Perhaps significantly, observational records and studies of beak mark damage to butterfly wings suggest that the major bird predators of butterflies are species which specialise in on-the-wing capture of insects e.g., jacamars (Chai, 1988).

Time of activity

The majority of the species of Spilomelinae (Pyralidae), Ennominae (Geometridae), Hedylidae and Pericopinae (Arctiidae), which resembled ithomiines at Jatun Sacha, were observed during the day only after they had been disturbed from low vegetation. Some of these species were collected only during the day, while others were collected by day and also at light after dark (see legends to Fig. 1-146). In addition, a few species (which closely resemble other species observed during day) were only recorded at light at night (see legends to Fig. 1-146). In contrast, all species of Dioptinae and Ctenuchinae which mimic ithomiines were only ever recorded during the day and the individuals observed were always in 'active flight'. These observations suggest that many of the species of Spilomelinae, Ennominae, Hedylidae and Pericopinae which resemble ithomiines are probably nocturnal and that they fly during the day only if they are disturbed and are forced to find new resting sites. These species are poor mimics when they are observed at rest (they have different resting postures to ithomiines) and it is unlikely that their resemblance to ithomiines when in flight has evolved in order to deceive nocturnal predators (their ithomiine models are diurnal). It therefore seems probable that mimicry in these species has evolved to protect them in flight against diurnal predators, possibly because they are frequently disturbed (e.g., by army ants, birds and large mammals) from their resting sites on low vegetation during the day.

POLYMORPHISM

Polymorphic species at Jatun Sacha

At Jatun Sacha, thirteen species were polymorphic: the ithomiines *Ithomia salapia* (Fig. 70-72), *Mechanitis mazaeus* (Fig. 96, 110, 123), *Mechanitis messenoides* (Felder & Felder) (Fig. 97, 111), *Hypothyris anastasia* (Bates) (Fig. 100, 112), *Hypothyris moebiusi* Haensch (Fig. 102, 113), *Callithomia alexirrhoe* (Fig. 103, 130), and *Ceratinia tutia* (Fig. 104, 131); the damselfly *Polythore mutata* (Fig. 35-36, 50); the dismorphiines *Dismorphia theucharila* (Fig. 43, 59) and *Moschoneura pinthaeus* (Linnaeus) (Fig. 77-78); the heliconiine *Heliconius numata* (Fig. 106, 115, 137); the nymphaline *Eresia pelonia* Hewitson (Fig. 107, 116, 139-140); and the charaxine *Consul fabius* (Fig. 108, 141). It is worth noting that the mimic *Dysschema buckleyi* (Druce) (Arctiidae: Pericopinae), although not polymorphic, is a dual sex-limited mimic, with the male (Fig. 90) an ithomiine mimic and the female (not illustrated) a mimic of *Parides* spp. (Papilionidae).

The morphs of eleven of the species listed above are clearly discrete and participate in different mimicry complexes. It is uncertain, however, whether the morphs of the other two species, *Ithomia salapia* (Ithomiinae) and *Moschoneura pinthaeus* (Pieridae: Dismorphiinae), belong to different complexes, so I have provisionally placed them in the same complex (the Small Yellow Transparent Complex, Fig. 66-81). However, as discussed earlier, there is some evidence to suggest that this complex may be an artificial amalgam of two (or perhaps more) discrete complexes and, if this is the case, then the morphs of these species may actually belong to separate complexes.

The majority of the polymorphic species at Jatun Sacha belong to subfamilies or genera which are either known or are thought to be unpalatable to predators (see above). The charaxine *Consul fabius* (Fig. 108, 141) is the only polymorphic species known to be palatable, but it is possible that the damselfly *Polythore mutata* (Odonata) (Fig. 35-36, 50), the dismorphiines *Dismorphia theucharila* (Fig. 43, 59) and *Moschoneura pinthaeus* (Fig. 77-78) (Pieridae), and the nymphaline *Eresia pelonia* (Fig. 107, 116, 139-140) may also be palatable. Even if a mimetic species is palatable, it may not be a 'true' Batesian mimic as it may have other (non-chemical) defences against predators. For example, some palatable mimetic species fly slowly like their protected models when undisturbed, but fly very rapidly when alarmed (e.g., *Consul fabius*) and it seems likely that this rapid escape flight constitutes a secondary defence against predators which have 'seen through' the mimetic disguise of these species.

Are the polymorphic species Batesian or Müllerian mimics?

Classical theory predicts that only Batesian mimics should exhibit polymorphism (e.g., Turner, 1977). At Jatun Sacha this prediction seems unlikely to be correct, at least in this simple form. It is usually assumed that unpalatable mimetic species of either equal or differing unpalatability mutually benefit from the relationship, because each species shares the burden of predator education (i.e., the mimicry is Müllerian). However, using a computer model, Speed (1993) has shown that if an unpalatable species is mimicked by a less unpalatable species, then under certain conditions, the former may experience greater predation than if it were not mimicked. Thus less unpalatable mimics of more unpalatable species may behave as Batesian or quasi-Batesian mimics, rather than as Müllerian co-mimics.

Although it is possible that none of the polymorphic species at Jatun Sacha is a classically 'undefended' Batesian mimic, some may be relatively more palatable than the ithomiine species which numerically dominate the mimicry complexes in which they participate. Comparative data on the relative unpalatabilities of butterfly species to the rufous-tailed jacamar (Srygley and Chai, 1990a; Srygley, 1994) suggest that species of *Heliconius*, *Dismorphia* and possibly *Eresia* may be relatively more palatable than ithomiines, and it is therefore possible that the polymorphic species which belong to these genera at Jatun Sacha (see above list) may be quasi-Batesian mimics. The polymorphic ithomiine species at Jatun Sacha, however, are likely to be 'true' Müllerian mimics, as no mildly unpalatable ithomiine species are known (see earlier discussion).

Apostatic selection

As pointed out above, classical theory predicts that only Batesian mimics should exhibit polymorphism. Müllerian mimics are predicted to be monomorphic, since the fitness of an aposematic pattern increases with its frequency and positive frequency-dependent selection should therefore select against rare phenotypes (e.g., Mallet, 1993) (but see below). In Batesian mimicry, the predation rate on both the model and mimic increases as the frequency of the 'parasitic' mimic increases relative to the model. Hence the rarer a Batesian mimic is relative to the model, the higher its fitness should be. This negative frequency-dependent selection (apostatic selection) is thought to maintain polymorphisms in Batesian mimics (e.g., Turner, 1977) and also possibly in quasi-Batesian mimics under certain conditions (Speed, 1993). For example, as the frequency of a morph increases, its fitness may decrease until it is lower that of a second morph, selection will then favour this second morph, which will therefore increase in frequency until such a point as its fitness is less than the first morph, the first morph will then increase in frequency, and so on. It is clear that a polymorphism will only be maintained given a scenario where an increase in the frequency of a morph relative to the model results in an increased predation rate. If all the morphs of a species are rare relative to their models, then selection should favour the fittest morph (i.e., the morph which mimics the best protected colour pattern). Although the frequency of this morph should therefore increase (and the frequency of the less fit morphs should decrease), its fitness may never decrease because it may never become common enough such that increased predation results on the mimicry complex in which it participates. If this occurs, then the less fit morphs will be lost and the species will become monomorphic (O'Donald and Pilecki, 1970).

At Jatun Sacha all of the polymorphic species which may be Batesian or quasi-Batesian mimics were very rare relative to the ithomiine individuals in the complexes in which they participate (Tables 1-3), and it therefore seems unlikely that apostatic selection could be operating to maintain polymorphism in these species. Although the data from the MRR study should be interpreted with caution as the sampling period was short, other studies (e.g., Bates, 1862; Poole, 1970) support the general rule that individuals of species which mimic ithomiines are very rare relative to ithomiine individuals in mimicry complexes. Although it appears unlikely that apostatic selection can operate to maintain polymorphism in Batesian or quasi-Batesian mimics which are at very low frequencies relative to their models (as appears to be the case at Jatun Sacha), experiments are needed to test this.

The above argument assumes that palatable mimics resemble their models perfectly, such that predators cannot distinguish them from their models. If, however, a species is a less-than-perfect Batesian mimic, then as its frequency increases relative to the model pattern, predators may develop a search image for it, and the mimic, but not the model, may therefore experience an increasing rate of predation (this is analogous to how predation is thought to operate on organisms with cryptic colour patterns: see Endler, 1988). If mimicry is imperfect, it seems possible that apostatic selection may begin to operate when a mimic is at a lower frequency relative to the model, than would be the case if the mimic resembled the model pattern perfectly.

Even if apostatic selection were responsible for maintaining polymorphisms in Batesian or quasi-Batesian ithomiine mimics, this cannot be the explanation for polymorphism in Müllerian mimics, such as the polymorphic ithomiine species found at Jatun Sacha.

Three theories have been proposed to account for the seemingly anomalous phenomenon of polymorphism in Müllerian mimics and I examine each of these in turn below. The first theory I discuss applies only to Müllerian mimics, while the remaining two could also explain polymorphism in Batesian and quasi-Batesian mimics.

Escape hypothesis

The higher the frequency of Batesian mimic individuals relative to model individuals in a mimicry complex, the higher the predation rate, and hence the lower the fitness of the models (assuming that the mimicry is high fidelity). If there is only a single model species in a complex with one or more species of Batesian mimic, then any decrease in fitness which the model experiences will obviously mean that it will have lower fitness than if it were not mimicked. If there are two or more model species in a complex (i.e., Müllerian co-mimics) then, although the fitness of each model species is partly a product of their combined population sizes, it is conceivable that 'parasitism' by one or more Batesian species may decrease the fitness conferred by the aposematic pattern such that one or more of the Müllerian species may have a lower fitness than if they were not involved in mimicry. Even though Batesian 'parasitism' may cause the fitness of a model species to fall below the fitness it would have if it were not mimetic, the model can only 'escape' if a mutation arises which gives it a resemblance to a better protected aposematic pattern of another species or mimicry complex (Sheppard *et al.*, 1985). If a novel colour pattern arises which does not resemble the colour pattern of any other species in the model's habitat it will not be initially recognised by predators as being unpalatable. It will therefore experience a higher predation rate than the 'wild-type' pattern and, because it is rare, it will probably become extinct before enough predators have learnt to avoid it (e.g., see experiments by Benson, 1972).

Although an unpalatable species may become polymorphic if a mimetic morph arises which has a higher fitness than the original 'parasitised' form, the polymorphism will be transient and the species will become monomorphic for the new colour pattern unless the fitness of the new mimetic colour pattern drops below that of the original pattern before the entire population of the unpalatable species is converted to the new pattern. If this occurs (e.g., due to an increase in the frequency of Batesian mimics of the 'new' colour pattern and/or a decrease in the frequency of Batesian mimics of the original pattern), then the polymorphism may be maintained. The polymorphism could be maintained indefinitely if the fitnesses of the new and the original colour patterns fluctuated relative to each other over time, such that the fitness of one pattern was sometimes greater and sometimes less than the fitness of the other. This could be caused, for example, by apostatic selection acting on both complexes as a result of the presence of an abundant polymorphic Batesian mimic which had morphs which participated in each complex.

The "escape hypothesis" may possibly explain some cases of polymorphism in Müllerian mimics (see example discussed by Gilbert, 1983). However, it seems unlikely that this mechanism is responsible for polymorphism in the Müllerian mimics at Jatun Sacha, as Batesian mimics appear to be very rare (Table 2).

Spatial and temporal fluctuations in the relative abundances of mimicry complexes

Brown and Benson (1974) postulated that polymorphism in the heliconiine *Heliconius numata* (which they believed to be a Müllerian mimic) is maintained because the different ithomiine mimicry complexes in which it participates fluctuate in relative abundance in an area, both spatially and temporally. These authors believed that ithomiines occur in concentrated "pockets" in forest and that these pockets tend to differ in the relative frequencies of the mimicry complexes represented, such that different ithomiine mimicry complexes numerically dominate different pockets. Furthermore, they suggested that the species composition of a pocket, as well as the relative abundances of the ithomiine species found in it, change over time and therefore different mimicry complexes may numerically dominate a pocket over time.

Given the above scenario, different mimetic morphs of a polymorphic species such as *H. numata* (or conceivably any polymorphic Batesian or Müllerian mimic) may be favoured in different areas of a habitat at different times and therefore a polymorphism could be maintained. However, random fluctuations in selective pressures on different morphs, such as those postulated, make it likely that the polymorphism will be unstable and that morphs will be lost by chance through time, thus leading to monomorphism (a similar criticism also applies to the "escape hypothesis" described above). For example, by chance all pockets in an area may be numerically dominated by the same mimicry complex for a long enough period so that morphs which mimic other rarer complexes are at a selective disadvantage and become extinct.

At Limoncocha, Ecuador, *H. numata* has three mimetic morphs and Drummond (1976) found that the relative abundances of the three ithomiine complexes in which these morphs participate remained fairly constant over the course of a 253 day MRR study conducted in a 0.5 hectare study plot. In addition, myself and others (e.g., J. Brachi and A. Neild, pers. comm.) have never observed ithomiine pockets of the type described above in Ecuador. It seems possible that ithomiine pockets are a phenomenon confined to regions with seasonally dry forest, such as those where Brown and Benson (1974) conducted their study. In such forests during the dry season, ithomiines aggregate in humid areas which are separated from other such areas by drier vegetation (e.g., Vasconcellos-Neto and Brown, 1982; Brown, 1988). The mechanism envisaged by Brown and Benson (1974) is therefore unlikely to provide a general explanation for mimetic polymorphism and, if it operates at all, it probably does not explain polymorphism in species found in regions which lack a pronounced dry season, such as the upper Amazon basin of Ecuador (e.g., at Jatun Sacha and Limoncocha). Additional criticisms of this hypothesis are given by Beccaloni (1995).

Microhabitat segregation of mimicry complexes

There is mounting evidence (reviewed in Beccaloni, 1995) to suggest that sympatric mimicry complexes (at least those dominated by ithomiines and heliconiines) are segregated from each other by microhabitat. Although there is some overlap in the habitat preferences of different complexes, each complex may numerically dominate a different microhabitat. The ithomiine-dominated complexes at Jatun Sacha, for example, have been shown by Beccaloni (in press) to fly in two different 'height bands': the majority of individuals which belong to the Clearwing (Fig. 1-36), Orange-Tip (Fig. 37-50), Small Dark Transparent (Fig. 51-65), and Small Yellow Transparent (Fig. 66-81) complexes fly below 1m; while the majority of the individuals which belong to the Large Yellow Transparent (Fig. 82-94), Yellow-Bar Tiger (Fig. 95-108), Orange and Black Tiger (Fig. 109-116), and Tiger (Fig. 117-146) complexes fly above this height and also range much higher (into the subcanopy or canopy). In addition, each of the four ithomiine complexes which fly within the same height band may be further segregated by vegetation type, such that each is the numerically dominant complex in a different vegetation type (Beccaloni, 1995). J. Smiley and L. E. Gilbert (in prep.) have shown that heliconiine-dominated mimicry complexes in Costa Rica (which all fly at similar heights) are segregated by vegetation type in this way.

If different mimicry complexes numerically dominate different microhabitats, then under certain conditions, mimetic polymorphism could arise and be maintained in species which occur in two or more microhabitats each of which is dominated by a different mimicry complex (Sheppard *et al*, 1985). Polymorphism can occur in such 'microhabitat generalist' species irrespective of whether they are Batesian, quasi-Batesian or Müllerian mimics. Probably the main requirement for polymorphism to be maintained in this system is that when a new mimetic morph arises through mutation, it must exhibit a behavioural preference for the microhabitat in which the aposematic pattern it mimics is the numerically dominant or otherwise 'best protected' pattern. In the absence of migration of morphs between microhabitats, the species would be monomorphic for each morph in different microhabitats, but if some migration occurred between microhabitats, then a balanced polymorphism may develop (Sheppard *et al.*, 1985).

Although very few studies have investigated whether the morphs of mimetic species exhibit different microhabitat preferences, there is evidence that this is the case for some polymorphic species at least (reviewed in Beccaloni, 1995). Detailed theoretical and ecological studies are, however, required before this hypothesis can be accepted.

SUMMARY

Species of ithomiine butterflies found at Jatun Sacha participate in at least eight mimicry complexes. I argue that the existence of polymorphism between many of these complexes provides indirect evidence that their natural predators perceive the colour patterns of these complexes to be discrete aposematic signals.

Other, unrelated insect species which also participate in these complexes are shown to be very rare in comparison with ithomiines, strongly suggesting that the ithomiines are the models for these complexes. This corroborates the beliefs of previous authors (e.g., Bates, 1862; Brown, 1988).

Evidence is reviewed which suggests that most species of ithomiine mimic are probably defended against predators, a finding which is consistent with the view that 'true' Batesian mimicry (in which the mimic is completely unprotected other that by its subterfuge) may be rare in nature (e.g., Vane-Wright, 1991).

Despite speculation by earlier authors (e.g., Turner, 1977; Silberglied, 1984) that mimetic insects may have 'hidden' UV reflectance patterns for intra- or inter-specific communication, none of the species examined in this study was found to possess such patterns. This is perhaps not surprising, as mounting evidence suggests that many vertebrate species can see UV light (Bennett, Cuthill and Norris, 1994; Tovée, 1995) and UV may therefore be too 'public' a channel to be used by mimetic insects for communication.

Although ithomiine and mimic species were observed to have similar flight behaviour, seemingly large differences were observed to occur between the resting behaviour of ithomiines and many species of mimic. These differences and other evidence suggest that selection for mimicry must be greatest when these insects are in flight. If correct, then experimental tests of mimicry which involve natural predators should be designed with this consideration in mind.

The observation that several ithomiine and mimic species are polymorphic at Jatun Sacha is puzzling, especially in view of the finding that possible Batesian (or pseudo-Batesian) mimics appear to be very rare relative to the probable ithomiine models of these complexes. Clearly more theoretical and ecological research is required before the phenomenon of polymorphism in these species is understood.

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