STUDIES ON THE ECOLOGY AND EVOLUTION OF NEOTROPICAL ITHOMIINE BUTTERFLIES (NYMPHALIDAE: ITHOMIINAE)

by

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To
my mother, Benjie
& Judy
in love and gratitude

ABSTRACT

Two aspects of the ecology of Neotropical ithomiine butterflies (Nymphalidae: Ithomiinae) are discussed: mimicry (Chapters 2, 3) and species richness (Chapters 4, 5). Chapter 2 defines eight mimicry complexes involving ithomiines and other insects found in eastern Ecuador. These complexes are dominated by ithomiine individuals. Hypotheses to explain polymorphism in Batesian and Müllerian mimics are assessed. In Chapter 3, evidence that sympatric ithomiine-dominated mimicry complexes are segregated by microhabitat is reviewed. Data confirm that sympatric complexes are segregated vertically by flight height. Flight height is shown to be positively correlated with larval host-plant height. Host-plant partitioning between species in a butterfly community results in the formation of microhabitat guilds of species, and evidence suggests that mimicry may evolve between species which share a guild, but not between guilds. Models for the evolution of mimicry complexes in sympatry, and for polymorphism and dual sex-limited mimicry in Müllerian mimics, are discussed in the light of these findings. Chapter 4 investigates relationships between species richness of families and subfamilies of Neotropical butterflies and overall butterfly species richness at local and regional scales. A strong positive correlation is demonstrated between ithomiine richness and the species richness of all other butterflies. The use of ithomiine richness to predict the total butterfly richness of an area is explored. Chapter 5 documents species richness patterns across the Neotropics for 101 of the 310 species of Ithomiinae, on a 1° x 1° grid. Richness in this sub-set increases with decreasing latitude (peaking just south of the equator), and with longitude from east to west. The richest cells are located in the eastern Andean foothills of Ecuador and Peru. Analysis of relationships between the species richness of this sub-set and all other ithomiines suggest that species richness patterns of this sub-set are representative for Ithomiinae as a whole.

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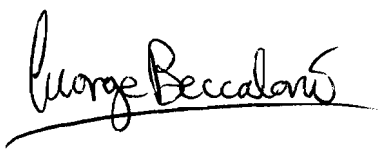
DECLARATION

Chapter 4 of this thesis is in the form of a paper co-authored with Dr K. J. Gaston, which was published in the journal *Biological Conservation* (1994, Vol. 71: 77-86). I was responsible for the main finding of this work (i.e. that the proportions of species in many families and subfamilies of Neotropical butterflies show relatively invariant or simple relationships with overall butterfly species richness at both local and regional scales). All of the data contained in the paper were compiled by myself and I performed the initial analyses of these data. In addition, I wrote the text and produced Figure [4.]1, and Tables [4.]1 and [4.]2. Dr Gaston helped with the data analysis and produced Figures [4.]2-[4.]5, using data which I supplied. Dr Gaston contributed the random-draw model and produced Figure [4.]6 (which shows the results of this model). He also read and corrected the text.



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-CHAPTER 1-

GENERAL INTRODUCTION

This thesis focuses on two aspects of the ecology of the Ithomiinae (ithomiine butterflies): mimicry (Chapters 2 and 3) and patterns in species richness (Chapters 4 and 5). The Ithomiinae are an exclusively Neotropical subfamily of Nymphalidae, containing some 310 species placed in 52 genera (Brown and Freitas, 1994; G. Lamas, in preparation). Ithomiines share many biological and ecological characteristics with the Danainae and with the monotypic Australasian Tellervinae. Ackery & Vane-Wright (1984) consider that these three subfamilies form a monophyletic group, although the relationships between them remain unresolved (Harvey, 1991). The Ithomiinae are characterised by the presence of a fringe of long androconial scales (hairpencils) on the costal margin of the male hindwing (Fox, 1956; Ehrlich, 1958). Female ithomiines lack hairpencils, with the exception of four species of the genus *Methona*.

Ithomiines possess aposematic wing patterns and are well known for their participation in mimicry complexes; indeed they were cited as the unpalatable models in the original proposals of both Batesian and Müllerian mimicry (Bates, 1862, and Müller, 1879, respectively). In Chapter 2, I define and describe the mimicry complexes which involve ithomiines at a site in eastern Ecuador (Jatun Sacha Biological Station, Napo Province). All species of insect which participate in these complexes are identified and illustrated, and aspects of their behaviour are discussed. The relative abundances of the ithomiine and other insect species which belong to these complexes are quantified using data from a mark-release-recapture study. Finally, I review hypotheses which have been proposed to explain polymorphism in Batesian and Müllerian mimics.

Müllerian mimicry theory predicts that there should be convergence among the unpalatable species in an area to give a single aposematic colour pattern. However, the observation that several discrete mimicry complexes centred around closely related species (such as ithomiines) often co-exist in the same locality contradicts this simple expectation, and suggests that divergence of mimetic colour patterns must sometimes occur. In Chapter 3, evidence is reviewed which demonstrates that sympatric mimicry complexes dominated by ithomiines are segregated by microhabitat. Original data (obtained during fieldwork at

Jatun Sacha Biological Station) are presented which confirm previous findings that sympatric ithomiine complexes are segregated vertically by flight height. Data are analysed to test the hypothesis that the flight heights of ithomiine species (and also non-mimetic British woodland butterfly species) are positively correlated with the heights of their larval host-plants. I review theories which have been proposed to explain divergence of mimetic colour patterns and argue that divergence of the patterns of model species could occur in sympatry, given prior microhabitat segregation of these species together with microhabitat-dependent selection on colour pattern. Models for the evolution of mimicry complexes in sympatry are presented and their plausibility is assessed. Next, I discuss predictions and implications of the hypothesised relationship between ithomiine community structure and patterns of mimicry complex diversity. Finally, I explore conditions required for the evolution and maintenance of polymorphism and dual sex-limited mimicry in Müllerian mimics.

Chapter 4 examines relationships between the species richness of families and subfamilies of Neotropical butterflies and overall butterfly species richness at both local and regional scales. The relationship between ithomiine species richness and the species richness of all other butterflies is discussed and the possibility of using ithomiine species richness to predict the species richness of all other butterflies in an area is evaluated.

Chapter 5 documents the patterns in species richness for 101 of the 310 species of Ithomiinae across the Neotropics at the scale of 1° x 1° grid cells. Plots showing the latitudinal and longitudinal gradients in species richness of this sub-set of ithomiines are presented. Relationships between the numbers of species of this sub-set and the numbers of all other ithomiine species are investigated at different spatial scales. These and other analyses are used to assess whether the patterns exhibited by this sub-set of species are representative for ithomiine species as a whole.

Format of the thesis chapters

Chapters 2-5 have been written in the form of scientific papers, one of which (Chapter 4) has been published. The remaining three are manuscript papers and these have been formatted in the styles of the journals to which they will ultimately be submitted. Instead of placing the legends of all the figures in a chapter together on a separate page (as required for submission to a journal), they have either been printed under the figures or on the page preceding a figure. The title pages of the thesis chapters have been standardised and do not include a suggested running title, the author's name, or the addresses of the institutions where the work was conducted. For clarity, the numbers of all figures, tables and appendices (except those in Chapter 4) have been prefixed by chapter numbers.

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-CHAPTER 2-

ECOLOGY, BEHAVIOUR AND NATURAL HISTORY OF SPECIES PARTICIPATING IN THE MIMICRY COMPLEXES DOMINATED BY ITHOMIINE BUTTERFLIES (NYMPHALIDAE: ITHOMIINAE) AT A SITE IN EASTERN ECUADOR

This chapter is in the form of a manuscript suitable for submission to the journal *Tropical Lepidoptera*.

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 subfamilies or families, 34 moth species, and 1 species of damselfly. All species are identified and illustrated, 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 ithomiine, five other butterfly species, and the single damselfly species were polymorphic at Jatun Sacha.

KEY WORDS: Batesian mimicry, behaviour, butterflies, damselflies, Ecuador, Ithomiinae, mimicry complexes, moths, Müllerian mimicry, Neotropics, polymorphism, ultraviolet patterns, unpalatability.

INTRODUCTION

The Ithomiinae is an exclusively Neotropical subfamily of Nymphalidae, which currently contains some 310 species placed in 52 genera (Brown and Freitas, 1994; G. Lamas, in preparation). Ithomiine butterflies occur in moist forests from sea level up to 3000m (Drummond, 1976) and range 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 belonging to other butterfly groups (Batesian mimics) had evolved to resemble them, thus gaining protection by 'deceiving' potential predators. Müller (1879) hypothesised that unrelated unpalatable species may also converge 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 bird (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 the females (Lamas and Pérez, 1981). Females obtain most of their PAs indirectly, via the spermatophore transferred by the males during mating (Brown, 1985; 1987). One 'primitive' species, *Tithorea harmonia* (Cramer), has been shown to sequester PAs directly from its larval host-plant *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.

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 (submitted) has shown that the number of sympatric ithomiine-dominated complexes increases with increasing local ithomiine species richness. 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. Ecological studies (reviewed by Beccaloni, submitted) 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 particular 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 (submitted) argues that divergence of the colour patterns of model species could occur in sympatry, given prior microhabitat segregation of these 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 (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 involving ithomiines at one of the richest sites for ithomiine species in the Neotropics (Jatun Sacha Biological Station, Ecuador). All the species involved are identified (most to

species level and a few to generic level only) 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 an elevation of 450 m. The reserve lies 20 km east of the base of the Andes, and the environment is transitional between the lower Andean slopes and 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 and the soil is largely red clay Oxisol (Dystropept) (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 4100 mm.

Fieldwork was conducted at Jatun Sacha during the following periods: 5th September - 14th October, 1991; 11th September - 7th November, 1992; and 22nd January - 15th February, 1994. A total of 30, 45 and 16 days respectively were actually 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 hand 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 in the reserve. The nets used had a diameter of 40 cm and a handle 30 cm in length, giving a total vertical reach of approximately 2.7 m. Sampling efficiency declined increasingly rapidly above about 2 m and became virtually non-existent above 2.7 m, firstly because low flying butterflies were more easily observed, and secondly because of the limited reach of the nets. A very low proportion of the individuals observed flying above 2.7 m were, however, captured, by jumping up, climbing on top of 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 collected were recorded.

Several species of mimic observed flying during the day were also attracted to light at night. These, together with any other species 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 (submitted).

The MRR study was conducted within a 1 hectare plot (permanent study plot "Parcela 5") of primary alluvial 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 595 m 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 *c.* 2 m 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 *c.* 3 ½ hours per day. Whenever possible, sampling was conducted between 9.30 AM and 1.30 PM.

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

THE 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 species of Lepidoptera and Zygoptera were collected which resembled ithomiines. These mimics represent 34 species of butterfly (25 genera, 9 subfamilies and 4 families), 34 species of moth (21 genera, 6 subfamilies and 5 families), and one species of damselfly. Seven species of ithomiine and six species of mimic (5 species of butterfly and the single damselfly species) were polymorphic.

Figures 2.1-2.146 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 so that they can be 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 (for an explanation of these terms see Vane-Wright, 1976).

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 (Figs 2.1-2.146) 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 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 appears to be 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 Figs 2.51-2.65), was not observed.

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 are perceived as mimetic by humans (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* (see Figure 6.2 in Tyler, Brown and Wilson, 1994), and *Heliconius numata* (see Brown and Benson, 1974). Interestingly, the female of *Metacharis regalis* (Fig. 2.46) only possesses 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. obs) and is presumably not mimetic.

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 represents a discrete signal to predators. At Jatun Sacha, polymorphism occurs between the Clearwing and

Orange-tip complexes (*i.e.* the female of *Polythore mutata*, Figs. 2.36 and 2.50), the Small dark transparent and the Orange-tip complex (*i.e. Dismorphia theucharila*, Figs 2.43 and 2.59), and between the Yellow-bar tiger, the Orange and black tiger, and the Tiger complexes (e.g., *Heliconius numata*, Figs 2.106, 2.115 and 2.137). There is, however, no polymorphism between the Small yellow transparent complex and any other complex, or the Large yellow transparent complex and any other complex.

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*, Fig. 2.7) 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 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*, Fig. 2.34, with *Heterosais nephele*, Fig. 2.2), are much better mimics when observed alive in their natural habitat. Bates (1862), referring to resemblances between species of ithomiine and riodinine butterflies, and dioptine moths stated, "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) 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*.

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 Figs 2.1-2.146 has a markedly different upperside and underside wing pattern. This exception is *Consul fabius* (Figs 2.108 and 2.141), which has an aposematic upperside wing pattern and a cryptic underside 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., *Napeogenes sylphis*, Fig. 2.37, *Hyposcada illinissa*, Fig. 2.51, *Napeogenes inachia*, Fig. 2.68, *Methona confusa*, Fig. 2.83, *Napeogenes achaea*, Fig. 2.98, and *Mechanitis lysimnia*, Fig. 2.122) 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 resting (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*, Fig. 2.132, with *Phaeochlaena hazara*,

Fig. 2.146). Unlike humans, however, 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: *Oleria agarista* (Fig. 2.53), *Hypothyris mamercus* (Fig. 2.101), *Hypothyris euclea* (Fig. 2.126), *Callithomia alexirrhoe* (Figs 2.103 and 2.130), *Ceratinia tutia* (Figs 2.104 and 2.131), *Mechanitis mazaeus* (Figs 2.96, 2.110 and 2.123), *Dismorphia theucharila* (Figs 2.43 and 2.59), *Eueides lampeto* (Figs 2.114), *Heliconius numata* (Figs 2.106, 2.115 and 2.137), and *Lycorea cleobaea* (Fig. 2.142). 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 forms. The morphs in question are as follows: the morph of *H. mamercus* differs from the typical form illustrated in Fig. 2.101 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. 2.131, 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* (Fig. 2.59) but lacks orange on the forewing; the morph of *H. numata* (*i.e.* f. *euphone* Felder & Felder) is similar to f. *euphrasius* (Fig. 2.106) but has a black bar on the hindwing, rather than a large black spot.

Although the reason for variation in the above species has not been established, one possibility is that this variation is a result of hybridisation between neighbouring parapatric mimetic races of these species (for a detailed discussion of hybridisation between geographical races of mimetic species see Mallet, 1993). 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 form *euphone* of *Heliconius numata* may be a recombinant between the mimetic morphs *laura*, Fig. 2.137, and *euphrasius*, Fig. 2.106).

ULTRAVIOLET PATTERNS OF ITHOMIINES AND MIMICS

Introduction

Unlike humans, many insects (including Lepidoptera) can see UV-A light (315-400 nm) (Silberglied, 1979; Bennett, Cuthill and Norris, 1994). 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 belonging to a mimicry complex may have converged in the 'visible' region 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 exhibited 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 the butterflies 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 that act as filters to the light entering individual cones, which may alter the number of hues they perceive (*ibid.*). These differences suggest that birds may perceive more colours and hues than humans.

If some, or all, of the predators responsible for selecting for mimicry between insects have UV vision, then species belonging to a mimicry complex should have converged in both the visible and UV elements of their colour patterns. Studies by Lutz (1933) 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

Figures 2.147-2.162 represent a preliminary attempt to investigate whether the species I have 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 Figs 2.147-2.162 are the same as those illustrated in Figs 2.1-2.146 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 *c.* 315-385 nm, with peak transmission at 350 nm). They were illuminated by natural sunlight which was incident on the plane of the specimens at an angle of *c.* 60°. Specimens were photographed against both a 'visible white' UV-reflecting background (Figs 2.147-2.154) and a 'visible black' UV-absorbing background (Figs 2.155-2.162). 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 Figs 2.1-2.146 and Figs 2.147-2.162 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 *Scada reckia* (Fig. 2.66), *Ithomia amarilla* (Fig. 2.69), *Ithomia salapia* f. *travella* (Fig. 2.70), *Ithomia salapia* f. *derasa* (Fig. 2.71), and *Hyphilaria nicia* (Fig. 2.81), and the hindwing marginal spots of *Pterourus zagreus* (Fig. 2.132) and *Consul fabius aequatorialis* (Fig. 2.141). The visible iridescent blue which overlays the visible black on the hindwing of *Hypocrita simulata* (Fig. 2.34) also reflects some UV. All other visible colours strongly absorb UV: with black absorbing the most strongly, and the orange on the forewings of *Hyalurga* sp. 2 (Fig. 2.29), *Metacharis regalis* (Fig. 2.46), and *Pheles heliconides* (Fig. 2.47), 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* (Fig. 2.45), all visibly transparent or translucent species which belong to the Small dark transparent complex (Figs. 2.51-2.65, 2.149 and 2.157), and some species which belong to the Clearwing complex (Figs. 2.1-2.36, 2.147 and 2.155).

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 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 (Figs 2.1-2.146, 2.150 and 2.158). The visible yellow areas of the wings of five of the species in this complex (*Scada reckia*, Fig. 2.66, *Ithomia amarilla*, Fig. 2.69, *Ithomia salapia* f. *travella*, Fig.

2.70, *Ithomia salapia* f. *derasa*, Fig. 2.71, and *Hyphilaria nicia*, Fig. 2.81) 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 would 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 artefacts of the technique used to examine the UV patterns of the species in this study. For example, although *Ithomiola cascella* (Fig. 2.45) appears to reflect UV more strongly than any other visibly transparent species in the Orange-tip complex (Figs 2.37-2.50, 2.148 and 2.156), 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 was examined (315-385 nm). 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 significant?

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 clear whether the natural predators of these insects have UV vision and, if they do, whether they perceive these differences to be significant. 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

Heterosais nephele, Fig. 2.2, with *Hypocrita simulata*, Fig. 2.34). 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 are 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 human-defined Small yellow transparent complex (Figs 2.1-2.146, 2.150 and 2.158): 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 discrete complexes is supported by the fact that one species, *Ithomia salapia*, has two morphs (*travella*, Fig. 2.70, and *derasa*, Fig. 2.71) which reflect UV, and a third morph (*salapia*, Fig. 2.72) 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 method used to produce the different visible yellow colours which they exhibit.

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 (submitted), while data on the mimic species sampled are presented in Table 2.1.

Representatives of all of the eight mimicry complexes illustrated in Figs 2.1-2.146 were collected during the MRR study. Table 2.2 lists the total numbers of ithomiine and mimic individuals belonging to each complex, while Table 2.3 lists the single most abundant species in each complex. These data show that ithomiines are the numerically dominant group of insects in all of these complexes, and that in each complex the most abundant single species is an ithomiine. It therefore seems likely that ithomiines are the model species of these complexes.

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 may 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 found to be highly protected. It is therefore likely that all of the ithomiine species which have been 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 *Consul fabius* (Figs 2.108 and 2.141). Chai (1990) found that 100% of individuals of this species presented to captive rufous-tailed jacamars were eaten.

Contrary to popular belief amongst entomologists, some Dismorphiinae may be unpalatable to insectivorous birds, including species of *Dismorphia* (Haber, 1978; Srygley and Chai, 1990a) - the genus which Bates (1862) used 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* (Fig. 2.133). 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 belonging to the Pierinae genera *Itaballia* and *Perrhybris* may be unpalatable (Haber, 1978, and Srygley and Chai, 1990a, respectively), although the species belonging to these genera at Jatun Sacha (Figs. 2.79, 2.80 and 2.105) 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 belonging 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 mimic not already discussed. Miller (1992) suggests that moths of the Notodontidae subfamily Dioptinae may be unpalatable, although no species have been tested. Many species of 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 on to the pattern of the numerically dominant unpalatable species in the complex (e.g., 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 2.1, 2.2 and 2.3), and it is therefore likely that these mimics have evolved to resemble 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 belong to a mimicry complex is usually very similar (pers. obs.). The only species which I did not observe flying naturally were *Myonia pales* (Fig. 2.23), which was obtained from a pupa, and those species of moth which were only collected at light (see legends to Figs. 2.1-2.146). The

members of 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. Four species, *Tithorea harmonia* (Fig. 2.117), *Consul fabius* (Figs 2.108 and 2.141), *Hypocrita simulata* (Fig. 2.34), and *Polythore mutata* (Figs 2.35, 2.36 and 2.50), can fly particularly fast when disturbed. All of the species which belong to the Large yellow transparent complex (Figs 2.82-2.94) 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 strongly 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 belonging to a mimicry complex is similar (at least during undisturbed flight), the resting postures of many of the mimic species are very different from 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*, Fig. 2.63, only). Most of the moth species observed rest with their wings folded over the abdomen, except *Genussa* spp. (Figs 2.13 and 2.14) which rest with their wings open and held flat (the other species of Ennominae were not observed at rest) and *Macrosoma lucivittata* (Fig. 2.17) 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). However, two species of Riodininae and four species of moth were

observed to perch under leaves (see legends to Figs 2.1-2.146) 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 mimic (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*, Figs. 2.108 and 2.141) are cryptic when at rest, and that other species (e.g., *Hypocrita simulata*, Fig. 2.34, and *Polythore mutata*, Figs. 2.35, 2.36 and 2.50) do not possess colour patterns accurately resembling those of ithomiines, but are never-the-less convincing mimics when seen in flight (*i.e.* mimicry is by "behavioural illusion"). In addition, 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, Ennominae, Hedylidae and Pericopinae 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 Figs 2.1-2.146). In addition, a few species (which closely resembled other species observed during day) were only recorded at light at night (see legends to Figs 2.1-2.146). 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 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 they are observed in flight) has

evolved in order to deceive nocturnal predators (ithomiines are diurnal). It therefore seems probable that mimicry in these species functions 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 observed to be polymorphic: *Ithomia salapia* (Figs 2.70, 2.71 and 2.72), *Mechanitis mazaeus* (Figs 2.96, 2.110 and 2.123), *Mechanitis messenoides* (Figs 2.97 and 2.111), *Hypothyris anastasia* (Figs 2.100 and 2.112), *Hypothyris moebiusi* (Figs 2.102 and 2.113), *Callithomia alexirrhoe* (Figs 2.103 and 2.130), *Ceratinia tutia* (Figs 2.104 and 2.131), *Polythore mutata* (Figs 2.35, 2.36 and 2.50), *Dismorphia theucharila* (Figs 2.43 and 2.59), *Moschoneura pinthaeus* (Figs 2.77 and 2.78), *Heliconius numata* (Figs 2.106, 2.115 and 2.137), *Eresia pelonia* (Figs 2.107, 2.116, 2.139 and 2.140), and *Consul fabius* (Figs 2.108 and 2.141). The first seven species are ithomiines and the six species which follow are mimics. It is worth noting that the mimic *Dysschema buckleyi*, although not polymorphic, is a dual sex-limited mimic, with the male (Fig. 2.90) an ithomiine mimic and the female (not illustrated) a mimic of *Parides* spp.

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 two remaining species, *Ithomia salapia* and *Moschoneura pinthaeus*, belong to different complexes, and I have therefore placed them in the same complex (the Small yellow transparent complex, Figs 2.66-2.81). There is some evidence, however, to suggest that this complex may be an artificial amalgam of two (or perhaps more) discrete complexes (see above) 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). *Consul*

fabius (Figs 2.108 and 2.141) is the only polymorphic species known to be palatable, but it is possible that *Polythore mutata* (Figs 2.35, 2.36 and 2.50), *Dismorphia theucharila* (Figs 2.43 and 2.59), *Moschoneura pinthaeus* (Figs 2.77 and 2.78), and *Eresia pelonia* (Figs 2.107, 2.116, 2.139 and 2.140) 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?

Theory predicts that only Batesian mimics should exhibit polymorphism (e.g., Turner, 1977) (but see below). 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, it 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, it is possible that some unpalatable species 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 above).

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 will 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 therefore increases 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. For example, 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), and 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 so, 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 2.1, 2.2 and 2.3), and it therefore seems unlikely that apostatic selection could be operating to maintain polymorphism in these species. Of the possibly Batesian or quasi-Batesian species sampled during the MRR study, the most abundant morph relative to the ithomiine individuals of the complex in which it participates was f.

euphrasius of *Heliconius numata* (Fig. 2.106), with a ratio of 1 f. *euphrasius* to 21.3 Yellow-bar tiger ithomiine individuals (see Tables 2.1 and 2.2). *H. numata* also has two other mimetic morphs at Jatun Sacha and the ratios of these recorded during the MRR study were: 1 f. *bicoloratus* (Fig. 2.115) to 23 Orange and black tiger ithomiines, and 1 f. *laura* (Fig. 2.137) to 184 Tiger ithomiines (Tables 2.1 and 2.2). Theory predicts that f. *laura* should have the highest fitness of these morphs, as it is the rarest morph relative to its models and also because the Tiger complex in which it participates is the relatively most abundant mimicry complex (the Tiger complex is more than eight times as abundant as the Yellow-bar tiger complex and more than twenty-three times as abundant as the Orange and black tiger complex, see Table 2.2). It is therefore puzzling why f. *laura* is so rare and it seems unlikely that apostatic selection would act on this morph, even if it were somewhat commoner. For example, even if all of the individuals of *H. numata* recorded during the MRR study were this morph, it would still be so rare relative to the ithomiine individuals of the Tiger complex that it seems improbable that its frequency would be high enough to cause increased predation on this complex (a total of 7 *H. numata* were recorded during the MRR study, Table 2.1, and if all were f. *laura*, then there would have been 1 individual of this morph to 79 Tiger ithomiine individuals).

Although the data from the MRR study should be interpreted with caution as the sampling period was short, a more detailed previous study (Brown and Benson, 1974) confirms that morphs of *H. numata* are always many magnitudes less abundant than the ithomiine individuals in a mimicry complex. In addition, 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 (presuming 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 the model's fitness will obviously mean that it will have a 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 was 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 will 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 of these complexes as a result of the presence of an abundant polymorphic Batesian mimic which has morphs which belonged to 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 2.2).

Spatial and temporal fluctuations in the relative abundances of mimicry complexes

Brown and Benson (1974) postulated that polymorphism in *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 species of 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 over 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 likely 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 (submitted).

Microhabitat segregation of mimicry complexes

There is mounting evidence (reviewed in Beccaloni, submitted) 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 between complexes, each complex is thought to numerically dominate a different microhabitat. The ithomiine-dominated complexes at Jatun Sacha, for example, have been shown by Beccaloni (submitted) to fly in two different 'height bands': the majority of individuals which belong to the Clearwing (Figs 2.1-2.36), Orange-tip (Figs 2.37-2.50), Small dark transparent (Figs 2.51-2.65), and Small yellow transparent (Figs. 2.66-2.81) complexes fly below 1.1m; while the majority of the individuals which belong to the Large yellow transparent (Figs 2.82-2.94), Yellow-bar tiger (Figs 2.95-2.108), Orange and black tiger (Figs 2.109-2.116), and Tiger (Figs 2.117-2.146) complexes fly above this height and also range much higher (into the subcanopy or canopy). In addition, it is thought that each of the four ithomiine complexes which fly in the same height band are probably further segregated by vegetation type, such that each is the numerically dominant complex in a different vegetation type (Beccaloni, submitted). J. Smiley and L. E. Gilbert (in preparation) 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 can arise and be maintained in species which occur in two or more microhabitats each of which is dominated by a different mimicry complex. Polymorphism can occur in such 'microhabitat generalist' species irrespective of whether they are Batesian, quasi-Batesian or Müllerian mimics. The main requirement for polymorphism to be maintained in this system is that when a new mimetic morph arises through mutation, it will establish only if it exhibits 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, submitted). A preliminary computer simulation model based on the conditions described above (G. W. Beccaloni, in preparation) indicates that they are sufficient to maintain a balanced polymorphism in a mimetic species. However, more theoretical and ecological studies are required before this hypothesis can be accepted.

SUMMARY

Species of ithomiine butterfly 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 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 species of vertebrate can see UV light (see Bennett, Cuthill and Norris, 1994) 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 exist 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 involving 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 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 can be understood.

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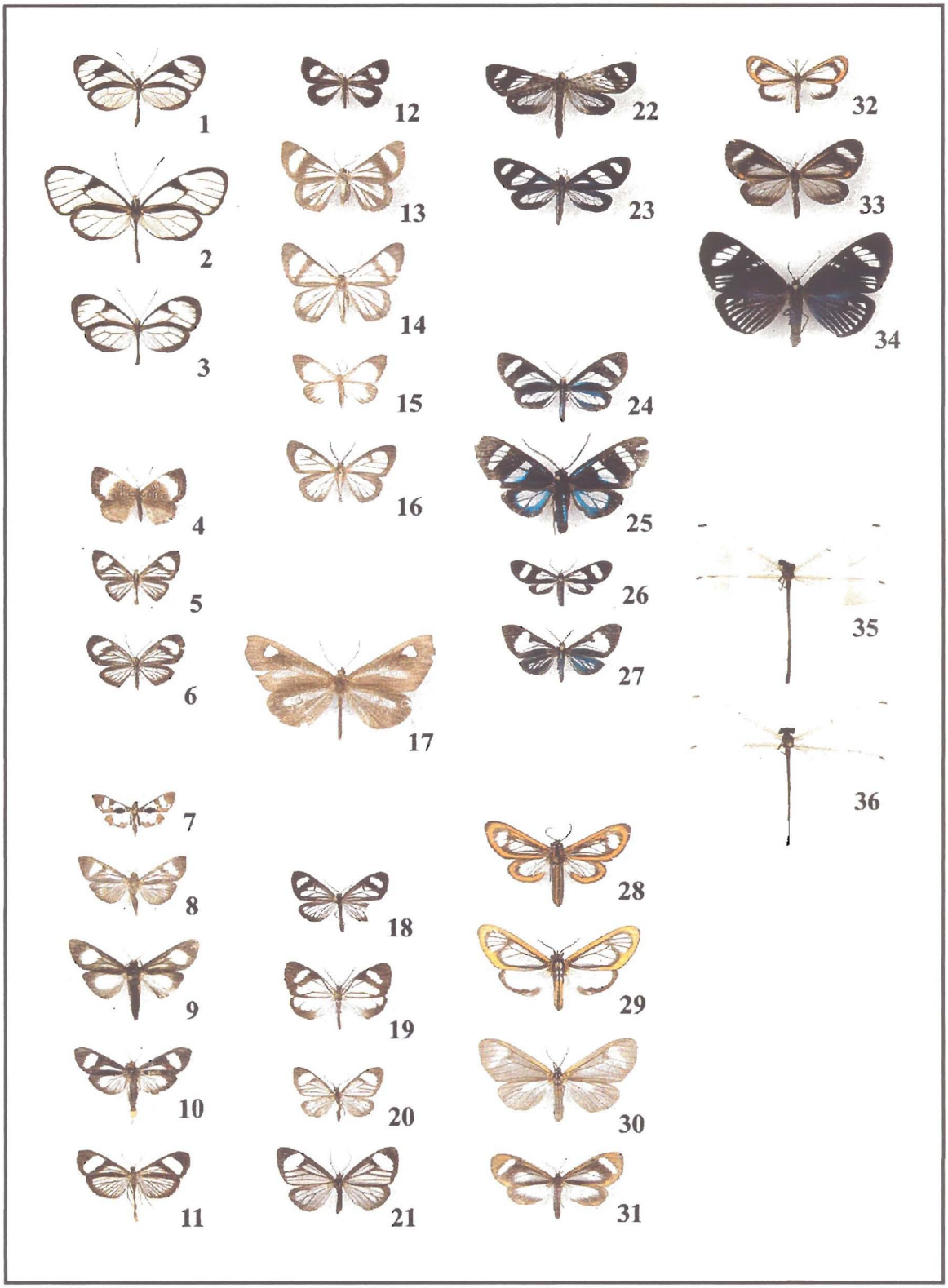
GENERAL LEGEND FOR FIGURES 2.1-2.146: "polymorphic" = the species is polymorphic and both sexes have the same mimetic morphs; "♀ polymorphic" = the female is polymorphic and the male is monomorphic (both sexes are mimetic); "♂ not mimetic" = the male has a different colour pattern to the female and is 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. 2.1-2.36. CLEARWING COMPLEX. **ITHOMIINAE, ITHOMIINI: 2.1**, *Ithomia agnosia agnosia* Hewitson. **GODYRIDINI: 2.2**, *Heterosais nephele nephele* (Bates); **2.3**, *Pseudoscada timna timna* (Hewitson). **LYCAENIDAE, RIODININAE: 2.4**, *Echenais alector alector* (Butler) ♀ (♂ not mimetic); **2.5**, *Esthemopsis celina celina* Bates; **2.6**, *Xynias christalla christalla* Grose-Smith (perches under leaves). **PYRALIDAE, SPILOMELINAE: 2.7**, *Desmia bajulalis bajulalis* Guenée (perches under leaves); **2.8**, *Erilusa* nr *leucoplagalis* (Hampson) (by day and at light; perches under leaves); **2.9**, *Omiodes hypoxantha hypoxantha* (Dognin) (at light); **2.10**, *Phostria* sp. (at light); **2.11**, *Phostria euryleucalis euryleucalis* Hampson; **GEOMETRIDAE, ENNOMINAE: 2.12**, *Emplocia* nr *pallor* (Druce); **2.13**, *Genussa* sp. (at light); **2.14**, *Genussa famulata famulata* Felder; **2.15**, *Nephodia panthea panthea* Druce; **2.16**, *Penthophlebia radiata radiata* (Felder) (by day and at light). **HEDYLIDAE: 2.17**, *Macrosoma lucivittata lucivittata* (Walker) ♀ (at light; ♂ lacks white fw spot and is probably not mimetic). **NOTODONTIDAE, DIOPTINAE: 2.18**, *Dioptis* nr *charila* Druce; **2.19**, *Euchontha frigida frigida* (Walker) (stridulates loudly when captured); **2.20**, *Monocreagra pheloides pheloides* Felder ♂; **2.21**, *Monocreagra pheloides pheloides* Felder ♀; **2.22**, *Myonia capena capena* (Druce); **2.23**, *Myonia pales pales* (Druce) (1 specimen ex. pupa - not observed in flight). **ARCTIIDAE, CTENUCHINAE: 2.24**, *Argyrta* nr *micilia* (Cramer); **2.25**, *Agyrtidia* nr *uranophila* (Walker); **2.26**, *Cacostatia* nr *ossa* (Druce); **2.27**, *Cyanopepla masia masia* (Dognin) (perches under leaves). **PERICOPINAE: 2.28**, *Hyalurga* sp. 1 (perches under leaves); **2.29**, *Hyalurga* sp. 2 (at light); **2.30**, *Hyalurga albovitrea albovitrea* Walker (at light); **2.31**, *Hyalurga osiba osiba* (Druce); **2.32**, *Hyalurga rufilinea rufilinea* (Walker) ♂; **2.33**, *Hyalurga rufilinea rufilinea* (Walker) ♀;

2.34, *Hypocrita simulata simulata* (Walker). **ZYGOPTERA, POLYTHORIDAE, POLYTHORINAE: 2.35**, *Polythore mutata mutata* (McLachlan) ♂; **2.36**, *Polythore mutata mutata* (McLachlan) ♀ (♀ polymorphic).

FIGURES 2.1-2.36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FIGURES 1 - 36

Fig. 2.37-2.65. ORANGE-TIP COMPLEX; see general legend on Fig. 2.1-2.36. **ITHOMIINAE, NAPEOGENINI: 2.37**, *Napeogenes sylphis caucayaensis* Fox & Real. **GODYRIDINI: 2.38**, *Hypoleria lavinia chrysodonia* (Bates); **2.39**, *Hypoleria sarepta aureliana* (Bates); **2.40**, "*Hypoleria*" *orolina orolina* (Hewitson); **2.41**, "*Hypoleria*" *seba oculata* (Haensch); **2.42**, "*Pseudoscada*" *florula aureola* (Bates). **PIERIDAE, DISMORPHIINAE: 2.43**, *Dismorphia theucharila* f. *erythroe* Bates (polymorphic). **LYCAENIDAE, RIODININAE: 2.44**, *Ithomeis corena corena* (Felder & Felder); **2.45**, *Ithomiola cascella cascella* (Hewitson); **2.46**, *Metacharis regalis regalis* Butler ♀ (♂ not mimetic); **2.47**, *Pheles heliconides heliconides* (Herrich-Schäffer); **2.48**, *Stalachtis euterpe latefasciata* Staudinger. **ARCTIIDAE, PERICOPINAE: 2.49**, *Hyalurga* nr *batesi* (Druce). **ZYGOPTERA, POLYTHORIDAE, POLYTHORINAE: 2.50**, *Polythore mutata mutata* (McLachlan) ♀ (♀ polymorphic). SMALL DARK TRANSPARENT COMPLEX. **ITHOMIINAE, OLERIINI: 2.51**, *Hyposcada illinissa ida* Haensch; **2.52**, *Hyposcada kena kena* (Hewitson); **2.53**, *Oleria agarista agarista* (Felder & Felder); **2.54**, *Oleria assimilis assimilis* (Haensch); **2.55**, *Oleria gunilla lota* (Hewitson); **2.56**, *Oleria lerda lerda* Haensch; **2.57**, *Oleria* ? *sexmaculata sexmaculata* (Haensch); **2.58**, *Oleria tigilla tigilla* (Weymer). **PIERIDAE, DISMORPHIINAE: 2.59**, *Dismorphia theucharila* f. *leuconoe* Bates (polymorphic). **NYMPHALIDAE, NYMPHALINAE: 2.60**, *Eresia clara clara* Bates; **2.61**, *Eresia plagiata plagiata* (Röber). **LIMENITINAE: 2.62**, *Vila cacica cacica* Staudinger. **LYCAENIDAE, RIODININAE: 2.63**, *Mesosemia phelina rubeola* (Stichel); **2.64**, *Nymphidium minuta minuta* Druce (perches under leaves). **ARCTIIDAE, PERICOPINAE: 2.65**, *Hyalurga padua padua* (Druce).

FIGURES 2.37-2.65

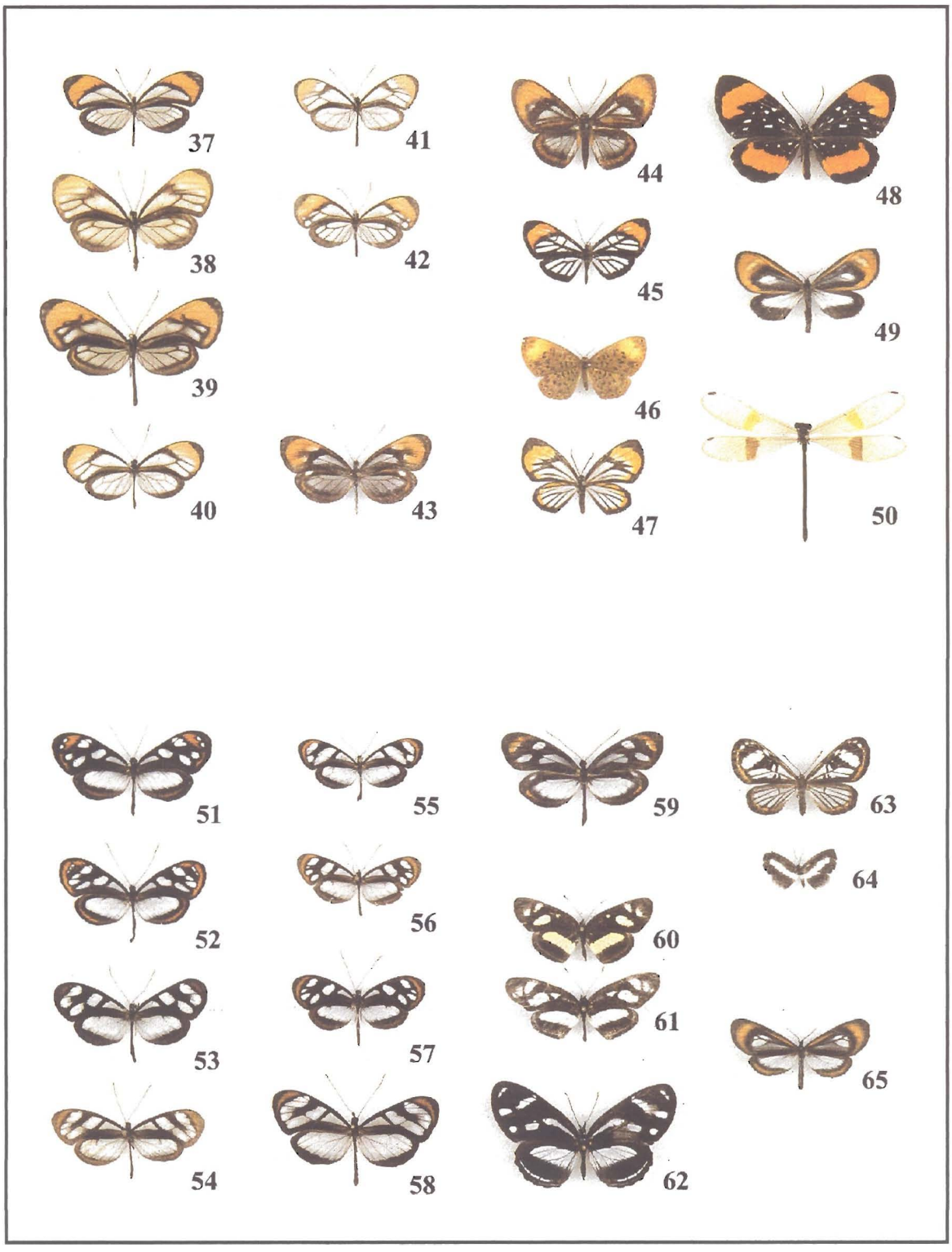
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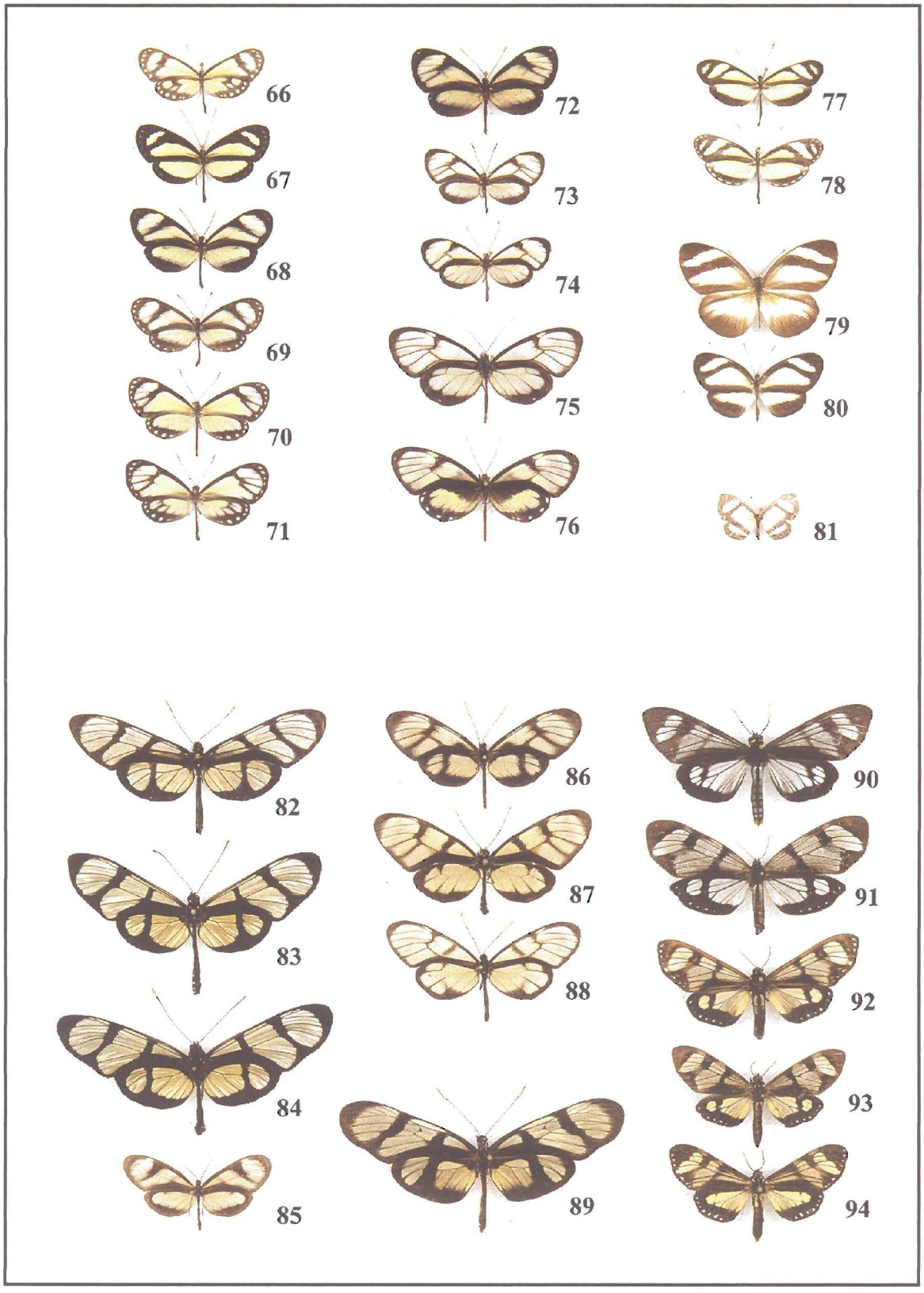
Fig. 2.66-2.94. SMALL YELLOW TRANSPARENT COMPLEX; see general legend on Fig. 2.1-2.36. **ITHOMIINAE, MECHANITINI: 2.66**, *Scada reckia ethica* (Hewitson). **NEW TRIBE: 2.67**, *Aeria eurimedea negricola* (Felder & Felder). **NAPEOGENINI: 2.68**, *Napeogenes inachia avila* Haensch. **ITHOMIINI: 2.69**, *Ithomia amarilla amarilla* Haensch; **2.70**, *Ithomia salapia* f. *travella* Haensch; **2.71**, *Ithomia salapia* f. *derasa* Hewitson; **2.72**, *Ithomia salapia* f. *salapia* Hewitson. **DIRCENNINI: 2.73**, *Ceratiscada hymen* ssp. n. Lamas; **2.74**, *Pteronymia vestilla sparsa* Haensch. **GODYRIDINI: 2.75**, *Godyris zavaleta matronalis* (Weymer) ♂; **2.76**, *Godyris zavaleta matronalis* (Weymer) ♀. **PIERIDAE, DISMORPHIINAE: 2.77**, *Moschoneura pinthaeus amelina* (Höpffer); **2.78**, *Moschoneura pinthaeus ithomia* (Hewitson). **PIERINAE: 2.79**, *Itaballia demophile demophile* (Linnaeus) ♀ (♂ not mimetic); **2.80**, *Itaballia pisonis pisonis* (Hewitson) ♀ (♂ not mimetic). **LYCAENIDAE, RIODININAE: 2.81**, *Hyphilaria nicia nicia* Hübner. LARGE YELLOW TRANSPARENT COMPLEX. **ITHOMIINAE, MECHANITINI: 2.82**, *Thyridia psidii ino* Felder & Felder. **METHONINI: 2.83**, *Methona confusa psamathe* Godman & Salvin; **2.84**, *Methona curvifascia curvifascia* Weymer. **NAPEOGENINI: 2.85**, *Napeogenes pharo pharo* (Felder & Felder). **DIRCENNINI: 2.86**, *Callithomia lenea zelie* (Guérin); **2.87**, *Dircenna loreta loreta* Haensch. **GODYRIDINI: 2.88**, *Godyris dircenna dircenna* (Felder & Felder). **PIERIDAE, DISMORPHIINAE: 2.89**, *Patia orise denigrata* (Rosenberg & Talbot). **ARCTIIDAE, PERICOPINAE: 2.90**, *Dysschema buckleyi buckleyi* (Druce) ♂ (by day and at light; ♀ mimics *Parides* spp. (Papilionidae)); **2.91**, *Dysschema mosera mosera* (Druce); **2.92**, *Dysschema* sp. (at light); **2.93**, *Dysschema grassator grassator* (Hering); **2.94**, *Dysschema hypoxantha hypoxantha* Hübner (by day and at light).

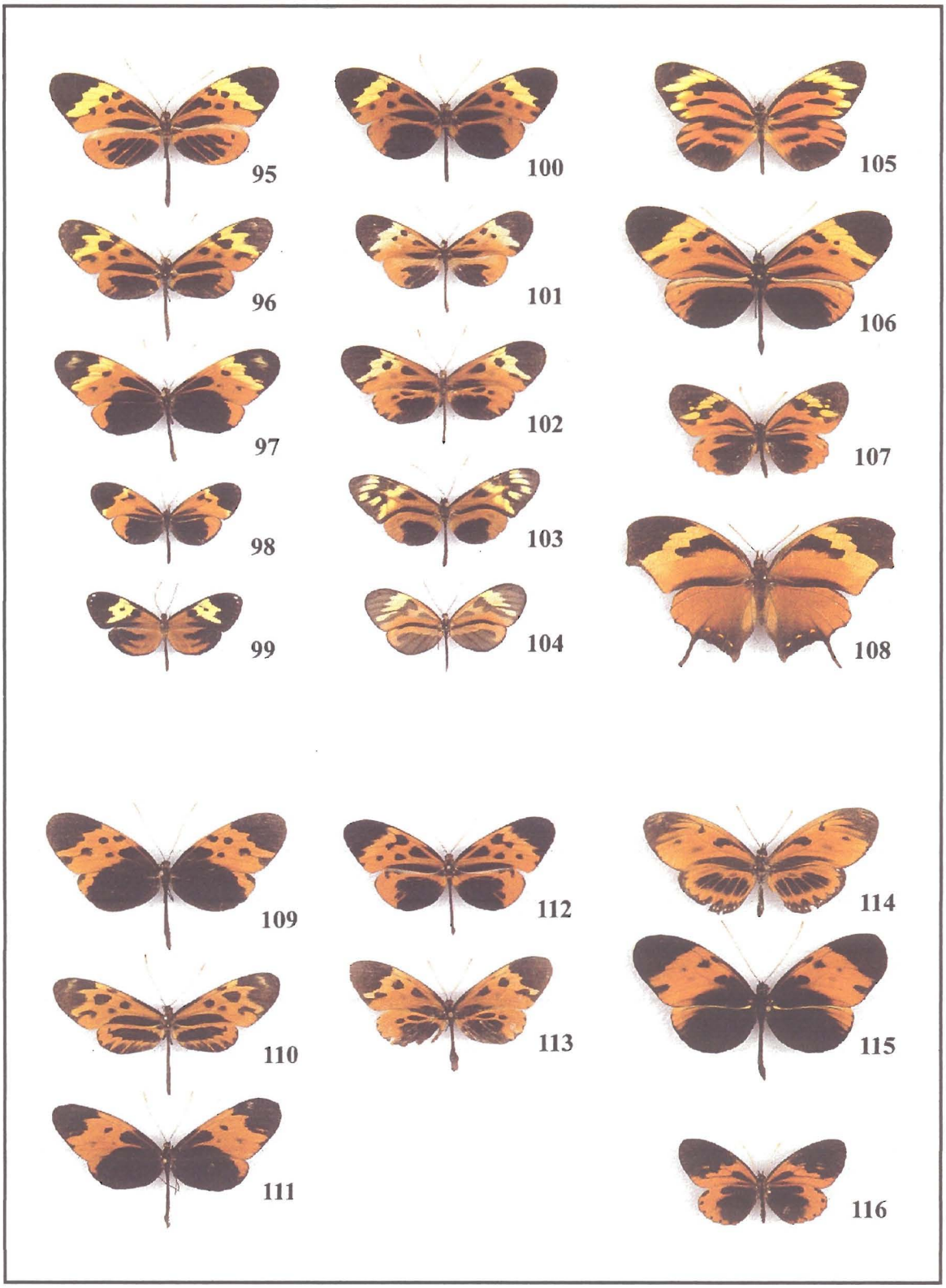
FIGURES 2.66-2.94



FIGURES 66 - 94

Fig. 2.95-2.116. YELLOW-BAR TIGER COMPLEX; see general legend on Fig. 2.1-2.36. **ITHOMIINAE, MELINAEINI: 2.95**, *Melinaea menophilus cocana* Haensch. **MECHANITINI: 2.96**, *Mechanitis mazaeus fallax* Butler (polymorphic); **2.97**, *Mechanitis messenoides messenoides* Felder & Felder (polymorphic). **NAPEOGENINI: 2.98**, *Napeogenes achaea achaea* (Hewitson); **2.99**, *Napeogenes stella* ssp. n. Brown; **2.100**, *Hypothyris anastasia honesta* (Weymer) (polymorphic); **2.101**, *Hypothyris mamercus mamercus* (Hewitson); **2.102**, *Hypothyris moebiusi moebiusi* (Haensch) (polymorphic). **DIRCENNINI: 2.103**, *Callithomia alexirrhoe* ssp. n. Lamas (polymorphic); **2.104**, *Ceratinia tutia poecila* f. *nigronascens* Haensch (polymorphic). **PIERIDAE, PIERINAE: 2.105**, *Perrhybris pamela amazonica* Fruhstorfer ♀ (♂ not mimetic). **NYMPHALIDAE, HELICONIINAE: 2.106**, *Heliconius numata* f. *euphrasius* Weymer (polymorphic). **NYMPHALINAE: 2.107**, *Eresia pelonia* f. *callonia* Staudinger ♀ (♀ polymorphic). **CHARAXINAE: 2.108**, *Consul fabius aequatorialis* f. *diffusus* Butler (polymorphic). ORANGE AND BLACK TIGER COMPLEX. **ITHOMIINAE, MELINAEINI: 2.109**, *Melinaea marsaeus mothone* (Hewitson). **MECHANITINI: 2.110**, *Mechanitis mazaeus mazaeus* Hewitson (polymorphic); **2.111**, *Mechanitis messenoides deceptus* Butler (polymorphic). **NAPEOGENINI: 2.112**, *Hypothyris anastasia bicolora* (Haensch) (polymorphic); **2.113**, *Hypothyris moebiusi unicolora* (Tessmann) (polymorphic). **NYMPHALIDAE, HELICONIINAE: 2.114**, *Eueides lampeto acacetes* Hewitson; **2.115**, *Heliconius numata* f. *bicoloratus* Butler (polymorphic). **NYMPHALINAE: 2.116**, *Eresia pelonia* f. *ithomiola* Salvin ♀ (♀ polymorphic).

FIGURES 2.95-2.116

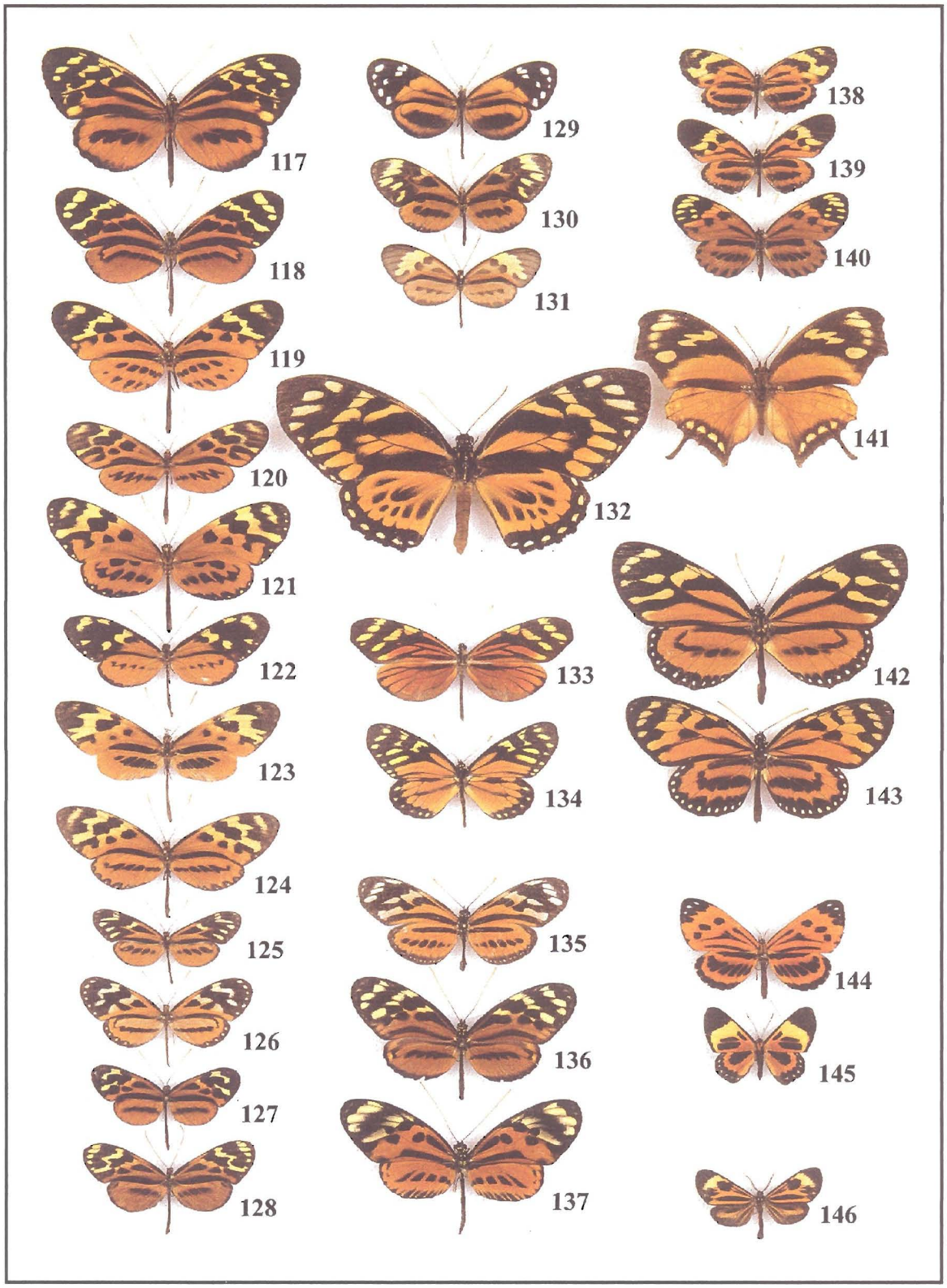


FIGURES 95 - 116

Fig. 2.117-2.146. TIGER COMPLEX; see general legend on Fig. 2.1-2.36.

ITHOMIINAE, TITHOREINI: 2.117, *Tithorea harmonia hermias* Godman & Salvin. **MELINAEINI: 2.118**, *Melinaea maelus maeonis* Hewitson; **2.119**, *Melinaea mnasias abitagua* Brown. **MECHANITINI: 2.120**, *Forbestra olivencia juntana* (Haensch); **2.121**, *Forbestra equicola equicoloides* (Godman & Salvin); **2.122**, *Mechanitis lysimnia elisa* (Guérin); **2.123**, *Mechanitis mazaeus visenda* Butler (polymorphic); **2.124**, *Mechanitis polymnia dorissides* Staudinger. **NAPEOGENINI: 2.125**, *Napeogenes aethra aethra* (Hewitson); **2.126**, *Hypothyris euclea intermedia* (Butler); **2.127**, *Hypothyris fluonia berna* (Haensch); **2.128**, *Hypothyris semifulva satura* (Haensch). **OLERIINI: 2.129**, *Hyposcada anchiala ecuadorina* Bryk. **DIRCENNINI: 2.130**, *Callithomia alexirrhoe butes* Godman & Salvin (polymorphic); **2.131**, *Ceratinia tutia poecila* (Bates) (polymorphic). **PAPILIONIDAE, PAPILIONINAE: 2.132**, *Pterourus zagreus zagreus* (Doubleday). **PIERIDAE, DISMORPHIINAE: 2.133**, *Dismorphia amphiona* ssp. n. Lamas. **PIERINAE: 2.134**, *Charonias eurytele eurytele* (Hewitson). **NYMPHALIDAE, HELICONIINAE: 2.135**, *Eueides isabella isabella* (Cramer); **2.136**, *Heliconius hecale quitalena* (Hewitson); **2.137**, *Heliconius numata* f. *laura* Neustetter (polymorphic). **NYMPHALINAE: 2.138**, *Eresia eunice eunice* (Hübner); **2.139**, *Eresia pelonia* f. *pelonia* Hewitson ♂; **2.140**, *Eresia pelonia* f. *pelonia* Hewitson ♀ (♀ polymorphic). **CHARAXINAE: 2.141**, *Consul fabius aequatorialis* (Butler) (polymorphic). **DANAINAE: 2.142**, *Lycorea cleobaea atergatis* Doubleday; **2.143**, *Lycorea pasinuntia brunnea* Riley. **LYCAENIDAE, RIODININAE: 2.144**, *Stalachtis calliope calliope* (Linnaeus); **2.145**, *Themone trivittata trivittata* Lathy. **NOTODONTIDAE, DIOPTINAE: 2.146**, *Phaeochlaena hazara hazara* (Butler).

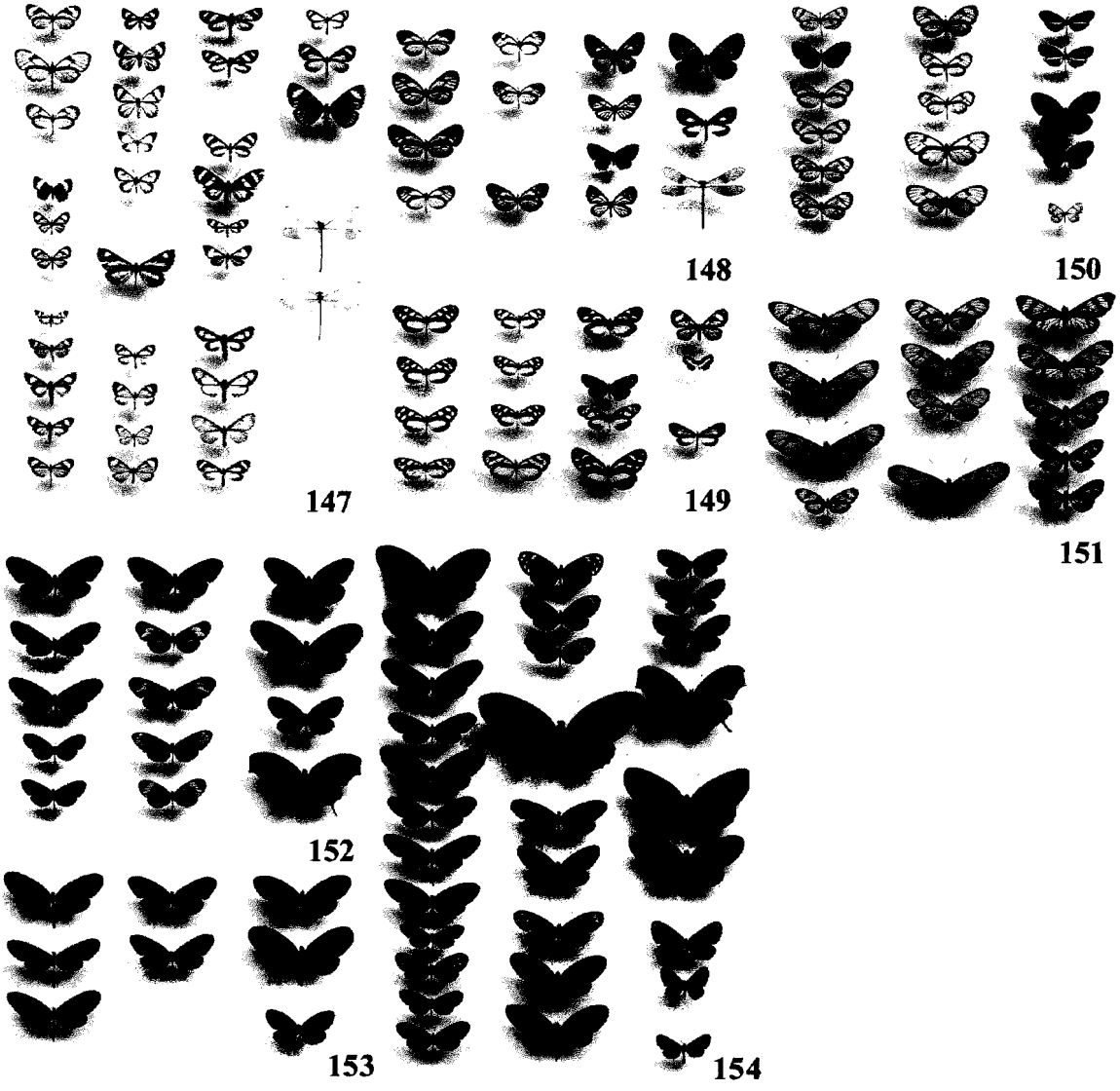
FIGURES 2.117-2.146



FIGURES 117 - 146

Fig. 2.147-2.154. 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 Figs 2.1-2.146. **2.147**, Clearwing complex (*cf.* Figs 2.1-2.36); **2.148**, Orange-tip complex (*cf.* Figs 2.37-2.50); **2.149**, Small dark transparent complex (*cf.* Figs 2.51-2.65); **2.150**, Small yellow transparent complex (*cf.* Figs 2.66-2.81); **2.151**, Large yellow transparent complex (*cf.* Figs 2.82-2.94); **2.152**, Yellow-bar tiger complex (*cf.* Figs 2.95-2.108); **2.153**, Orange and black tiger complex (*cf.* Figs 2.109-2.116); **2.154**, Tiger complex (*cf.* Figs 2.117-2.146).

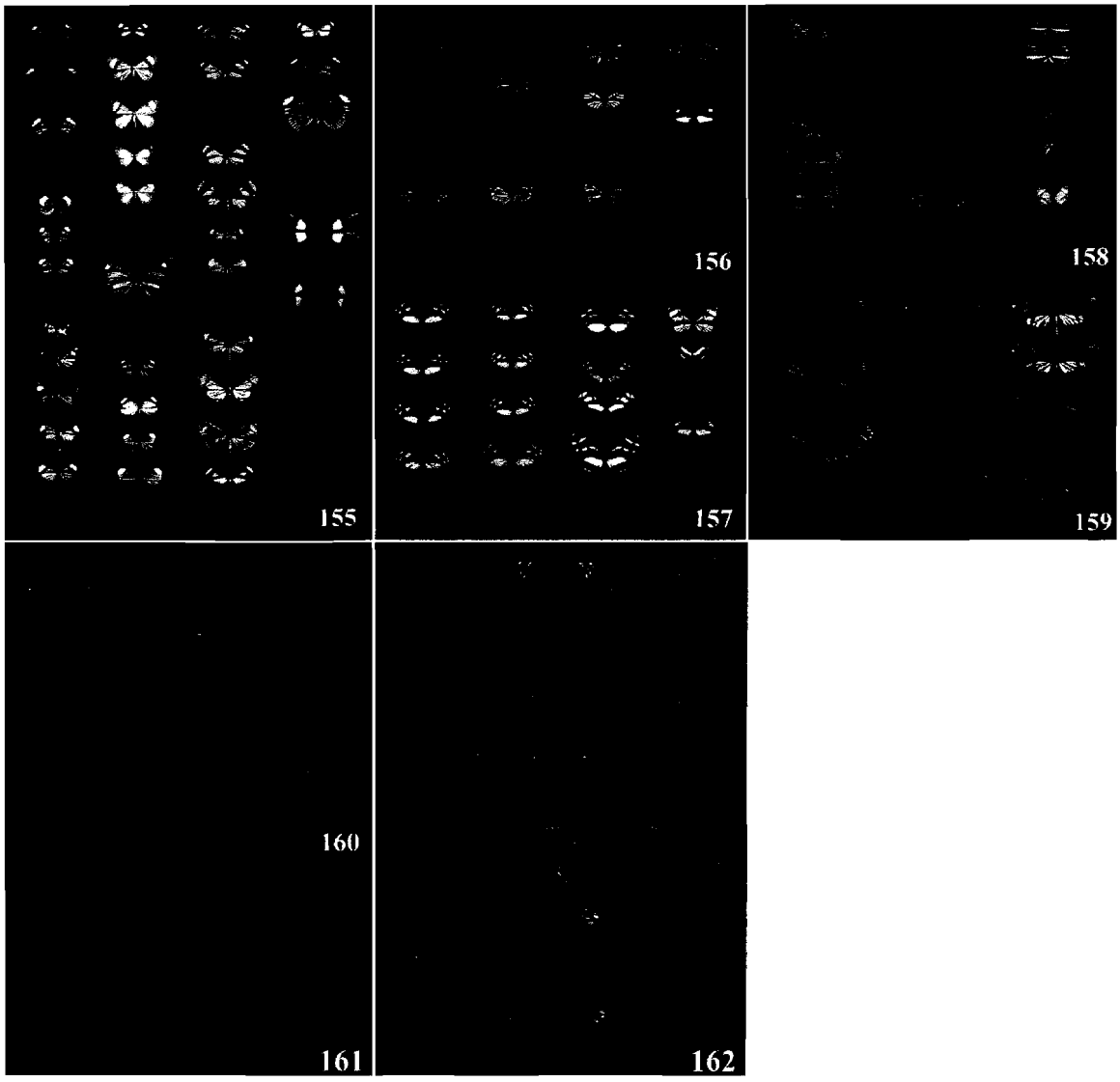
FIGURES 2.147-2.154



FIGURES 147 - 154

Fig. 2.155-2.162. 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 Figs 2.1-2.146. **2.155**, Clearwing complex (*cf.* Figs 2.1-2.36); **2.156**, Orange-tip complex (*cf.* Figs 2.37-2.50); **2.157**, Small dark transparent complex (*cf.* Figs 2.51-2.65); **2.158**, Small yellow transparent complex (*cf.* Figs 2.66-2.81); **2.159**, Large yellow transparent complex (*cf.* Figs 2.82-2.94); **2.160**, Yellow-bar tiger complex (*cf.* Figs 2.95-2.108); **2.161**, Orange and black tiger complex (*cf.* Figs 2.109-2.116); **2.162**, Tiger complex (*cf.* Figs 2.117-2.146).

FIGURES 2.155-2.162



FIGURES 155 - 162

TABLE 2.1. 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				
Polythoridae				
Polythorinae				
Polythore mutata mutata	♂ and ♀: Clearwing;	3	3	
	♀: Orange-tip	-	1	7

TABLE 2.2. 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 RECORDED OF COMPLEX	% 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 2.3. 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

-CHAPTER 3-

MICROHABITAT SEGREGATION OF GUILDS OF NEOTROPICAL ITHOMIINE BUTTERFLIES (NYMPHALIDAE: ITHOMIINAE) AND THE EVOLUTION OF MIMICRY

This chapter is in the form of a manuscript suitable for submission to the *Biological Journal of the Linnean Society*. The table of contents required by this journal has been omitted. Appendix 3.2 is not intended for publication.

ABSTRACT

Müllerian mimicry theory predicts that there should be convergence among the unpalatable species in an area to give a single aposematic colour pattern. Thus, the observed sympatry of many different butterfly mimicry complexes throughout much of the Neotropical forests requires explanation. Evidence is reviewed which demonstrates that sympatric mimicry complexes dominated by unpalatable Ithomiinae (ithomiines) and also Heliconiinae (heliconiines), are spatially segregated by microhabitat. Data are presented which confirm that sympatric ithomiine complexes are segregated vertically by flight height. Flight height of ithomiines was found to be positively correlated with the height of their larval host-plants. Thus members of a mimicry complex utilise host-plants of similar heights. Flight height and host-plant height were also found to be positively correlated for non-mimetic British woodland butterflies, which suggests that this relationship is independent of mimicry. These and other data indicate that host-plant partitioning between butterfly species in a community results in the formation of microhabitat guilds of species. Mimicry complexes are microhabitat guilds, which suggests that mimicry has evolved between species which share a guild and not between guilds, perhaps through the action of microhabitat-dependent selection. Models for the evolution of mimicry complexes in sympatry are presented and hypotheses for the evolution of polymorphism and dual sex-limited mimicry in Müllerian mimics are discussed.

ADDITIONAL KEY WORDS:-Neotropics - Ithomiinae - Heliconiinae - mimicry complexes - vertical stratification - host-plants - ecology - community structure - polymorphism.

INTRODUCTION

Background

Ithomiines (Nymphalidae: Ithomiinae) are an exclusively Neotropical group of forest-dwelling butterflies, currently comprising 310 species placed in 52 genera and 10 tribes (Brown & Freitas, 1994; G. Lamas, unpublished). Ithomiines possess aposematic wing patterns and are known to be unpalatable to birds (Brower & Brower, 1964; Haber, 1978; Chai, 1990) and to other predators (Belt, 1874; Vasconcellos-Neto & Lewinsohn, 1982; Brown, 1984). They are defended by dehydropyrrolizidine alkaloids which are usually sequestered pharmacophagously by the adults (primarily males) from the flower nectar and decomposing foliage of certain species of Eupatorieae (Compositae) and Boraginaceae, and occasionally other sources (Brown, 1985, 1987a). These compounds are transferred to the female during mating via the male spermatophore and females use them both for their own defence and for protection of their eggs (Brown, 1987a; Brown *et al.*, 1991).

Ithomiines are well known for their participation in mimicry complexes, indeed they were cited as the unpalatable models in the original proposals of both Batesian and Müllerian mimicry (Bates, 1862, and Müller, 1879, respectively). These complexes are usually comprised of many co-mimicking ithomiine species (which often belong to several different genera and even tribes), plus many other species of Müllerian and Batesian mimics which belong to a wide variety of families and subfamilies of butterflies and moths, and even to other insect orders such as Odonata and Homoptera (Brown, 1988). Ithomiines are believed to be the principal models (or "prime movers": Brown, 1988) of the majority of these complexes, as they dominate them in terms of relative abundance of individuals (Poole, 1970; Brown & Benson, 1974; G. W. Beccaloni, unpublished). For example, Poole (1970) found that over 85% of the individuals in the mimicry complexes he studied in Venezuela were ithomiines.

Müllerian mimicry theory predicts that unpalatable species in an area should converge onto a single shared colour pattern, in order to minimise the number of different aposematic patterns naive or forgetful predators have to learn and therefore maximise the fitness of individual participating co-mimics (the larger the 'pool' of co-mimics, the lower the probability of any individual being predated). Once convergence has taken place then positive frequency-dependent stabilising selection should select against rare novel morphs and prevent divergence of members of the complex from the consensus colour pattern. An apparent contradiction to this is the observation that in most areas of the Neotropics (below about 2000 m), several (up to a maximum of about eight) discrete ithomiine mimicry complexes occur sympatrically (Brown, 1988). This study will focus on and explore this phenomenon.

Are mimicry complexes ecologically segregated?

Evidence

Convergence of sympatric mimicry complexes could be prevented and divergence facilitated, if complexes are temporally or spatially segregated from one another within a habitat.

Sympatric mimicry complexes have been shown not to be segregated temporally. Papageorgis (1974, 1975) demonstrated that the ithomiine and heliconiine (Nymphalidae: Heliconiinae) complexes she studied in Peru were not segregated by diurnal activity times (my own observations in Ecuador support this). Drummond (1976) found that although the numbers of ithomiine individuals fluctuated over the course of a 253 day mark-release-recapture study at Limoncocha, Ecuador, the relative abundances of the mimicry complexes to which they belonged remained fairly constant.

Growing evidence (presented and summarised below) suggests, however, that sympatric (or more precisely, syntopic) mimicry complexes are spatially segregated (horizontally

and/or vertically) by microhabitat. Complexes are thus comprised of microsyntopic species (*i.e.* species which occupy the same microhabitat) and complexes which share a macrohabitat are microallotopic to the other complexes in that macrohabitat (*i.e.* they occur in different microhabitats) [the terms "syntopic" and "allotopic" refer to species found in the same or different macrohabitats respectively (Rivas, 1964)].

Horizontal microhabitat segregation

Only a small number of studies have examined whether butterfly mimicry complexes are segregated horizontally within a habitat (e.g., by vegetation type). Poole (1970) observed that ithomiine species exhibit microhabitat fidelity and that species which occurred together in a particular microhabitat tended to possess similar colour patterns (*i.e.* they were members of the same mimicry complex). Data presented by Haber (1978) suggest that ithomiine species which share a complex have roughly similar biological characteristics (*i.e.* adult size, egg size, and number of mature eggs per female) and that members of a complex also tend to utilise host-plants which grow in similar microhabitats and have similar patterns of dispersion (e.g., clumped or more uniformly spaced).

Benson (1978) demonstrated that a similar situation exists in the case of heliconiine mimicry complexes. He found that heliconiine species exhibit microhabitat fidelity in their choice of host-plants and that species which utilise host-plants in a particular microhabitat are usually co-mimics. Species which belong to different mimicry complexes usually use host-plants which grow in different microhabitats. Host-plants within a microhabitat are partitioned between different heliconiine species (usually members of the same complex) according to species of plant, plant part or growth condition, and a particular species of plant may be partitioned by microhabitat between species which belong to different mimicry complexes.

In a complementary study, J. Smiley & L. E. Gilbert (unpublished) have shown that adult microhabitat overlap is significantly greater between heliconiine co-mimics than it is

between non-mimics, and that different heliconiine complexes numerically dominate different microhabitats (i.e. different successional stages of forest). Although this study did not examine the host-plant utilisation patterns of the different complexes, data presented by Benson (1978) suggest that the microhabitats in which the complexes studied by J. Smiley & L. E. Gilbert (unpublished) are numerically dominant, are those microhabitats in which the host-plants of the species which belong to these complexes are largely found (both adult abundance data and host-plant data are from Costa Rica). For example, Benson showed that the co-mimics *Heliconius melpomene* (L.) and *H. erato* (L.) select host-plants which grow in early successional stages of forest (hosts are partitioned between them), and J. Smiley & L. E. Gilbert (unpublished) demonstrated that this microhabitat is where the adults of both species are most abundant, and where the mimicry complex represented by the two species is numerically dominant.

Vertical microhabitat segregation

Vertical stratification of ithomiine mimicry complexes was first noted by Poole (1970) in Venezuela, after initial observations by Ross (1964) and Brown & Mielke (1967) that ithomiine species appeared to have relatively discrete vertical flight height ranges. Subsequent studies conducted in many areas of the Neotropics (e.g., Mexico: Ross, 1976; Llorente & Garcés, 1983; Costa Rica: Haber, 1978; Panama: Burd, 1994; Ecuador: Drummond, 1976; Beccaloni, this study; Peru: Papageorgis, 1974, 1975; Medina, Robbins & Lamas, in press; and Brazil: Brown, 1988) have confirmed that sympatric ithomiine complexes are vertically segregated. In general, complexes characteristically fly in one of two principal vertical strata: below *c.* 1 m; or above this height (often ranging into the forest canopy or subcanopy). Medina *et al.* (in press) have demonstrated that the flight heights of ithomiine complexes do not change significantly over the course of a day, and that there is no significant difference between the flight heights of males and females of a species.

Heliconiine mimicry complexes have also been reported as being vertically stratified by flight height (Papageorgis, 1974, 1975; Brown, 1988), but this has been disputed by Mallet & Gilbert (1995), who have shown that they are, however, stratified by roosting height. Mallet & Gilbert found that overlap in roosting height was significantly greater between species which belong to the same complex than it was between non-mimics, that co-mimics tended to share roosts, and that species which belong to the same complex tended to roost in the same microhabitat.

A study of a community of non-mimetic fruit-feeding nymphalid butterflies in Costa Rica (DeVries, 1988) suggests that vertical stratification of species may be a general feature of Neotropical rainforest butterfly communities. Of the 46 species trapped during this study, 24 were caught only in the canopy, 15 were caught only in the understorey, and only 7 were caught in both strata.

Concluding a discussion of mimicry complex vertical segregation, Gilbert & Smiley (1978) stated "...how these species differences in average height of flight relate to utilisation of host plants is unknown." It is this aspect which I address in the experimental section of this study.

Aims of the present study

During fieldwork in Ecuador in 1991, I observed that the flight heights of ithomiine species appeared to be positively correlated with the heights of their larval host-plants. In addition, I noted that mimicry occurred between low flying species which utilised short hosts and between higher flying species which utilised tall hosts, but not between high and low flying species. An attempt was made to quantify these observations. Using these data I first test whether the flight heights of ithomiine species, and the mimicry complexes in which they participate, are positively correlated with the heights of their larval host-plants. I then ask whether a correlation between host-plant height and mimicry complex flight height exists for ithomiine communities in other areas [in this case Costa Rica]. Next,

using host-plant data for British woodland butterflies, I test whether the flight heights of non-mimetic species are correlated with their host-plant heights. Finally, I attempt to place these findings into a wider ecological context and I explore their implications for the evolution of sympatric mimicry complexes and the evolution of polymorphism and dual sex-limited mimicry in Müllerian mimics.

DATA FROM JATUN SACHA, ECUADOR

Introduction and methods

Study site

Data were gathered during three periods of fieldwork at Jatun Sacha Biological Station, Napo Province, Ecuador, South America (5th September - 14th October, 1991; 11th September - 7th November, 1992; and 22nd January - 15th February, 1994). A total of 30, 45 and 16 days respectively were actually spent in the field during these periods.

Jatun Sacha is situated in the upper Amazon basin, at 01° 04' S, 77° 36' W. The reserve lies on the southern bank of the Rio Napo (a tributary of the Amazon) at an elevation of 450 m. The core of the reserve comprises about 700 hectares of Tropical Wet Forest (Holdridge, 1967), of which 75% is primary and the remainder is secondary regrowth. The average annual precipitation is about 4100 mm. This 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. Jatun Sacha lies 20 km east of the base of the Andes and the environment is transitional between the lower Andean slopes and Amazon lowlands. The terrain is mostly steeply dissected hills crossed by small streams and the soil is largely red clay Oxisol (Dystropept) (Castner, 1990; D. Neill, pers. comm.).

Species list and host-plant data

Ithomiines were sampled with hand nets from a representative range of the different vegetation types found in the reserve during fieldwork in 1991 and 1992. Specimens were set and identified to species on return to Britain and a species list was compiled. All specimens collected during this study have been deposited in the collections of the Natural History Museum, London, or the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.

In 1991 and 1992, an attempt was made to locate the early stages and host-plants of as many ithomiine species as possible. A variety of techniques were used, including: searching all locatable plants of Solanaceae and Gesneriaceae for eggs and larvae; following females engaged in apparent host-plant searching behaviour; and locating females engaged in oviposition. All eggs and larvae found were reared through to the adult stage in order to identify them to species. When early stages were located, their height on the host-plant and the total height of the plant were measured and recorded. The growth-form and growth stage of host-plants were also noted. Voucher specimens of host-plants, in flower and/or fruit if possible, were collected and pressed for future identification.

Mark-release-recapture study

During fieldwork in 1994 a 16 day mark-release-recapture (MRR) study was conducted to quantify the flight heights of ithomiine species, thereby enabling flight height distributions of the mimicry complexes to which they belong to be produced. The total sampling time was 57 field hours: an average of *c.* 3 ½ hours per day. Whenever possible, sampling was conducted between 9.30 AM and 1.30 PM. The study was conducted within a 1 hectare plot (permanent study plot "Parcela 5") of primary alluvial 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. The terrain was flat. A transect line of nylon string, approximately 595 m in length, was strung up through this area in four main loops, in such a way that almost all

of the area was sampled. The transect line consisted of two strands of coloured string: a white strand strung at 1 m above the ground, and a red strand suspended 1 m directly above this.

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. Butterflies were captured using an insect net of 40 cm diameter and a handle 30 cm in length, giving a total vertical reach of approximately 2.7 m. 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, flying or perched, were sampled within a *c.* 2 m band on either side of the transect. Data on the insect species which mimic ithomiines will form the basis of a future paper and will not be discussed in detail here. Captured ithomiines were gently removed from the net, identified to species (using, if necessary, a set of previously prepared photographic plates illustrating the majority of the Jatun Sacha ithomiine species), and sexed. They were then marked using a quick-drying permanent marker pen and released. Recaptures were noted, but are not included in the data analysis.

Flight or perched heights were recorded within 0.10 m categories (0.01-0.10 m, 0.11-0.20 m etc.) from ground level to 5 m. In subsequent analyses, both heights were combined as 'flight height', since perched height must equal the height at which a butterfly was flying before it landed. The flight height of an individual was taken to be the height at which we first observed it flying. Flight heights were estimated by comparison with the known height of the nearest strand of the transect line. Butterflies flying significantly above 2 m could be assigned a height by noting a nearby landmark and then estimating or measuring its height.

Sampling efficiency declined increasingly rapidly above about 2 m and became virtually non-existent above 2.7 m, first, because low flying butterflies were easier to observe, and

second, because of the limited reach of the nets. In addition, higher flying species tended to fly upward out of net reach when disturbed, unlike lower flying species which usually flew downwards (this difference in the escape behaviours of the two groups was also noted by Drummond, 1976). A very low proportion of the individuals observed flying above 2.7 m were captured, however, by jumping up, climbing on top of fallen logs, or waiting for them to descend to within net reach.

A total of 64 ithomiine taxa belonging to 56 species have been documented to date at Jatun Sacha (G. W. Beccaloni, unpublished) and during the 1994 MRR study 1361 ithomiine individuals representing 45 taxa belonging to 41 species were recorded (Appendix 3.1). One species, *Hyalyris coeno norellana* (Haensch) (two individuals observed), is not included in the MRR totals. It was excluded from the analysis on the basis that it does not have any co-mimics at Jatun Sacha.

Results

Ithomiine mimicry complexes at Jatun Sacha

The ithomiine taxa found at Jatun Sacha can be divided into eight discrete mimicry complexes on the basis of their wing colour patterns and the taxa observed during the MRR study have been classified accordingly (see Appendix 3.1). The terminology used to describe the complexes is based on a combination of that of Drummond (1976), Haber (1978) and Brown (1988). For the purpose of analysis I have classified *Aeria e. negricola* as a member of the SYT complex, but it may be the sole ithomiine member of the BY complex (see Costa Rican data below) present at Jatun Sacha.

Do ithomiine species fly at the heights of their host-plants?

The host-plants and early stages of 16 ithomiine taxa (which belong to 15 species placed in 11 genera and 7 tribes) were located (Table 3.1). For simplicity I mainly refer to these taxa as 'species'. The species, grouped by mimicry complex, are illustrated in Fig. 3.1. They include representatives of six of the eight ithomiine mimicry complexes found at Jatun Sacha.

At Limoncocha, Ecuador, which has a very similar ithomiine fauna and environment to Jatun Sacha, Drummond (1976) observed that ithomiine species with SDT, OT, CW or SYT colour patterns usually flew below 1 m, while species possessing T, YBT, OBT or LYT patterns usually flew above this height. I hypothesised that colour pattern and flight height of ithomiines at Jatun Sacha are correlated in a similar way and I have therefore divided the species with host-plant records into two flight height groups (termed "A" and "B") accordingly (Table 3.1). Species in group A (T and LYT patterns represented) are predicted to fly above *c.* 1 m, while species in group B (SDT, OT, CW and SYT patterns represented) are predicted to fly below this height.

Species in group A have hosts > 1.5 m tall (shrubs, trees and a vine) and their early stages were found above 1.1 m, while the species in group B have hosts ≤ 1.5 m tall (herbs and shrubs) and their early stages were found at or below 1.1 m (Table 3.1). The only exception is the group A species *Mechanitis polymnia dorissides*, which has both a tall host (*Solanum rugosum*) and a short host (*Solanum quitöense*). The latter plant, however, is a non-native cultivated species. In addition, on three of the four occasions when eggs of *M. p. dorissides* were located they were found on the taller *S. rugosum*, tentatively suggesting that this species is the most frequently used. *M. p. dorissides* has therefore been classed as utilising tall hosts.

The combinatorial probability that the species predicted to be 'high' flying (group A) would also be those with the tallest hosts (and highest early stages), and that the species predicted

to be 'low' flying (group B) would be those with the shortest hosts (and lowest early stages) is 8!8!/16! = 0.00008.

Eggs of one group B species, *Hyposcada illinissa ida*, were recorded up to 1.1 m (Table 3.1) and the female(s) which laid these must have consequently flown at least as high as this. I have therefore chosen to define Drummond's (1976) "high" and "low" flying colour pattern groups with respect to this height in subsequent analyses: the high flying group are predicted to fly on average above 1.1 m; while the low flying group are predicted to fly on average at or below this height.

Flight height data

During the MRR study, individuals of 14 of the 16 species with host-plant records were observed (Appendix 3.1, Table 3.1). The median flight heights of the 8 group A species are all greater than 1.1 m, while those of the 6 group B species are all less than this height (Table 3.2). Considering just the 9 species with > 20 flight height observations: > 50% of the flight height observations of the species in group A are above 1.1 m; while > 50% of individuals of the species in group B were recorded at or below this height. Pair-wise chi-square tests corrected for continuity (Siegel, 1956), with the number of flight height observations above 1.1 m, and at or below 1.1 m, show significant differences between all comparisons involving pairs of species belonging to the two different groups; comparisons made within the two groups, however, were not significant in 9 out of 16 pair-wise tests (Table 3.3).

These results support the predicted division of the species on the basis of colour pattern into the two flight height groups. The probability that the 14 species were assigned to the correct flight height groups by chance is 8!6!/14! = 0.0003. Excluding species with low sample sizes (< 20 flight observations) this probability becomes 0.008 (4!5!/9!). Fig. 3.2 shows the aggregated, weighted flight height frequency distributions of each of these two groups (excluding species with low sample sizes).

Are the Jatun Sacha mimicry complexes vertically segregated?

Flight height frequency distributions for the eight mimicry complexes found at Jatun Sacha are illustrated in Fig. 3.3.

In four complexes (T, YBT, OBT and LYT), most individuals were recorded above 1.1 m, while in the case of the other four (SDT, OT, CW and SYT), most individuals were recorded at or below this height. The median flight heights of the former group are higher than those of the latter. The numbers of individuals in each complex recorded above 1.1 m, and at or below 1.1 m, are significantly different in all pair-wise comparisons involving one 'high' and one 'low' flying complex (e.g., T vs. SDT), whereas 9 out of the 12 comparisons made between complexes within each of the two groups (e.g., SDT vs. OT) are not significant (Table 3.4).

These results confirm the prediction that the T, YBT, OBT and LYT complexes fly on average above the SDT, OT, CW and SYT complexes.

Observer-bias in recording flight height

Sampling was heavily biased towards individuals flying below 2.7 m. This will have biased the flight height frequency distributions of the high flying complexes downwards, but it will not have affected the distributions of the low flying complexes as much or at all. Never in the course of the MRR study (or during other fieldwork) at Jatun Sacha were individuals which belong to the low flying complexes SDT, OT, CW and SYT observed to fly above about 2.4 m, whereas individuals which belong to the T, YBT and OBT complexes were frequently observed flying 5-20 m or more above the ground. Members of the LYT complex often flew above 2.4 m, but they did not fly as high as the other high flying complexes. If it had been possible to sample with equal efficiency from canopy height (estimated at *c.* 30 m) to ground level, then it is likely that the observed division between the flight height frequency distributions of the high and low flying mimicry

complexes would have been much greater than is shown in Fig. 3.3. In other words, the frequency distributions of the high flying complexes probably have modes at considerably greater heights than indicated in Fig. 3.3.

Do members of a mimicry complex utilise host-plants of similar heights?

Of the sixteen ithomiine species with host-plant records, the eight which belong to high flying mimicry complexes (group A) have high early stages/tall hosts, while the eight which belong to low flying complexes (group B) have low early stages/short hosts (Table 3.1, Fig. 3.3). As it is unlikely that the correlation between flight height and host-plant height is a result of chance (see above), it is probable that the other species which belong to the two high and to the four low flying complexes represented by these species also utilise tall and short hosts respectively.

Although there are no host-plant records from Jatun Sacha for any of the species which belong to the high flying YBT and OBT mimicry complexes, I predict that they utilise tall hosts. This prediction is supported by host-plant records from other areas, where some of the species participating in these complexes at Jatun Sacha are found. For instance, the high flying YBT species, *Melinaea menophilus cocana*, elsewhere feeds on epiphytic solanaceous shrubs of the genera *Juanulloa* and *Markea* (Drummond & Brown, 1987), which grow in the canopy or subcanopy of mature forest (Haber, 1978). So too does *M. marsaeus* (Hewitson), which at Jatun Sacha belongs to the OBT complex as subspecies *mothone* (Hewitson). Unlike *M. m. cocana*, this species was not recorded during the MRR study, but personal observations suggest that it is high flying.

Table 3.1, although based on a small total number of observations, shows that host-plant species are only ever shared between ithomiine species which share a flight band. Thus at Jatun Sacha, overlap of host-plant utilisation was never observed to occur between species which belong to complexes which fly at different heights.

Observer-bias in recording host-plants

As with flight height records (see above), the Jatun Sacha host-plant data set (and all data of a similar nature) is heavily biased by the physical height of the human observer in favour of recording short hosts. Thus hosts of butterfly species which utilise tall plants will be relatively poorly documented, and if a species uses both short and tall hosts then it will be difficult or impossible to accurately determine the frequency with which it uses the two height classes. At Jatun Sacha, species which belong to low flying mimicry complexes were never observed to fly above 2.4 m (Fig. 3.3) and it is therefore likely that these species only utilise short hosts. In contrast, high flying species spend a proportion of their time flying low (Fig. 3.3) and they may therefore occasionally utilise short hosts. As short hosts are probably more likely to be recorded than tall hosts, this could bias the observed utilisation patterns of these species in favour of short hosts. Fortunately, in ithomiine communities with high species richness (such as at Jatun Sacha) the majority of ithomiine species are probably monophagous (see Discussion), so it is likely that few host-plant species remain to be documented at Jatun Sacha for the species with host records (Table 3.1). I therefore cautiously conclude that the conclusions derived so far are not seriously in error because of inadequate host-plant records, although more observations of the species with host records, as well as host-plant records for other Jatun Sacha ithomiine species, would be desirable.

Mimics of ithomiines

There is evidence that the flight height distributions of butterfly and moth species which mimic ithomiines are similar to the those of their ithomiine models (Papageorgis, 1974, 1975; Drummond, 1976; Brown, 1988) and that they, like ithomiines, utilise host-plants which correspond to their usual flight heights. For example, at Jatun Sacha I located the host-plants of two ithomiine mimics: *Lycorea cleobaea atergatis* Doubleday (Nymphalidae: Danainae), which belongs to the high flying T complex; and *Moschoneura pinthaeus amelina* (Höpffer) (Pieridae: Dismorphiinae), which belongs to the low flying

SYT complex. *L. c. atergatis* was observed ovipositing at a height of 2.5 m on a 3.5 m tall cultivated *Carica papaya* L. tree, and at approximately the same height on *c.* 4 m tall native *Carica* sp., while *M. p. amelina* was observed ovipositing at a height of *c.* 0.1 m on a 0.3 m tall unidentified herbaceous plant. Both of these mimics were recorded during the 1994 MRR study and from these data the following flight height statistics were calculated: *L. c. atergatis* (3 individuals observed) has a flight height range of 1.35-2.85 m, a median flight height of 2.75 m, and no individuals flew at or below 1.1 m; while *M. p. amelina* (11 individuals observed) has a flight height range of 0.25-1.35 m, a median flight height of 0.68 m, and 72.7% of individuals flew at or below 1.1 m. Thus the flight height distributions of both species correspond to the heights of the host-plants they utilise and, in addition, their flight height distributions and the heights of the hosts they utilise are similar to those of the ithomiine species they resemble (see Table 3.1, Fig. 3.3).

COSTA RICAN ITHOMIINE HOST-PLANT DATA

Introduction and methods

The host-plant relationships of Costa Rican ithomiine species are probably the best documented of any regional fauna and this large data set was therefore selected for comparison with the Jatun Sacha data. Host-plant records exist for 48 of the 61 ithomiine species found in Costa Rica (Drummond & Brown, 1987, supplemented by DeVries, 1987, and DeVries, 1991) (Appendix 3.2). Only host-plants identified to species level were used in the analysis, except in three cases where only the genus was given but the growth-form of the host was recorded in the primary literature.

A total of 103 host records, representing 53 species of plants in 13 genera, have been documented for Costa Rican ithomiines (Appendix 3.2). The hosts are primarily Solanaceae (mostly species which belong to the huge genus *Solanum*), but a few are Apocynaceae (the hosts of *Tithorea* and *Aeria* only) and Gesneriaceae (the hosts of *Hyposcada* only).

Growth-forms (and maximum mature growth heights) of the host-plants were taken from Standley & Morton (1938), Standley & Williams (1969), D'Arcy (1973), Gentry & Standley (1974), and Gibson (1974). Host-plant species were classified as having one of the following growth-forms (maximum mature height in brackets): herb (≤ 1.5 m); shrub (> 1.5 m and ≤ 3.5 m); tree (> 3.5 m); epiphytic shrub (usually found in the forest canopy or subcanopy >> 3.5 m above ground level); shrub/tree (< or > 3.5 m); and vine (mature height uncertain). The latter two categories have been excluded from the data analysis on the basis that they are uninformative with regard to mature height. Thus "shrub/tree" includes plants with a variable mature height of < or > 3.5 m, while the mature height of a vine will depend on the nature of the support it is growing up etc. If botanical authorities classified the growth-form of a species differently, then the original literature source of the host record (Young, 1972; Young, 1973; Young, 1974a, b, c; Young, 1977; Young, 1978a, b; Haber, 1978; DeVries, 1991) was consulted to see whether the author had stated the growth-form of the host and, if so, this was used. If, however, it was not stated, then the most frequently quoted growth-form in the botanical literature was used, or alternatively, if authorities were divided as to whether the plant was a shrub or a tree (this category was the most contentious) then it was placed in the "shrub/tree" category and therefore excluded from the analysis.

Ithomiine species were classified into one of five mimicry complexes (see Fig. 3.4) using the terminology and groupings of Haber (1978) and the plates in DeVries (1987). Representatives of these complexes are illustrated in Fig. 3.4. I consider Haber's BY complex to include only the following three Costa Rican species: *Aeria eurimedea agna* Godman & Salvin, *Scada zibia xanthina* (Bates), and *Oleria zelica pagasa* (Druce). I have arbitrarily classified species which exhibit dual sex-limited mimicry (Evans, 1968) (*i.e.* the sexes each belong to a different mimicry complex) according to the female colour pattern, as in all such cases both sexes belong to complexes which are known to fly at similar heights.

All five Costa Rican mimicry complexes are usually sympatric at mid-elevation sites between *c.* 600-1300 m. Below *c.* 600 m the GT complex is absent. With increasing elevation between *c.* 1300 m and *c.* 3000 m (no ithomiine species occur above this altitude) complexes are progressively lost, *i.e.* first the BY, then the T and BR, next the GT, and finally the CW complex (Haber, 1978; DeVries, 1987).

The BY and CW complexes are known to be the lowest flying, while the other three usually fly higher (Haber, 1978; Brown, 1988). Brown gives the following approximate flight height ranges for these complexes (in primary forest): BY, 0-1.5 m; CW, 0-2.5 m; GT, 1.5-7+ m (to subcanopy); BR, 3-7+ m (to subcanopy); and T, 2.5-5+ m (to subcanopy). Ross (1976) observed that (in Mexico) species which belong to the CW and BY complexes usually did not fly above about 0.6-0.9 m, while the T and GT complexes usually flew above about 1.8 m (the BR complex was absent from Ross's study site). Thus although the flight heights of ithomiine mimicry complexes in Costa Rica have not been quantitatively studied, it seems reasonable to assume that the CW, BY complexes fly below about 1.5 m on average, and that the other complexes fly on average above this height.

Results

Species which belong to the two low flying complexes (CW, BY) use short (≤ 3.5 m) hosts exclusively (Fig. 3.4). The host-plants of the three higher flying complexes (T, BR, GT) include representatives of all growth-form categories, but the majority are trees and epiphytic shrubs. Note that epiphytic shrubs are in a sense the tallest hosts of all, as they usually grow in the forest canopy or subcanopy and are often higher than even the tallest solanaceous trees.

Mimicry complexes were grouped into two categories, low (CW and BY) and high (T, BR and GT) flying, and the number of short (herbs and shrubs) and tall (trees and epiphytic shrubs) host-plants recorded for each of the two groups was calculated (Table 3.5). Low

and high flying complexes are significantly different ($P << 0.001$) with respect to the frequencies of short and tall hosts they utilise (Fisher's exact test - Siegel, 1956). Low flying complexes utilise only low growing plants, while high flying complexes utilise all height classes, but the greater proportion of their hosts are tall.

The data points (host records) in Table 3.5 are, however, not strictly independent for two reasons: a host-plant species may be represented more than once within a category in a row; and second, the hosts of butterfly species with more than one host may fall into two categories. In order to alleviate these problems, three additional Fisher tests were performed. In the first, each plant species was counted only once within each category. In the second, each ithomiine species was classed as either feeding on short or tall hosts by its tallest recorded host (therefore each ithomiine species was only counted once). In the third, each ithomiine species was classed by its shortest host. The first and second tests gave $P << 0.001$, while the third gave $P = 0.002$. I therefore conclude that the flight height range of a mimicry complex in Costa Rica mirrors the height range of the host-plants utilised by the members of the complex.

Caveats and elaborations

These data are prone to many potential errors including: misidentification of host-plants; mis-association of ithomiines with their hosts; a bias towards plants growing in human-disturbed areas (these are the areas most frequented by lepidopterists), which may be infrequently or never (e.g., if non-native) utilised under natural conditions; and a bias towards low growing hosts (these are the ones most likely to be observed). In addition, host-plant growth-form and mature height (as used in the above and subsequent analyses) may not be accurate indicators of the height of the hosts actually selected by females for oviposition, because an ithomiine species may only utilise immature individuals of tall host species (e.g., seedlings of tree species). Another potential problem is that low flying ithomiine species may have tall hosts, but may only utilise low foliage of these. Note also that an undetermined number of the host-plants considered in the above analysis are

species introduced to Costa Rica and are therefore not natural hosts for Costa Rican ithomiines.

Overlap in host-plant utilisation between high and low flying species

There are only two records of any member of a high flying complex utilising herbs as hosts (see Appendix 3.2). Both are hosts of the T species, *Mechanitis menapis saturata* Godman, and one, *Solanum* (*Acanthophora*) *capsicoides* Allioni, is not a native of Central America (it originates from Coastal Brazil (Nee, 1986)). *M. m. saturata* has also been recorded as using four other species of host (1 shrub, 2 shrub/trees and 1 vine) and I predict that herbs are infrequently used by this species.

Although vines were not considered in the above analysis due to their uncertain growth height, close examination of some individual cases of vine feeding suggests that if more information were available a positive correlation would probably be found between the flight height of the mimicry complexes and the height of the vines they utilise. For example, some of the highest flying members of the BR (*Olyras crathis staudingeri* Godman & Salvin), GT (*Eutresis hypereia theope* Godman & Salvin) and T (*Melinaea lilis imitata* Bates) complexes are known to feed on the large canopy vine *Solandra grandiflora* Swartz. Interestingly, the only other hosts recorded for these ithomiine genera are epiphytic canopy shrubs of the genera *Markea* (*Olyras*, *Eutresis* and *Melinaea*) and *Juanulloa* (*Melinaea* only) (Drummond & Brown, 1987). In Costa Rica two species of vine are hosts to species belonging to high and low flying complexes. One of these, *Prestonia* (Apocynaceae), is host to a BY species, *Aeria eurimedea agna*, a T species, *Tithorea harmonia helicaon* Godman & Salvin, and a BR species, *T. tarricina pinthias* Godman & Salvin. *A. e. agna* flies below 1 m (Haber, 1978) and oviposits on *Prestonia* seedlings less than 0.2 m tall (Young, 1978b), while the higher flying *T. t. pinthias* is known to select large plants (Fountaine, 1913). The other "vine" used by several mimicry complexes is *Solanum* (*Micracantha*) *siparunoides* Ewan and it is host to one CW, one BY, two T, one BR and one GT species. *S. siparunoides* is unusual in that in open areas it

grows as a sprawling shrub, while in forest it assumes the form of a straggling climber and often ascends to subcanopy or canopy level (Haber, 1983). I speculate that either: members of the low flying complexes utilise the former growth-form of this plant and members of the high flying complexes use the latter; or that they partition this host by growth stage (low flying species on seedlings and high flying ones on mature plants). Complexes which share a flight stratum may partition this host between them by horizontal microhabitat.

Despite the uncertainties in the Costa Rican records, it is worth noting that a total of only 9 out of the 53 species of host-plants are shared between the two low and three high flying complexes. Four of these are shrubs, three are shrub/trees and two are vines. The general picture that emerges is therefore that host-plants are partitioned between mimicry complexes according to height class.

Haber (1978), who is responsible for the majority of the Costa Rican ithomiine host-plant records, stated that low flying ithomiine species usually select small plants or the seedlings of trees and vines, while high flying species utilise tall hosts. Although Haber did not quantify this statement, it suggests that if the actual heights of the individual plants selected by females were known (as well as the frequency of use of each species of host if there is more than one) then the separation between the utilisation patterns of high and low flying complexes would probably be even greater than that demonstrated above.

BRITISH WOODLAND BUTTERFLY HOST-PLANT DATA

Introduction and methods

Data on the host-plant relationships of British woodland butterflies were chosen for comparison with the Neotropical ithomiine data, to test whether flight height and host-plant height are positively correlated for species of butterflies not involved in mimicry.

Dennis (1992a) has divided the British butterfly fauna into categories defined by habitat associations. For the purpose of this study "woodland butterflies" were taken to be those species which Dennis lists in the following two categories: "Broadleaved woodland dependence on climax component"; and "Broadleaved woodland understorey component; coppice". The principal host-plants of these species in Britain and the growth-forms of these plants were taken from Dennis (1992b), while the average mature heights of the hosts were taken from Clapham, Tutin & Warburg (1968). The butterfly species have been grouped according to the forest stratum (canopy or understorey) where individuals of the species spend the greater proportion of their time flying, based on personal observations and a variety of literature sources including Frohawk (1934), Emmet & Heath (1989) and Thomas (1989).

The British woodland butterfly community is comprised of species which belong to a wide variety of different butterfly families and subfamilies (*i.e.* Pieridae: Dismorphiinae, Coliadinae and Pierinae; Lycaenidae: Lycaeninae and Riodininae; Nymphalidae: Limenitinae, Apaturinae, Nymphalinae, Heliconiinae and Satyrinae), and these exploit a wide taxonomic range of host-plants. Appendix 3.3 lists the butterfly species, principal host-plants, their mature heights and growth-forms and Table 3.6 summarises these data (excluding vines).

Results

Canopy and understorey species groups have significantly different ($P << 0.001$; Fisher's exact test) patterns of host-plant utilisation. Canopy species exclusively utilise tall hosts (shrubs and trees), while the majority (*c.* 88%) of the hosts of understorey species are low growing herbs and grasses (Table 3.6). As with the Costa Rican data, this test suffers from the fact that a host-plant species may be represented more than once within a category in a row. I corrected for this by counting each plant species within a category only once, and a similar result was obtained on re-testing ($P << 0.001$). It was not considered necessary to control for correlations between the categories in a row (caused when a butterfly's host-

plants fall into more than one height category), as only one species (*P. c-album*) utilises more than one height category of host.

P. c-album is the only understorey species which utilises trees (*Ulmus procera* and *U. glabra*) as hosts. However, these are rarely used and a herb, common nettle (*Urtica dioica*), is the preferred host (Emmet & Heath, 1989).

DISCUSSION

Flight height and host-plant height

Non-mimetic butterflies

Data presented above for British woodland butterflies suggest that the positive correlation between butterfly flight height and host-plant height is independent of mimicry, and I believe that the relationship is probably a general one which applies to most forest butterflies. There is much qualitative (but unfortunately little quantitative) data to support this belief. For example, cryptically coloured, forest-dwelling Madagascan butterflies of the subtribe Mycalesina (Satyrinae: Elymiini) which feed on low growing grasses are low fliers, while other similarly cryptic species of this subtribe which utilise tall bamboo hosts fly much higher and are usually only captured in subcanopy traps (D. Lees, pers. comm.).

Butterfly host-plant relationships and microhabitat fidelity

Vertical microhabitat fidelity

Female butterflies spend most of their total flight time searching for host-plants (Benson, 1978; Papaj & Rausher, 1983) and they probably fly at the height of their hosts because this maximises the probability of encountering plants of the correct species and growth stage. Females attempting to locate their host-plants usually flutter slowly and evenly

between plants which are of a similar height to their hosts (note that the host-plants of oligophagous or polyphagous species usually all have similar heights, e.g., Table 3.1, Appendix 3.2, Appendix 3.3). This behaviour is characteristic of ithomiine females (Drummond, 1976; pers. obs.) and females of species belonging to many other butterfly groups (Owen, 1971; Benson, 1978; Singer, 1984; Pollard & Yates, 1993; Porter, 1992). Female butterflies probably identify hosts on the basis of leaf chemical cues and leaf size and shape (Rausher, 1978; Wiklund, 1984; Tyler, Brown & Wilson, 1994) and they therefore have to fly at 'leaf height' in order to detect hosts. Thus host-plant architecture probably influences female flight height.

Males of most butterfly species spend much of their time attempting to find conspecific females with which to mate. In species where the females spend most or all of their adult lives in a particular stratum, selection should favour males which fly in the same stratum. Drummond (1976) has shown that male ithomiines perch and wait for conspecific females at the level at which the females usually fly and it is probable that the males of many other butterfly species exhibit similar behaviour.

Horizontal microhabitat fidelity

Butterfly species (both mimetic and non-mimetic) are often horizontal microhabitat specialists (Benson 1978; Gilbert & Smiley 1978; Gilbert 1984; Courtney 1984; Singer, 1984; Porter, Steel & Thomas, 1992). In fact, it is thought that this may be the primary niche dimension partitioned between species, with host-plants differentially used only as an indirect result of microhabitat choice (Gilbert, 1984). For females of many butterflies, the initial stage of host-plant searching involves locating the microhabitat where the host-plants are found and where environmental conditions are suitable (Porter, 1992). Microhabitat selection may greatly increase female searching efficiency, resulting in a high contact rate with hosts (Courtney, 1984).

The males of many butterfly species perch and wait for females, or actively search for them, in the microhabitats where their host-plants are found. Males of some species even locate the larval host-plants and wait for newly eclosed virgin females or conspecific females searching for hosts (Scott, 1975; Tyler, Brown & Wilson, 1994). Males of certain *Heliconius* species search larval host-plants for female pupae which they 'rape' as they begin to eclose (Deinert, Longino & Gilbert, 1994), and the males of many other *Heliconius* species are known to patrol host-plants in order locate newly emerged females (e.g., Mallet & Jackson, 1980).

Microhabitat fidelity and host-plant shifts

As female butterflies fly at 'host-plant height' when searching for hosts, they are more likely to come into contact with plants which have a similar height and growth-form to their hosts, than they are with plants which belong to different height or growth-form categories. I speculate that host-plant shifts are therefore more likely to occur between plants which have a similar height and growth-form to a species' original hosts. Indirect evidence for this is that the host-plants of butterfly species which utilise more than one host, either at a given locality, or in different parts of their geographical range, usually all belong to the same height class (e.g., Table 3.1, Appendix 3.2, Appendix 3.3). This may explain why the plants utilised by a butterfly species often seem to be more closely united by height and growth-form, than they are related phylogenetically. For example, some ithomiine species only utilise tree hosts and these often belong to several different genera and even sections of Solanaceae, although more closely related plants with different heights and growth-forms (many genera of Solanaceae contain species with tree, shrub, herb and vine growth-forms) may grow in the same habitat and may be utilised by other sympatric ithomiine species. Horizontal microhabitat fidelity may also constrain host-plant switches, with switches between plant species which occur in the same horizontal microhabitat being more likely than switches between species which grow in different horizontal microhabitats (see Chew & Robbins, 1984). Host switches will obviously also

be constrained by other factors, such as the degree of chemical similarity between existing host and potential host (Miller, 1987; Brown, 1987a; Tyler, Brown & Wilson, 1994).

Spatial segregation and mimicry

I have argued that forest butterfly species often exhibit vertical and horizontal microhabitat fidelity and I have suggested that this behaviour is directly (in females) or indirectly (in males) related to a species pattern of host-plant utilisation. Butterfly communities are divided into guilds of microsyntopic species, each of which is comprised of species which utilise host-plants which grow in the same microhabitat and are of similar growth heights. Evidence suggests that ithomiine and heliconiine species which belong to the same mimicry complex utilise host-plants of similar heights (ithomiines and possibly heliconiines) which grow in the same horizontal microhabitat (heliconiines and probably ithomiines). Mimicry complexes are therefore microhabitat guilds of species, which (like medieval human guilds!) each have their own distinctive livery.

Why are there so many mimicry complexes?

Evolution of mimicry complexes in allopatry

There are a large number of different ithomiine, heliconiine and other butterfly mimicry complexes in the Neotropics (see Brown, 1988, for an overview). Some complexes have wide geographical distributions, e.g., the ithomiine T complex, which is found throughout much of the Neotropical forests (below about 2000 m), from southern Mexico (20°N) to southern Brazil (32°S) (see maps in Brown, 1979). Other complexes in contrast, are relatively localised, e.g., the ithomiine OT complex which occurs in the upper Amazon basin of eastern Ecuador, south-eastern Colombia and north-eastern Peru, and in south-western Venezuela and the western Amazonas region of Brazil (Drummond, 1976). Mimicry complexes often vary in colour pattern geographically, a fact noted by Bates

(1862). The T complex, for example, is divided into numerous parapatric colour pattern races or 'sub-complexes' over its range (Brown, 1979).

Turner (1976, 1982, 1984b), Brown (1979, 1982, 1987b), Sheppard *et al.* (1985) and others have proposed that butterfly mimicry complexes evolved in allopatry in forest "refuges" isolated by savannah during glacial periods of the Pleistocene, when drier climatic conditions were thought to have prevailed over the Neotropics. In order to provide a sufficient explanation of mimicry complex diversity, the refuge theory must assume that before the Pleistocene, either a single mimicry complex occurred throughout the Neotropical forests (*i.e.* all butterflies possessed the same colour pattern), or alternatively, that no mimicry existed (*i.e.* each butterfly species had a unique colour pattern). In the first scenario, a mechanism is then needed to explain divergence in the face of the strong stabilising selection predicted by Müllerian mimicry theory. Mallet (1993) has pointed out that the second scenario (discussed in full by Turner, 1982, 1984b) is unlikely, as at least in the case of *Heliconius*, there are now more racial mimetic patterns than there are species mimicking each other! This would imply that many model species (*i.e.* the dominant unpalatable species around which mimicry complexes are thought to have formed in the putative refuges) have gone extinct. For example, this scenario assumes that before the Pleistocene the two co-mimics *Heliconius erato* and *H. melpomene* each had different colour patterns and that each species was monomorphic throughout its geographical range. It is supposed that during the last glacial period (with a cold, dry peak between 13000 and 18000 years ago), sub-populations of the two species were isolated in different refuges, and that each refuge contained a different dominant model species with a different colour pattern, onto which both *Heliconius* species then converged. It is believed that this process produced the twenty-two parallel geographical races of *H. erato* and *melpomene* seen today (Turner, 1984b), and as these species are now the dominant models of these mimicry complexes (they are often the sole members), the original model species are presumed to have all become extinct. This scenario does not seem plausible.

Müllerian mimicry theory predicts that there should be convergence of sympatric mimicry complexes, so the observed sympatry of different ithomiine and heliconiine mimicry complexes throughout much of the Neotropics (e.g., the eight ithomiine complexes at Jatun Sacha) requires explanation. This apparent anomaly is thought by proponents of the refuge theory to be due to spread and overlap of complexes formed originally in different refuges (e.g., Brown & Benson, 1974). When wetter climatic conditions returned to the Neotropics after the glacial period, forest refuges expanded until they met and mimicry complexes were free to spread through the newly continuous habitat. Convergence of overlapping complexes has not occurred, however (despite the reasonable assumption that some sympatric complexes must be better protected than others and therefore selection should favour convergence onto the single 'fittest' colour pattern in an area), because it is claimed that the colour patterns are so different developmentally that mutations which would enable convergence cannot arise, or simply have not arisen (e.g., Turner, 1977, 1984a, b; Sheppard *et al.*, 1985). This *ad hoc* hypothesis is, however, seemingly contradicted by the existence of Müllerian mimics which are polymorphic (e.g., *Heliconius numata* (Cramer)), or exhibit dual sex-limited mimicry (e.g., the ithomiine, *Pteronymia notilla notilla* Butler & Druce). In these cases the required mutations obviously have arisen, so lack of convergence onto a single colour pattern requires explanation. Brown & Benson (1974) proposed that polymorphism in *H. numata* is maintained because the relative abundances of the ithomiine mimicry complexes in which morphs of this species participate, vary temporally and spatially. Thus different morphs of *H. numata* are thought to be favoured in different parts of a habitat and at different times. Data presented by Brown & Benson were, however, insufficient to prove that the relative abundances of the ithomiine complexes in which *H. numata* participates fluctuate in the manner suggested. In addition, a detailed study by Drummond (1976) at Limoncocha, Ecuador, where *H. numata* has three morphs, demonstrated that the relative abundance of the three ithomiine complexes in which these morphs participate, remained fairly constant in a 0.5 hectare study plot over the course of a 253 day study. Thus the mechanism proposed by Brown & Benson cannot be accepted until supporting evidence is available (for a theoretical criticism of this mechanism see Papageorgis, 1974).

Dual sex-limited mimicry in Müllerian mimics presents an additional problem for the refuge theory, as clearly the males and females of these species could not have been separately isolated in different refuges, as has been proposed in the case of morphs of polymorphic Müllerian mimics (Brown & Benson, 1974). In addition, given that mimicry complexes are microhabitat guilds of species, it is difficult to envisage how individual ecological guilds could have been individually isolated in different refuges. Other theoretical objections to the refuge theory are discussed by Benson (1982) and Mallet (1993).

Evolution of mimicry complexes in parapatry

Benson (1982) argued that divergence of mimicry complexes could occur in parapatry and that such a model would provide an equal or better explanation of observed phenomena than a model based on allopatric isolation. Mallet (1993) reviews evidence supporting parapatric divergence of mimicry complexes and proposes a mechanism for divergence of mimetic colour patterns in parapatry based on Sewall Wright's "shifting balance" (Wright, 1977). Mallet argues that in a small population a novel colour pattern morph may, through kin-founding or genetic drift, rise above the critical frequency needed for it to be favoured by positive frequency-dependent selection and spread to fixation within the deme or "neighbourhood" in which it arose. If it is fitter than the ancestral mimetic pattern (e.g., if it is more memorable to predators) it may then spread to adjacent demes by interdemic selection, or through a continuous population as a moving hybrid zone, until it is trapped by a barrier (e.g., a large river, mountain ridge etc.). If the fitness of a novel pattern is habitat dependent, then it will spread only within the habitat in which it is adaptive. Such a change in the colour pattern of one species in a mimicry complex should result in selection for convergence of the other species in the complex onto this new pattern, as this derived pattern must have higher fitness than the ancestral mimetic pattern. In this way, parapatric 'populations' of a mimicry complex could diverge in colour pattern over evolutionary time.

This hypothesis provides a plausible explanation for the observed phenomenon of parapatric mimicry complexes, which differ in colour pattern to a lesser or greater degree.

However, I do not find Mallet & Gilbert's (1995) suggestion that sympatric mimicry complexes initially diverged in parapatry and then became sympatric, convincing, in view of the evidence which suggests that sympatric complexes are ecological guilds.

Evolution of mimicry complexes in sympatry

Background

Given that communities of non-mimetic butterflies are divided into microhabitat guilds of species and that in communities of mimetic butterflies, mimicry complexes represent guilds, it seems likely that mimicry has evolved between microsyntopic species. The alternative hypothesis, that mimicry evolved between microallotopic species, which then became microsyntopic (e.g., that species with different microhabitat preferences first converged in colour pattern and secondarily evolved similar microhabitat preferences), appears to be much less likely.

Accepting the first hypothesis as a basis for further discussion, I now explore how discrete mimicry complexes may evolve in a butterfly community which is divided into two or more guilds under two extreme scenarios: first, in a community in which all species initially possessed different colour patterns (and there was therefore no mimicry); and second, in a community where all species initially possessed the same colour pattern (thus there was initially a single mimicry complex). I will refer to these as the "convergence" and "divergence" scenarios respectively.

Convergence scenario

In a butterfly community where all species possessed different colour patterns, if microsyntopic species converged in colour pattern, but microallotopic species did not, then multiple sympatric mimicry complexes will obviously result. Species within a guild may either converge onto the colour pattern of the dominant model species (*i.e.* the most

abundant and/or unpalatable species) in the microhabitat occupied by the guild (Müllerian and Batesian mimicry), or species with similar abundance and degree of unpalatability which share a microhabitat, may evolve a pattern intermediate between their ancestral patterns (Müllerian mimicry only) (Turner, 1984a).

Geographical divergence of a mimicry complex may occur in at least two ways: if the species composition of a guild changes over its geographical range and convergence is therefore onto a different combination of colour patterns in different areas (e.g., if species in a guild converge onto different model species in different areas); or, if after convergence of species in a guild, a geographic barrier divides the range of the guild, then divergence in colour pattern may occur between parapatric or allopatric 'sub-populations' of the guild (see parapatric divergence hypothesis above).

Divergence scenario

In a community of butterflies in which all guilds shared the same mimetic pattern, if the model species of a guild diverged in colour pattern (see parapatric divergence hypothesis above for a mechanism), this may lead to re-convergence of microsyntopic species, but no selection for convergence between microallotopic species. Thus the mimetic colour pattern of guilds of species may diverge from those of other guilds within a habitat, and the colour pattern of individual guilds may also diverge geographically, if barriers prevent novel colour patterns of model species from spreading throughout their geographical ranges.

The convergence and divergence scenarios discussed above are not mutually exclusive. For example, formation of sympatric mimicry complexes through convergence of microsyntopic species onto different model patterns (the convergence scenario), may be followed by colour pattern divergence of these complexes (the divergence scenario) through time. Alternatively, sympatric complexes may arise as a consequence of divergence of guilds from a single mimetic colour pattern, but species entering the

community after divergence has taken place may converge onto the colour pattern of the complex with which they share a microhabitat.

Microhabitat-dependent selection

If mimicry has evolved within, but not between, guilds of butterflies, this suggests that selection on colour pattern is probably microhabitat-dependent. Two plausible reasons why selection may operate in this way are discussed in turn below.

The first possibility is that communities of visually hunting predators may be spatially structured in a similar way to butterfly communities, thus each guild of butterflies may be subject to selection by a different set of predator species. Birds are the best studied (and probably most important) group of potential butterfly predators. It is well established that forest-dwelling insectivorous bird species in both temperate and tropical regions exhibit both horizontal and vertical spatial segregation in foraging behaviour (Colquhoun & Morley, 1943; MacArthur & MacArthur, 1961; Cody, 1974). Vertical segregation is believed to be "the single most important factor in the segregation of species' feeding activities." (Cody, 1974). The possibility therefore exists that butterfly species and their bird predators may be partitioned by microhabitat in a similar way.

The second possibility is that microhabitat-dependent selection may occur without microhabitat-specific predation. For example, the abiotic environments of different microhabitats may favour different patterns (e.g., selection for thermoregulatory ability may favour melanic colour patterns in dark microhabitats such as the forest understorey, and light colours in sunny microhabitats such as the forest canopy). One hypothesis, first proposed by Poole (1970) and supported by Papageorgis (1974, 1975) and Brown (1988), is that the colour patterns of ithomiine, heliconiine and other mimicry complexes are adapted for concealment against the background light-structure (the pattern of light and shadow) of their microhabitats. This may reduce overall predation on a complex, because some predators may overlook members of a complex entirely, while forgetful predators

may overlook individuals which they otherwise may have sampled. Individuals detected by educated predators, however, are perceived to be aposematic and are avoided. In forest, light-structure changes vertically, so if the colour patterns of guilds of mimetic species which fly at different levels were selected to be eucryptic or disruptive against the background light-structure of the stratum in which they fly, then stratified mimicry complexes would evolve. Background light-structure may also change horizontally within a stratum (according to vegetation type etc.), thus favouring the evolution of different colour patterns in different horizontal microhabitats. Microhabitat-specific predation is not necessary, although if it were present it may facilitate the process of adaptation. For ease of argument I will consider microhabitat-specific predation and microhabitat-dependent selection for crypsis as independent factors. Experiments with artificial dough prey have demonstrated that crypsis and unpalatability can have an additive protective advantage (Papageorgis, 1974, 1975). However, no field experiments have tested whether the colour patterns of butterfly mimicry complexes are cryptic to predators when viewed against their natural backgrounds. To the human observer in the field, some (e.g., the ithomiine CW complex) do appear cryptic, while others seem to be conspicuous.

Models for the evolution of mimicry complexes in sympatry

Conditions

Fig. 3.5 illustrates in schematic form conditions which may enable mimicry complexes to evolve in sympatry. I will treat the convergence and divergence scenarios as separate models and discuss them with reference to Fig. 3.5. For simplicity I only consider vertical microhabitat segregation, but similar arguments could apply to guilds segregated by horizontal microhabitat.

Both models assume a community of four aposematic butterfly species ("a", "b", "c" and "d"). These species are equally unpalatable, their colour patterns are equally memorable to predators, but they are not equally abundant. The species are divided into two microhabitat

guilds: a 'canopy' guild (species "a" and "b") and an 'understorey' guild (species "c" and "d"). In terms of relative abundance, species "a" is the dominant 'model' of the canopy guild, while species "c" is the dominant 'model' of the understorey guild.

In both models, microhabitat-dependent selection is either the result of microhabitat-specific predation, or microhabitat-dependent selection for crypsis. Thus, either each guild is predated largely by a different species of bird (species "x" or "y") and colour pattern has a solely aposematic function, or both guilds are predated by the same bird species and colour pattern has a dual cryptic/aposematic function (thus there is selection for crypsis against the different light-structure backgrounds of the vertical microhabitats in which the guilds fly).

Convergence model

In this model the four butterfly species ("a" through "d") initially each possess different colour patterns (and there is therefore no mimicry). Two sympatric mimicry complexes (a canopy and an understorey complex) could evolve under microhabitat-dependent selection as follows.

Under microhabitat-specific predation: butterfly species "b" may converge onto the pattern of model species "a" under selection from bird "x"; while species "d" may converge onto the pattern of model species "c" under selection from bird "y".

Under microhabitat-dependent selection for crypsis, selection by a single bird species on the four butterfly species, may result in: selection for species "b" and "a" to evolve similar cryptic patterns for concealment against the light-structure background of the canopy, as well as selection for mimetic convergence of "b" onto "a"; and, selection for species "d" and "c" to evolve similar cryptic patterns for concealment against the light-structure background of their understorey microhabitat, as well as selection for mimetic convergence of species "d" onto "c".

Divergence model

In this model the four butterfly species initially possess the same colour pattern (thus there is only a single mimicry complex). Two sympatric mimicry complexes (a canopy and an understorey complex) could evolve under microhabitat-dependent selection as follows.

Under microhabitat-specific predation: if model species "a" diverges in colour pattern, selection by bird "x" may lead to convergence of species "b" onto this new pattern; and/or, if model species "c" diverges in pattern, selection by bird "y" may result in species "d" converging onto this pattern.

Under microhabitat-dependent selection for crypsis, selection by a single bird species on the four butterfly species, may result in: model species "a" evolving a pattern adapted for concealment in the canopy microhabitat, and convergence of species "b" onto this pattern; and/or model species "c" evolving a pattern adapted for concealment in the understorey microhabitat, and convergence of species "d" onto this pattern.

Remarks on the convergence and divergence models

A computer simulation of the convergence model with microhabitat-specific predation (G. W. Beccaloni, unpublished) demonstrates that convergence will occur between microsyntopic species and not between microallotopic species (as hypothesised above), even if there is some overlap in the spatial distributions of different guilds. For example, Fig. 3.5 shows the hypothetical distributions of four species which overlap each other, but in which overlap is greatest between "a" and "b" and between "c" and "d". Both members of the canopy guild ("a" and "b") enter the foraging range of bird species "y", and similarly, both members of the understorey guild ("c" and "d") enter the foraging range of bird species "x". However, if predation by birds "x" and "y" is frequency-dependent against rarity, then within the foraging range of bird species "x", butterfly species "a" will have the highest fitness of the four butterfly species which occur in this region of space. If

individuals of species "b" moved randomly between the canopy and understorey microhabitats, but spent the greater part of their time in the former environment (as indicated by the frequency distribution of species "b" in Fig. 3.5), then a novel mutation which arose in the population of "b" which gave individuals a resemblance to "a", will have higher fitness than the wild-type "b" pattern and will be favoured. However, if mutations arose which gave individuals of "b" a resemblance to either species "c" or "d", then these phenotypes will have lower fitness than the "b" wild-type pattern and will be at a selective disadvantage. A similar argument to the above can explain why species "d" is only likely to converge onto the pattern of species "c". Computer tests of this model show that once mimicry complexes have evolved they will not converge, provided that each is the most frequent pattern in the foraging range of a different predator species.

The conditions necessary for the evolution and non-convergence of mimicry complexes in the convergence model with microhabitat-specific predation, are probably very similar to those required by the divergence model with microhabitat-specific predation. However, the convergence and divergence models with microhabitat-dependent selection for crypsis are more complex, and computer models are needed to assess their plausibility and explore the conditions necessary for the evolution and non-convergence of mimicry complexes in sympatry.

Possible evidence for the evolution of mimicry complexes in sympatry

Do sympatric mimicry complexes each dominate a different microhabitat?

Under the convergence and divergence models with microhabitat-specific predation, microallotopic mimicry complexes are only likely to co-exist without converging given two conditions: first that complexes are selected by different predators; and second, that each complex represents the most abundant pattern in the microhabitat occupied by the species which belong to the complex. Although the first condition is possibly not required by the

convergence and divergence models with microhabitat-dependent selection for crypsis, the second may be.

J. Smiley & L. E. Gilbert (unpublished) have demonstrated that each of the three heliconiine mimicry complexes they studied numerically dominated a different horizontal microhabitat, but this possibility has not been quantitatively investigated in the case of ithomiine mimicry complexes. There is evidence, however, that at Jatun Sacha, different ithomiine mimicry complexes are numerically dominant at different heights in primary forest (Fig. 3.6): the SDT complex is the relatively most abundant complex at or below 0.7 m; the SYT complex is the relatively most abundant pattern from 0.71 m to 1.10 m; and the T complex is the relatively most abundant pattern above this height. Personal observations suggest that the Jatun Sacha ithomiine mimicry complexes are probably further segregated by horizontal microhabitat e.g., in secondary forest, the CW complex appeared to be the relatively most abundant of the low flying complexes and the LYT complex seemed to be the relatively most abundant of the high flying complexes. It is not known whether foraging ranges of predators correspond to the horizontal or vertical microhabitats discussed above.

Host-plant utilisation patterns and guild structure

Increasing species richness of communities of ecologically closely related butterfly species leads to greater niche segregation of the species in a community (Gilbert, 1984). The primary niche dimension partitioned between species is thought to be microhabitat (perhaps as a result of indirect competition mediated by microhabitat specific polyphagous parasitoids or predators (see Lawton, 1986)), with host-plants used differentially only as an indirect result of habitat choice (Gilbert & Smiley, 1978; Courtney, 1984). Thus theory predicts that increasing species richness of butterfly communities leads to increasing microhabitat segregation of species, which in turn results in greater host-plant specialisation of the species in a community.

Benson's (1978) study on host-plant partitioning in heliconiine butterflies supports this hypothesis. Benson found that heliconiine species exhibited a higher degree of host-plant specialisation in two communities with high species richness (in Costa Rica and Trinidad), than in a third, less species-rich community (in south-east Brazil). Heliconiine species in the two communities with high species richness utilised fewer species of host-plants on average than did species in the community with lower species richness and, as expected, the (horizontal) microhabitat restriction of species was found to be greater in the two communities with higher species richness (*i.e.* the species in these communities were more finely partitioned spatially). Species in the low species richness community overlapped little in (horizontal) microhabitat preferences, thus heliconiine species in this community partitioned host-plants largely by microhabitat. Microhabitat overlap was much greater, however, between heliconiine species in the two communities with higher species richness and species which shared a microhabitat partitioned host-plants between them by plant species, plant part or growth condition. Benson observed that whereas mimicry did not occur between the *Heliconius* species in the low species richness community, it did between *Heliconius* species in the two communities with high species richness, and that co-mimicking species in these communities shared microhabitats.

Benson's (1978) study demonstrates that increasing species richness of heliconiine communities leads, first, to increasing microhabitat restriction of species, and second, to more species sharing a particular microhabitat. Consequently, there should be a greater number of guilds of microsyntopic species, and hence mimicry complexes, in communities with high species richness, than in communities with lower species richness.

Ithomiine community structure

Table 3.7 brings together all available data for sites with more than 2 months' sample time, to test the hypothesis that ithomiine species, like heliconiines, exhibit an increasing degree of host-plant specialisation with increasing community species richness. The data appear to be consistent with this idea; for example, the observed proportion of monophagous

ithomiine species in the five communities listed in Table 3.7 is: 20% at Sumaré, with 23 ithomiine species; 13% at Campinas, with 25 ithomiine species; 28% at Monteverde, with 40 ithomiine species; 82% at Limoncocha, with 52 ithomiine species; and 87% at Jatun Sacha, with 56 ithomiine species. The observed proportion of monophagous ithomiine species and the total number of ithomiine species recorded at a site are significantly correlated ($R^2 = 0.89$, $P < 0.01$).

Also notice the concomitant decrease in the degree of overlap in the utilisation of host-plant species, indicated by the increase in the proportion of host-plant species observed to be utilised by a single ithomiine species only. The proportion of host-plant species observed to be utilised by a single ithomiine species and the number of ithomiine species recorded at a site are significantly correlated ($R^2 = 0.94$, $P = 0.001$). Unfortunately, sampling effort (number of months of observation) is not equal for the sites. Since increasing intensity and duration of study may reveal rare use of occasional host-plants by particular butterfly species, one would expect that the lower the sampling effort, the greater the observed degree of monophagy. The possibility therefore exists that the data in Table 3.7 are artefactually consistent with the hypothesis that more species-rich ithomiine communities exhibit a greater degree of host-plant specialisation. The observed proportion of monophagous ithomiine species and $\log_{10}$ % sample time (months) are not significantly correlated ($R^2 = 0.60$, NS), while $\log_{10}$ % monophagous ithomiine species observed and $\log_{10}$ % sample time (months) are significantly correlated ($R^2 = 0.71$, $P < 0.05$). A multiple regression of % monophagous ithomiine species observed (Y) versus $\log_{10}$ % sample time (months) (X_1) and number of ithomiine species recorded at a site (X_2), has a lower level of significance ($R^2 = 0.81$, $P < 0.025$), than the simple regression of % monophagous ithomiine species observed and number of ithomiine species recorded at a site ($R^2 = 0.89$, $P < 0.01$). Thus the total number of ithomiine species in a community appears to affect the observed proportion of monophagous ithomiine species at a site more than sampling time, and I therefore cautiously conclude that the observed increase in the degree of monophagy with increasing species richness of ithomiine communities is probably a real trend.

However, more studies of the host-plant utilisation patterns of ithomiine communities (using equal sampling effort) are clearly desirable.

An increasing degree of host-plant specialisation of ithomiine species with increasing community species richness, if real, is probably a direct result of increasing microhabitat fidelity (probably largely horizontal) of the species in these communities. For discussion of how parasitism of early-stages and other factors may lead to microhabitat partitioning and host-plant specialisation in ithomiines see Haber (1978), Gilbert (1984), and Vasconcellos-Neto (1986, 1991).

Increasing species richness of communities, coupled with increasing microhabitat fidelity of species, should result in an increasing number of microhabitat guilds, and hence an increasing number of mimicry complexes. Table 3.7 demonstrates that the number of mimicry complexes does indeed increase with increasing species richness of the communities documented (a pattern that is extremely unlikely to be an artefact of sampling effort). This relationship is significant ($R^2 = 0.91$, $P < 0.01$).

The positive correlation between the species richness of ithomiine communities and the number of mimicry complexes represented in these communities appears to hold throughout the Neotropics (pers. obs.). Ithomiine communities at the northern (central Mexico) and southern (southern Brazil, Uruguay, and northern Argentina) limits of the Neotropical forests have low species richness and in those with the lowest species richness only the CW complex is represented (those with slightly more species include representatives of both the CW and T complexes) (see maps in Brown, 1979; pers. obs.). Ithomiine species richness and the number of sympatric mimicry complexes both increase towards the equator and reach a maximum at altitudes of *c.* 500 m in the upper Amazon basin of Ecuador, Peru and Brazil. Jatun Sacha in eastern Ecuador, for example, is one of the richest of all Neotropical sites in terms of both ithomiine species richness and the number of sympatric ithomiine mimicry complexes (Table 3.7). The correlation between the species richness of ithomiine communities and the number of mimicry complexes also

appears to hold for Caribbean islands e.g., Tobago with only three ithomiine species has a single mimicry complex (the CW complex), while Trinidad with sixteen ithomiine species has two mimicry complexes (the CW and T complexes) (Barcant, 1970).

Species richness of ithomiine communities and the number of mimicry complexes both also decline with increasing elevation throughout the Neotropics (few if any ithomiine species are found above *c.* 3000 m), and typically only one complex (the CW complex) is found at high elevation sites with low species richness. Within Costa Rica, for example, the species richness of ithomiine communities peaks at mid-elevation sites between *c.* 1100 m and 1400 m, and decreases both below and above this altitudinal belt, to about two thirds of the maximum in the lowlands, and to zero species above *c.* 3000 m (Haber, 1978; DeVries, 1987; also see Fig. 3.2 in Gilbert, 1984, modified from Haber, 1978). The number of mimicry complexes, however, remains positively correlated with the species richness of these communities. Thus all five Costa Rican mimicry complexes are usually represented in high species richness communities between about 600-1300 m, e.g., at San Vito, Puntarenas Prov., 1100 - 1200 m, with 42 ithomiine species (Haber, 1978, supplemented by DeVries, 1983). Below 600 m the GT complex is absent, e.g., at La Selva, Heredia Prov., 50 m, with 26 ithomiine species (Haber, 1978, supplemented by DeVries, 1983). With increasing elevation above 1300 m, community species richness and the number of sympatric complexes both progressively decline, until only the CW complex is represented in communities with *c.* 4 or fewer species between *c.* 2600 m and 3000 m (DeVries, 1987).

Studies of how changes in the species richness of ithomiine communities with latitude and altitude relate to the numbers and types of mimicry complexes present in these communities, may provide insights into how changes in species richness affect the spatial structuring of ithomiine communities. For example, ithomiine communities with the lowest species richness, both at high latitudes and high elevations, typically only include representatives of the low flying CW complex (Haber, 1978; pers. obs.). As the species richness of ithomiine communities increases with decreasing latitude, the second complex

to be represented always seems to be a high flying complex (usually the T complex) (pers. obs.). Similarly, as the species richness of ithomiine communities increases with decreasing elevation, the second complex to be represented also always seems to be a high flying complex (usually the GT complex) (pers. obs.). As the species richness of ithomiine communities increases further with decreasing latitude or decreasing elevation, both high and low flying complexes are progressively added, until an observed maximum of four high and four low flying sympatric mimicry complexes is reached in communities where ithomiine species richness is highest (the upper Amazon basin). These observations suggest that as the species richness of ithomiine communities increases, ithomiine species first partition microhabitat vertically into two flight strata, and I predict that as the species richness of communities increases further, species probably increasingly segregate by horizontal microhabitat within each stratum.

It is interesting that there are two sympatric mimicry complexes which are confined to the upper Amazon basin - the region of the Neotropics where the species richness of ithomiine communities is highest. One of these is a high flying complex (the OBT complex), while the other is a low flying complex (the OT complex). The other high flying (T, YBT and LYT) and low flying (SDT, CW and SYT) complexes found in this region, also occur in other regions where the species richness of ithomiine communities is lower. Thus the higher species richness of ithomiine communities in the upper Amazon basin (in comparison with other regions of the Neotropics), may have resulted in greater horizontal microhabitat fidelity of species in this region and hence more microhabitat guilds (and therefore mimicry complexes), sub-dividing each horizontal stratum.

The number of mimicry complexes in a region should reflect the maximum degree to which local communities in a region are spatially structured and hence the maximum species richness reached by communities within a region. Thus mimicry complex diversity is a product of local, rather than regional, species richness. For example, there are 61 ithomiine species and 5 mimicry complexes in Costa Rica as a whole, while the Jatun Sacha site in eastern Ecuador has fewer species (56) and yet more mimicry complexes (8). The plausible

reason is that the richest ithomiine communities in Costa Rica have many fewer species than the richest communities in eastern Ecuador. San Vito (see above) with 42 ithomiine species has the highest documented species richness of any ithomiine community in Costa Rica, and all 5 complexes are found in this community.

Phylogenetic relatedness, mimicry and flight height

As hypothesised earlier, ithomiine species are probably more likely to make host-plant switches between plants which belong to the same height class, than between hosts which belong to different height classes. Thus the more closely related ithomiine taxa are phylogenetically, the greater the probability that they utilise hosts of similar growth heights (even if these hosts are not closely related). Taxa which utilise hosts of similar heights should belong to mimicry complexes which fly in the same height stratum and I therefore predict that the more closely ithomiine taxa are related phylogenetically, the greater is the probability that they belong to complexes which fly at similar heights.

Comparisons between ithomiine taxa at different taxonomic levels appear to support this prediction. Mimetic morphs of polymorphic ithomiine species appear to always belong to complexes that fly at similar heights (pers. obs). Likewise (with a few rare possible exceptions e.g., *Godyris zavaleta* (Hewitson) - see below) all sub-species/different mimetic races of an ithomiine species seem to belong to complexes that fly at similar heights (Brown, 1979; D'Abrera, 1984; pers. obs.). For example, twelve ithomiine species are shared between Costa Rica as a whole and the Jatun Sacha site in Ecuador (each species is represented by a different sub-species in each of these areas). The sub-species of six of these ithomiine species belong to the high flying T complex in both areas; the sub-species of two species belong to the low flying CW in both areas; and the sub-species of one species belong to the low flying BY/SYT complex in both areas. Of the three remaining species, the sub-species of one (*Thyridia psidii* (L.)) belong to the high flying BR complex in Costa Rica and to the high flying LYT complex at Jatun Sacha, the sub-species of another (*Hypoleria lavinia* (Hewitson)) belong to the low flying CW complex in Costa

Rica and to the low flying OT complex at Jatun Sacha, while the sub-species of the third (*Godyris zavaleta*) belong to the high flying BR complex in Costa Rica and to the low flying SYT complex at Jatun Sacha.

The majority of the 52 ithomiine genera contain species which belong exclusively to either high - or to low - flying complexes. Those which contain species which belong to both high and low flying mimicry complexes include: *Godyris*, *Hyalyris*, *Hypoleria*, *Hyposcada*, *Ithomia*, *Napeogenes*, *Pteronymia*, and *Scada* (see Brown, 1988, for details of the mimicry complexes and flight heights of species in these genera). Seven of the ten ithomiine tribes contain species which belong to both high and low flying complexes. The three tribes which contain species which all belong to complexes which are thought to fly at similar heights are the Melinaeini, the Methonini, and the Tithoreini (all taxa in these tribes belong to high flying complexes).

Although closely related ithomiine taxa seem to usually belong to complexes which fly at similar heights they often belong to different complexes, which if sympatric, are presumably segregated by horizontal microhabitat. Thus vertical microhabitat preference may possibly be more highly conserved than horizontal microhabitat preference over evolutionary time.

Polymorphism and dual sex-limited mimicry in Müllerian mimics

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. It is well known, however, that several species of Müllerian mimic are polymorphic over most or all of their geographic ranges e.g., the ithomiine *Mechanitis mazaeus* and the heliconiine *Heliconius numata*, both of which have

two or more sympatric mimetic morphs which participate in various ithomiine-dominated mimicry complexes (Brown & Benson, 1974).

Hypotheses to account for the apparently anomalous phenomenon of polymorphism in Müllerian mimics were reviewed by Sheppard *et al.* (1985). These authors believed that the most plausible hypothesis (originally proposed by Papageorgis, 1974) is that Müllerian polymorphisms are maintained by spatial heterogeneity in selection for the different mimetic morphs. They described the scenario they envisaged as follows: "If two warningly coloured species (or mimicry rings) with different patterns have such ecological requirements that they tend not to fly together, then a third species with less restricted requirements that flies with both would be subject to selection for possession of one pattern in one type of locality and the second pattern in the other locality. In the absence of migration the species would be monomorphic for the two forms in different places, but if it migrated to some extent between the two habitats it could be polymorphic."

Given that mimicry complexes are segregated by microhabitat, this hypothesis seems plausible. It predicts that polymorphic Müllerian mimics must be microhabitat generalists, which range across two or more microhabitats each dominated by a different aposematic species or mimicry complex. In such species, mimetic morphs would probably only be maintained if they exhibited a preference for the microhabitat in which the complex they mimicked was the numerically dominant or otherwise best protected pattern (*i.e.* if the genes coding for the mimetic colour pattern were linked with appropriate behaviour modifier genes for microhabitat preference). Polymorphism would result if there was some movement (and interbreeding) of morphs between microhabitats. Preliminary tests of a computer simulation model of this scenario (G. W. Beccaloni, unpublished), indicate that a polymorphism in a Müllerian mimic can be maintained given these conditions.

At present, there is insufficient ecological data available for any species of polymorphic Müllerian mimic to evaluate this hypothesis. However, fragmentary qualitative observations of a few unpalatable polymorphic mimetic butterfly species suggest that, as

predicted, they are microhabitat generalists and that different mimetic morphs exhibit different microhabitat preferences. It is not known whether the microhabitat preferences of the morphs of these species correspond to those of the mimicry complexes in which they participate, but this seems likely. *H. numata*, for example, is known to be a microhabitat generalist (Benson, 1978). Brown & Benson (1974) observed that the sympatric 'silvana' and 'superioris' morphs of this species exhibit different behaviour, and A. Neild (pers. comm.) observed that in Venezuela these morphs appear to exhibit different microhabitat preferences, with 'silvana' preferring relatively undisturbed forest, and 'superioris' preferring more disturbed vegetation types. Another polymorphic butterfly species where the mimetic morphs are known to exhibit different microhabitat preferences is the African *Hypolimnas anthedon* (Doubleday) (Nymphalidae: Nymphalinae). In South Africa this species has two sympatric morphs, 'mima' and 'wahlbergi', and these participate in different danaine mimicry complexes. The morph 'mima' occurs mainly in forest, while 'wahlbergi' is found largely in open areas (Leigh, 1906; Poulton, 1915). The flight pattern and resting behaviour of these morphs are also different, and correspond to the behavioural patterns exhibited by their different models (*ibid.*). It is not known whether *H. anthedon* is unpalatable, but the related species *Hypolimnas bolina* (L.) has been shown to have the capacity to store cardioactive substances (Marsh *et al.*, 1977; Clarke *et al.*, 1989).

Under this hypothesis, selection should act to increase the microhabitat fidelity of mimetic morphs and this in turn may result in reduced interbreeding between morphs. It is conceivable that this process, perhaps coupled with selection for microhabitat specific adaptations (other than colour pattern), could ultimately lead to sympatric morphs evolving into distinct species (for discussion of speciation of sympatric microhabitat races see Diehl & Bush, 1989; Tauber & Tauber, 1989; Bush, 1994).

Dual sex-limited mimicry

Classical theory predicts that Müllerian mimics should be monomorphic, so the existence of unpalatable species which exhibit dual sex-limited mimicry (e.g., the ithomiine

Pteronymia notilla notilla) is therefore puzzling. It would be possible, however, for dual sex-limited mimicry to evolve (and be maintained) in 'protected' species, if the males and females exhibited different microhabitat preferences and associated with different (microallotopic) mimicry complexes for the majority of their adult lives (a hypothesis originally proposed by Evans, 1968, 1969). For example, if the males and females of an unpalatable non-mimetic monomorphic species occupied different microhabitats, each dominated by a different mimicry complex (or guild of aposematic species), then divergence of the male and female colour patterns could occur via either the convergence or the divergence scenarios discussed above. The conditions required by this hypothesis seem reasonable, given the evidence that mimicry complexes are segregated by microhabitat, and the fact that the males and females of some non-mimetic butterfly species are known to exhibit different microhabitat preferences. For example, the males of some butterfly species congregate at prominent landmarks (e.g., hill tops), located in habitats different to that of the larval host-plants, and females briefly visit these leks to mate, before flying to the microhabitats where their host-plants are found (Shields, 1967; Scott, 1974, 1975; Rutowski, 1984).

In possibly all cases where the ecology of dual sex-limited mimics has been studied, the males and females have been found to occupy different microhabitats and to associate with different microallotopic mimicry complexes (as predicted by this hypothesis). For example, Brown & Benson (1975) found that female *Heliconius demeter bouqueti* Nöldner fly in the understorey and mimic *Heliconius erato erato* which flies in this microhabitat, while male *H. d. bouqueti* fly in the forest canopy and mimic *Heliconius egeria* (Cramer), a species which is largely restricted to this stratum. Other examples of dual sex-limited mimics where the sexes are known to associate with different microallotopic mimicry complexes include: *Heliconius nattereri* Felder (Brown, 1972), *Eresia phillyra* Hewitson (Nymphalidae: Nymphalinae) (Ross, 1976; Llorente & Garcés, 1983), and *Eresia coela* Druce (DeVries, 1987). It is not known for certain whether the above mentioned species are Müllerian or Batesian mimics, however, it is likely that all species of *Heliconius* are

unpalatable (see Gilbert, 1991), and Srygley (1994) suggests that *Eresia* are probably unpalatable.

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Figure 3.1. Ithomiine species reared at Jatun Sacha Biological Station, Ecuador, (Table 3.1) grouped by mimicry complex. Tiger (T) complex: 1, *Hyposcada a. ecuadorina* Bryk, ♂; 2, *Mechanitis l. elisa* (Guérin), ♂; 3, *Mechanitis p. dorissides* Staudinger, ♀; 4, *Hypothyris e. intermedia* (Butler), ♀; 5, *Ceratinia t. poecila* (Bates), ♂. Small dark transparent (SDT) complex: 6, *Hyposcada i. ida* Haensch, ♀; 7, *Hyposcada k. kena* (Hewitson), ♀; 8, *Oleria a. agarista* (Felder & Felder), ♀. Orange-tip (OT) complex: 9, *Napeogenes s. caucayaensis* Fox & Real, ♀. Clearwing (CW) complex: 10, *Ithomia a. agnosia* Hewitson, ♂. Large yellow transparent (LYT) complex: 11, *Methona c. psamathe* Godman & Salvin, ♂; 12, *Thyridia p. ino* Felder & Felder, ♂; 13, *Dircenna l. loreta* Haensch, ♀. Small yellow transparent (SYT) complex: 14, *Godyris z. matronalis* (Weymer), ♀; 15, *Ithomia s. derasa* Hewitson, ♀; 16, *Ithomia s. salapia* Hewitson, ♀.

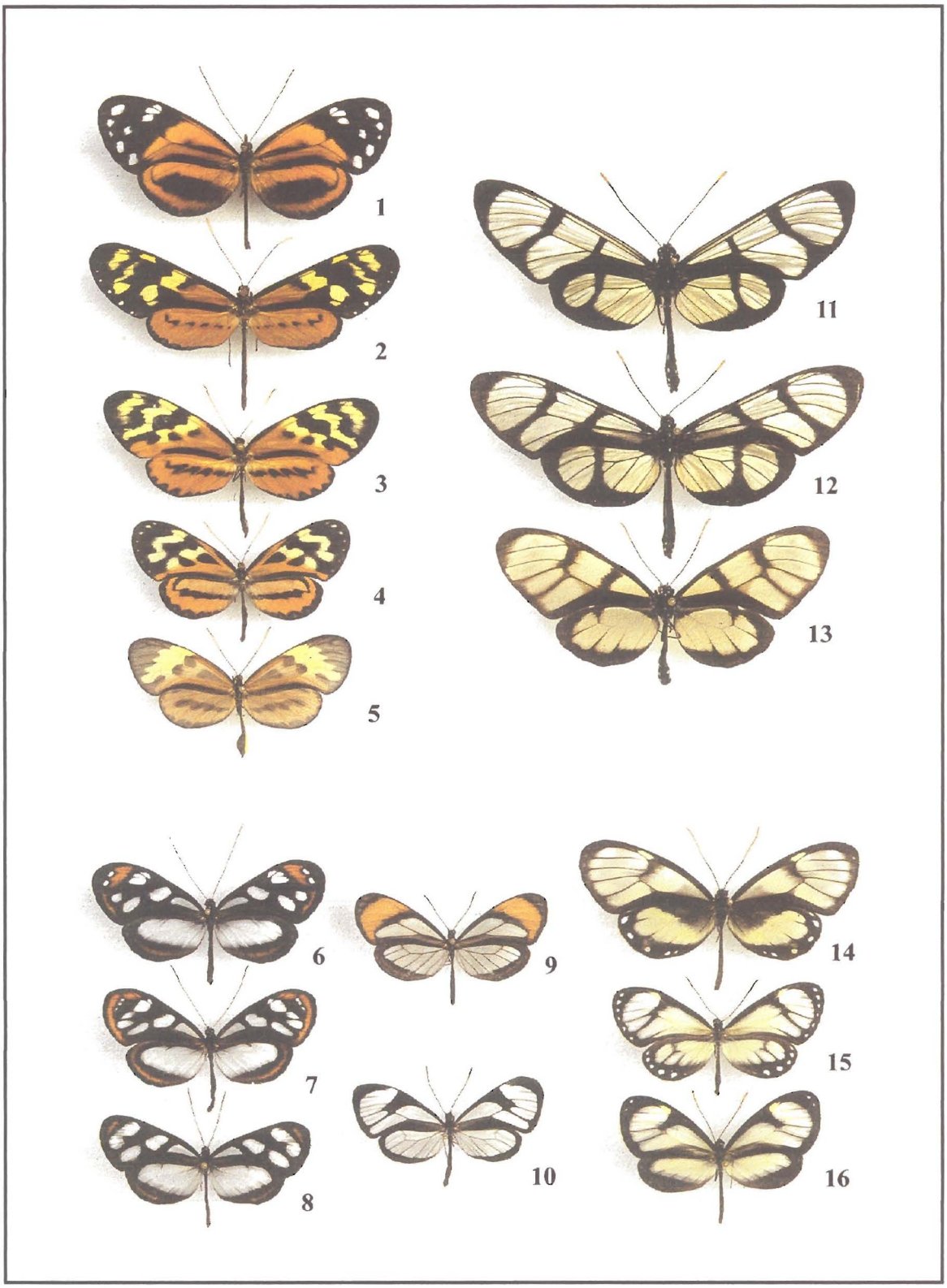

FIGURE 3.1

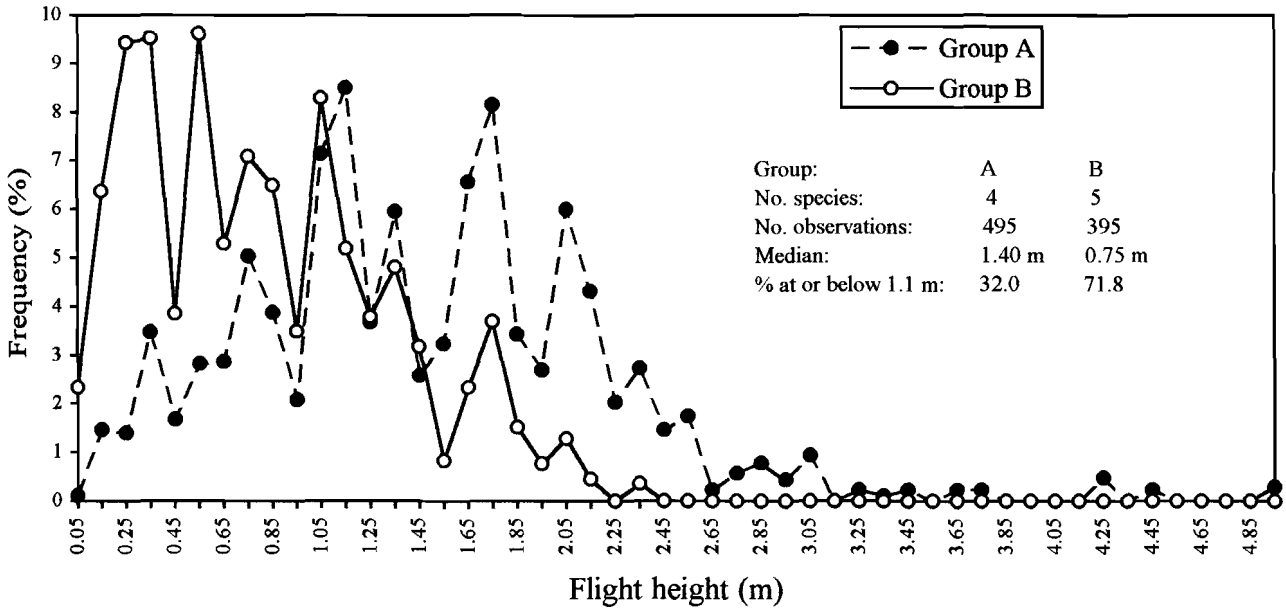

Figure 3.2. Aggregated flight height distributions of reared ithomiine species from Jatun Sacha with > 20 flight height observations, belonging to groups A (host-plants > 1.5 m tall/early stages above 1.1 m) and B (host-plants ≤ 1.5 m tall/early stages at or below 1.1 m). Flight height distributions of the species belonging to a group were equally weighted before they were combined, so that the group distributions were not biased by numerically dominant species.

Figure 3.3. Flight height distributions of the ithomiine mimicry complexes found at Jatun Sacha. Flight height distributions of species sharing a mimetic colour pattern recorded during the MRR study (Appendix 3.1) were combined.

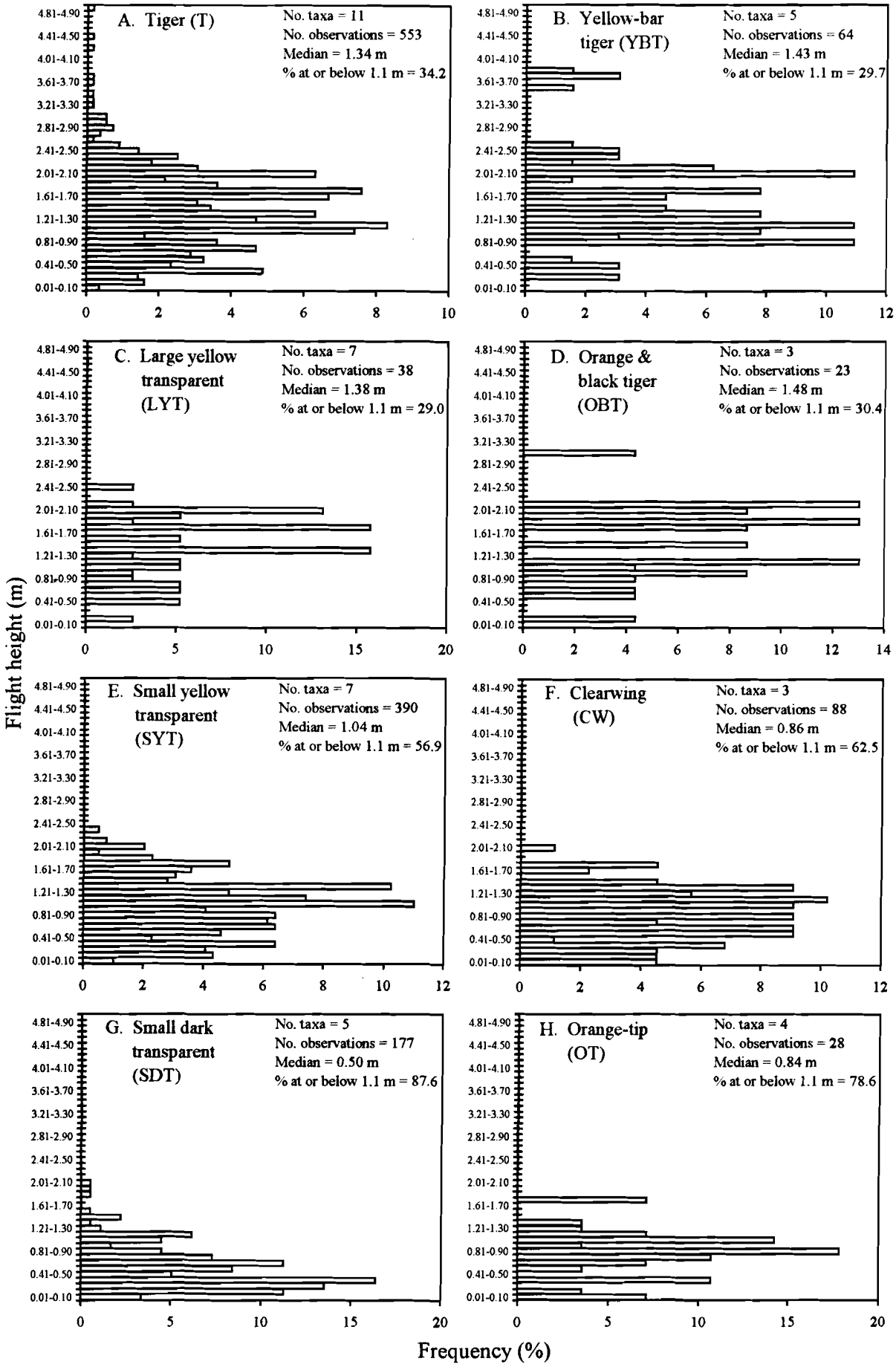
A. Tiger (T)
No. taxa = 11
No. observations = 553
Median = 1.34 m
% at or below 1.1 m = 34.2
B. Yellow-bar tiger (YBT)
No. taxa = 5
No. observations = 64
Median = 1.43 m
% at or below 1.1 m = 29.7
C. Large yellow transparent (LYT)
No. taxa = 7
No. observations = 38
Median = 1.38 m
% at or below 1.1 m = 29.0
D. Orange & black tiger (OBT)
No. taxa = 3
No. observations = 23
Median = 1.48 m
% at or below 1.1 m = 30.4
E. Small yellow transparent (SYT)
No. taxa = 7
No. observations = 390
Median = 1.04 m
% at or below 1.1 m = 56.9
F. Clearwing (CW)
No. taxa = 3
No. observations = 88
Median = 0.86 m
% at or below 1.1 m = 62.5
G. Small dark transparent (SDT)
No. taxa = 5
No. observations = 177
Median = 0.50 m
% at or below 1.1 m = 87.6
H. Orange-tip (OT)
No. taxa = 4
No. observations = 28
Median = 0.84 m
% at or below 1.1 m = 78.6
Flight height (m)
Frequency (%)

FIGURE 3.3

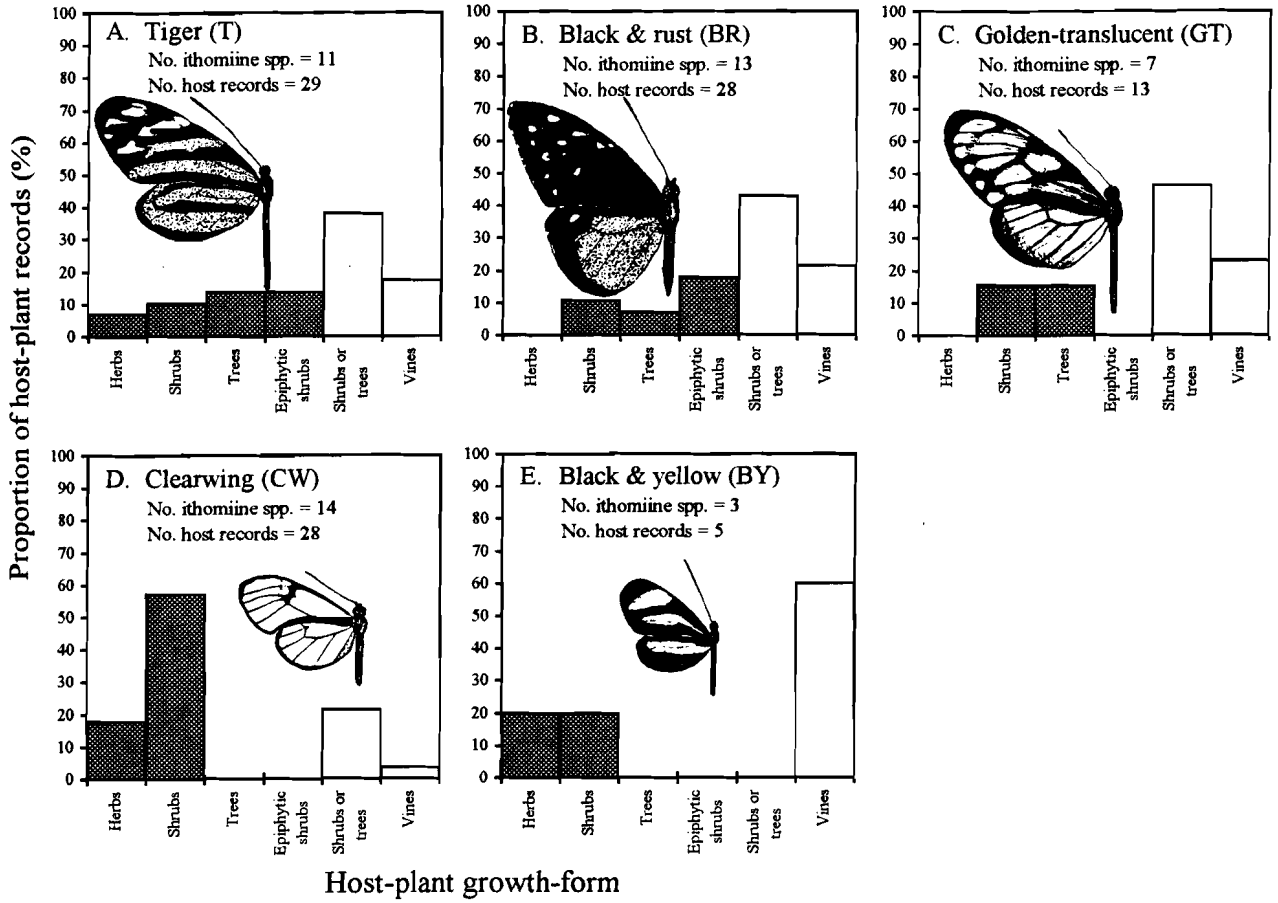

Figure 3.4. Growth-form/height class distributions of host-plants recorded for Costa Rican ithomiine species. Hosts of ithomiine species which share a mimetic colour pattern were combined (see text). Shaded columns are growth-form categories containing plant species of known maximum mature growth height; unshaded columns are categories containing plant species of uncertain mature height (these were excluded from subsequent analyses). A typical representative of each complex is illustrated (all drawn to the same scale) and these are as follows: *Melinaea lilis imitata* Bates, ♀ (A. Tiger); *Tithorea tarricina pinthias* Godman & Salvin, ♂ (B. Black & rust); *Eutresis hypereia theope* Godman & Salvin, ♀ (C. Golden-translucent); *Pteronymia artena artena* (Hewitson), ♂ (D. Clearwing); *Aeria eurimedea agna* Godman & Salvin, ♂ (E. Black & yellow).

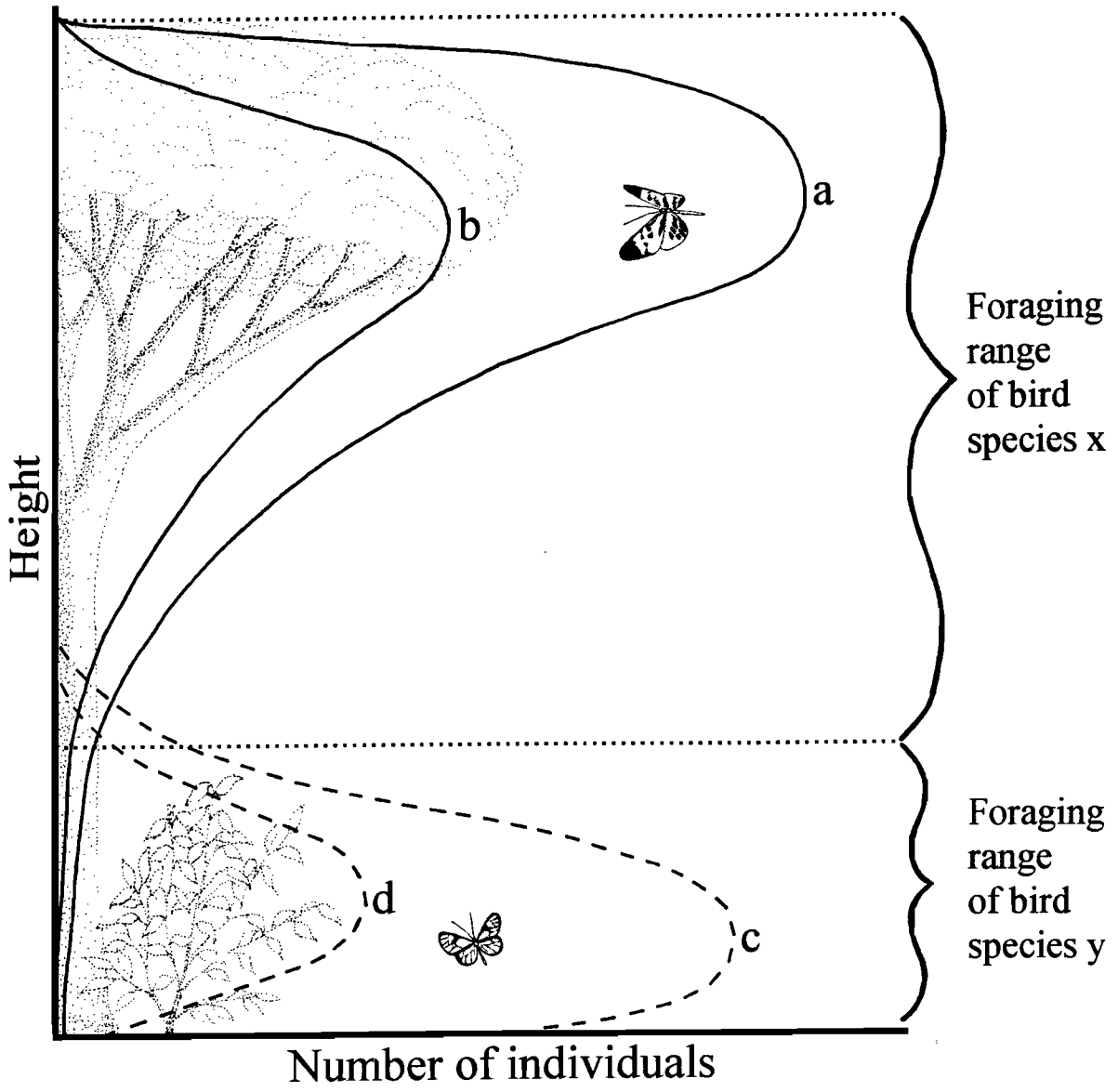

Figure 3.5. Schematic representation of conditions for the evolution of mimicry complexes in sympatry (see text). Flight height frequency distributions of four hypothetical species of butterfly ("a", "b", "c" and "d") are shown in relation to the foraging ranges of two species of insectivorous bird ("x" and "y") and to the vertical structure of forest vegetation.

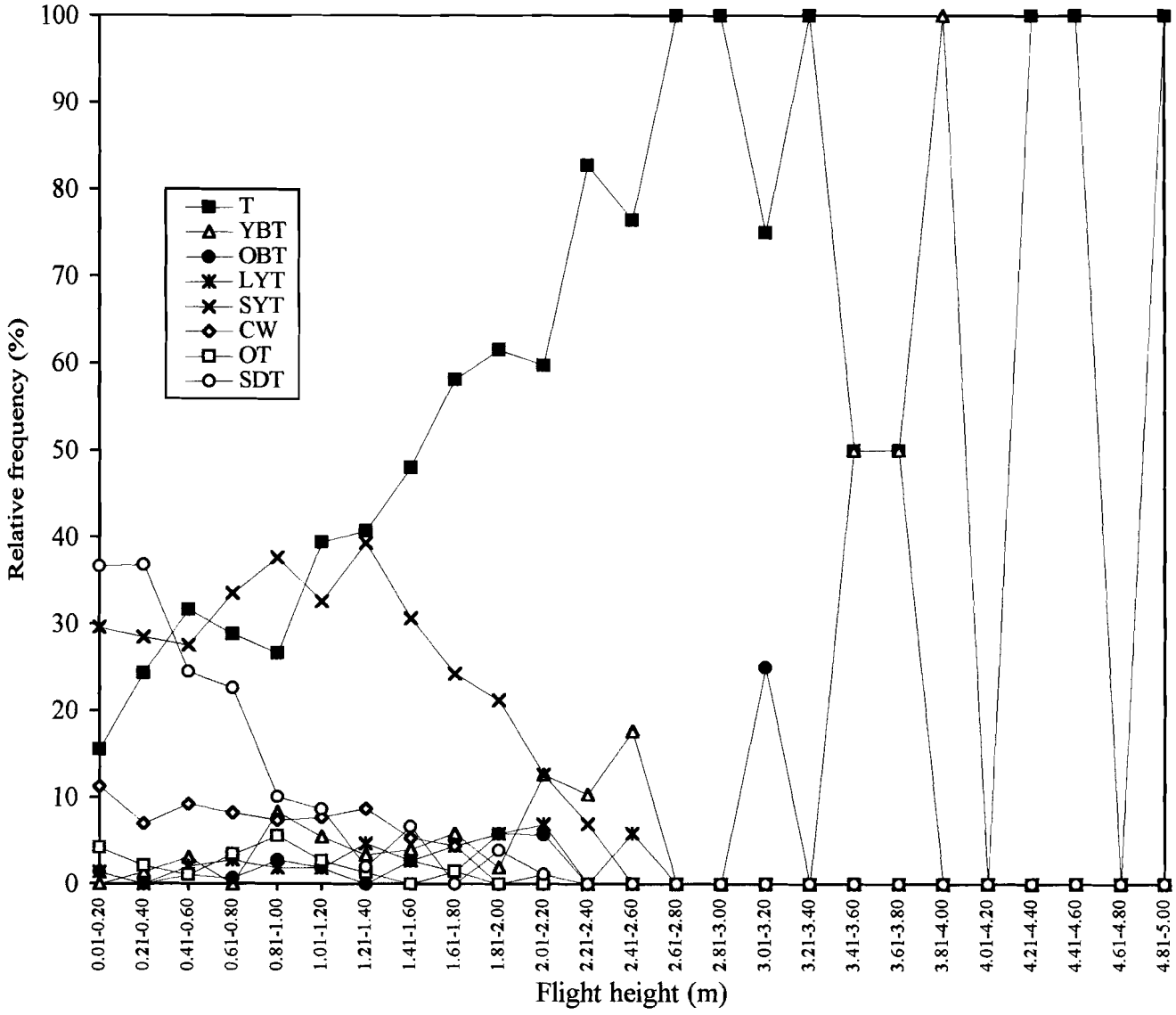

Figure 3.6. Relative vertical frequency distributions of the eight ithomiine mimicry complexes found at Jatun Sacha. Flight height frequency distributions of the eight complexes (see Fig. 3.3) were combined and the relative frequencies of the complexes in each height interval were calculated. Height intervals of 0.2 m were used for clarity.

TABLE 3.1. Host-plant records of Jatun Sacha ithomiine species, grouped according to host-plant height/height of early stages, and mimicry complex of adult.

(Explanations of the codes of the mimicry complexes are given in the footnote to Appendix 3.1. e, female observed ovipositing and/or eggs found; l, larvae found; ma, mature; s, sapling; se, seedling)

Ithomiine species	Mimicry complex	Type of observation	Number of records	Height of early stages on host-plant (m)[a]	Host-plant species (all are Solanaceae unless stated otherwise)	Growth-form of host-plant	Growth stage of host-plant	Height of host-plant (m)[a]
Group A: host-plants > 1.5 m tall/early stages above 1.1 m								
Mechanitis l. elisa	T	l	1	1.5	*Cyphomandra pilosa* Bohs	tree	s	2.5
Mechanitis p. dorissides	T	e	3	2.5	*Solanum* (*Brevantherum*) *rugosum* Dunal	tree	ma	6.0
		e	1	1.0	*Solanum* (*Lasiocarpa*) *quitöense* Lam.[b]	shrub	ma	1.5
Hypothyris e. intermedia	T	e	3	2.5	*Solanum* (*Brevantherum*) *rugosum* Dunal	tree	ma	6.0
Ceratinia t. poecila	T	e	1	3.0	*Solanum* (*Geminata*) *nudum* Dunal	tree	ma	6.0
		e	1	1.5			s	2.0
		l	6	1.5			s	2.0
Hyposcada a. ecuadorina	T	e[c]	1	4.0	*Drymonia oxysepala* Leeuwenberg (Gesneriaceae)	vine	ma	5.0
		l	1	3.0			ma?	4.0
Methona c. psamathe	LYT	e	> 10	1.5-2.0	*Brunfelsia grandiflora* D.Don	shrub	ma	3.6
		l	> 10	1.5-2.0			ma	3.6
Thyridia p. ino	LYT	l	1	3.0	*Cyphomandra pilosa* Bohs	tree	ma?	4.0
Dircenna l. loreta	LYT	e	4	2.5	*Solanum* (*Brevantherum*) *rugosum* Dunal	tree	ma	6.0
		l	2	2.5			ma	6.0
Group B: host-plants ≤ 1.5 m tall/early stages at or below 1.1 m								
Godyris z. matronalis	SYT	l	1	1.0	*Cestrum* sp.	shrub	ma?	1.5
Ithomia s. salapia	SYT	e	> 5	0.15-0.70	*Witheringia solanacea* L'Herit	herb	all stages	0.10-1.0
		e & l	> 10	0.10-0.70			all stages	0.10-1.0
Ithomia s. derasa	SYT (variant)	e	> 5	0.20-0.60	*Witheringia solanacea* L'Herit	herb	all stages	0.10-1.0
		e & l	> 10	0.10-0.70			all stages	0.10-1.0
Ithomia a. agnosia	CW	e	2	0.20	*Physalis* nr *peruviana* L.	herb	ma	0.30
		l	2	0.20			ma	0.30
Napeogenes s. caucayaensis	OT	e	3	0.20	*Solanum* (*Extensum*) nr *extensum* Bitter	shrub	se	0.35
		e & l	> 10	0.05-0.35			se	0.35
Hyposcada k. kena	SDT	e	3	0.20	*Gasteranthus corallinus* (Fritsch) Wiehler (Gesneriaceae)	herb	ma	0.30
Hyposcada i. ida	SDT	e	1	0.45	*Besleria aggregata* (Martius) Hanstein (Gesneriaceae)	herb	s	0.50
		e & l	13	0.60-1.1			ma	1.5
Oleria a. agarista	SDT	e	> 5	0.20-0.40	*Solanum* (*Nemorense*) *barbeyanum* Huber	shrub	ma	0.60
		e & l	> 10	0.10-0.50			ma	0.60
		e & l	> 10	0.10-0.25	*Solanum* (*Pteroidea*) *mite* Ruiz & Pavón	herb	ma	0.25
		l	1	1.0	*Solanum* (*Pteroidea*) *anceps* Ruiz & Pavón	shrub	ma	1.5

[a]Heights ≤ 1 m are accurate to *c.* ± 0.05 m; heights between 1 m and 4 m are accurate to *c.* ± 0.1 m; heights ≥ 4 m are accurate to *c.* ± 0.5 m. Note that height records representing > 1 observation are averages and the ranges are given if variation exceeds the limits stated.
[b]Cultivated: not native to the area (see text).
[c]D. Murray (pers. comm.).

TABLE 3.2. Flight height statistics for ithomiine species with host-plant records observed during MRR study at Jatun Sacha. Species have been divided into two groups (A or B) according to host-plant height/early stage height recorded for the species (Table 3.1).

Ithomiine species	Number of individuals recorded	Flight height range (m)[a]	Median flight height (m)	Proportion of individuals at or below 1.1 m
Group A: host-plants > 1.5 m tall/early stages above 1.1 m				
Mechanitis l. elisa	109	0.25-4.45	1.70	18.4
Mechanitis p. dorissides	53	0.15-4.25	1.71	32.1
Hypothyris e. intermedia	245	0.05-3.35	1.24	38.8
Ceratinia t. poecila	88	0.15-4.95	1.25	38.6
Hyposcada a. ecuadorina	13	0.25-2.15	1.23	46.2
Methona c. psamathe	2	1.15-1.55	1.35	0
Thyridia p. ino	2	1.05-2.05	1.55	50.0
Dircenna l. loreta	5	0.65-2.05	1.75	20.0
Group B: host-plants ≤ 1.5 m tall/early stages at or below 1.1 m				
Godyris z. matronalis	209	0.05-2.35	1.06	56.0
Ithomia s. salapia	77	0.15-2.35	1.03	55.8
Ithomia s. derasa	2	0.45-1.55	1.00	50.0
Ithomia a. agnosia	51	0.05-1.75	0.78	68.6
Hyposcada i. ida	35	0.15-2.05	0.43	82.9
Oleria a. agarista	23	0.05-1.15	0.53	95.7

[a]Taken from the mid-point of the flight height class

TABLE 3.3. Pair-wise χ^2 tests, corrected for continuity, on flight heights (number of individuals recorded above 1.1 m, and at or below 1.1 m) for pairs of species with host-plant records (Table 3.1) and > 20 flight height observations (Table 3.2). Underlined values are results of comparisons made between pairs of species in the same host-plant height/early stage height group (A or B).

(d.f. = 1; n.s., not significant at 5% level; $*P < 0.05$; $**P < 0.02$; $***P < 0.01$; $****P < 0.001$)

	M. l. elisa	*M. p. dorissides*	*H. e. intermedia*	*C. t. poecila*	*G. z. matronalis*	*I. s. salapia*	*I. a. agnosia*	*H. i. ida*
M. p. dorissides	3.07 n.s.	-	-	-	-	-	-	-
H. e. intermedia	13.44 ****	0.57 n.s.	-	-	-	-	-	-
C. t. poecila	9.08 ***	0.37 n.s.	0.01 n.s.	-	-	-	-	-
G. z. matronalis	39.85 ****	8.74 ***	12.73 ****	6.78 ***	-	-	-	-
I. s. salapia	26.67 ****	6.21 **	6.29 **	4.22 *	0.01 n.s.	-	-	-
I. a. agnosia	36.74 ****	12.47 ****	14.08 ****	10.45 ***	2.20 n.s.	1.60 n.s.	-	-
H. i. ida	46.28 ****	19.80 ****	22.37 ****	17.87 ****	7.93 ***	6.52 **	1.52 n.s.	-
O. a. agarista	48.81 ****	23.47 ****	25.39 ****	21.49 ****	11.98 ****	10.65 ***	5.10 *	1.11 n.s.

TABLE 3.4. Pair-wise χ^2 tests, corrected for continuity, on flight heights (number of individuals recorded above 1.1 m, and at or below 1.1 m) for pairs of mimicry complexes (see text). Complexes T, YBT, OBT & LYT have the highest median flight heights and a majority of individuals flying above 1.1 m; complexes SDT, OT, CW & SYT have the lowest median flight heights and a majority of individuals flying at or below 1.1 m. Pair-wise comparisons within each of these two groups (high & low) are underlined.

(Explanations of the codes of the mimicry complexes are given in Appendix 3.1; d.f. = 1; n.s., not significant at 5% level; $*P < 0.05$; $**P < 0.02$; $***P < 0.01$; $****P < 0.001$)

	T	YBT	OBT	LYT	SYT	CW	OT
YBT	0.34 n.s.	-	-	-	-	-	-
OBT	0.02 n.s.	0.04 n.s.	-	-	-	-	-
LYT	0.23 n.s.	0.02 n.s.	0.03 n.s.	-	-	-	-
SYT	47.20 ****	15.30 ****	5.14 *	9.83 ***	-	-	-
CW	24.64 ****	14.68 ****	6.36 **	10.67 ***	0.70 n.s.	-	-
OT	20.83 ****	16.91 ****	10.05 ***	13.96 ****	4.19 *	1.79 n.s.	-
SDT	151.27 ****	75.60 ****	39.54 ****	57.81 ****	49.96 ****	20.96 ****	0.99 n.s.

TABLE 3.5. Numbers of host-plant records in two height class categories utilised by high (T, BR and GT) and low (CW and BY) flying Costa Rican mimicry complexes.

Mimicry complexes	No. ithomiine species	No. herbs & shrubs	No. trees & epiphytic shrubs	Total host-plant records
T + BR + GT	16	10	17	27
CW + BY	14	23	0	23

TABLE 3.6. Numbers of host-plant records in two height class categories utilised by high (canopy) and low (understorey) flying species of British woodland butterflies.

Flight stratum	No. butterfly species	No. herbs & grasses	No. shrubs & trees	Total host-plant records
Canopy	6	0	10	10
Understorey	13	29	4	33

TABLE 3.7. Species richness, number of mimicry complexes and degree of host-plant specificity of ithomiine species, at five of the best studied Neotropical sites.

Locality	Source	Sample time (months)	Total number of ithomiine species recorded from site	No. of ithomiine mimicry complexes at site	No. of ithomiine species with host records	No. of host-plant records[a]	No. of host-plant species[a]	Mean number of host-plant records per ithomiine species	Mean number of host-plant species per ithomiine species	Observed number of monophagous ithomiine species, with proportion of monophagous species at the site in brackets	No. host-plant species utilised by only a single ithomiine species, with proportion of total in brackets
Sumaré Forestry Station, São Paulo State, Brazil	Vasconcellos-Neto, 1991	48	23	3[d]	5	25	11	5.0	2.2	1 (20%)	5 (46%)
Campinas, São Paulo State, Brazil	Brown, 1987a	96[b] ?	25	3[d,e]	16[g]	63[g]	35[g]	3.9	2.2	2 (13%)	20 (57%)
Monteverde, Puntarenas Prov., Costa Rica	Haber, 1978	10	40[c]	4[e]	18	47	32	2.6	1.8	5 (28%)	20 (63%)
Limoncocha, Napo Prov., Ecuador	Drummond, 1976; 1986	15	52	8[f]	28	39	33	1.4	1.2	23 (82%)	28 (85%)
Jatun Sacha, Napo Prov., Ecuador	Beccaloni, this study	2.5	56	8	15	18	15	1.2	1.0	13 (87%)	13 (87%)

[a]Introduced non-native plant species have not been removed from the host-plant data sets.
[b]Estimated - the actual total is probably greater.
[c]Total includes four species added by DeVries (1983).
[d]These complexes are geographical variants of the T, LYT and CW complexes.
[e]Only one ithomiine species with a BY colour pattern is present at these sites and I therefore consider the BY complex to be absent.
[f]The complexes at this site are the same as those at Jatun Sacha (see text).
[g]Verified host-plants records for ithomiine populations within a 5 km diameter circle between Campinas and Barão Geraldo (see Brown, 1987a).

APPENDIX 3.1. ITHOMIINE SPECIES RECORDED DURING MRR STUDY AT JATUN SACHA BIOLOGICAL STATION, ECUADOR.

Ithomiine species (arranged by tribe)[a]	Mimicry complex[b]	Number of individuals recorded (both sexes)
Melinaeini		
Melinaea maelus maeonis Hewitson	T	5
Melinaea menophilus cocana Haensch	YBT	4
Mechanitini		
Forbestra equicola equicoloides (Godman & Salvin)	T	2
Forbestra olivencia juntana (Haensch)	T	4
Mechanitis lysimnia elisa (Guérin)	T	109
Mechanitis mazaeus mazaeus Hewitson	OBT	1
Mechanitis mazaeus visenda Butler	T	29
Mechanitis messenoides deceptus Butler	OBT	21
Mechanitis messenoides messenoides Felder & Felder	YBT	2
Mechanitis polymnia dorissides Staudinger	T	53
Thyridia psidii ino Felder & Felder	LYT	2
New tribe Brown, *in litt.*		
Aeria eurimedea negricola (Felder & Felder)	SYT	13
Methonini		
Methona confusa psamathe Godman & Salvin	LYT	2
Methona curvifascia curvifascia Weymer	LYT	2
Napeogenini		
Hypothyris anastasia bicolora (Haensch)	OBT	1
Hypothyris anastasia honesta (Weymer)	YBT	3
Hypothyris euclea intermedia (Butler)	T	245
Hypothyris mamercus mamercus (Hewitson)	YBT	24
Hypothyris moebiusi moebiusi (Haensch)	YBT	31
Hypothyris semifulva satura (Haensch)	T	2
Napeogenes inachia avila Haensch	SYT	26
Napeogenes pharo pharo (Felder & Felder)	LYT	6
Oleriini		
Hyposcada anchiala ecuadorina Bryk	T	13
Hyposcada illinissa ida Haensch	SDT	35
Oleria agarista agarista (Felder & Felder)	SDT	23
Oleria assimilis assimilis (Haensch)	SDT	6
Oleria gunilla lota (Hewitson)	SDT	112
Oleria tigilla tigilla (Weymer)	SDT	1
Ithomiini		
Ithomia agnosia agnosia Hewitson	CW	51
Ithomia amarilla amarilla Haensch	SYT	1
Ithomia salapia derasa Hewitson	SYT (variant)	2
Ithomia salapia salapia Hewitson	SYT	77
Dircennini		
Callithomia alexirrhoe butes Godman & Salvin	T	3
Callithomia lenea zelie (Guérin)	LYT	6
Ceratinia tutia poecila (Bates)	T	88

APPENDIX 3.1 - continued

Dircenna loreta loreta Haensch	LYT	5
Pteronymia vestilla sparsa Haensch	SYT	62
Godyridini		
Godyris dircenna dircenna (Felder & Felder)	LYT	15
Godyris zavaleta matronalis (Weymer)	SYT	209
Heterosais nephele nephele (Bates)	CW	5
Hypoleria lavinia chrysodonia (Bates)	OT	7
"*Hypoleria*" *orolina orolina* (Hewitson)	OT	11
"*Hypoleria*" *seba oculata* (Haensch)	OT	3
"*Pseudoscada*" *florula aureola* (Bates)	OT	7
Pseudoscada timna timna (Hewitson)	CW	32

[a]Nomenclature of ithomiine species is largely based on a recent systematic list (G. Lamas, unpublished).

[b]Codes of mimicry complexes: SDT, small dark transparent; OT, orange-tip; CW, clearwing; SYT, small yellow transparent; LYT, large yellow transparent; OBT, orange & black tiger; YBT, yellow-bar tiger; T, tiger.

APPENDIX 3.2. COSTA RICAN ITHOMIINE SPECIES WITH HOST-PLANT RECORDS (SEE TEXT).

Ithomiine species (arranged by tribe)	Mimicry complex	Host-plant species	Growth-form of host-plant	Height of mature host-plant (m)
Tithoreini				
Eutresis hypereia theope G. & S.	GT	*Solandra grandiflora*	vine	-
Olyras crathis staudingeri G. & S.	BR	*Solandra grandiflora*	vine	-
Tithorea harmonia helicaon G. & S.	T	*Prestonia portobellensis*	vine	-
Tithorea tarricina pinthias G. & S.	BR	*Prestonia portobellensis*	vine	-
		Prestonia guatemalensis	vine	-
Melinaeini				
Melinaea lilis imitata Bates	T	*Juanulloa mexicana*	epiphytic shrub	-
		Markea (*Merinthopodium*) *neurantha*	epiphytic shrub	-
		Solandra grandiflora	vine	-
Melinaea scylax scylax Salvin	T	*Juanaloa mexicana*	epiphytic shrub	-
		Markea (*Merinthopodium*) *neurantha*	epiphytic shrub	-
Mechanitini				
Mechanitis lysimnia doryssus Bates	T	*Solanum* (*Brevantherum*) *rugosum*	shrub/tree	1-9
		Solanum (*Brevantherum*) *umbellatum*	shrub/tree	1-6
		Solanum (*Micracantha*) *siparunoides*	vine	-
Mechanitis menapis saturata Godman	T	*Solanum* (*Leptostemonum*) *hispidum*	shrub/tree	1-5(-7)
		Solanum (*Micracantha*) *siparunoides*	vine	-
		Solanum (*Lasiocarpa*) *quitöense*	shrub	3
		Solanum (*Acanthophora*) *acerifolium*	herb	1.5
		Solanum (*Acanthophora*) *capsicoides*	herb	1.5
		Solanum torvum	shrub/tree	1-5(-6)
Mechanitis polymnia isthmia Bates	T	*Solanum* (*Brevantherum*) *schlechtendalianum*	shrub/tree	1.5-5(-8)
		Solanum (*Brevantherum*) *asperum*	shrub/tree	1-7
		Solanum (*Leptostemonum*) *ochraceo-ferrugineum*	shrub/tree	1-5(-?12)
		Solanum (*Leptostemonum*) *hispidum*	shrub/tree	1-5(-7)
		Solanum (*Leptostemonum*) *jamaicense*	shrub	1-3.5
		Solanum (*Micracantha*) *lancaeifolium*	vine	-
Scada zibia xanthina (Bates)	BY	*Solanum* (*Brassovia*?) *enchylozum*	shrub	?
		Solanum (*Micracantha*) *siparunoides*	vine	-
Thyridia psidii melantho Bates	BR	*Cyphomandra hartwegii*	tree	4 (-12)
		Cyphomandra crassicaulis	shrub/tree	4
New tribe Brown, *in litt.*				
Aeria eurimedea agna G. & S.	BY	*Prestonia portobellensis*	vine	-
		Prestonia sp.	herb (vine?)	0.2
Napeogenini				
Hyalyris excelsa decumana (G. & S.)	BR	*Solanum* (*Leptostemonum*) *accrescens*	shrub/tree	1.5-5
		Solanum (*Micracantha*) *siparunoides*	vine	-
		Solanum (*Micracantha*) *lancaeifolium*	vine	-
Hypothyris euclea leucania (Bates)	T	*Solanum* (*Brevantherum*) *rugosum*	shrub/tree	1-9
		Solanum (*Brevantherum*) *umbellatum*	shrub/tree	1-6
Hypothyris lycaste callispila (Bates)	BR	*Solanum torvum*	shrub/tree	1-5(-6)
Napeogenes tolosa amara Godman	BR	*Lycianthes* nr. *multiflora*	shrub	3.5
Oleriini				
Hyposcada virginiana evanides Haensch	BR	*Columnea consanguinea*	epiphytic shrub	-
		Columnea grata	epiphytic shrub	-
		Drymonia conchocalyx	epiphytic shrub	-
		Drymonia sp.	epiphytic shrub	-
Oleria paula (Weymer)	CW	*Lycianthes* nr. *multiflora*	shrub	3.5
Oleria rubescens (Butler & Druce)	CW	*Solanum* (*Micracantha*) *siparunoides*	vine	-
Oleria vicina (Salvin)	CW	*Lycianthes multiflora*	shrub	3.5
		Solanum (*Bassovia*) *trizygum*	herb	1
Oleria zelica pagasa (Druce)	BY	*Solanum* (*Potatoe*) *evolvulifolium*	vine	-
Ithomiini				
Ithomia celemia plaginota Butler & Druce	T	*Cuatresia riparia*	tree	4.5
Ithomia diasia hippocrenis Bates	CW	*Witheringia asterotricha*	herb	0.5(-4)
		Witheringia solanacea	herb	0.5(-4)

APPENDIX 3.2 - continued

Ithomia iphianassa heraldica Doubleday	T	*Cuatresia riparia*	tree	4.5
		Witheringia morii	tree	?
		Acnistus arborescens	tree	3-6
Ithomia patilla Hewitson	CW	*Lycianthes multiflora*	shrub	3.5
		Witheringia solanacea	herb	0.5(-4)
Ithomia xenos (Bates)	GT	*Cuatresia riparia*	tree	4.5
		Witheringia cuneata	shrub	2.5-3
		Acnistus arborescens	tree	3-6
Dircennini				
Callithomia hezia hezia (Hewitson)	BR	*Lycianthes sanctaeclarae*	epiphytic shrub	-
		Solanum (*Androceras*) nr. *granelianum*	vine	-
Ceratinia tutia dorilla (Bates)	T	*Solanum* (*Geminata*) *antillarum*	shrub	3
Dircenna dero euchytma (Felder & Felder)	T	*Solanum* (*Leptostemonum*) *ochraceo-ferrugineum*	shrub/tree	1-5(-?12)
Dircenna jemina chiriquensis Haensch	GT	*Solanum* (*Micracantha*) *siparunoides*	vine	-
Dircenna klugii ssp. n. Lamas, *in litt.*	GT	*Solanum* (*Brevantherum*) nr. *rugosum*	shrub/tree	1-9
		Solanum (*Brevantherum*) *umbellatum*	shrub/tree	1-6
		Solanum (*Leptostemonum*) *hispidum*	shrub/tree	1-5(-7)
		Solanum (*Leptostemonum*) *ochraceo-ferrugineum*	shrub/tree	1-5(-?12)
		Solanum (*Micracantha*) *lancaeifolium*	vine	-
Dircenna olyras relata Butler & Druce	BR	*Solanum* (*Brevantherum*) *cordavense*	shrub/tree	1-5
		Solanum (*Brevantherum*) nr. *rugosum*	shrub/tree	1-9
		Solanum (*Brevantherum*) *umbellatum*	shrub/tree	1-6
		Solanum (*Leptostemonum*) *hispidium*	shrub/tree	1-5(-7)
		Solanum torvum	shrub/tree	1-5(-6)
Episcada salvinia opleri Lamas	CW	*Solanum* (*Geminata*) *antillarum*	shrub	3
		Solanum (*Geminata*) *nudum*	shrub	3.5
Pteronymia artena artena (Hewitson)	CW	*Lycianthes multiflora*	shrub	3.5
		Lycianthes escuitlensis	shrub	1-3.5
		Lycianthes synanthera	shrub/tree	1-3.5(-10)
Pteronymia cotytto (Guérin)	CW	*Solanum* (*Geminata*) *nudum*	shrub	3.5
Pteronymia fulvimargo Butler & Druce	GT	*Solanum* (*Geminata*) nr. *antillarum*	shrub	3
Pteronymia latilla fulvescens G. & S.	GT	*Solanum* (*Geminata*) *brenesii*	shrub/tree	2-4
Pteronymia notilla notilla Butler & Druce	BR	*Solanum* (*Geminata*) *arboreum*	shrub/tree	1-8
		Solanum (*Geminata*) *brenesii*	shrub/tree	2-4
		Solanum (*Geminata*) *roblense*	shrub/tree	2-7
		Cestrum megalophyllum	shrub	2-3
Pteronymia obscurata agalla G. & S.	GT	*Solanum* (*Geminata*) *brenesii*	shrub/tree	2-4
Pteronymia simplex simplex (Salvin)	CW	*Solanum* (*Geminata*) *antillarum*	shrub	3
		Solanum (*Geminata*) *arboreum*	shrub/tree	1-8
		Solanum (*Geminata*) *brenesii*	shrub/tree	2-4
Talamancana lonera (Butler & Druce)	BR	*Cyphomandra hartwegii*	tree	4 (-12)
Godyridini				
Godyris zavaleta caesiopicta (Niepelt)	BR	*Solanum* (*Geminata*) *brenesii*	shrub/tree	2-4
Godyris zygia (G. & S.)	BR	*Cestrum nocturnum*	shrub	1-3.5
Greta morgane oto (Hewitson)	CW	*Cestrum lanatum*	shrub/tree	2-5
Greta nero ssp. n. Lamas, *in litt.*	CW	*Cestrum standleyi*	herb	1
Hypoleria lavinia cassotis (Bates)	CW	*Cestrum megalophyllum*	shrub	3
		Solanum (*Geminata*) sp.	shrub	3
Hypomenitis annette championi (Lamas)	CW	*Cestrum fragile*	shrub	?
		Solanum (*Brevantherum*) *cordavense*	shrub/tree	1-5
Hypomenitis polissena umbrana (Haensch)	CW	*Cestrum fragile*	shrub	?
		Cestrum megalophyllum	shrub	2-3
		Cestrum nocturnum	shrub	1-3.5
		Cestrum rugulosum	shrub	3(-5)
		Cestrum lanatum	shrub/tree	2-5

APPENDIX 3.3. BRITISH WOODLAND BUTTERFLY SPECIES AND THEIR PRINCIPAL HOST-PLANTS, GROUPED BY USUAL FLIGHT STRATUM (CANOPY OR UNDERSTOREY) OF ADULT.

Butterfly species	Principal host-plants in Britain	Average height of mature host-plant (m)	Growth-form of host-plant
Canopy species			
Quercusia quercus (L.)	*Quercus robur* L.	30.0(-40.0)	tree
	Quercus petraea (Mattuschka) Liebl.	30.0(-40.0)	tree
Satyrium w-album (Knoch)	*Ulmus glabra* Huds.	up to *c.* 40.0	tree
	Ulmus procera Salisb.	up to 30.0	tree
Satyrium pruni (L.)	*Prunus spinosa* L.	1.0-4.0	shrub
Celastrina argiolus (L.)	*Ilex aquifolium* L.	3.0-15.0	shrub
	Hedera helix L.	up to 30.0	vine
Apatura iris (L.)	*Salix caprea* L.	3.0-10.0	shrub
	Salix cinerea L.	2.0-10.0	shrub
Nymphalis polychloros (L.)	*Ulmus glabra* Huds.	up to *c.* 40.0	tree
	Ulmus procera Salisb.	up to 30.0	tree
Understorey species			
Leptidea sinapis (L.)	*Lathyrus pratensis* L.	0.30-1.2	herb
	Lathyrus montanus Bernh.	0.15-0.40	herb
	Vicia cracca L.	0.60-2.0	herb
	Lotus corniculatus L.	0.10-0.40	herb
Gonepteryx rhamni (L.)	*Rhamnus catharticus* L.	4.0-6.0(-10.0)	shrub
	Frangula alnus Mill.	4.0-5.0	shrub
Anthocharis cardamines (L.)	*Cardamine pratensis* L.	0.30-0.60	herb
	Alliaria petiolata (Bieb.) Cavara & Grande	0.20-1.2	herb
Hamearis lucina (L.)	*Primula veris* L.	0.05-0.15(-0.20)	herb
	Primula vulgaris Huds.	0.08-0.15(-0.20)	herb
Ladoga camilla (L.)	*Lonicera periclymenum* L.	up to 6.0	shrub/vine
Inachis io (L.)	*Urtica dioica* L.	0.30-1.5	herb
Polygonia c-album (L.)	*Urtica dioica* L.	0.30-1.5	herb
	Ulmus procera Salisb.	up to 30.0	tree
	Ulmus glabra Huds.	up to *c.* 40.0	tree
	Humulus lupulus L.	3.0-6.0	vine
Boloria selene ([Denis & Schiffermüller])	*Viola riviniana* Reichb.	0.02-0.20(-0.40)	herb
	Viola palustris L.	0.01-0.04	herb
Boloria euphrosyne (L.)	*Viola riviniana* Reichb.	0.02-0.20(-0.40)	herb
	Viola palustris L.	0.01-0.04	herb
Argynnis adippe ([Denis & Schiffermüller])	*Viola riviniana* Reichb.	0.02-0.20(-0.40)	herb
	Viola hirta L.	0.02-0.06	herb
Argynnis paphia (L.)	*Viola riviniana* Reichb.	0.02-0.20(-0.40)	herb
Mellicta athalia (Rottemburg)	*Plantago lanceolata* L.	(0.02)0.10-0.15(0.30)	herb
	Melampyrum pratense L.	0.08-0.60	herb
	Veronica chamaedrys L.	0.20-0.40	herb
Pararge aegeria (L.)	*Brachypodium sylvaticum* (Huds.) Beauv.	0.30-0.90	grass
	Dactylis glomerata L.	up to 1.0	grass
	Poa trivialis L.	0.20-0.60	grass
	Holcus lanatus L.	0.20-0.60	grass
	Festuca rubra L.	0.10-0.70	grass
	Bromus ramosus Huds.	0.60-1.9	grass
	Agrostis stolonifera L.	0.10-1.4	grass
Aphantopus hyperantus (L.)	*Elymus repens* (L.) Gould	0.30-1.0	grass
	Poa pratensis L.	0.10-0.80	grass

-CHAPTER 4-

PREDICTING THE SPECIES RICHNESS OF NEOTROPICAL FOREST BUTTERFLIES: ITHOMIINAE (LEPIDOPTERA: NYMPHALIDAE) AS INDICATORS

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PREDICTING THE SPECIES RICHNESS OF NEOTROPICAL FOREST BUTTERFLIES: ITHOMIINAE (LEPIDOPTERA: NYMPHALIDAE) AS INDICATORS

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Abstract

The proportions of species in many of the 14 butterfly families and subfamilies found in the tropical forests of mainland Central and South America show relatively invariant or simple relationships with overall butterfly species richness at both local and regional scales. These relationships suggest that it may be possible to use the species total of a single butterfly group (an indicator) to predict the overall species richness of all other butterflies in an area. For practical purposes (ease of sampling, etc.), ithomiine butterflies (Nymphalidae: Ithomiinae) are a logical choice. There is a strong positive correlation between ithomiine species richness and the overall species richness of all other butterflies across all areas, and the proportion of this subfamily is reasonably invariant. It should therefore be possible to use the mean proportion (4·6%) to predict the overall butterfly species richness of an area for which the ithomiine total is known.

Keywords: butterflies, indicator groups, Ithomiinae, Neotropics, species richness.

INTRODUCTION

Attempts at rational prioritisation of areas for conservation often rely on comparisons of relative or absolute numbers of species (species richness) (e.g. Myers, 1990 (hot-spots); Mittermeier, 1988 (megadiversity)). Ideally, decisions should also be based on the identities and genealogical relationships of all taxa in the areas, so that taxon turnover (complementarity: Vane-Wright *et al.*, 1991) and taxic or phylogenetic differences of the subsets of species in areas (Faith, 1992; Williams *et al.*, 1993) can additionally be taken into account. However, this information is not often readily available; indeed data on the absolute species richness of most areas are non-existent. Even for small well-studied groups such as birds or butterflies, data are often sparse, especially for regions with high species richness. Demand is therefore high for methods which enable the species richness of areas to be predicted and several surrogates have been proposed to achieve this. These include the use of indicator groups, environmental variables, and higher-taxon richness (Gaston & Williams, 1993; Williams & Gaston, 1994). At best the last two methods can usually only allow areas to be compared on the basis of their relative species richness, and the first (indicator groups) is also commonly used in this way.

A wide variety of groups of organisms has been proposed as indicators, including plants (Cronk, 1988), butterflies (Brown, 1991; Kremen, 1992), tiger beetles (Pearson & Cassola, 1992), birds (ICBP, 1992), and mammals (Mittermeier, 1988). Most studies have attempted to use indicators to identify areas of high overall biodiversity, by seeking positive correlations between the species richness of the chosen groups and the richness of other groups for which information is available. Of necessity, however, comparisons are usually made at a coarse spatial scale, often across widely different habitats or ecosystems, and between groups of organisms which do not necessarily share the same, or even similar, ecological requirements. While this approach may be valuable for comparing the relative diversity of large geographic regions, it is probably of limited use for finer scale comparisons. Prendergast *et al.* (1993), for example, demonstrate that (at least within Britain) attempts to use indicator groups in this way often meet with little success.

This study adopts a more focused approach, by restricting comparisons to phylogenetically and ecologically related groups (families and subfamilies of butterflies), sharing the same general habitat (tropical forests of mainland Central and South America). First, we assess the broad potential of each group as an indicator for predicting the absolute richness of all other butterfly groups at both local and regional scales. Subsequently, we concentrate on a single group (the Ithomiinae) and investigate its value as an indicator of overall butterfly richness in more detail.

METHODS

The many distinct vegetation types found in the Neotropics can be classified into two broad categories, tropical forest and non-tropical-forest vegetation (see Fig. 1 for details of the vegetation types included in these categories). Each of these macrohabitats has a relatively discrete butterfly fauna (tropical forest and non-tropical-forest species respectively), as few species are shared between the two systems (Brown, 1987; Pinheiro & Ortiz, 1992).

The tropical forests of Central and South America form a more or less continuous block, ranging from southern Mexico to southern Brazil and northern Argentina (Fig. 1). Even the forests of the Atlantic region of south-eastern Brazil, usually thought of as isolated, are connected to the Amazonian forests by corridors of gallery forest along watercourses and 55% of the butterfly species found in the former are shared with the latter system (Brown, 1991).

Species totals for the 14 commonly recognised butterfly families and subfamilies (Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae, Libytheidae, Nymphalidae: Nymphalinae, Satyrinae, Brassolinae, Morphinae, Heliconiinae, Acraeinae, Danainae and Ithomiinae) were gathered from the literature and other sources to represent three contrasting spatial scales: collecting sites, countries, and the whole of the Neotropics. Totals for two Caribbean islands (Trinidad and Jamaica) were also included for comparison with the mainland data-set. Details of the areas, including their location, size (km^2), major vegetation type, collecting effort, and the sources from which information was obtained, are given in Table 1. Data on the

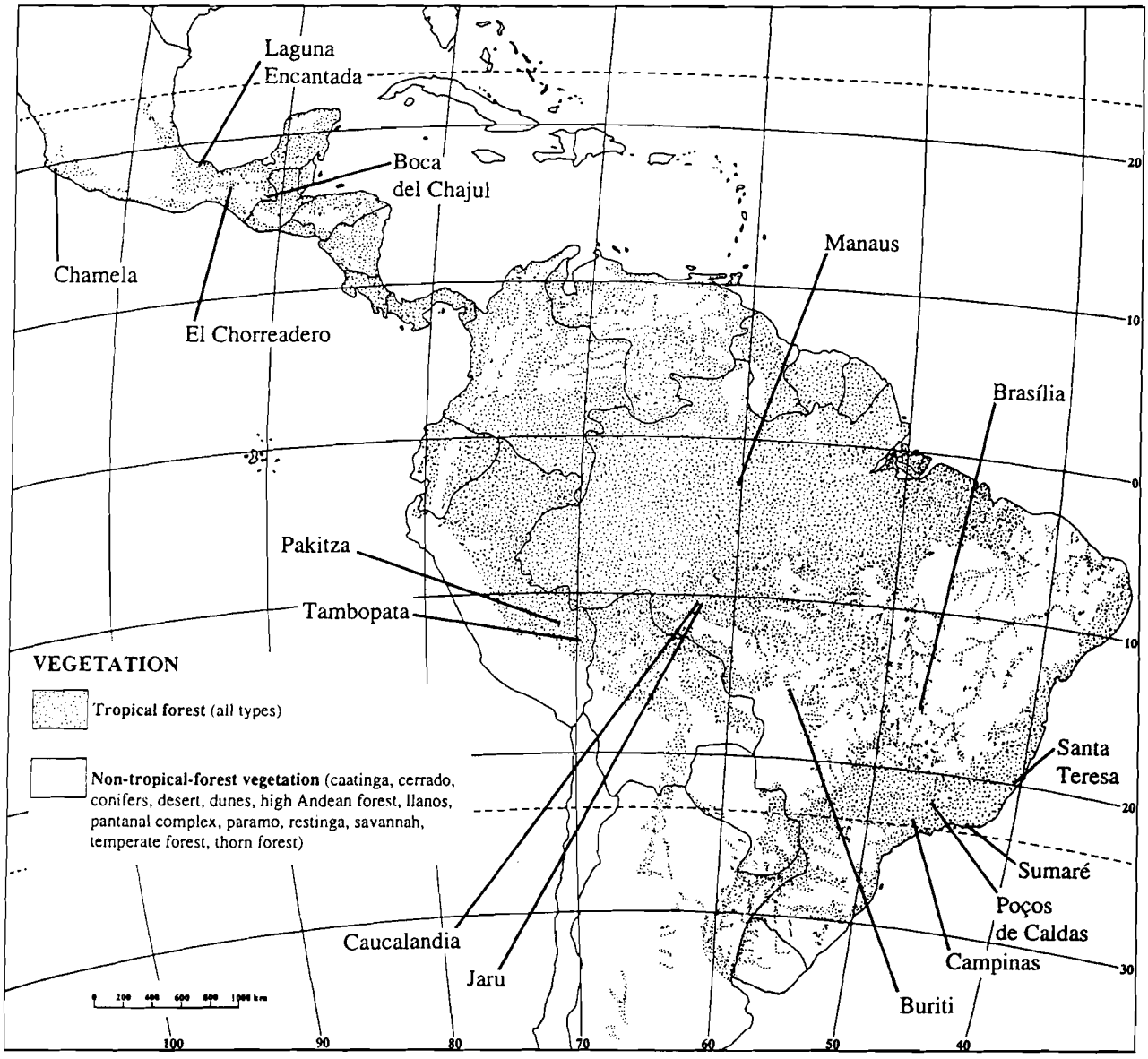

Fig. 1. Map of the Neotropics showing natural cover of the two major vegetation types (tropical forest and non-tropical-forest vegetation) and locations of the collecting sites discussed in text (adapted from Brown, 1982).

Table 1. Details of the areas discussed in text, and sources from which the butterfly totals in Table 2 were obtained

Areas	Area (km^2)	Major vegetation type(s)	Collecting effort (various measures) and spread of collecting effort (in brackets)	Sources
Collecting sites				
Laguna Encantada, Veracruz, Mexico; 350 m	0·56	Lower montane rainforest	6 weeks (consecutive)	Raguso & Llorente-Bousquets (1991)
Boca del Chajul, Chiapas, Mexico; 140 m	10	Lowland rainforest	4 years (consecutive?)	De la Maza & White López (1990); Raguso & Llorente-Bousquets (1991)
El Chorreadero, Chiapas, Mexico; 680 m	<1	Montane rainforest	>24 months (over 2 years)	Beutelspacher (1983)
Chamela[a], Jalisco, Mexico; 120 m	0·044	Dry forest	12 months (over 2 consecutive years)	Beutelspacher (1982)
Pakitza biological station, Manu National Park, Madre de Dios, Peru; 350 m	<1	Lowland rainforest	200 person-hours (over 17 consecutive days)	Lamas *et al.* (1991)
Tambopata Natural Reserve, Madre de Dios, Peru; 300 m	2	Lowland rainforest	>1000 person-hours (over 6 years)	Lamas (1985)
Manaus, Amazonas, Brazil; *c.* 100 m	10	Lowland rainforest	1000 person-hours (over many months)	Brown (1984)
Brasília area, Distrito Federal, Brazil; 1020–1110 m	?	Humid forest & cerrado	43 days (over 4 years)	Brown (1972)
Poços de Caldas area, Minas Gerais, Brazil; 1000–1500 m	?	Montane rainforest	37 days (over 3 years)	Ebert (1969)
Santa Teresa area, Espírito Santo, Brazil; *c.* 200–1200 m	?	Rainforest	100 days (over 2 consecutive years)	Brown (1972)
Sumaré, Parque Nacional da Tijuca, Rio de Janeiro, Brazil; *c.* 600–1200 m	?	Rainforest	40 days (over 5 consecutive years)	Brown (1972)
Campinas, São Paulo, Brazil; 800 m	4	Semideciduous forest	2000 person-hours (over many years)	Brown (1984)
Buriti area, Mato Grosso, Brazil. *c.* 500–1000 m	?	Rainforest	44 days (over 5 consecutive years)	Brown (1972)
Jaru, Rondônia, Brazil, Rondônia; 250–350 m	1	Lowland rainforest	300 person-hours (over 2 years)	Brown (1984)
Caucalandia area, Rondônia, Brazil; 160–350 m	<314	Lowland rainforest	>3 months (over 2 years)	Emmel & Austin (1990)
Islands				
Trinidad[a]	4,828	—	?	Barcant (1970)
Jamaica[a]	11,650	—	?	Brown & Heineman (1972)
Mainland countries				
Mexico[a]	1,972,550	—	?	De la Maza *et al.* (1989, 1991)
Costa Rica	51,100	—	?	De Vries (1983, 1987); Austin (1992)
Panama	75,650	—	?	Robbins (1982); Haber (1978)
Colombia	1,138,910	—	?	Brown (1991)
Venezuela	912,050	—	?	A. Neild (pers. comm.)
Peru	1,285,215	—	?	Brown (1991); Lamas (1985)
Brazil	8,511,970	—	?	Brown (1991)
Neotropics	17,500,000	—	?	Brown (1991); Heppner (1991); Robbins (1982, 1992)

[a]Not included in data analysis — see text for details.

butterflies found in each of these areas are summarised in Table 2.

The collecting sites, which are widely scattered throughout the Neotropical forests (Fig. 1), represent the most intensively sampled localities for butterflies in Central and South America. Only sites with a minimum collecting effort of 200 person-hours or 37 person-days (measures are those stated in original sources and could not be standardised) and those sampled for all butterfly families and subfamilies were included in this study. The collecting sites are relatively small areas, with only one, Caucalandia, exceeding 10 km^2 (note that the actual area sampled at Caucalandia is probably much less than the 314 km^2 stated in Table 1), and all possess a single major forest type. The sites therefore in effect represent point diversity for tropical forest butterflies.

One dry (deciduous) forest site, Chamela (Mexico), is included in Tables 1 and 2 for comparison with the other sites. The butterfly fauna of this site probably

Table 2. Total butterfly species richness of areas, and the proportions of species in the families and subfamilies of butterflies recorded from each

Areas	Total butterfly species	% of total													
		Hespe.	Papil.	Pieri.	Lycae.	Riodi.	Libyt.	Nymph.	Satyr.	Brass.	Morph.	Helic.	Acrae.	Danai.	Ithom.[c]
Sites															
Laguna Encantada	182	19·78	4·95	8·79	10·99	9·34	0	26·92	5·50	0·55	1·10	4·95	0·55	1·65	4·95
Boca del Chajul	544	27·21	4·78	5·70	11·77	13·97	0	20·96	4·78	2·39	0·55	3·31	0·18	0·74	3·68
El Chorreadero	177	20·34	6·22	14·12	7·35	7·91	0·57	29·38	2·83	0·57	0·57	2·83	0·57	2·26	4·52
Chamela[a]	150	30·00	9·33	14·67	5·33	6·67	0·67	26·67	1·33	0	0·67	2·00	0	2·67	0
Pakitza	616	23·54	1·30	2·92	17·70	21·92	0	11·20	9·42	1·46	0·65	2·44	0·16	0·16	7·14
Tambopata	1122	31·82	2·23	2·23	12·66	18·72	0·09	14·62	8·73	1·87	0·98	2·14	0·09	0·27	3·57
Manaus	365	14·25	1·92	1·92	13·97	30·41	0	12·60	10·69	1·92	1·92	4·93	0	0·55	4·93
Brasília	755	33·11	1·59	3·58	17·75	17·22	0·13	12·58	5·96	1·72	0·53	1·72	0·80	0·40	2·91
Poços de Caldas	572	38·99	2·80	6·12	15·21	8·22	0·18	13·29	5·94	1·22	0·87	1·57	1·22	0·70	3·67
Santa Teresa	513	29·24	2·53	6·82	6·43	13·65	0·20	17·54	7·80	3·90	1·56	3·31	1·37	0·59	5·07
Sumaré	658	38·00	3·04	5·47	15·65	12·16	0·15	11·40	3·19	1·98	0·76	2·43	0·91	0·46	4·41
Campinas	537	31·29	3·17	5·40	10·06	11·17	0·19	21·42	5·21	2·61	0·93	2·42	1·30	0·75	4·10
Buriti	533	31·90	4·13	3·75	9·76	15·01	0·19	16·14	8·44	1·69	0·38	2·63	0·56	0·75	4·69
Jaru	956	29·18	2·41	2·72	9·31	20·50	0·11	13·81	9·94	2·41	0·84	2·51	0·11	0·21	5·96
Caucalandia	838	27·57	2·15	3·46	10·38	24·22	0	15·04	6·68	0·96	1·31	2·98	0	0·36	4·89
Islands															
Trinidad[a]	616	37·34	2·44	4·38	15·10	17·37	0·16	11·53	3·90	1·62	0·16	2·44	0·33	0·65	2·60
Jamaica[a]	119	29·41	5·88	17·65	14·29	0	0·84	24·37	0·84	0	0	2·52	0·	3·36	0·84
Mainland countries															
Mexico[a]	1696	42·63	3·36	4·42	13·86	10·14	0·12	15·27	4·84	1·00	0·35	1·24	0·41	0·35	2·01
Costa Rica	1251	28·06	3·36	5·60	10·23	17·75	0·08	18·63	6·00	1·60	0·88	2·08	0·40	0·48	4·88
Panama	1550	32·26	1·87	4·19	?	?	?	?	?	?	?	?	?	0·39[b]	4·58
Colombia	3100	?	2·07	?	?	?	?	?	?	?	?	?	?	0·19[b]	4·13[d]
Venezuela	2316	23·75	2·16	4·58	17·27	23·75	0·04	12·09	6·47	1·34	0·91	1·81	0·39	0·35	5·10
Peru	3055	?	1·87	6·55	?	?	0·03	?	?	1·31	0·59	1·64	0·75	0·23[b]	5·47[d]
Brazil	3132	34·67	2·17	1·88	13·70	22·99	0·03	9·67	6·19	1·57	0·67	1·41	0·70	0·26[b]	4·09
Neotropics	7179	28·08	1·85	4·50	18·15	18·22	0·03	14·35	6·97	1·13	0·77	0·91	0·63	0·13	4·30[d]

Hespe., Hesperiidae; Papil., Papilionidae; Pieri., Pieridae; Lycae., Lycaenidae; Riodi., Riodinidae; Libyt., Libytheidae; Nymph., Nymphalinae; Satyr., Satyrinae; Brass., Brassolinae; Morph., Morphinae; Helic., Heliconiinae; Acrae., Acraeinae; Danai., Danainae; Ithom., Ithomiinae.

[a]Not included in data analysis — see text for details.

[b]Taken from Ackery and Vane-Wright (1984)

[c]Nomenclature of Ithomiinae was updated, where possible, using a recent systematic list (G. Lamas, pers. comm.), thus totals may be different from original literature source.

[d]Calculated using G. W. Beccaloni (unpublished) distributional data and/or G. Lamas (pers. comm.) systematic list.

largely or solely comprises non-tropical-forest species, as the majority of tropical forest species are unable to tolerate the long dry periods characteristic of this seasonal habitat. It has been excluded from the analysis on this basis. Brasília (Brazil) has a component of non-tropical-forest vegetation (cerrado: savannah with trees) and the total for this site is therefore probably inflated by non-tropical-forest butterfly species.

For the regional totals (the countries and the Neotropics), it was not possible selectively to include only figures for tropical forest butterflies, as species lists giving the habitat preferences of the butterfly species found in these areas are not available. However, an estimated 90% of all Neotropical butterfly species are confined to tropical forest habitats, the remaining 10% being non-tropical-forest species (mostly grass-feeding Hesperiidae and Satyrinae). This source of error is therefore probably relatively small, especially considering that the greater proportion of the surface area of the countries, and the Neotropics as a whole, is covered with tropical forest. Mexico may be considered an exception, as it has only a relatively small proportion of tropical forest and the greater part of the country (the northern and central portions) is dry and has a temperate Nearctic butterfly fauna.

These kinds of data are prone to many sources of error, including unequal sampling effort across areas, unequal rates of species accumulation for different groups of butterfly within areas, and taxonomic problems of species recognition and separation. Under-recording of species will affect the totals of the least rich areas (the sites) relatively more than those of the richest areas (countries and Neotropics as a whole). At the site level, however, under-recording is likely to be greatest at the richest sites. At the country level, actual figures for each of the 14 groups of butterfly are only available for Costa Rica and Brazil. The figures for the overall total butterfly species richness of Panama, Colombia, Venezuela and Peru are estimates and should be treated with care.

RESULTS AND DISCUSSION

Patterns in species richness

The proportions of species in many of the 14 butterfly families and subfamilies are relatively constant, independent of size or total species richness of an area of tropical forest on mainland Central and South America (Fig. 2). However, the proportions of Lycaenidae and Riodinidae increase with total species richness, whilst in the case of the Papilionidae, Nymphalinae, Heliconiinae and Danainae they decrease.

The fact that the proportions of many of the butterfly families and subfamilies are reasonably invariant, or show comparatively simple patterns with total species richness, means that it is possible to use the known species totals of one or more of these groups (the indicators) in an area to predict the total butterfly species richness of that area. Care should be exercised with those groups whose proportions decrease with increasing total

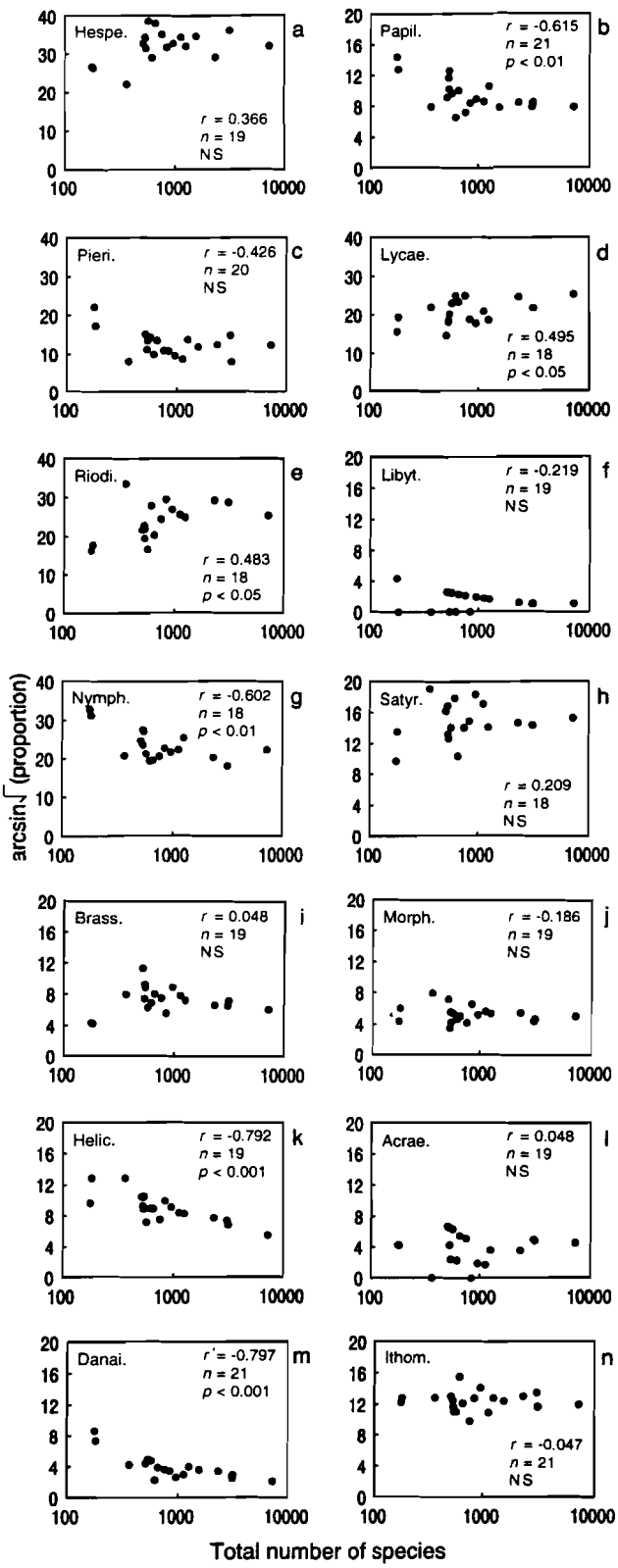

Fig. 2. Relationships between the proportions of species in a given butterfly family or subfamily (arcsin √ transformed) and the overall butterfly species richness ($\log_{10}$-transformed) of collecting sites, countries and Neotropics as a whole: a, Hesperiidae; b, Papilionidae; c, Pieridae; d, Lycaenidae; e, Riodinidae; f, Libytheidae; g, Nymphalinae; h, Satyrinae; i, Brassolinae; j, Morphinae; k, Heliconiinae; l, Acraeinae; m, Danainae; n, Ithomiinae.

species richness. If this is due to saturation the group will be of little value as an indicator. Saturation is most likely to be a problem with very small groups and it can be detected by plotting the number of species in a group (rather than proportions) against the total richness of all the other butterflies. Saturation is suggested if the relationship becomes asymptotic.

Selecting an indicator group

For a group to be a good indicator, there should be low variance about the relationship between the species richness of this group and the species richness of the group we wish to predict. It is advantageous if the relationship is linear, as linear relationships are simpler and may require less detailed documentation to establish. Caution should be exercised when comparing the variance of different potential indicator groups, as small groups may appear to have lower variance than larger groups, although the converse may in fact be true. For example, the proportions of a relatively small group may fluctuate between 2 and 4% across areas, which is the same magnitude as the proportions of a larger group fluctuating between 20 and 40% across these areas.

Ideally, relatively large groups (or perhaps several groups combined) should be used as indicators, because the larger the group, the proportionally less each species contributes to the group total and thus the less each individual species will influence the prediction of total butterfly richness.

Why choose the Ithomiinae as indicators?

Given a choice between a number of potentially equally good indicator groups, how do we choose between them? Choosing a single group is a compromise between many different factors, but for practical purposes we would want a group which is taxonomically well-known, relatively small in total number of species, easy to sample, etc. Brown (1991) listed the desirable qualities that an indicator group should ideally possess and scored various Neotropical insect orders, families and subfamilies accordingly. Of the butterfly groups Brown considered, the Heliconiinae and Ithomiinae were jointly ranked as the best indicators. It can be argued, however, that the Ithomiinae are better indicators than the Heliconiinae, as they are a larger group (representing 4·3%, as opposed to 0·9%, of the Neotropical total) and the comparatively invariant relationship exhibited by this subfamily (Fig. 2(n)) is simpler than the negative relationship shown by the Heliconiinae (Fig. 2(k)). We will therefore take the Ithomiinae as an example and investigate their value as an indicator of total butterfly richness in more detail below.

The Ithomiinae (ithomiines) are an exclusively Neotropical subfamily of Nymphalidae, currently comprising 309 species placed in 51 genera (G. Lamas, pers. comm.). They are one of the taxonomically and ecologically best known groups of Neotropical butterflies and detailed distribution maps exist for approximately one-third of the species (Brown, 1979).

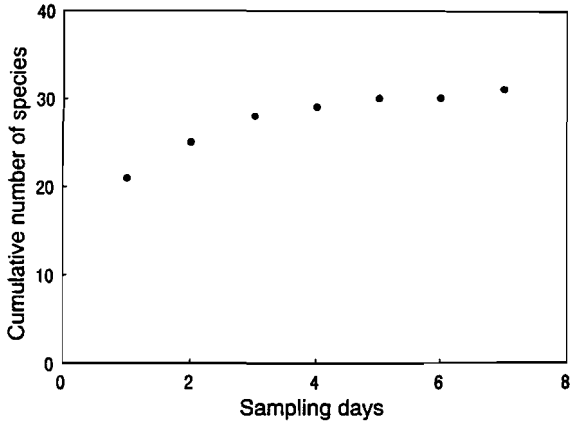

Fig. 3. Accumulation curve for ithomiine species in primary premontane rainforest at Valle Escondido, 750 m, Cartago Province, Costa Rica (redrawn from Haber, 1978).

With the possible exceptions of the Brassolinae and Morphinae, ithomiines are the only major group of Neotropical butterflies entirely restricted to tropical forest habitats. They occur in all tropical forest types from sea level to approximately 3000 m elevation (Drummond, 1976) and range throughout the whole of the Neotropics. Ithomiine species richness as a whole increases towards the equator and peaks at elevations of approximately 500 m on the eastern Andean slope in Ecuador and Peru (G. W. Beccaloni, unpublished data).

Ithomiines are continuously brooded, have overlapping generations, and adults have been estimated to live for over 6 months (Drummond, 1976). They can therefore be collected throughout the year. The adults have conspicuous aposematic wing patterns, are generally low-flying, have slow flapping flight, and species often have high relative abundances. In addition, adult ithomiines (predominantly the males) can be baited easily using plant material (e.g. wilted *Heliotropium*) containing pyrrolizidine alkaloids (Masters, 1968; Pliske, 1975). These factors make ithomiines perhaps the easiest single group of Neotropical butterflies to sample, and species accumulation curves for sites are typically steep and rapidly become asymptotic (Fig. 3).

Are ithomiines good indicators?

Figure 4 demonstrates that there is a strong positive relationship between ithomiine species richness and the overall species richness of all other butterflies across sites, countries, and the Neotropics as a whole ($\log_{10}$–$\log_{10}$ plot: $r = 0{\cdot}977$, $n = 21$, $p < 0{\cdot}001$). The histogram (Fig. 5) demonstrates that the variance of ithomiine proportions across the areas is reasonably low, with ithomiines constituting 4–5% of the butterfly species of 12 out of 21 areas.

Two sites, Brasília and Pakitza, could justifiably have been excluded from this analysis, thereby increasing the level of correlation. The former (Brasília) has the lowest proportion of ithomiines (2·9%) of all sites. It is also the only site where non-tropical-forest vegetation

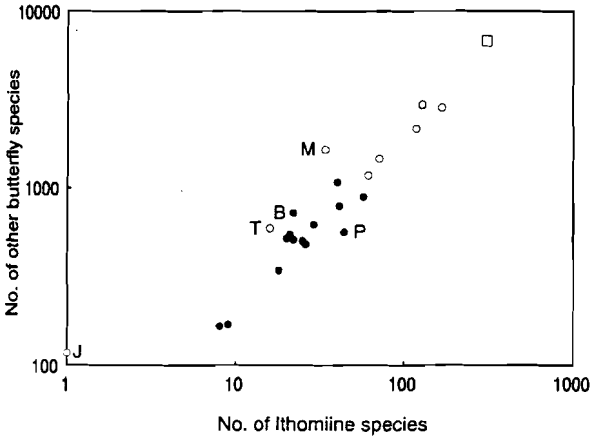

Fig. 4. Log_{10}–log_{10} plot of butterfly species richness (excluding ithomiines) versus ithomiine species richness, for collecting sites (●), countries (○) and the Neotropics as a whole (□) (r = 0·977, n = 21, p < 0·001). B, Brasília; P, Pakitza. Areas excluded from analysis (○): J, Jamaica; T, Trinidad; M, Mexico.

(cerrado) was sampled in addition to tropical forest, and the species total therefore includes non-tropical-forest butterfly species which will have decreased the proportional representation of the tropical forest species (such as the exclusively forest-dwelling ithomiines). Pakitza, in contrast, has the highest proportion of ithomiines of all sites (7·1%). It is the least sampled site, with only 200 person-hours of collecting effort (Table 1). As ithomiines are probably the most easily sampled of the 14 butterfly groups, the majority of ithomiine species at Pakitza, but a relatively smaller percentage of the other butterfly species, will have been recorded, and the proportion of ithomiines will therefore be inflated. Lamas *et al.* (1991) predicted a total of 905 butterfly species at Pakitza, based on the results of a species accumulation study. If we assume that the 44 ithomiine species known from Pakitza represent all the ithomiine species present at this site and that 905 is the actual total for all butterfly species, then ithomiines represent only 4·9% of the site total. The

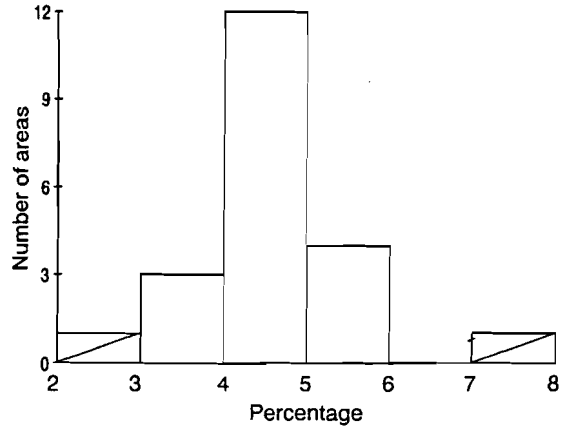

Fig. 5. Distribution of the ithomiine proportions of collecting sites, countries, and the Neotropics as a whole (n = 21). Hatched columns: left, Brasília; right, Pakitza.

only other site at which a similar species accumulation study has been conducted is Laguna Encantada and here a total of 234 butterfly species was predicted (Raguso & Llorente-Bousquets, 1991). If we take the number of ithomiines recorded from this site (nine species) as the absolute total, then ithomiines represent 3·9% of the predicted total of butterflies calculated for the site. This is closer to the Neotropical proportion for ithomiines (4·3%) than is the observed figure given in Table 2 for Laguna Encantada (5·0%). Jaru, with 300 person-hours of collecting effort, probably represents the second least well-sampled site, and this factor is the likely explanation why it has the second highest proportion of ithomiines (6·0%) of any site.

In the case of all the plots given (Figs 2 and 4), the data are not strictly independent, they suffer from spatial autocorrelations, and take the form of the nested set: (Neotropics(Countries(Sites))). The significance tests associated with the various relationships should therefore be treated with caution.

A combined data set for the site and country data was tested against a random-draw model, in which the proportion of ithomiines in each area was assumed to equal that for the whole of the Neotropics. Two Neotropical pools were used, one based on all butterfly species in the Neotropics (309 ithomiines and 6870 other species), and the other with the numbers of non-ithomiines discounted by 10% to allow for non-tropical-forest butterfly species (309 ithomiines and 6183 others). In both cases, correlations between the numbers of ithomiines observed and expected to occur in each area are high, and the relationships are well fitted by a slope of 1 (Fig. 6). As anticipated, expected values based on the discounted regional pool are closer to the observed values.

CONCLUSION

The reasonably invariant relationship between proportions of ithomiine species and overall butterfly species richness means that it should be possible to use the average proportion of ithomiines across all areas (4·6%) to predict the total butterfly species richness of an area of mainland Neotropical forest for which the ithomiine total is known.

Predicting the butterfly species richness of an area in this way is probably less reliable than the two methods currently used to obtain the absolute species richness of an area: (1) counting all the butterfly species in the area; or (2) conducting a species accumulation study of all butterflies in the area and predicting where the accumulation curve will become asymptotic. The former method is, however, expensive in terms of time and resources, especially in areas with high species richness. For example, Lamas *et al.* (1991) calculated that it would take 24,497 person-hours (about 9 years of collecting effort) to collect 99·5% of the 905 butterfly species predicted to occur at Pakitza. The second method (a species accumulation study) is less demanding on time and resources, but it is still many orders of

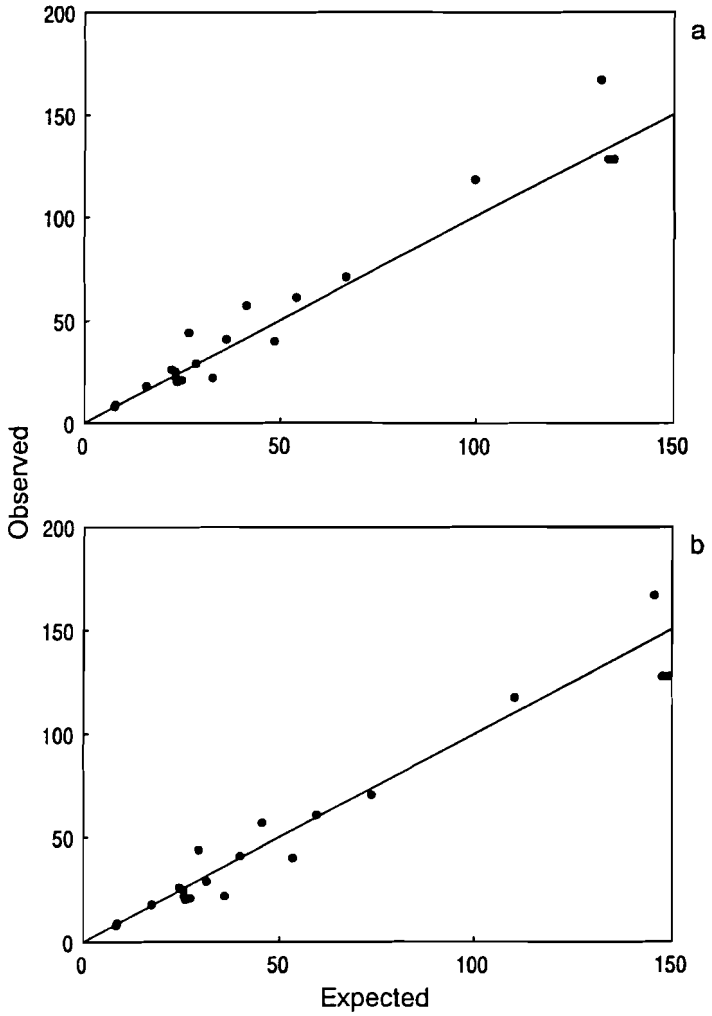

Fig. 6. Relationships between the numbers of ithomiines observed and expected to occur in different collecting sites and countries, with expected values based on the assumption that ithomiines constitute the same proportion of butterfly species as in the regional pool. Plot (a) assumes a regional pool of 7179 butterfly species, and plot (b) one of 6492 (see text for details). The slopes are not fitted lines, but represent equality of observed and expected values. For both plots $r = 0{\cdot}970$, $n = 20$, $p < 0{\cdot}001$.

magnitude more demanding than simply collecting the species of a single easily sampled group (such as the Ithomiinae), because the overall shape of the accumulation curve (for all butterfly species) needs to be well established before robust predictions can be made. In addition, the choice of model fitted to the data may significantly influence the prediction (Soberón & Llorente, 1993), and species accumulation studies can only practically be conducted within relatively small areas.

The main advantage of the method we propose over alternative techniques is therefore its cost effectiveness in terms of time and resources, and it could be valuable in situations where the total butterfly species richness of an area is required rapidly for conservation evaluation.

Using the figure for the overall butterfly richness of an area it should be possible to generate approximate estimates for the species totals of the individual butterfly groups in the area, on the basis of the known relationships between total butterfly species richness and the species richness of the groups across all areas (providing that these are strong). This would, of course, be less satisfactory than actually counting the number of species of each group in the area, but it would be considerably easier than either this method or the alternative of constructing individual species accumulation curves for each group.

Pearson and Cassola (1992) stated that it would take decades of work to determine the patterns of butterfly species richness across the Amazon Basin. However, using ithomiine richness as a predictor of total butterfly richness it may soon be possible to produce a map of predicted butterfly species richness for much of the tropical forests of mainland Central and South America. Distributions of 99 species of Ithomiinae have already been plotted onto a 1° × 1° grid covering the Neotropics (G. W. Beccaloni, unpublished data), and providing these patterns of species richness are representative for the Ithomiinae as a whole, then — using the method proposed above — this map could easily be converted into one representing the approximate richness of all tropical forest butterfly species.

Although we have restricted our analysis to the tropical forest butterfly fauna of the Neotropics, preliminary work suggests that the proportions of the butterfly families and subfamilies found in the forests of the Afrotropical region are also often reasonably invariant or demonstrate simple relationships with overall butterfly richness (for examples see Larsen *et al.*, 1980; Larsen, 1991) and could be used as indicators in a similar way.

NOTE ADDED IN PROOF

Since acceptance of this paper, G. Lamas has provided the authors with the following updated species totals for Peru and for the two Peruvian collecting localities discussed in this paper. Peru: 3352 butterfly species, 202 ithomiine species; Tambopata Natural Reserve: 1234 butterfly species, 42 ithomiine species; Pakitza biological station: 1300 butterfly species, 62 ithomiine species. The proportions of ithomiines in these areas are now 6·03, 3·40 and 4·77% respectively. The largest change is in the case of Pakitza, where the ithomiine proportion has decreased from 7·14% to a value close to the mean proportion of ithomiines across all of the 21 areas analysed (note that with inclusion of the updated figures this proportion decreases from 4·6 to 4·5%). As predicted above, the formerly inflated proportion of ithomiines at Pakitza was probably an artifact of the low collecting effort at this site.

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-CHAPTER 5-

PATTERNS IN SPECIES RICHNESS OF A SUB-SET OF NEOTROPICAL ITHOMIINE BUTTERFLIES (NYMPHALIDAE: ITHOMIINAE): ARE THESE PATTERNS THE SAME FOR OTHER SPECIES OF ITHOMIINE, OR EVEN ALL SPECIES OF FOREST BUTTERFLIES?

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SUMMARY

The geographical distributions of ithomiine butterflies (Nymphalidae: Ithomiinae) are among the best known of any group of organisms in the Neotropical region. Ithomiine butterflies are an exclusively Neotropical group, and extensive distribution records are available for 101 of the 310 currently recognised species. This study documents the patterns in species richness of this sub-set of 101 species across the Neotropics at the scale of 1° x 1° grid cells. The species richness of this group increases with decreasing latitude and peaks to the south of the equator. A greater mean number of species per grid cell with records was found to occur to the south of the equator than to the north. Species richness increases with longitude from east to west in South America and the richest grid cells are located in the eastern foothills of the Andes in Ecuador and Peru. Relationships between the numbers of species of this sub-set and the numbers of all other ithomiine species were investigated at different spatial scales. It is concluded that there is some evidence that the species richness patterns exhibited by this sub-set are representative for ithomiine butterfly species as a whole.

INTRODUCTION

Few quantitative studies exist which document the species richness patterns of groups of organisms across the Neotropical region at spatial scales smaller than that of a country, despite the importance of such data for conservation planning and for the development and testing of biogeographical and ecological hypotheses. Some exceptions are a study on latitudinal gradients of species richness of swallowtail butterflies (Papilionidae) (Slansky 1972; Scriber 1973; Scriber & Gage 1995), and a recent comprehensive study by T. M. Blackburn & K. J. Gaston (in preparation) which documents the species richness patterns of all species of Neotropical birds. Even these studies, however, were conducted at relatively coarse spatial scales - the former used 10° belts of latitude, while the latter used equal area grid cells, each with a surface area of approximately 611000 km².

The present study aims to document the patterns of species richness across the Neotropical region for ithomiine butterflies (Nymphalidae: Ithomiinae), at the scale of 1° x 1° grid cells. In terms of published distribution data, the Ithomiinae are probably the best known relatively large group of Neotropical butterflies (possibly even the best known group of Neotropical insects). Although large data sets exist for heliconiine butterflies (Nymphalidae: Heliconiinae) and swallowtail butterflies (see Brown 1979, and Tyler *et al.* 1994, respectively), heliconiine butterflies are a relatively small group (*c.* 65 species), while the published distribution maps for swallowtail butterflies (Tyler *et al.* 1994) are heavily interpolated and the records on which they are based are not available.

The Ithomiinae are an exclusively Neotropical group of forest-dwelling butterflies, currently comprising some 310 species placed in 52 genera (Brown and Freitas 1994; G. Lamas, in preparation). They occur in moist tropical forests from sea level up to 3000m (Drummond 1976) and range from Mexico (23°N latitude) to Argentina (35°S latitude). Ithomiines are probably the most easily sampled of all groups of Neotropical butterflies, as they are continuously brooded, have long-lived adults, are relatively slow flying, can be baited, and species are often abundant in terms of numbers of individuals (Beccaloni & Gaston 1994).

In consequence, ithomiines are relatively well represented in collections of Neotropical butterflies and the species level distribution records which have been compiled are probably more extensive than for species which belong to other groups of butterfly. Here, using the published distribution data for ithomiines, I identify areas of high regional species richness and present plots showing latitudinal and longitudinal gradients of species richness.

Beccaloni & Gaston (1994) demonstrated that the proportions of species in many of the fourteen families and subfamilies of butterflies found in the tropical forests of mainland Central and South America, show relatively invariant or simple relationships with overall butterfly species richness at both local and regional scales. A statistically strong positive relationship was found between the numbers of species of Ithomiinae and all other butterfly species in an area, such that the proportion of ithomiine species relative to all other butterfly species is relatively constant, independent of the total butterfly species richness or size of an area. This suggests that the species richness patterns of Ithomiinae should mirror the species richness patterns exhibited by all other species of butterfly that occur in the tropical forests of mainland Central and South America.

Unfortunately, extensive distribution data are only readily available for approximately one third of ithomiine species. However, if this sub-set of species and the remaining 209 species of ithomiine exhibit similar patterns of species richness across the Neotropics, then it is plausible that the patterns of species richness documented for this sub-set are representative for Neotropical forest butterfly species as a whole. This possibility is explored in the latter part of this paper.

METHODS

A literature search revealed that distribution records had been compiled and published for 101 species of ithomiine belonging to 26 genera. These species together with the sources of the distribution data are listed in Appendix 5.1. Of the 26 genera represented, 24 include all of the currently recognised species placed in them. In the case of *Napeogenes*, no distribution

records have been compiled for four species (*N. flossina* Butler, *N. larilla* (Hewitson), *N. sodalis* Haensch, and *N. verticilla* (Hewitson)), while in the case of *Hypothyris*, no records are available for one recognised but as yet undescribed species (*Hypothyris* sp. n. Lamas).

Distribution records for all species listed in Appendix 5.1 were compiled in the literature at the level of subspecies, except those for *Melinaea mneme* which had been compiled at species level. The records for the majority of the taxa are contained in Brown (1979) as lists of subspecies recorded in 30' x 30' grid cells grouped by country. Records for the remaining taxa published in other literature sources (see Appendix 5.1) were in the form of lists of collecting localities. Where co-ordinates of these were not given, gazetteers of Neotropical collecting sites (Lamas 1973; Brown 1979) were used to determine their geographical positions. Records taken from the primary sources listed in Appendix 5.1 were supplemented with additional records from the collecting sites listed in Table 5.1.

Species level distribution maps were required for analysis and these were produced in two stages. First, distribution maps for the 597 recognised subspecies of the 101 species listed in Appendix 5.1 were plotted, and second, the maps of all subspecies of each species were combined to produce species level distribution maps (Appendix 5.2). The WORLDMAP computer program (Williams 1992; 1993) was used to produce all distribution maps. The map employed includes most of Mexico, all of Central America and the tropical portion of South America (30°N to 30°S) and is divided into 1° x 1° grid cells. The grid cells on the map used range in area from *c.* 12321 km² (cells between 1° north or south of the equator) to *c.* 10438 km² (cells between 29° and 30° north or south). Unfortunately, an equal-area grid could not be used because the bulk of the distribution records (*i.e.* those contained in Brown 1979) were listed by quarter degree grid cells, and the collecting site(s) where each taxon was recorded within a cell was not given. However, even the equal-area grid maps used in other studies (e.g., Gaston *et al.* 1995; T. M. Blackburn & K. J. Gaston, in preparation) suffer because the topography of the land area covered by a cell is not considered and therefore cells could differ substantially in the amount of surface area (or suitable habitat) included within them.

For ease of subsequent discussion I will refer to the 101 ithomiine species with distribution maps as the 'mapped species' and to the remaining sub-set of species without distribution maps as the 'unmapped species'. Only *c.* 4 of the mapped species range further south than 30°S and none range further north than 30°N.

Using the species distribution maps (Appendix 5.2), the number of species recorded in each 1° x 1° grid cell was counted (Figure 5.1). A total of 734 grid cells contain one or more species records and the total number of species records is 5521 (Figure 5.1). These data cannot be corrected for differences in sampling effort between grid cells because the amount of sampling effort in a grid cell is unknown. Even the number of collecting localities within each grid cell could not be determined because of the way in which the bulk of the data (in Brown 1979) were recorded. Brown (1979) presented lists of taxa recorded in quarter degree grid cells and listed the locality with the greatest number of taxa for each grid cell, plus localities which added new taxa to the list for a cell. Thus the number of localities listed for a grid cell in Brown (1979) will be less than or equal to the number of taxa recorded from it.

The data used to plot Figure 5.2*a-b* were calculated from the species distribution maps (Appendix 5.2). For both plots, the mean number of ithomiine species per grid cell with records within each 1° band of latitude or longitude (*i.e.* the total number of species records in a band divided by the number of grid cells with records in the band) was calculated (Figure 5.2*a-b* lower line) in order to minimise area effects (*i.e.* the greater the number of grid cells with records in a band, the greater the area sampled and hence the greater the expected total number of species in a band). This method does not, however, remove the area effect caused by the fact that 1° grid cells increase in land area with decreasing latitude. In addition, the unknown differences in sampling effort between bands cannot be taken into account. Figure 5.2*a-b* should therefore be interpreted with caution.

The data contained in Table 5.1 were compiled in order to examine the relationship between the numbers of mapped and unmapped ithomiine species across Neotropical areas of different sizes (*i.e.* collecting sites and islands, countries, and the Neotropics as a whole). These data are based on all the reliable and comprehensive species lists of ithomiines

(published and unpublished) known to the author. In the case of most of these lists, the sampling effort was not recorded. However, it is likely that most of the site lists are complete (or almost so), as ithomiines are a relatively easy group to sample and species accumulation curves for sites are typically steep and rapidly become asymptotic (see Beccaloni & Gaston 1994). The country lists and the list for the Neotropics as a whole are also probably largely complete, as ithomiines are a well collected and relatively well studied group of butterflies.

In the case of the plots based on data from Table 5.1 (*i.e.* Figures 5.3 and 5.4), the data suffer from spatial autocorrelations and are therefore not strictly independent. The significance tests associated with the various relationships should therefore be treated with caution.

RESULTS

Patterns in species richness of the mapped ithomiine species

Figure 5.1 illustrates the patterns of richness of the mapped ithomiine species. The grid cell with the greatest number of recorded species (52 species) is situated in the Napo Province of eastern Ecuador in the Andean foothills in the upper Amazon basin. The five next richest cells (47-39 species) are located in the eastern foothills of the Andes in Ecuador and Peru, and the seventh richest cell (35 species) is located in the state of Rondônia, Brazil. Four of the five next richest cells (34-32 species) are located in eastern foothills of the Andes in Ecuador and Peru, while one is in the eastern foothills of the Cordillera Oriental in Colombia. Of the eight next richest cells (30-27 species), one is situated in western foothills of the Cordillera Oriental in Colombia, five in the eastern foothills of the Andes in Ecuador and Peru, another in Acre State, Brazil, and the remaining cell in Rondônia State, Brazil. All of the remaining 714 grid cells with records have less than 27 mapped ithomiine species. The general pattern that emerges is that species richness of the mapped ithomiine species peaks in the eastern foothills of the Andes in Ecuador and Peru between 0° and 12°S, and that smaller subsidiary peaks

occur around the rim of the Amazon basin in south-western Brazil, and in the foothills of the Cordillera Oriental in Colombia.

The mean number of ithomiine species per grid cell with records within a 1° latitudinal band (Figure 5.2*a*) increases with decreasing latitude and is greatest to the south of the equator between 4°S and 5°S (mean of 12.8 species). The second to fifth highest values are: 10°S-11°S (mean of 12.2 species), 1°-2°S (mean of 11.8 species), 3°-4°S (mean of 11.6 species), and 4°N-5°N (mean of 11.4 species). The value of the grid cell with the greatest number of species within a band of latitude also increases towards the equator and peaks to the south (Figure 5.2*a*).

Overall, species richness is greater to the south of the equator than to the north: the mean number of species per grid cell with records south of the equator is 7.9 (s.e.=0.39, n=468), while cells to the north of the equator have a mean of 6.8 species (s.e.=0.35, n=266). These means are significantly different (unpaired heteroscedastic t-test: t=-2.2, d.f.=712, p<0.05).

The mean number of ithomiine species per grid cell with records within a 1° band of longitude (Figure 5.2*b*) is greatest for the band 75°W-76°W (mean of 17.9 species), and the six bands between 74°W and 80°W all have a greater mean number of species per cell with records than do any of the other bands of longitude. The six grid cells with the greatest recorded number of species in the Neotropics are located between 75°W and 79°W (Figure 5.2*b*). Thus not only do bands of longitude in the extreme west of South America contain the grid cells with the greatest recorded numbers of mapped ithomiine species in the Neotropics, but these bands also have a greater mean number of species per cell with records than do any of the other longitudinal bands.

Relationships between species richness of the mapped and unmapped ithomiine species.

Beccaloni & Gaston (1994) found that ithomiine butterflies represent a fairly constant proportion (*c.* 4.5%) of the total of all species of butterfly present in an area of tropical forest on mainland Central and South America, irrespective of the total butterfly species richness or

size of the area examined. A relationship such as the one observed can be explained by a random-draw model (Beccaloni & Gaston 1994), *i.e.* if the species in an area had been randomly drawn from the 'pool' of all species of butterfly in the Neotropical forests, then on average, the proportions of the families and subfamilies of butterflies found in an area will be similar to the proportions of these groups in the total pool.

If such a proportional relationship existed between the mapped and unmapped ithomiine species, then the patterns of species richness exhibited by the mapped species at the scale of a 1° grid cell should be similar to those exhibited by the unmapped species at this spatial scale. Figure 5.3 demonstrates that there is a strong positive relationship between the numbers of mapped and unmapped species at the scale of a site or island ($\log_{10}$-$\log_{10}$ plot of untransformed data: r^2=0.84, n=32, p<0.001) and at the scale of a country ($\log_{10}$-$\log_{10}$ plot of untransformed data: r^2=0.99, n=6, p<0.001). If the relationships observed between the species richness of each of these sub-groups of ithomiines at these two different spatial scales are consistent with each other, then it would be reasonable to infer that a similar relationship exists at intermediate spatial scales e.g., the scale of a 1° grid cell. Unfortunately, although the relationship for a combined data set of sites, islands, countries and the Neotropics as a whole is strong ($\log_{10}$-$\log_{10}$ plot of untransformed data: r^2=0.88, n=39, p<0.001) it is not valid statistically to combine the data in this way, because they take the form of the nested set: (Neotropics(countries(sites and islands))). It is also not possible to statistically compare the regression line for the site and island data with the regression line for the country data, as the range of values of these data sets only partially overlap. Nevertheless, the data are qualitatively consistent with, and certainly do not refute the hypothesis that species richness of the mapped and unmapped ithomiines are likely to be highly positively correlated at the scale of 1° grid cells. However, the precise form of the correlation requires further examination.

To investigate this problem in more detail, data for each of the sites, islands and countries (Table 5.1) were tested against a random-draw model (listed in Appendix 5.3), in which the relative proportions of mapped and unmapped species in an area were assumed to be equal to the relative proportions of these groups in the Neotropics as a whole. The model assumes a

Neotropical pool of 310 ithomiine species, of which 101 are mapped species and the remaining 209 are unmapped species. For each of 38 areas (Table 5.1), a number of species - equal to the total number of ithomiine species observed in the area - were randomly drawn without replacement from the Neotropical pool and the numbers of mapped and unmapped species sampled were recorded. This was performed 10000 times for each area and the number of these iterations with expected numbers of mapped species less than, equal to, and greater than, the observed value were calculated. If 97.5% or more of the total iterations for an area had an expected number of mapped species either greater than or less than the observed number of mapped species in the area, then the number of mapped species observed is significantly different to the number expected at the 5% confidence level.

The relative proportions of mapped and unmapped species in 32 of the 38 areas can be explained by the random-draw model, while in the case of six of these areas (all of them sites) the relative proportions of these groups are significantly different from those expected (Table 5.1). I therefore conclude that a random-draw model cannot provide a general explanation for the relationships observed between the numbers of mapped and unmapped species across all areas (see Figure 5.3). However, as the relationships observed between the numbers of mapped and unmapped species at the scale of site or island and at the scale of country appear to be similar, it is possible that they represent the same relationship. If so, then the relationship between the numbers of mapped and unmapped species at the scale of a 1° grid cell may also be the same, and therefore the patterns of species richness exhibited by these two groups at this spatial scale are also likely to be similar.

Figure 5.4 shows that a strong positive relationship exists between the number of unmapped species recorded from a site or island and the total number of mapped species recorded from the grid cells in which the sites or islands are situated ($\log_{10}$-$\log_{10}$ plot of untransformed data: r^2=0.71, n=32, p<0.001). This finding, together with the fact that a strong positive relationship exists between the numbers of mapped and unmapped species at the scale of a site or island (Figure 5.3), suggests that the species richness patterns exhibited by these groups are probably very similar at the scale of a 1° grid cell.

DISCUSSION

In common with many other groups of organisms (both terrestrial and aquatic), the species richness of the mapped ithomiines increases with decreasing latitude and is highest around the equator (for reviews of latitudinal gradients in species richness see Rohde 1992, and Gaston & Williams, in press). At least 14 different hypotheses have been proposed to explain this general pattern, but support for none of them is conclusive (Gaston & Williams, in press; T. M. Blackburn & K. J. Gaston, in preparation). T. M. Blackburn & K. J. Gaston (in preparation) have pointed out that part of the problem with establishing a plausible theory to explain latitudinal gradients in species richness, is that it may be simplistic to view richness as symmetric about the equator. Platnick (1991) suggested that decline in richness with latitude may be faster in the northern than in the southern hemisphere - therefore species richness is greater to the south of the equator. Several groups of taxa are known to exhibit this pattern (reviewed in Gaston & Williams, in press), including New World spiders (Platnick 1991) and New World birds (T. M. Blackburn & K. J. Gaston, in preparation), and the current study demonstrates that the mapped ithomiine species are no exception. The reasons for such asymmetric latitudinal patterns in species richness are currently unknown and it remains to be shown whether they are a general phenomenon.

Few studies have examined longitudinal gradients in species richness for groups of organisms in the Neotropical region. One exception is a study of the New World avifauna by T. M. Blackburn & K. J. Gaston (in preparation). This study shows that species richness of Neotropical birds increases with longitude from east to west. The mapped ithomiine species also exhibit a pattern of increasing species richness with longitude from east to west. Interestingly, Bates (1862) was first to observe this pattern for ithomiines. He stated, "I found the number of species to increase in travelling from east to west, from the Lower Amazons towards the eastern slopes of the Andes."

In the case of both Neotropical birds (T. M. Blackburn & K. J. Gaston, in preparation) and the mapped ithomiine butterflies, the Neotropical grid cells with the greatest species richness

are situated in the Andean region of western South America. This coincidence suggests that the greater richness of these cells (compared with eastern cells in the same latitudinal band) may, at least partly, be a product of environmental heterogeneity e.g., habitat or topographic diversity (T. M. Blackburn & K. J. Gaston, in preparation). Thus grid cells situated in the Andean region (and therefore also the longitudinal bands which include this region) may have higher species richness because they include a greater number of different types of habitat (each habitat containing different species) than do grid cells further to the east in South America. In addition, it seems plausible that more range restricted species occur in the Andean region because of its rugged topography and, if true, this would also inflate the species richness of grid cells in this region.

Topographic and habitat diversity may not, however, supply the complete explanation. The richest known Neotropical collecting sites for mapped ithomiine species (and ithomiine species as a whole) are situated in the Andean region (more specifically in the eastern Andean foothills of Ecuador and Peru), with the exception of the Caucalandia site in Rondônia State, Brazil (Table 5.1). This suggests that point diversity of ithomiine species probably peaks in the upper Amazon basin of western South America (the sites are relatively small and usually only possess a single major type of habitat). All of the richest grid cells for mapped species include part of the eastern Andean foothills. Andean cells to the west of these are less species rich (Figure 5.1), including those cells which cover part of the western Andean foothills and which probably possess similar environmental heterogeneity to the richer eastern cells (e.g., habitats ranging from lowland tropical moist forest to high altitude Andean cloud forest). It therefore seems likely that environmental heterogeneity can at best only partly explain why eastern Andean grid cells have high species richness. A major reason for the high richness of these cells may be that they include the habitat type with possibly the greatest density of ithomiine species in the Neotropics (*i.e.* the forests of the eastern Andean foothills).

The positive correlation observed between the numbers of mapped and unmapped ithomiine species recorded from a site or island (Figure 5.3), and the positive correlation seen between the number of unmapped ithomiine species recorded from a site or island and the

number of mapped species recorded from the grid cells in which these areas are located (Figure 5.4), suggest that the numbers of mapped and unmapped species are likely to be positively correlated at the scale of a 1° grid cell. In addition, the apparently similar positive relationships observed between the numbers of mapped and unmapped species at the scale of a site or island and between these groups at the scale of a country (Figure 5.3), further suggest that this is probably the case. If this suggestion is correct, then the species richness patterns of the mapped and unmapped species across the Neotropics should at least be broadly similar, and therefore so too may be the species richness patterns exhibited by Neotropical forest butterfly species as a whole (see Introduction). However tempting this speculation may be, it cannot be accepted until further supporting evidence is available.

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Figure 5.1. Maps of species richness of the mapped ithomiine butterflies (101 species in total) (*a*) number of species recorded in a 1° x 1° grid cell, (*b*) the number of species in a grid cell represented by grey-scale intensities (light grey represents the minimum value, black with a white cross the maximum, while white areas are those with no data or no species).

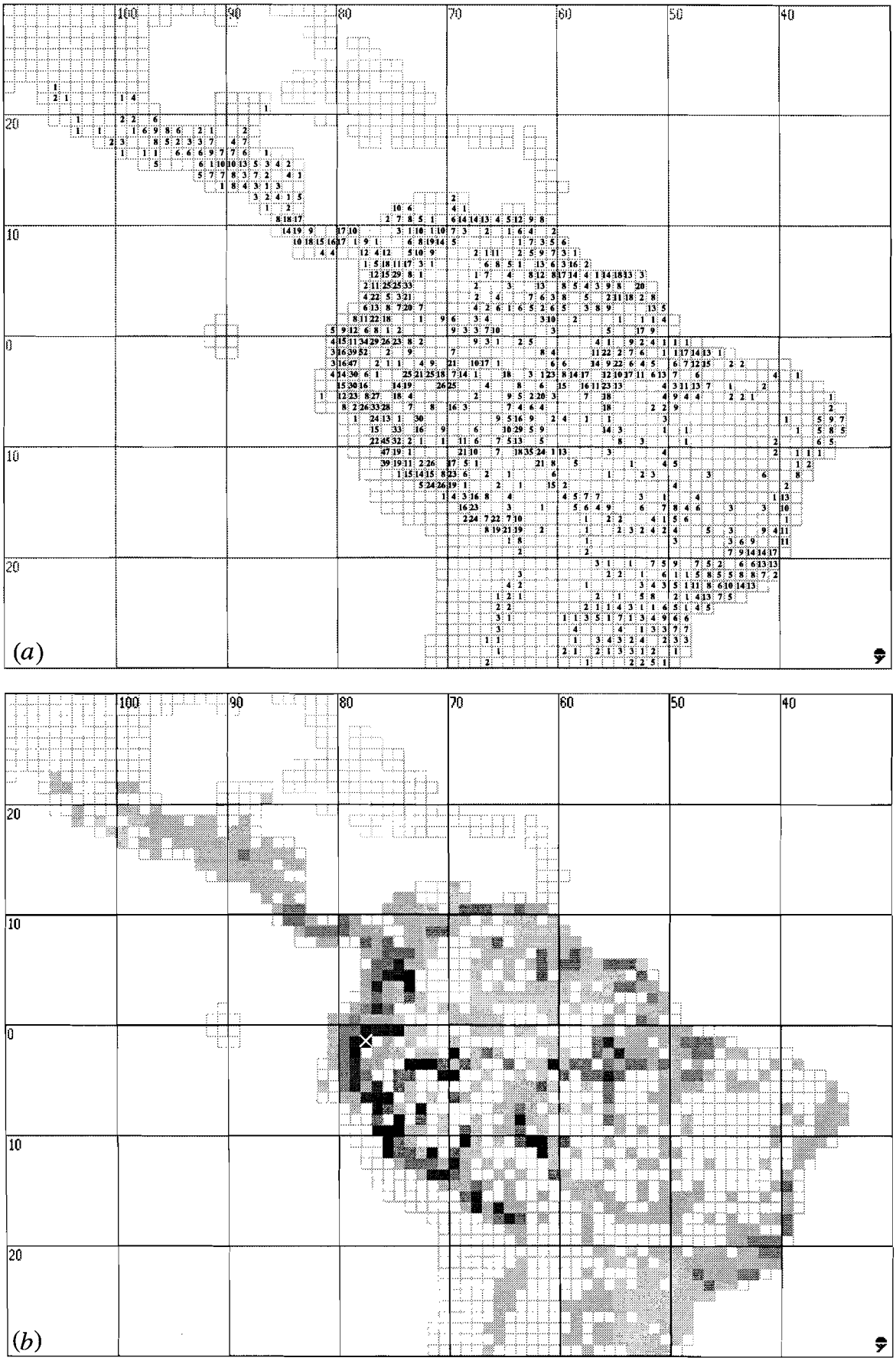
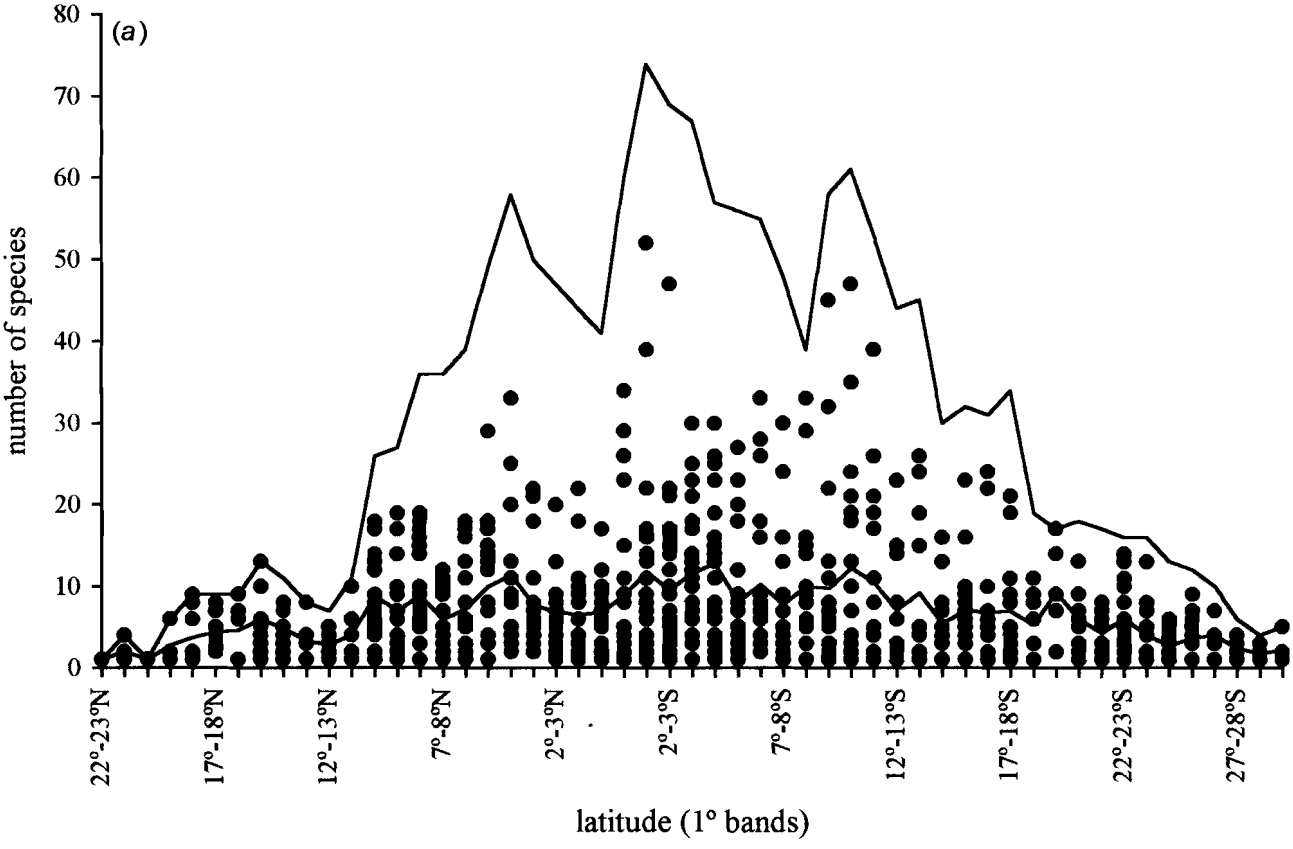

100
90
80
70
60
50
40
20
10
0
10
20
(a)
100
90
80
70
60
50
40
20
10
0
10
20
(b)

FIGURE 5.1

Figure 5.2. Gradients in species richness of the mapped ithomiine butterflies (101 species in total) (*a*) latitudinal gradient, (*b*) longitudinal gradient. For both plots, the data markers represent the number of species recorded in the 1° x 1° grid cells within a 1° band; the upper line is the total number of species in a 1° band; while the lower line is the mean number of species per 1° grid cell with records within each 1° band.


(a)
number of species
0
10
20
30
40
50
60
70
80
22°-23°N
17°-18°N
12°-13°N
7°-8°N
2°-3°N
2°-3°S
7°-8°S
12°-13°S
17°-18°S
22°-23°S
27°-28°S
latitude (1° bands)

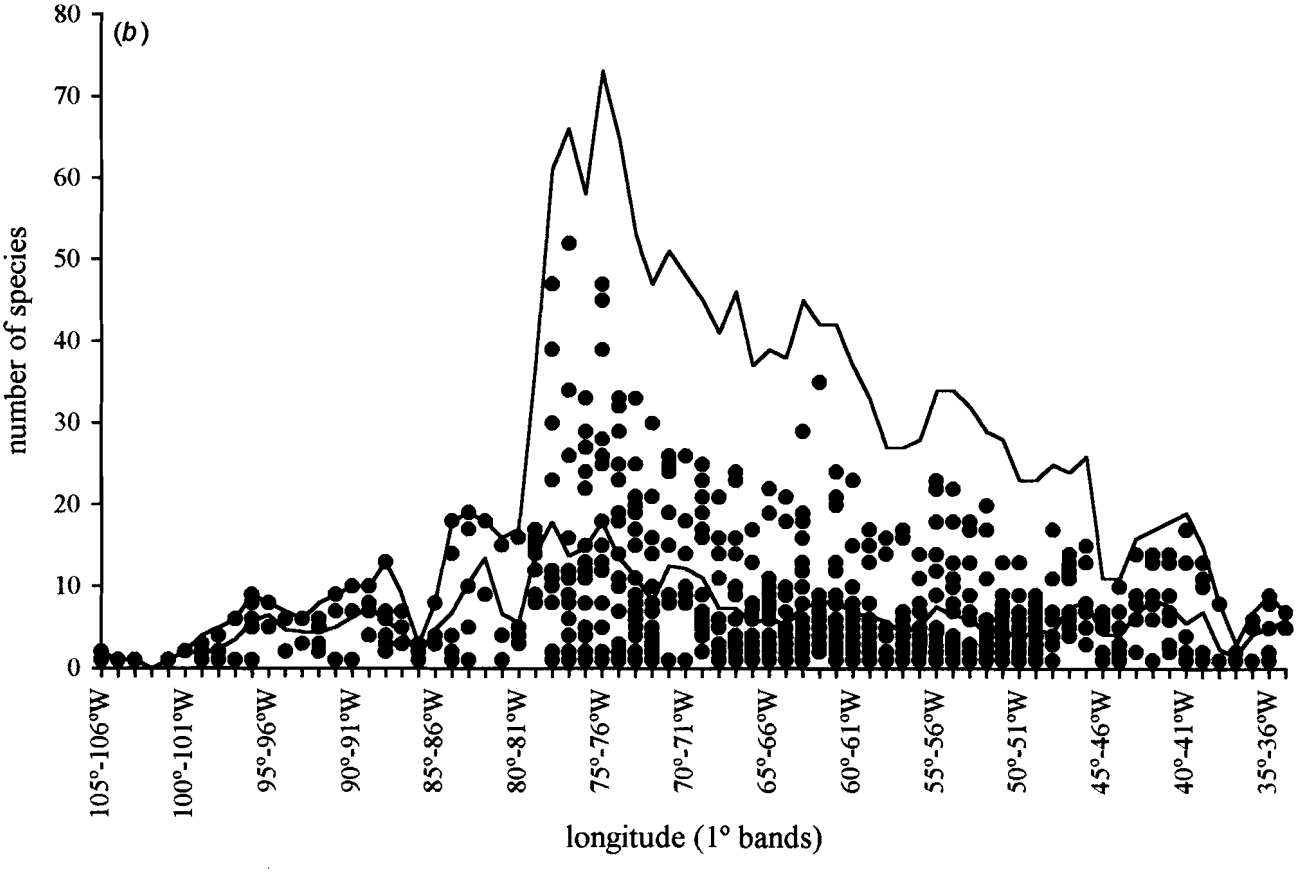

(b)
number of species
0
10
20
30
40
50
60
70
80
105°-106°W
100°-101°W
95°-96°W
90°-91°W
85°-86°W
80°-81°W
75°-76°W
70°-71°W
65°-66°W
60°-61°W
55°-56°W
50°-51°W
45°-46°W
40°-41°W
35°-36°W
longitude (1° bands)

FIGURE 5.2

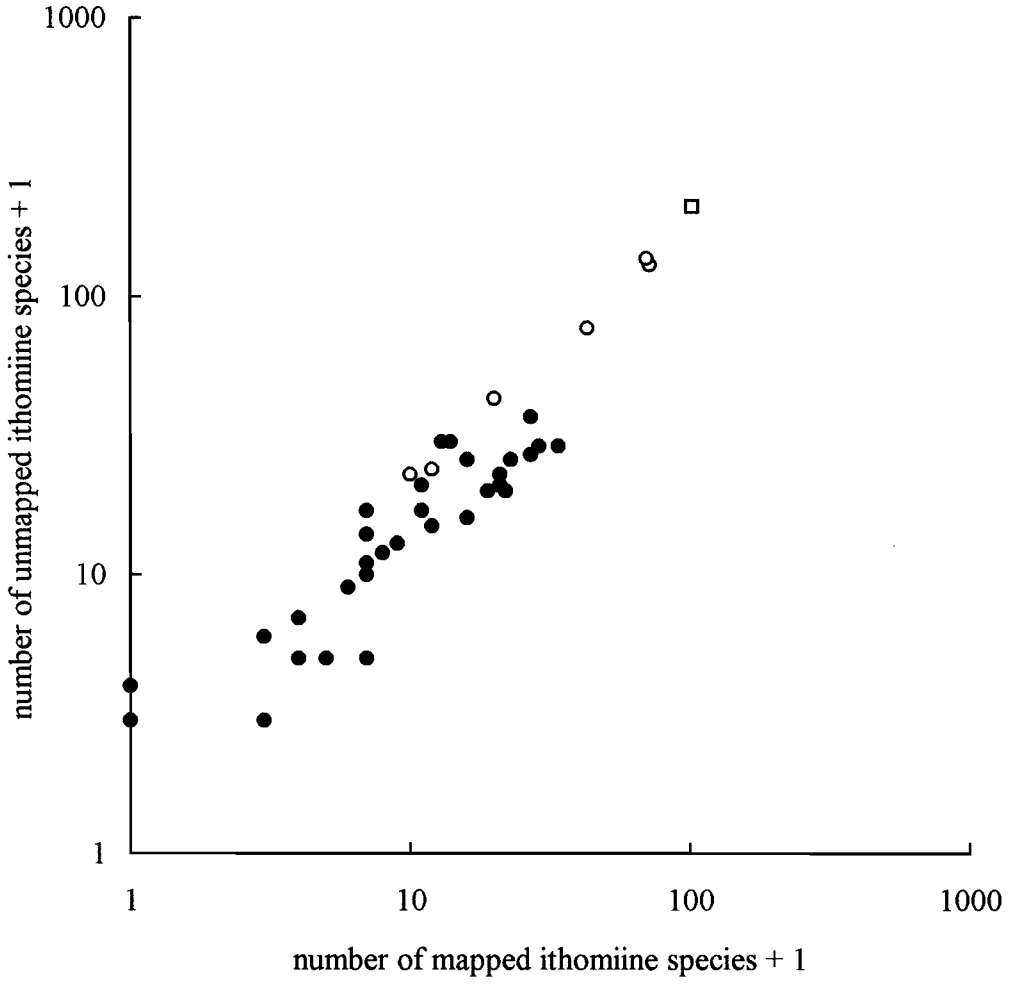


Figure 5.3. Log-log plot of the number of unmapped ithomiine species versus the number of mapped ithomiine species, for collecting sites or islands (●), countries (○) and the Neotropics as a whole (□).

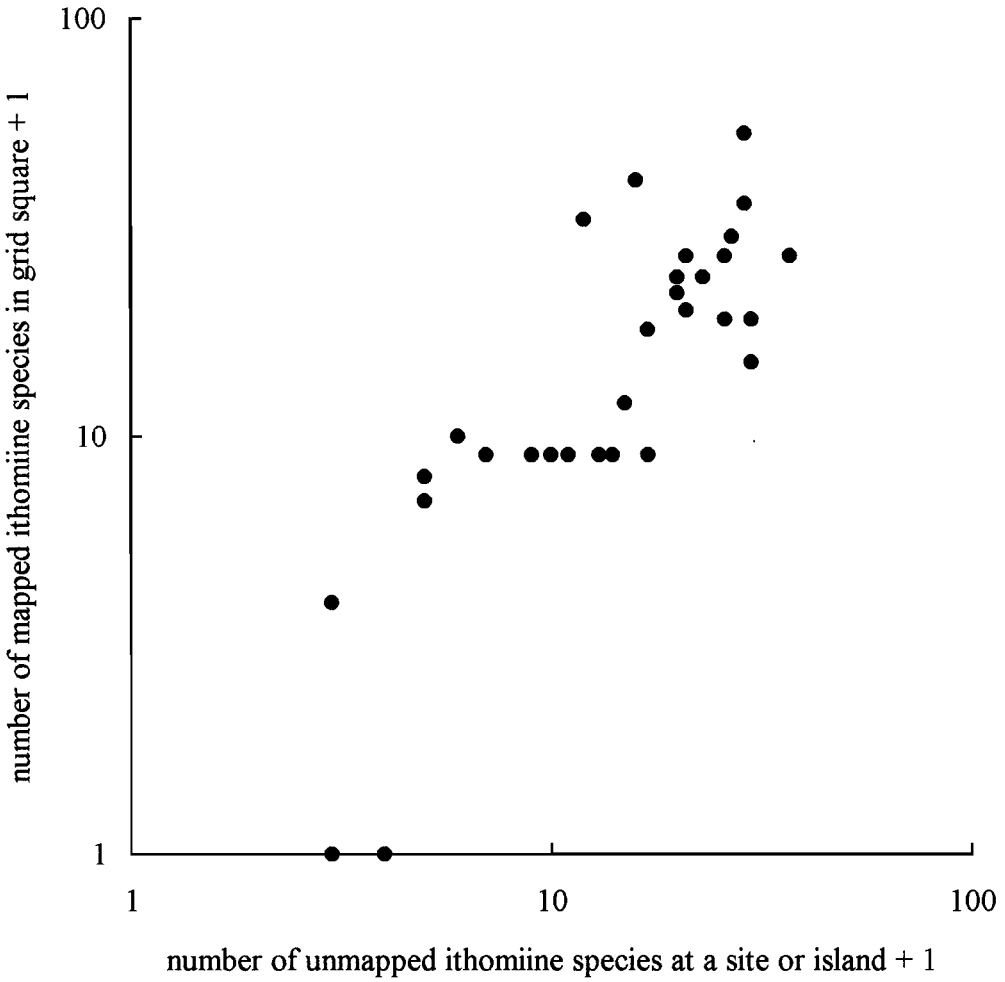


Figure 5.4. Log-log plot showing the relationship between the numbers of unmapped ithomiine species recorded from a collecting site or island and the numbers of mapped ithomiine species recorded from the 1° x 1° grid cells in which these areas are located.

Table 5.1. *Neotropical areas with reliable and comprehensive species lists of ithomiine butterflies*

(NS, not significantly different to expected value at 5% level)

areas	sources	total number of ithomiine species[a]	number of mapped ithomiine species[a]	probability that the observed number of mapped species is explained by a random-draw model (see text)
Collecting sites				
Las Minas, Veracruz, Mexico. *c.* 19°45'N, 97°06'W.	Beutelspacher (1975)	2	0	NS
Sierra de Tuxtla, Veracruz, Mexico. 18°45'N, 95°27'W - 18°10'N, 94°42'W.	Ross (1976)	19	6	NS
Estacion de Biologia Tropical "Los Tuxtlas", Veracruz, Mexico. *c.* 18°35'N, 95°05'W.	Raguso & Llorente-Bousquets (1991)	13	5	NS
Laguna Encantada, Veracruz, Mexico. 18°28'N, 95°12'W.	Raguso & Llorente-Bousquets (1991)	9	3	NS
La Soledad, Oaxaca, Mexico. *c.* 17°50'N, 96°10'W.	De la Maza (1979a)	15	6	NS
La Esperanza, Oaxaca, Mexico. 17°40'N, 96°10'W.	De la Maza (1980)	22	6	NS
Metates, Oaxaca, Mexico. *c.* 17°34'N, 96°17'W.	De la Maza (1979b)	19	6	NS
El Chorreadero, Chiapas, Mexico. *c.* 16°43'N, 93°00'W.	Beutelspacher (1983)	8	4	NS
Augustine Camp, Cayo, Belize. 16°58'N, 88°58'W.	Ross (1964)	7	3	NS
La Selva, Heredia, Costa Rica. 10°26'N, 83°59'W.	Haber (1978); DeVries (1983)	26	10	NS
Monteverde, Puntarenas, Costa Rica. 10°18'N, 84°48'W.	Haber (1978); DeVries (1983)	40	15	NS
Turrialba, Cartago, Costa Rica. 09°54'N, 83°41'W.	Haber (1978)	30	10	NS
San Vito, Puntarenas, Costa Rica. 08°47'N, 83°00'W.	Haber (1978); DeVries (1983)	42	13	NS
Rancho Los Chorros, Sucre, Venezuela. 10°35'N, 62°08'W.	Convey (1990)	7	2	NS
Rancho Grande, Aragua, Venezuela. 10°21'N, 67°41'W.	Fox & Fox (1947); Beebe (1950); Lamas & Pérez (1981)	41	12	NS
Limoncocha, Napo, Ecuador. 00°24'S, 76°38'W.	Drummond (1976)	52	26	$p < 0.05$
Jatun Sacha Biological Station, Napo, Ecuador. 01°04'S, 77°36'W.	G. Beccaloni (unpublished)	56	28	$p < 0.05$
Castaña, Rio Napo, Loreto, Peru. 00°48'S, 75°14'W.	G. Lamas (unpublished)	47	22	$p < 0.05$
Arcadia, Rio Napo, Loreto, Peru. 00°59'S, 75°19'W.	G. Lamas (unpublished)	40	20	$p < 0.05$
Yanamono, Rio Amazonas, Loreto, Peru. *c.* 03°27'S, 72°48'W.	G. Lamas (unpublished)	40	21	$p < 0.05$

Table 5.1 - continued

Cordillera del Condor, Amazonas, Peru. 03°54'S, 78°26'W - 04°01'S, 78°24'W.	G. Lamas (unpublished)	30	15	NS
Cordillera del Sira, Huánuco, Peru. *c.* 09°25'S, 74°45'W.	G. Lamas (unpublished)	18	7	NS
Pakitza Biological Station, Manu National Park, Madre de Dios, Peru. 11°55'S, 71°15'W.	G. Lamas (unpublished)	62	26	NS
Cuzco Amazonico, Rio Madre de Dios, Madre de Dios, Peru. 12°35'S, 69°05'W.	G. Lamas (unpublished)	37	18	NS
Tambopata Natural Reserve, Madre de Dios, Peru. 12°50'S, 69°17'W.	Lamas (1994a)	42	20	NS
Pampas del Heath, Madre de Dios, Peru. 12°57'S, 68°52'W - 12°57'S, 68°54'W.	Lamas (1994b)	10	6	NS
Caucalandia area, Rondônia, Brazil. 10°18'S, 62°60'W.	G. Austin (unpublished)	61	33	$p < 0.05$
Poços de Caldas area, Minas Gerais, Brazil. 21°47'S, 46°33'W.	Ebert (1969)	20	8	NS
Campinas, São Paulo, Brazil. 22°53'S, 47°05'W.	Brown (1987)	25	11	NS
Cafayate, Salta, Argentina. 26°05'S, 65°58'W.	Hayward (1966)	4	2	NS
Islands				
Trinidad	Barcant (1970)	16	6	NS
Tobago	Barcant (1970)	3	0	NS
Countries				
Mexico	De la Maza *et al.* (1989)	34	11	NS
Costa Rica	DeVries (1987)	61	19	NS
Venezuela	A. Neild (unpublished)	118	42	NS
Ecuador	T. Racheli (unpublished)	200	71	NS
Peru	G. Lamas (unpublished)	205	69	NS
Argentina	Hayward (1973)	31	9	NS
Neotropics	G. Lamas (in preparation)	310	101	-

[a]Nomenclature of ithomiine species was updated, where possible, using a recent systematic list (G. Lamas, in preparation), thus species totals may be different from the original literature source.

APPENDIX 5.1. List of the mapped ithomiine species, sources of distribution records and reference numbers to the species distribution maps in Appendix 5.2

species (arranged by tribe)[a]	map number	sources of distribution records[b]
Tithoreini		
Roswellia acrisione (Hewitson)	1	Brown (1979)
Athesis clearista Doubleday	2	Fox (1956)
Patricia demylus (Godman & Salvin)	3	Brown (1979)
Patricia dercyllidas (Hewitson)	4	Brown (1979)
Patricia oligyrtis (Hewitson)	5	Brown (1979)
Eutresis dilucida Staudinger	6	Brown (1979)
Eutresis hypereia Doubleday	7	Brown (1979)
Olyras crathis Doubleday	8	Brown (1979)
Olyras insignis Salvin	9	Brown (1979)
Athyrtis mechanitis Felder & Felder	10	Brown (1979)
Elzunia humboldt (Latreille)	11	Brown (1979)
Elzunia pavonii (Butler)	12	Brown (1979)
Tithorea harmonia (Cramer)	13	Brown (1979)
Tithorea tarricina Hewitson	14	Brown (1979)
Melinaeini		
Melinaea crameri Godman & Salvin	15	Brown (1979)
Melinaea ethra (Godart)	16	Brown (1979)
Melinaea idae (Felder & Felder)	17	Brown (1979)
Melinaea isocomma Forbes	18	Brown (1979)
Melinaea lilis (Doubleday)	19	Brown (1979)
Melinaea ludovica (Cramer)	20	Brown (1979)
Melinaea maelus (Hewitson)	21	Brown (1979)
Melinaea marsaeus (Hewitson)	22	Brown (1979)
Melinaea menophilus (Hewitson)	23	Brown (1979)
Melinaea mnasias (Hewitson)	24	Brown (1979)
Melinaea mneme (Linnaeus)	25	Fox (1960)
Melinaea satevis (Doubleday)	26	Brown (1979)
Melinaea scylax Salvin	27	Brown (1979)
Mechanitini		
Paititia neglecta Lamas	28	Lamas (1979)
Thyridia psidii (Linnaeus)	29	Lamas (1973)
Sais browni Takahashi	30	Brown (1979)
Sais rosalia (Cramer)	31	Brown (1979)
Forbestra equicola (Cramer)	32	Brown (1979)
Forbestra olivencia (Bates)	33	Brown (1979)
Forbestra proceris (Weymer)	34	Brown (1979)
Mechanitis lysimnia (Fabricius)	35	Brown (1979)
Mechanitis mazaeus Hewitson	36	Brown (1979)
Mechanitis menapis Hewitson	37	Brown (1979)
Mechanitis messenoides Felder & Felder	38	Brown (1979)
Mechanitis polymnia (Linnaeus)	39	Brown (1979)
Scada batesi Haensch	40	Brown (1979)
Scada karschina (Herbst)	41	Brown (1979)

APPENDIX 5.1 - continued

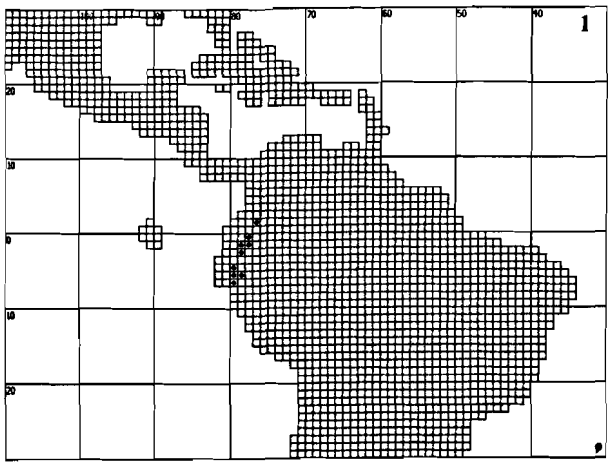
Scada kusa (Hewitson)	42	Brown (1979)
Scada reckia (Hübner)	43	Brown (1979)
Scada zemira (Hewitson)	44	Brown (1979)
Scada zibia (Hewitson)	45	Brown (1979)
New tribe		
Placidula euryanassa (Felder & Felder)	46	Brown (1979)
Methonini		
Methona confusa Butler	47	Lamas (1973)
Methona curvifascia Weymer	48	Lamas (1973)
Methona grandior (Forbes)	49	Lamas (1973)
Methona maxima (Forbes)	50	Lamas (1973)
Methona megisto Felder & Felder	51	Lamas (1973)
Methona singularis (Staudinger)	52	Lamas (1973)
Methona themisto (Hübner)	53	Lamas (1973)
Napeogenini		
Aremfoxia ferra (Haensch)	54	Fox & Real (1971); plus data from 3 specimens in the collection of The Natural History Museum (London)
Epityches eupompe (Geyer)	55	Brown (1979)
Garsauritis xanthostola (Bates)	56	Brown (1979)
Rhodussa cantobrica (Hewitson)	57	Brown (1979)
Hyalyris antea (Hewitson)	58	Brown (1979)
Hyalyris coeno (Doubleday)	59	Brown (1979)
Hyalyris excelsa (Felder & Felder)	60	Brown (1979)
Hyalyris fiammetta (Hewitson)	61	Brown (1979)
Hyalyris frater (Salvin)	62	Brown (1979)
Hyalyris juninensis Fox & Real	63	Brown (1979)
Hyalyris latilimbata (Weymer)	64	Brown (1979)
Hyalyris leptalina (Felder & Felder)	65	Brown (1979)
Hyalyris oulita (Hewitson)	66	Brown (1979)
Hyalyris praxilla (Hewitson)	67	Brown (1979)
Napeogenes achaea (Hewitson)	68	Brown (1979)
Napeogenes aethra (Hewitson)	69	Brown (1979)
Napeogenes apulia (Hewitson)	70	Brown (1979)
Napeogenes cranto Felder & Felder	71	Brown (1979)
Napeogenes glycera Godman	72	Brown (1979)
Napeogenes harbona (Hewitson)	73	Brown (1979)
Napeogenes inachia (Hewitson)	74	Brown (1979)
Napeogenes omissa Strand	75	Brown (1979)
Napeogenes peridia (Hewitson)	76	Brown (1979)
Napeogenes pharo (Felder & Felder)	77	Brown (1979)
Napeogenes rhezia (Geyer)	78	Brown (1979)
Napeogenes stella (Hewitson)	79	Brown (1979)
Napeogenes sylphis (Guérin)	80	Brown (1979)
Napeogenes tolosa (Hewitson)	81	Brown (1979)
Hypothyris anastasia (Bates)	82	Brown (1979)
Hypothyris connexa (Hall)	83	Brown (1979)

APPENDIX 5.1 - continued

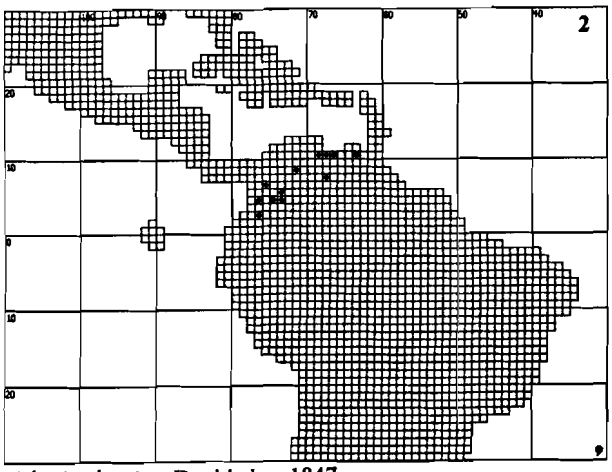
Hypothyris daphnis d'Almeida	84	Brown (1979)
Hypothyris euclea (Godart)	85	Brown (1979)
Hypothyris fluonia (Hewitson)	86	Brown (1979)
Hypothyris gemella Fox	87	Brown (1979)
Hypothyris leprieuri (Feisthamel)	88	Brown (1979); Brown (1980)
Hypothyris lycaste (Fabricius)	89	Brown (1979)
Hypothyris mamercus (Hewitson)	90	Brown (1979)
Hypothyris mansuetus (Hewitson)	91	Brown (1979)
Hypothyris meterus (Hewitson)	92	Brown (1979)
Hypothyris moebiusi (Haensch)	93	Brown (1979)
Hypothyris ninonia (Hübner)	94	Brown (1979)
Hypothyris semifulva (Salvin)	95	Brown (1979)
Hypothyris thea (Hewitson)	96	Brown (1979)
Hypothyris vallonia (Hewitson)	97	Brown (1979)
Ithomiini		
Pagyris cymothoe (Hewitson)	98	Lamas (1986)
Pagyris priscilla Lamas	99	Lamas (1986)
Pagyris ulla (Hewitson)	100	Lamas (1986)
Godyridini		
Veladyris pardalis (Salvin)	101	Lamas (1980)

[a] Taxonomy largely follows a recent systematic list (G. Lamas, in preparation).
[b]Additional distribution records were taken from the lists of species recorded from the collecting sites listed in Table 5.1.

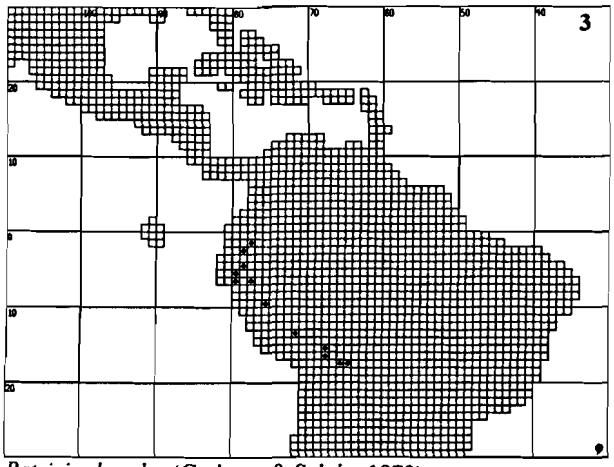
APPENDIX 5.2. Distribution maps of ithomiine species (see text and Appendix 5.1)



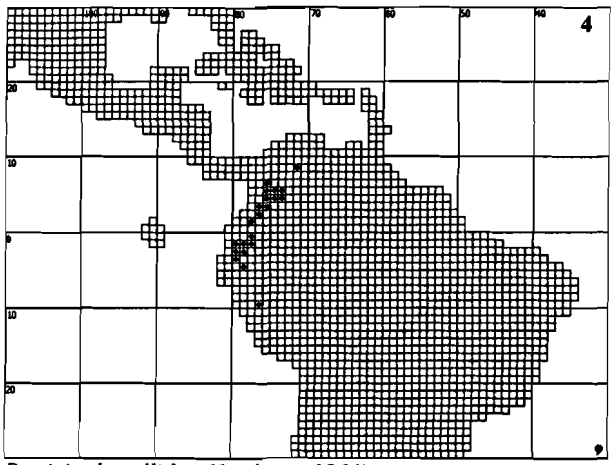
Roswellia acrisione (Hewitson, 1869)



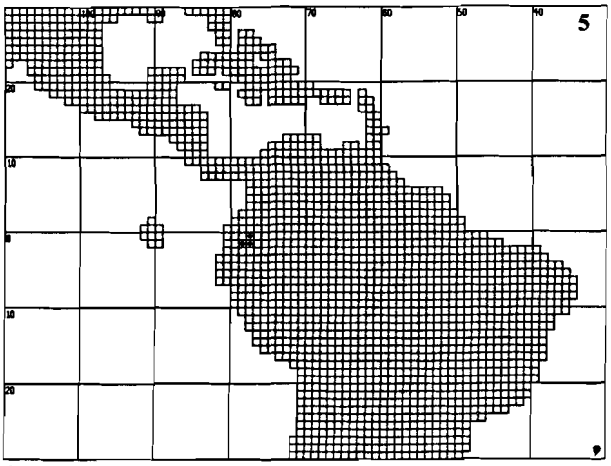
Athesis clearista Doubleday, 1847



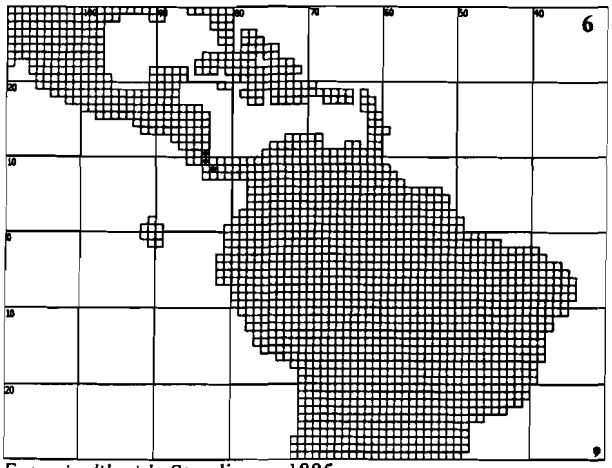
Patricia demylus (Godman & Salvin, 1879)



Patricia dercyllidas (Hewitson, 1864)

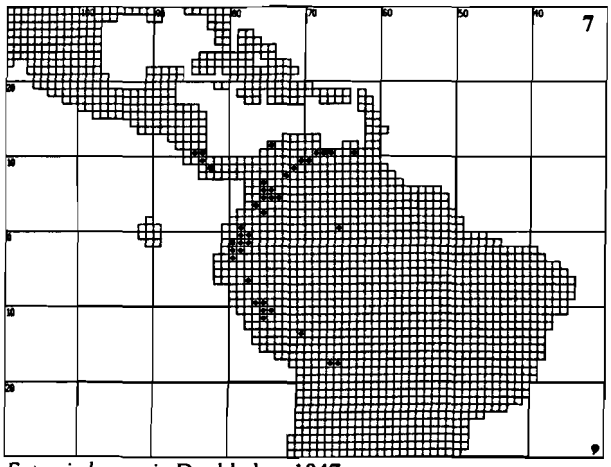


Patricia oligyrtis (Hewitson, 1877)

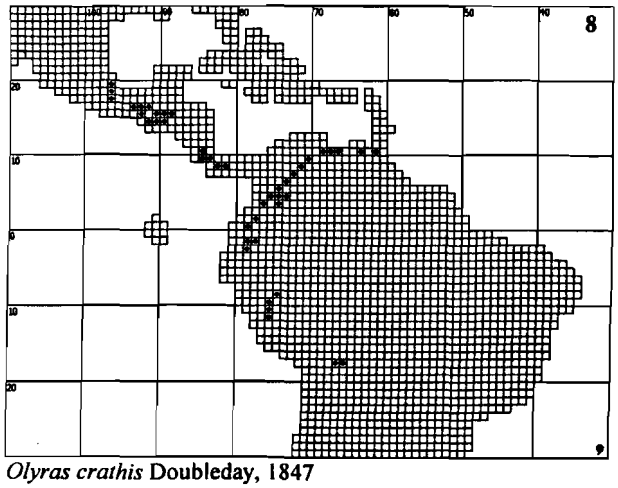


Eutresis dilucida Staudinger, 1885

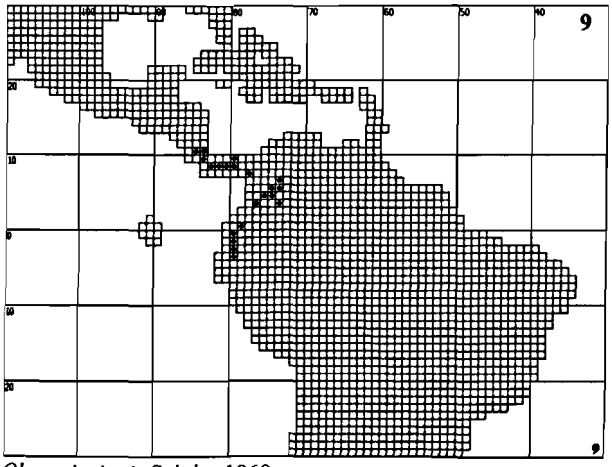
APPENDIX 5.2 - continued



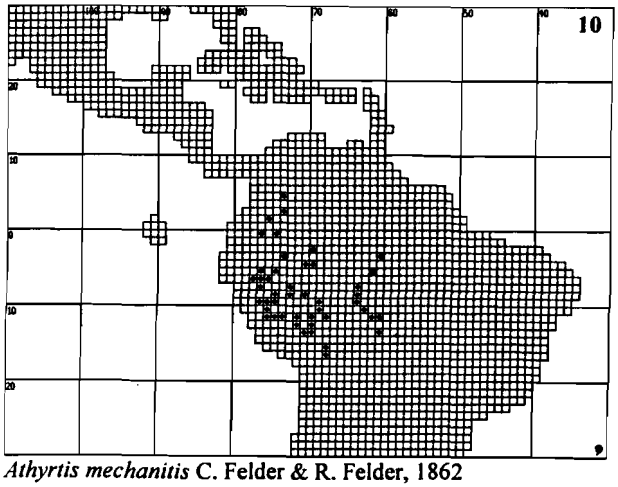
Eutresis hypereia Doubleday, 1847



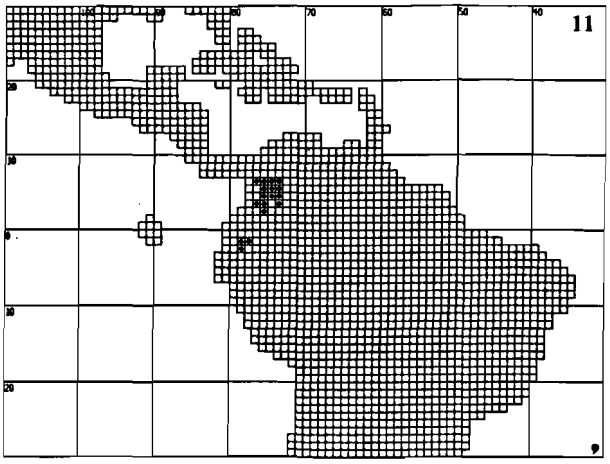
Olyras crathis Doubleday, 1847



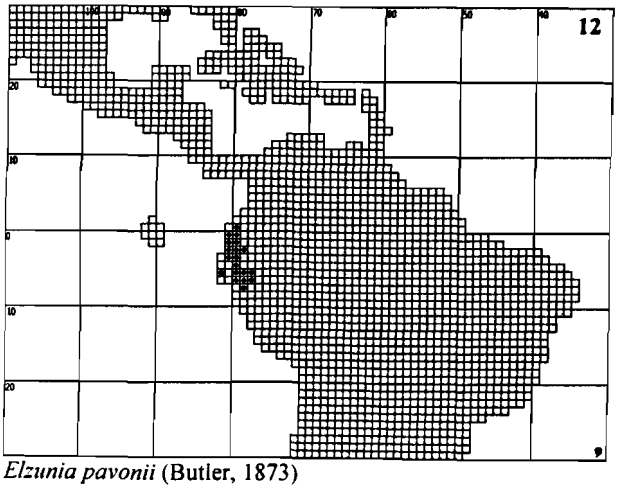
Olyras insignis Salvin, 1869



Athyrtis mechanitis C. Felder & R. Felder, 1862

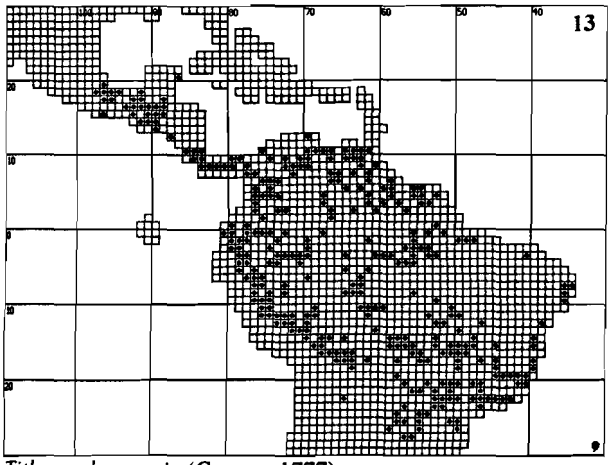


Elzunia humboldt (Latreille, [1809])

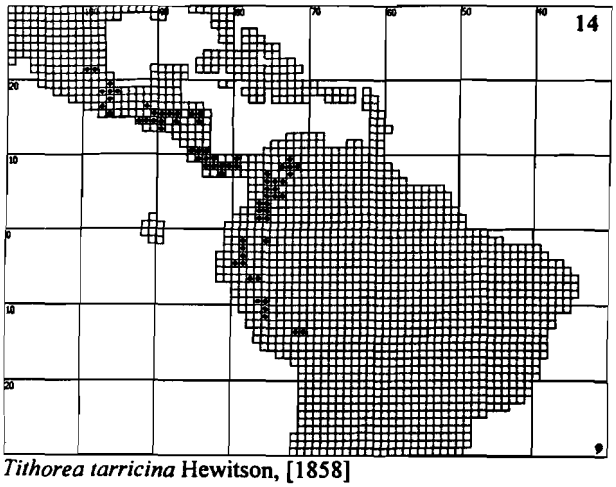


Elzunia pavonii (Butler, 1873)

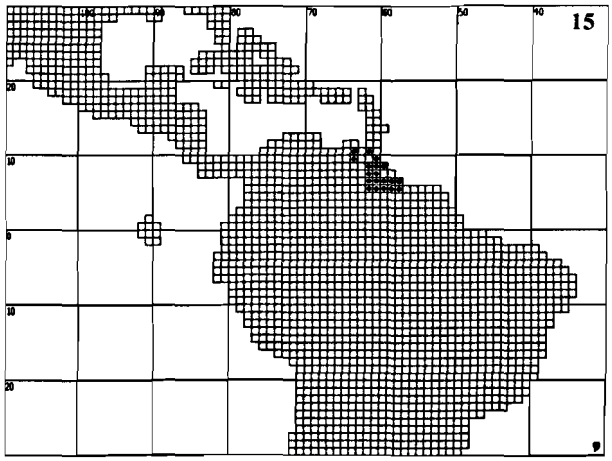
APPENDIX 5.2 - continued



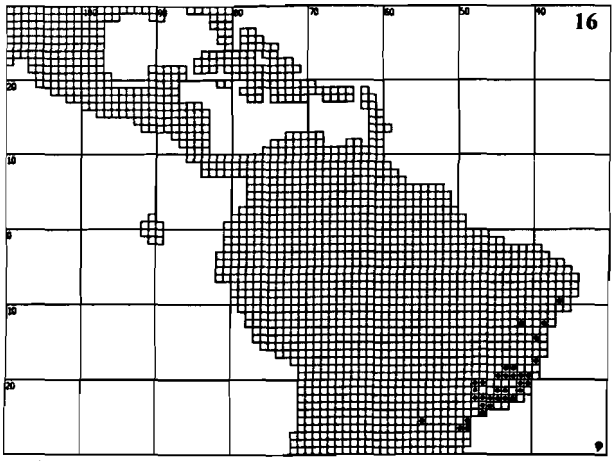
Tithorea harmonia (Cramer, 1777)



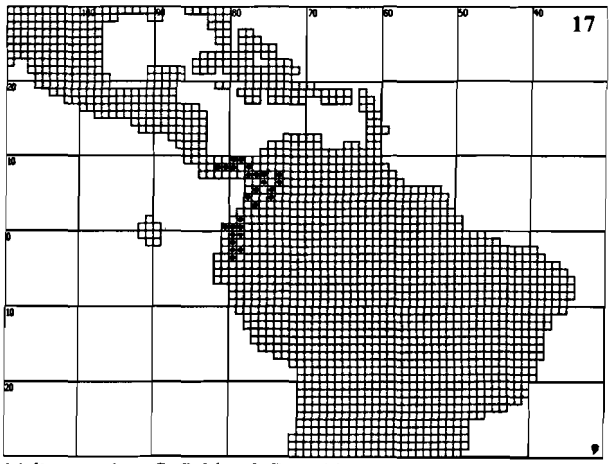
Tithorea tarricina Hewitson, [1858]



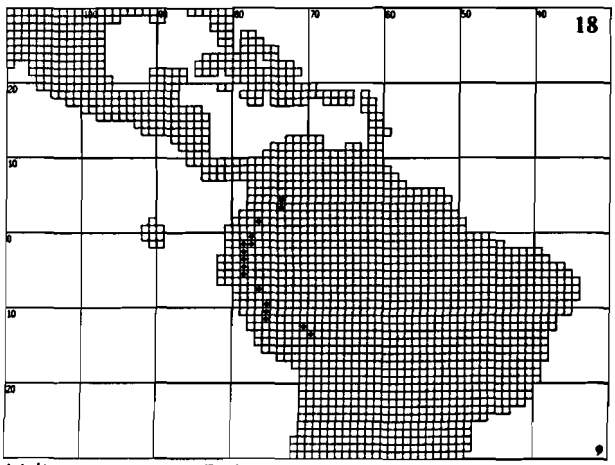
Melinaea crameri Godman & Salvin, 1898



Melinaea ethra (Godart, 1819)

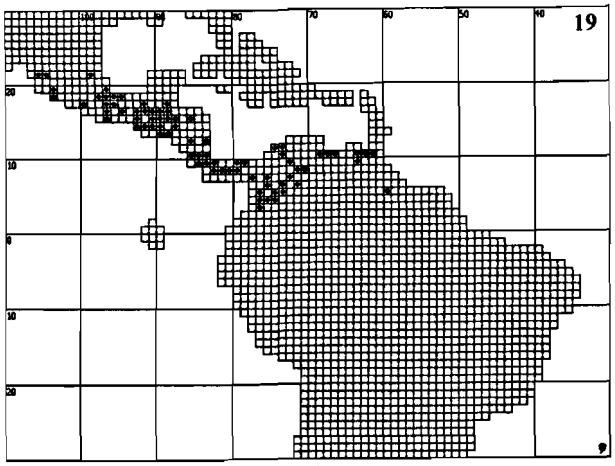


Melinaea idae (C. Felder & R. Felder, 1862)

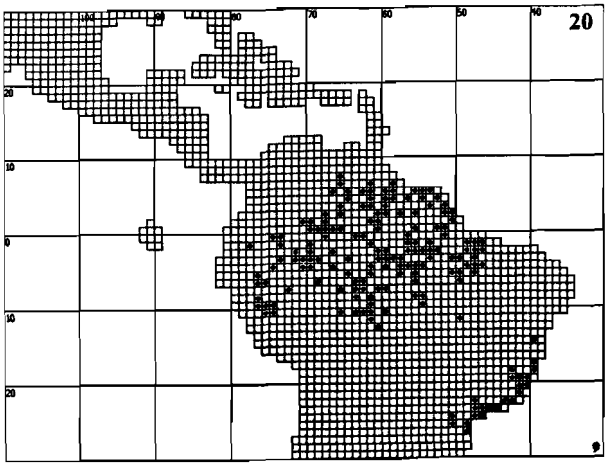


Melinaea isocomma Forbes, 1948

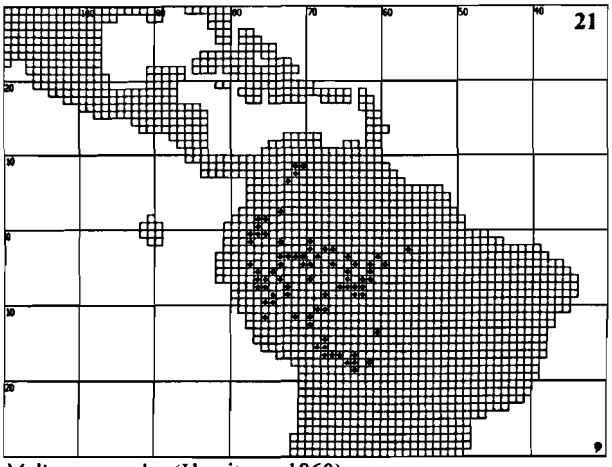
APPENDIX 5.2 - continued



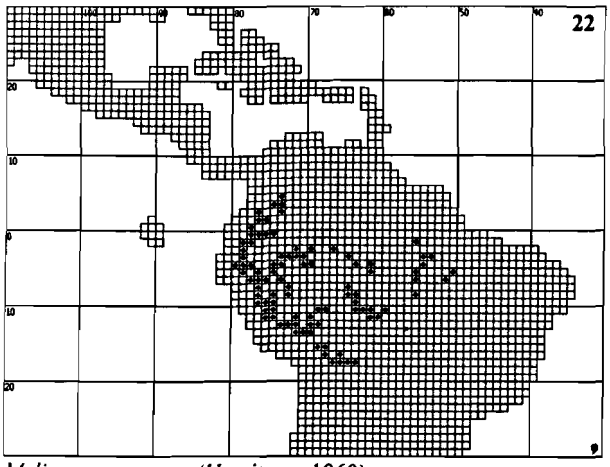
Melinaea lilis (Doubleday, 1847)



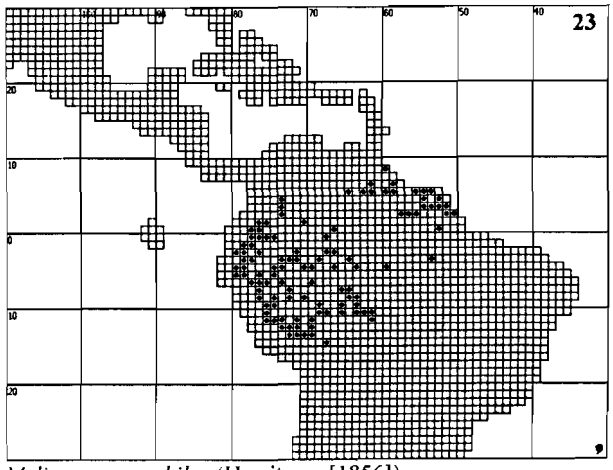
Melinaea ludovica (Cramer, 1782)



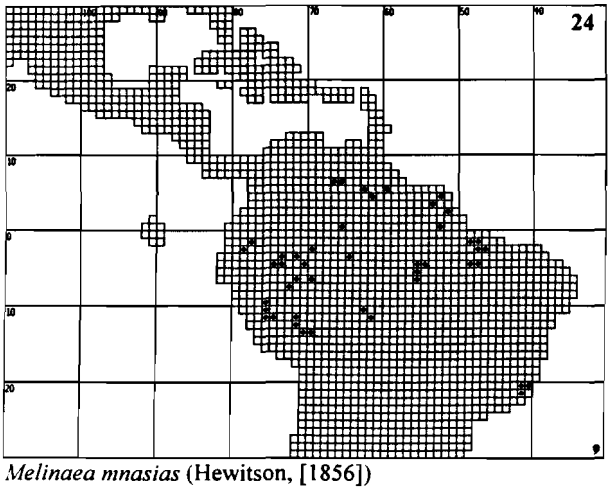
Melinaea maelus (Hewitson, 1860)



Melinaea marsaeus (Hewitson, 1860)

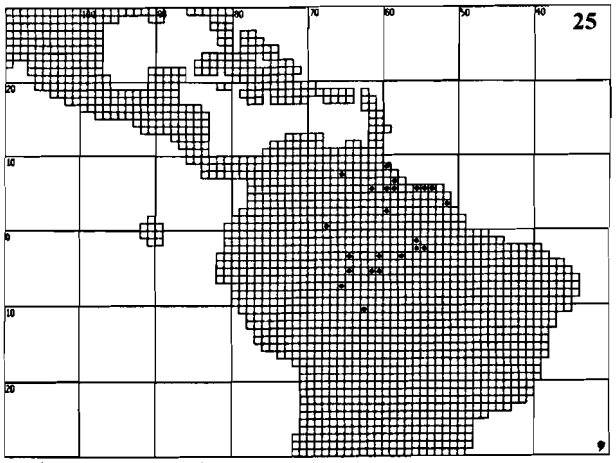


Melinaea menophilus (Hewitson, [1856])

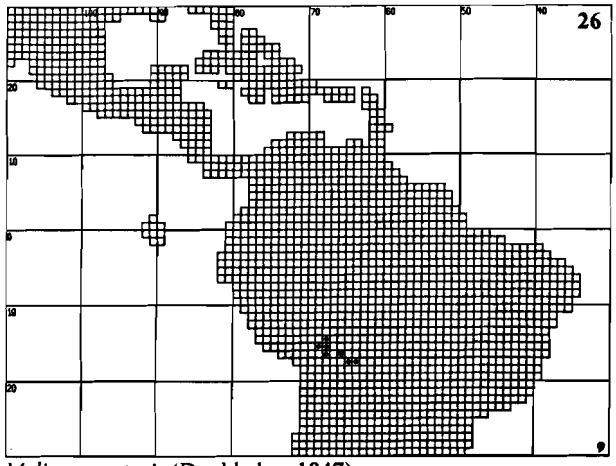


Melinaea mnasias (Hewitson, [1856])

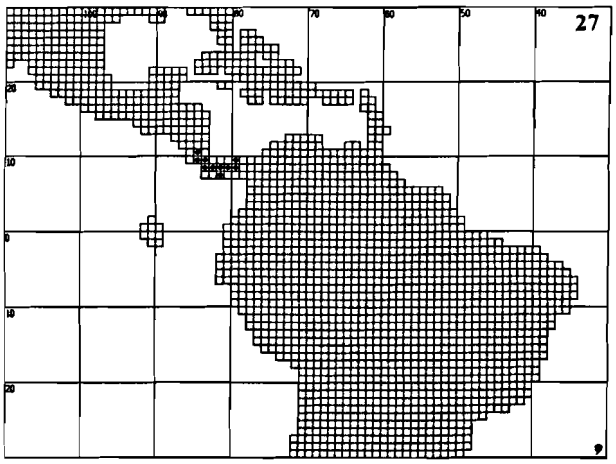
APPENDIX 5.2 - continued



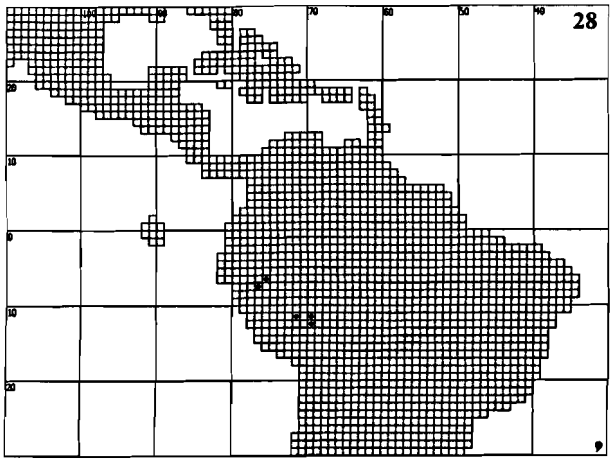
Melinaea mneme (Linnaeus, 1763)



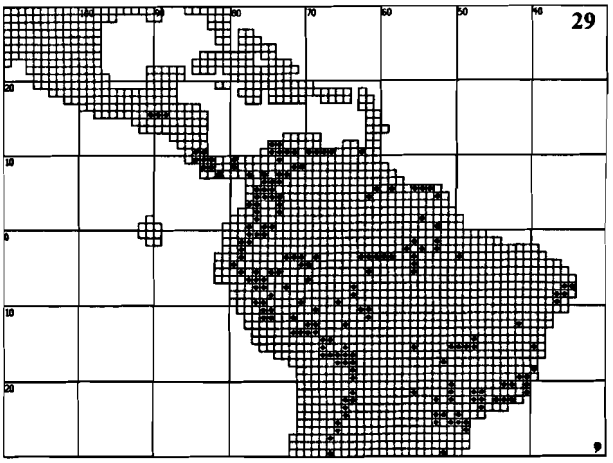
Melinaea satevis (Doubleday, 1847)



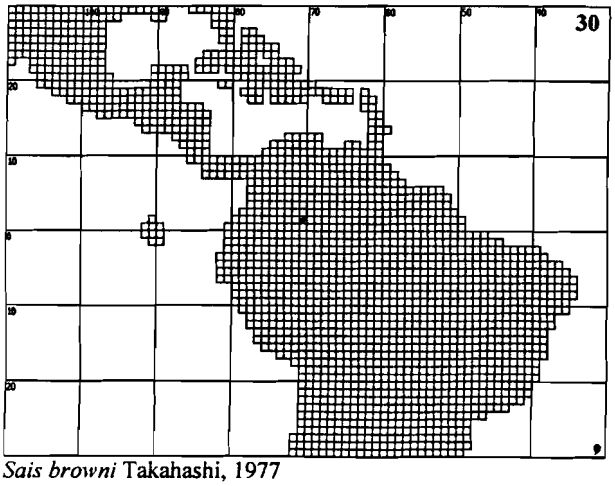
Melinaea scylax Salvin, 1871



Paititia neglecta Lamas, 1979

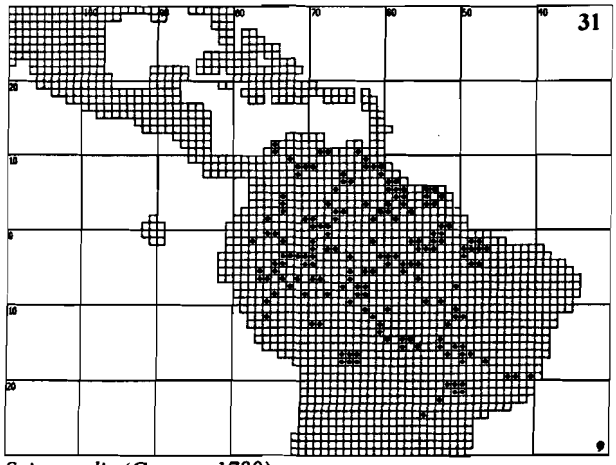


Thyridia psidii (Linnaeus, 1758)

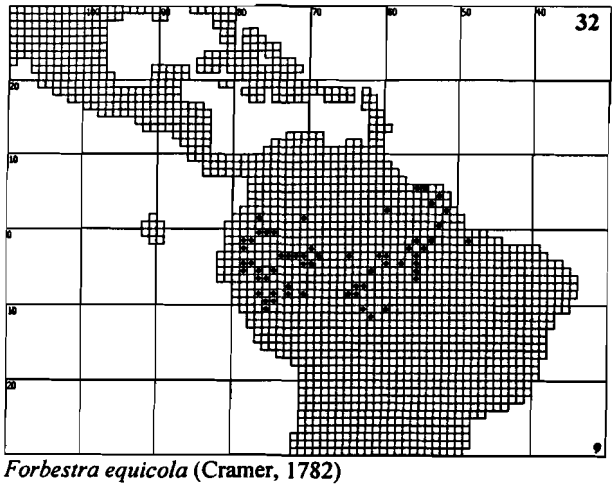


Sais browni Takahashi, 1977

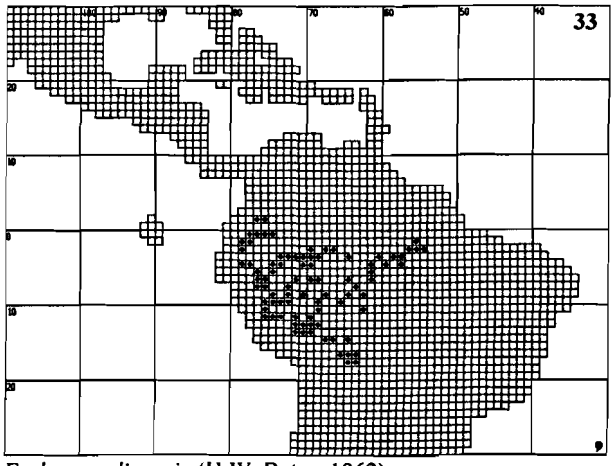
APPENDIX 5.2 - continued



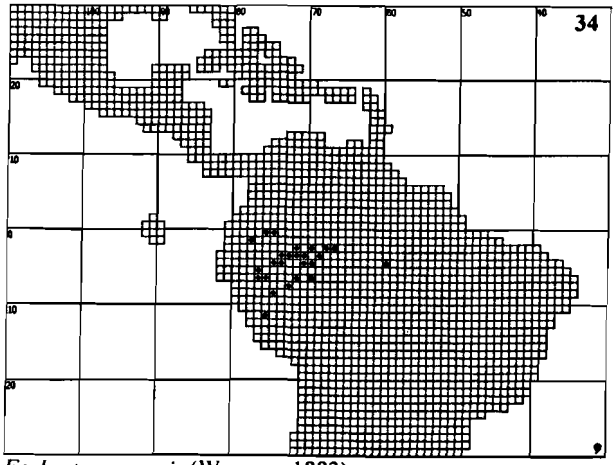
Sais rosalia (Cramer, 1780)



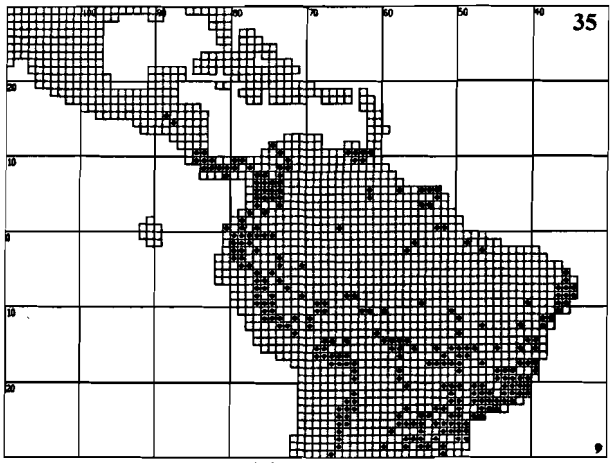
Forbestra equicola (Cramer, 1782)



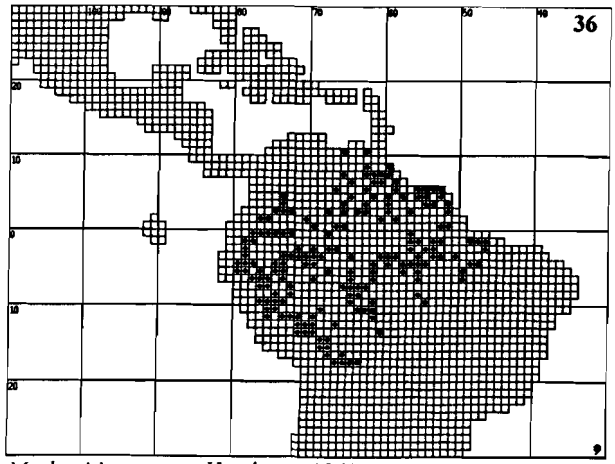
Forbestra olivencia (H.W. Bates, 1862)



Forbestra proceris (Weymer, 1883)

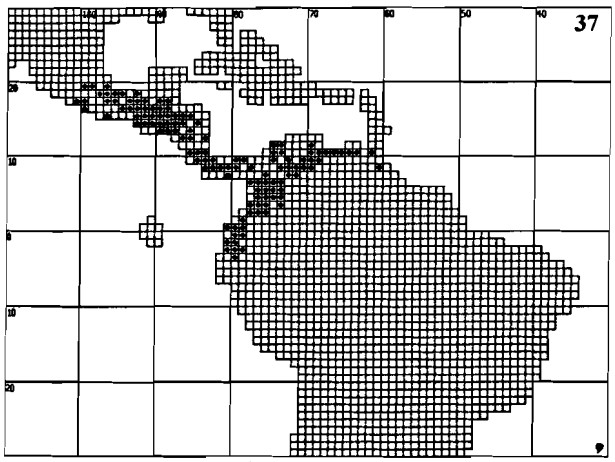


Mechanitis lysimnia (Fabricius, 1793)

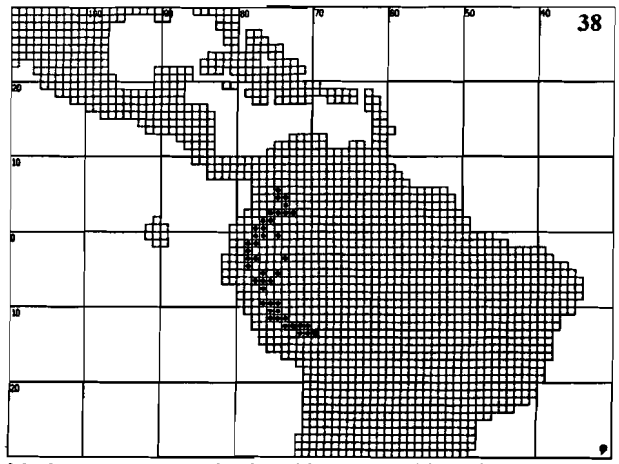


Mechanitis mazaeus Hewitson, 1860

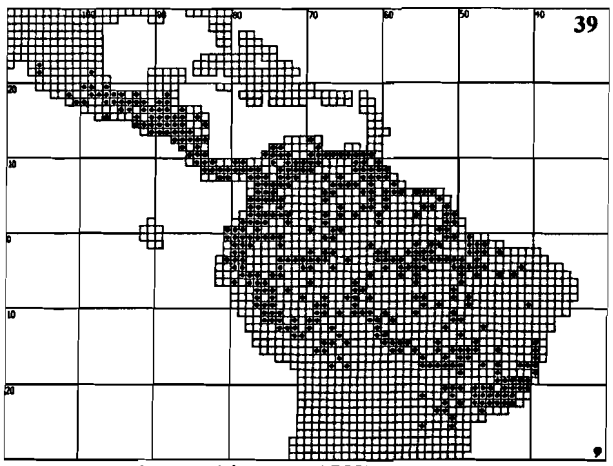
APPENDIX 5.2 - continued



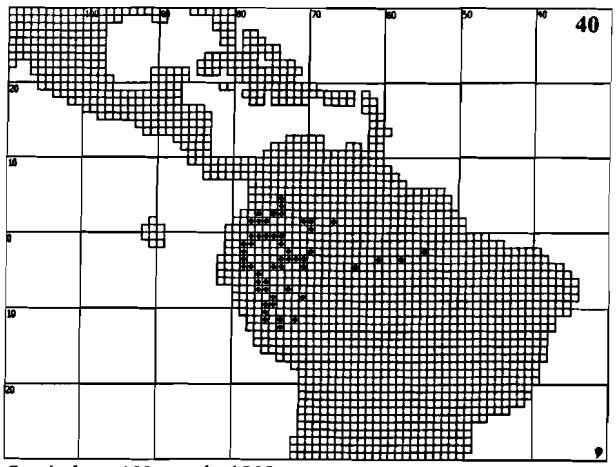
Mechanitis menapis Hewitson, [1856]



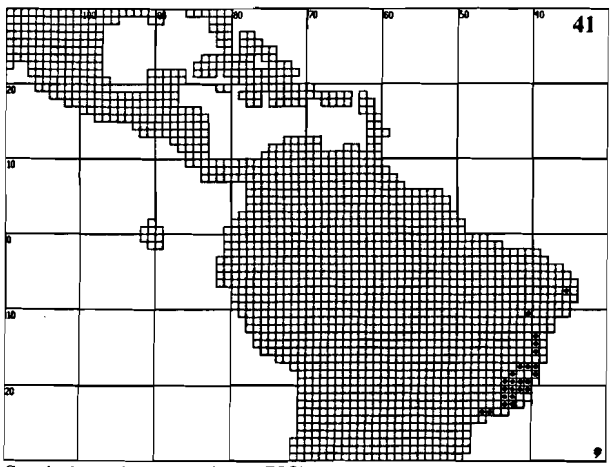
Mechanitis messenoides C. Felder & R. Felder, 1865



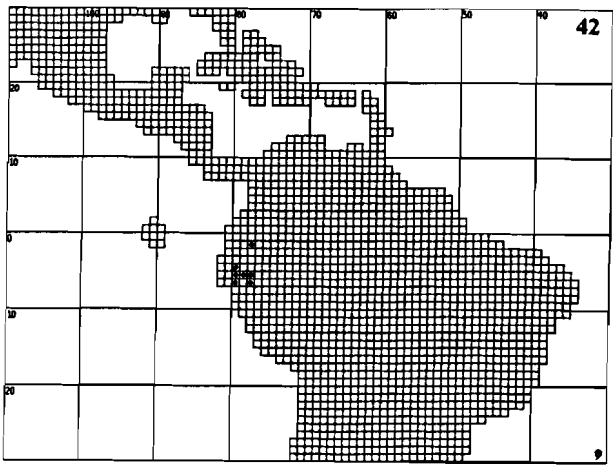
Mechanitis polymnia (Linnaeus, 1758)



Scada batesi Haensch, 1903

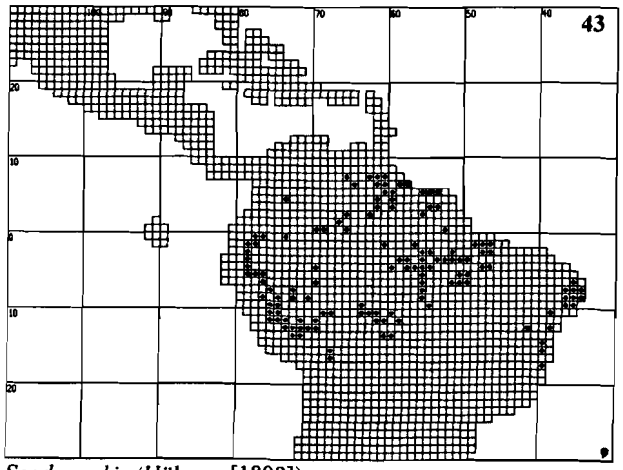


Scada karschina (Herbst, 1792)

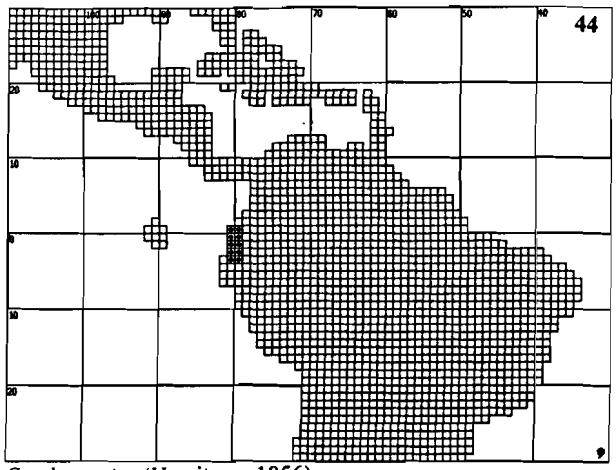


Scada kusa (Hewitson, 1872)

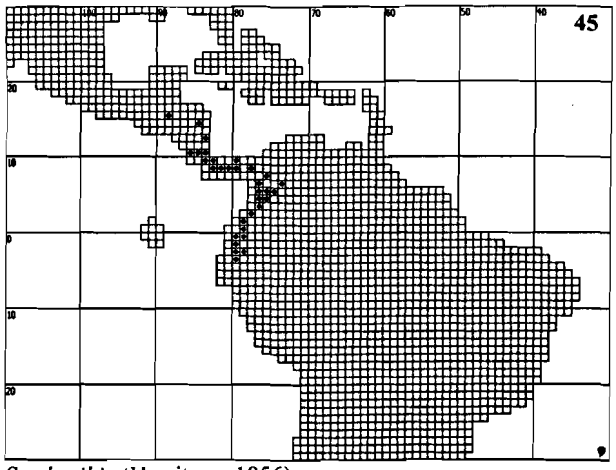
APPENDIX 5.2 - continued



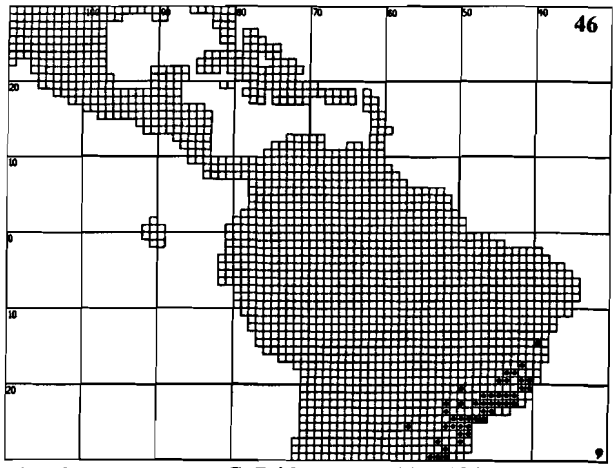
Scada reckia (Hübner, [1808])



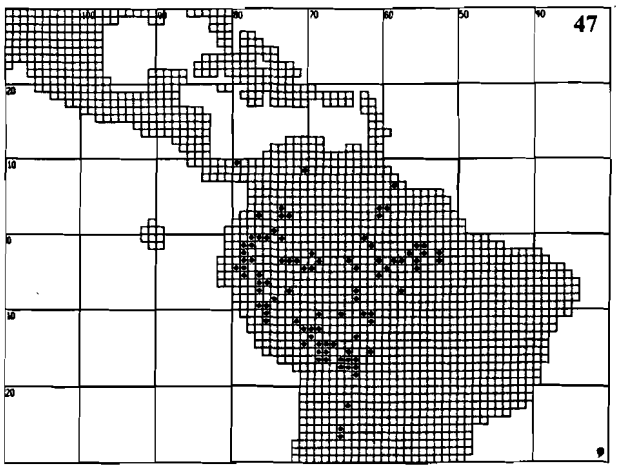
Scada zemira (Hewitson, 1856)



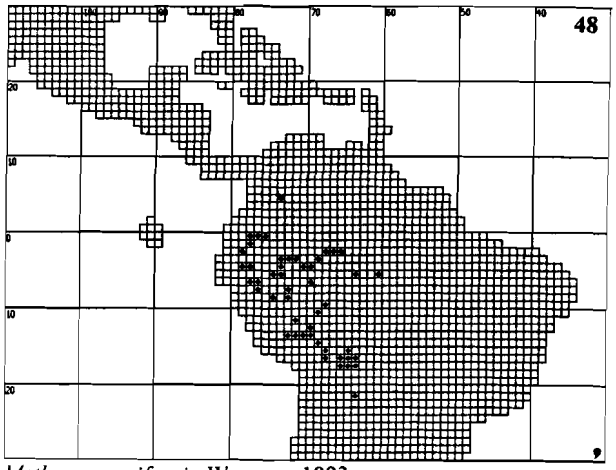
Scada zibia (Hewitson, 1856)



Placidula euryanassa (C. Felder & R. Felder, 1865)

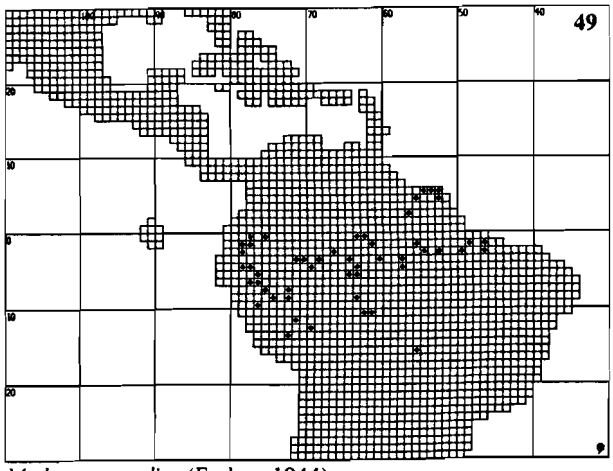


Methona confusa Butler, 1873

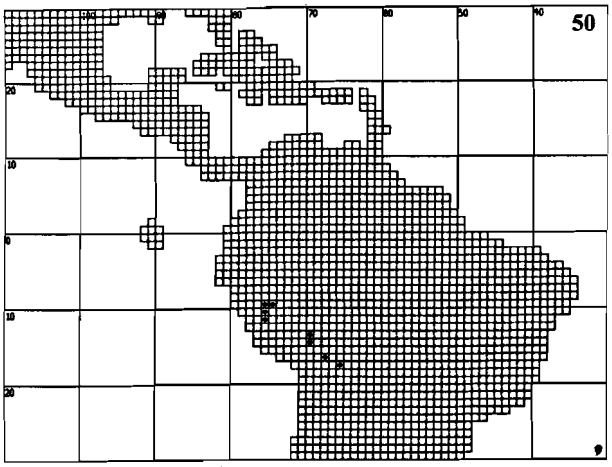


Methona curvifascia Weymer, 1883

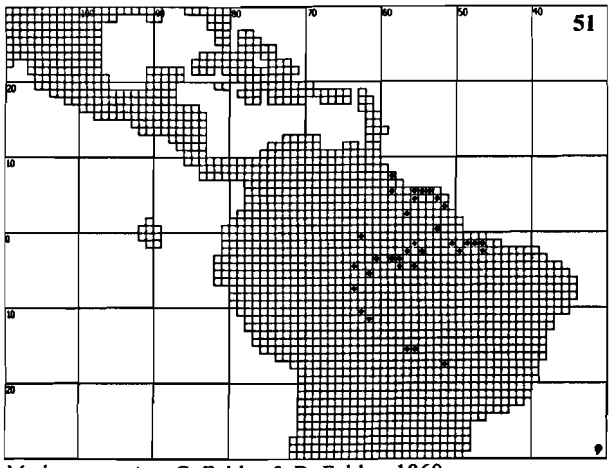
APPENDIX 5.2 - continued



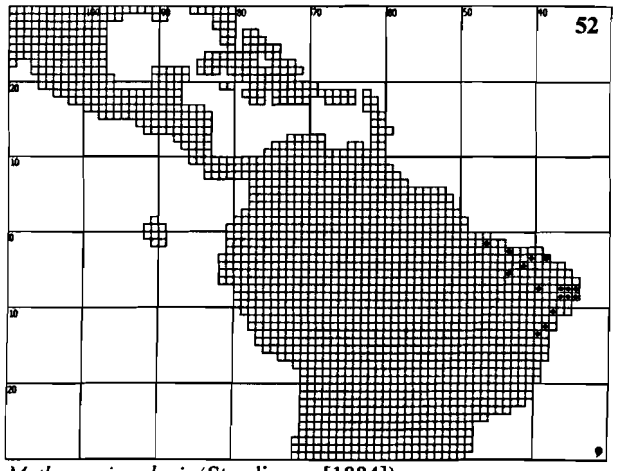
Methona grandior (Forbes, 1944)



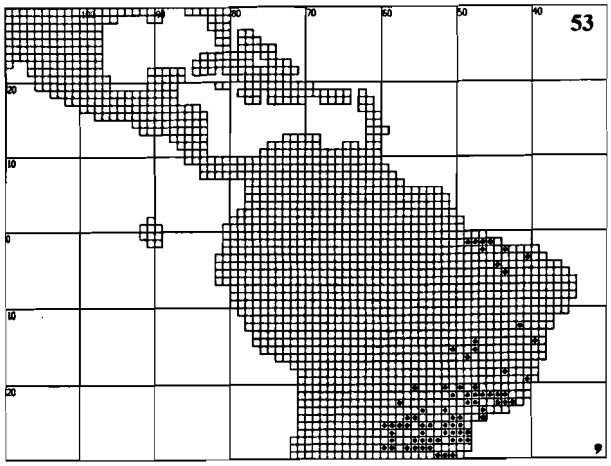
Methona maxima (Forbes, 1944)



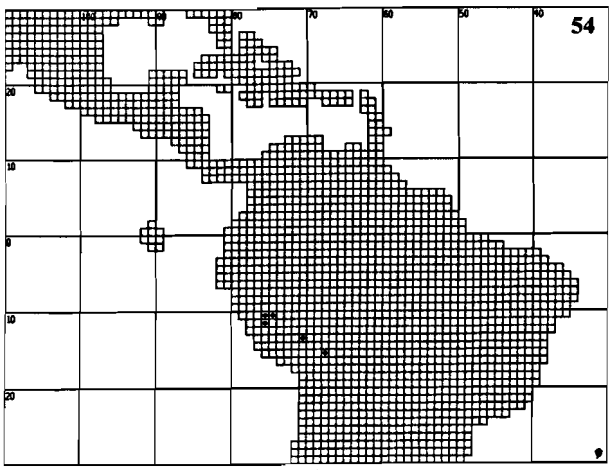
Methona megisto C. Felder & R. Felder, 1860



Methona singularis (Staudinger, [1884])

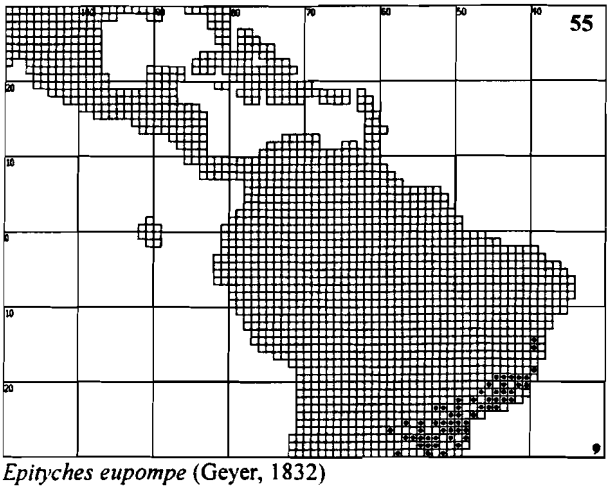


Methona themisto (Hübner, 1818)

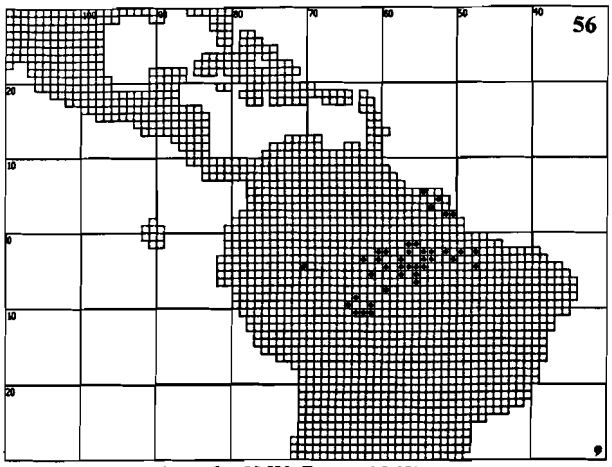


Aremfoxia ferra (Haensch, 1909)

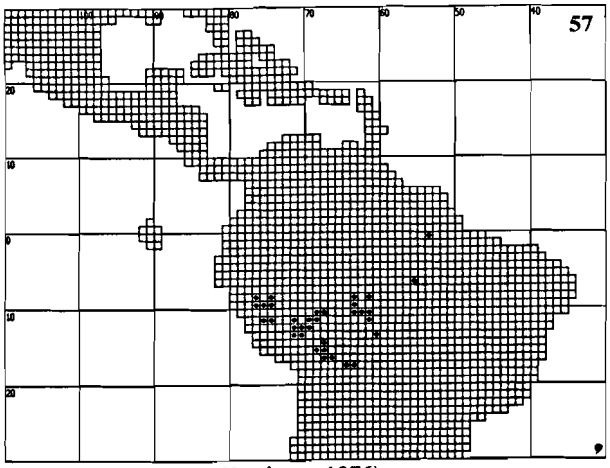
APPENDIX 5.2 - continued



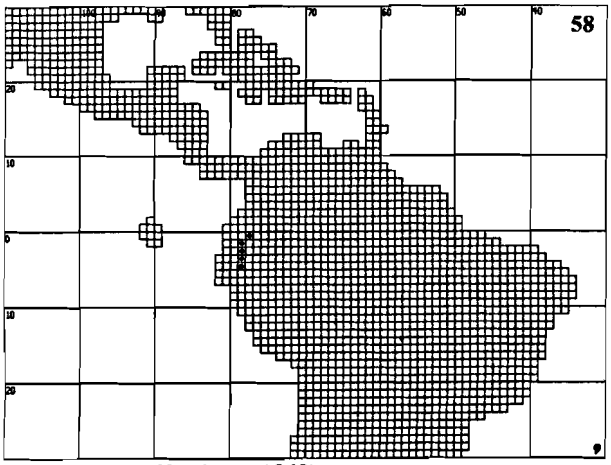
Epityches eupompe (Geyer, 1832)



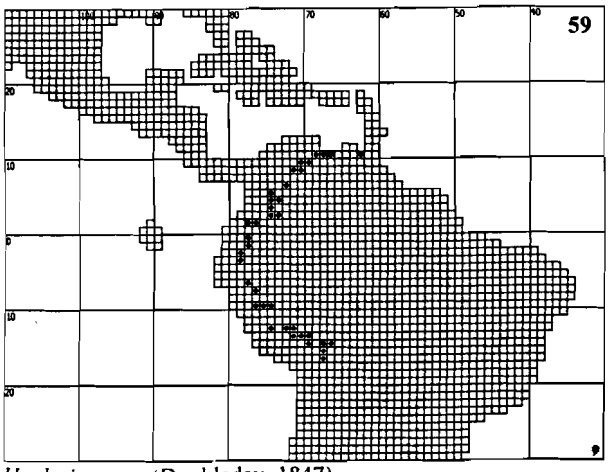
Garsauritis xanthostola (H.W. Bates, 1862)



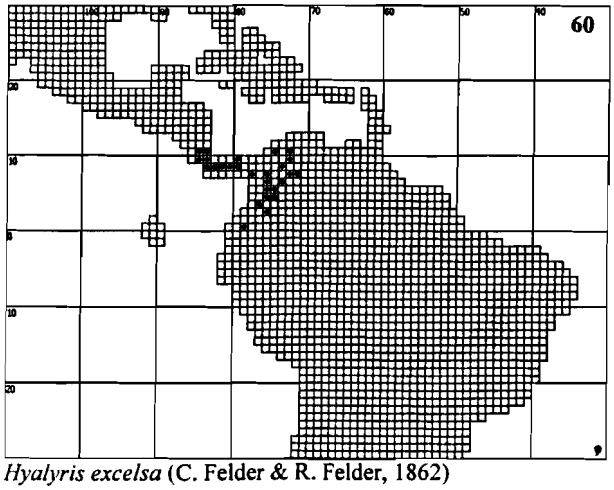
Rhodussa cantobrica (Hewitson, 1876)



Hyalyris antea (Hewitson, 1869)

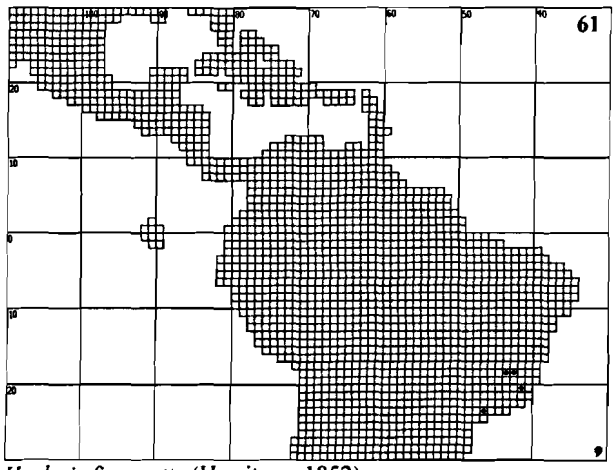


Hyalyris coeno (Doubleday, 1847)

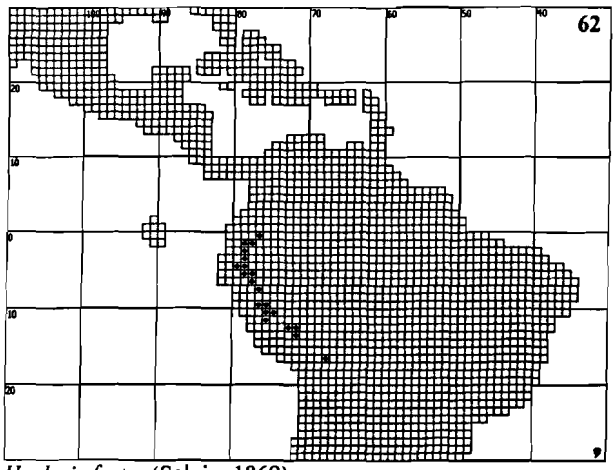


Hyalyris excelsa (C. Felder & R. Felder, 1862)

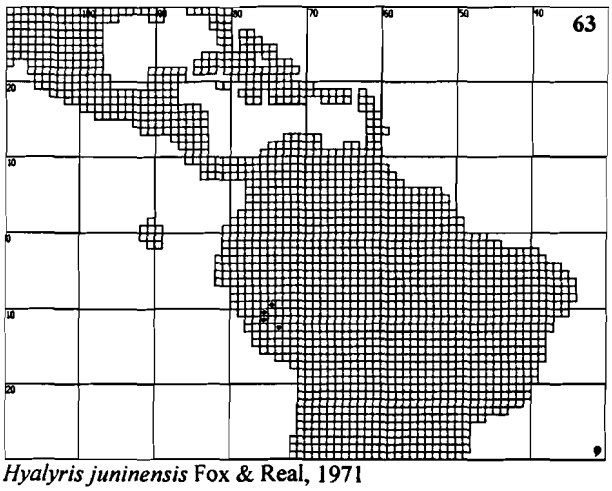
APPENDIX 5.2 - continued



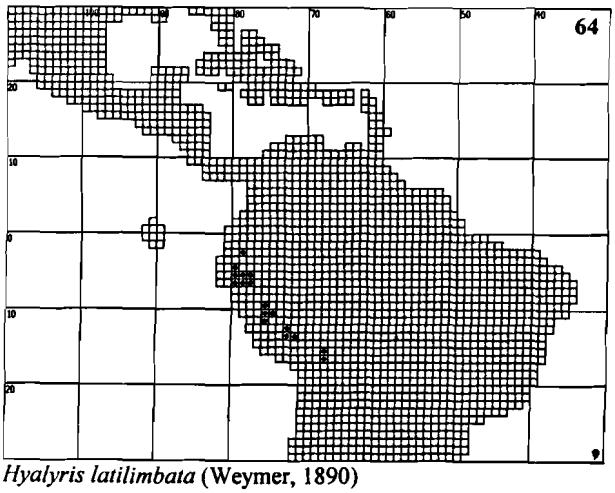
Hyalyris fiammetta (Hewitson, 1852)



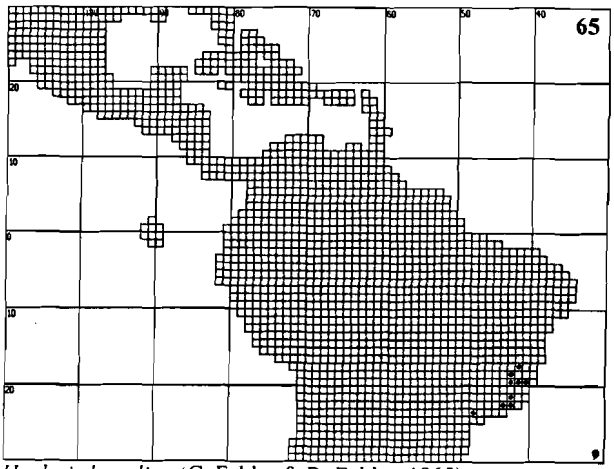
Hyalyris frater (Salvin, 1869)



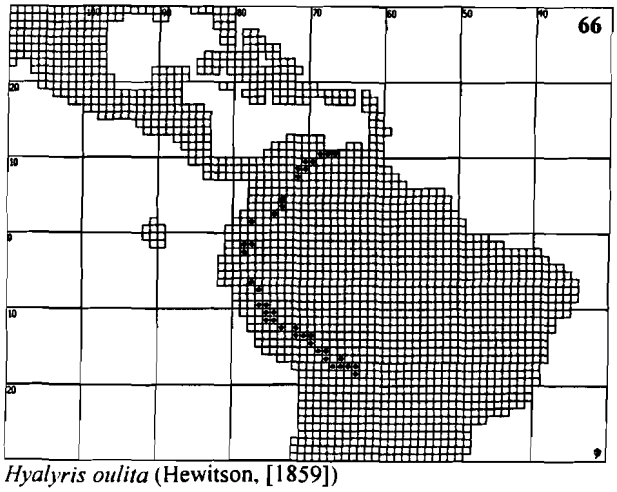
Hyalyris juninensis Fox & Real, 1971



Hyalyris latilimbata (Weymer, 1890)

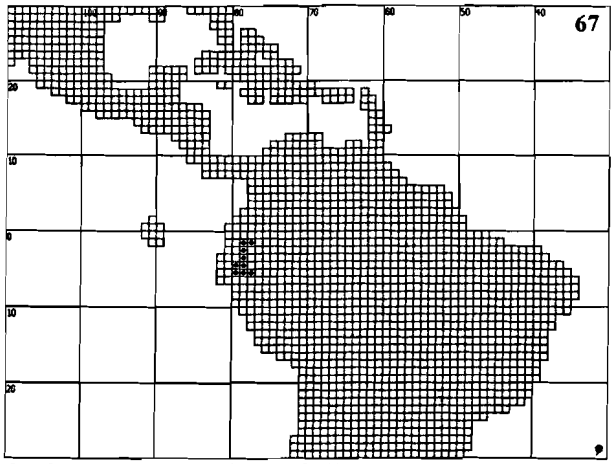


Hyalyris leptalina (C. Felder & R. Felder, 1865)

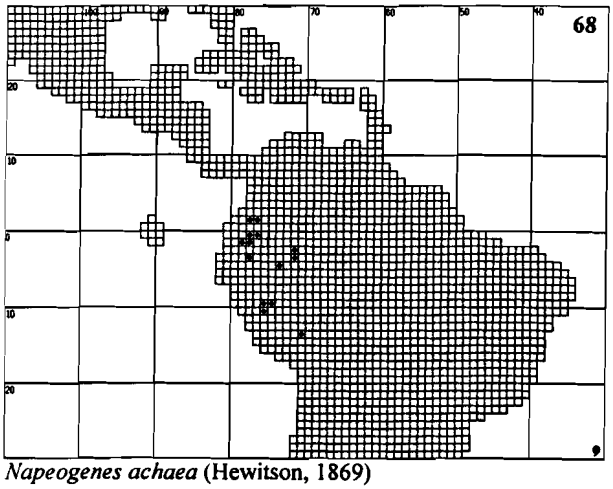


Hyalyris oulita (Hewitson, [1859])

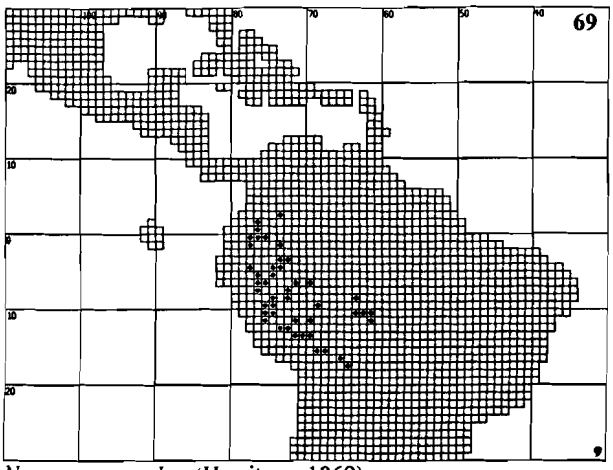
APPENDIX 5.2 - continued



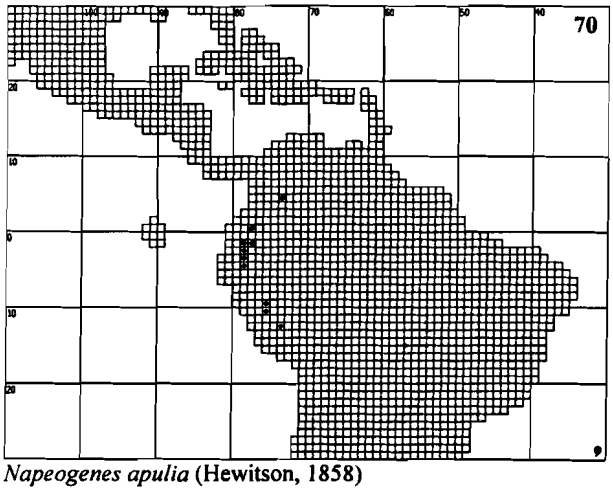
Hyalyris praxilla (Hewitson, 1870)



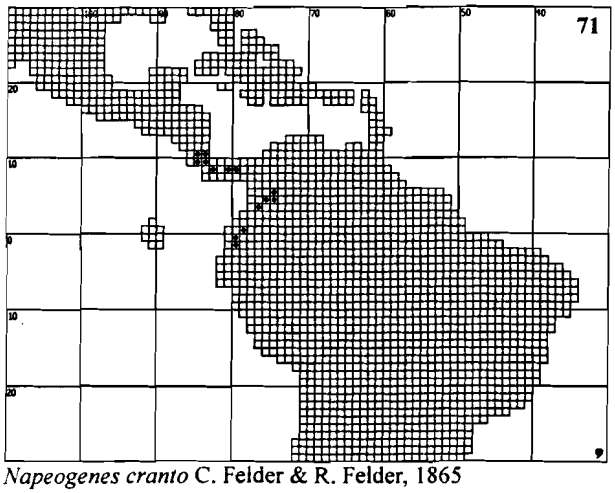
Napeogenes achaea (Hewitson, 1869)



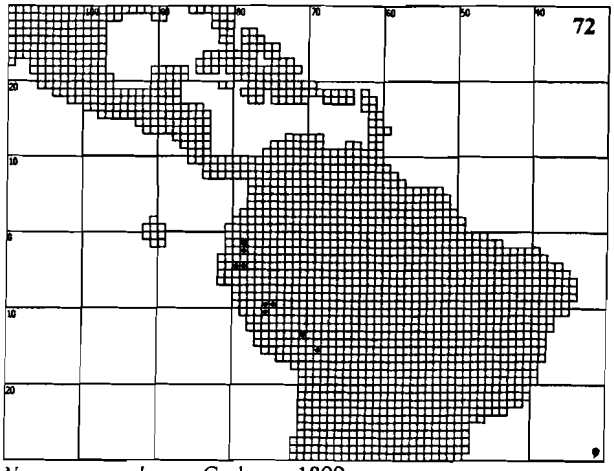
Napeogenes aethra (Hewitson, 1869)



Napeogenes apulia (Hewitson, 1858)

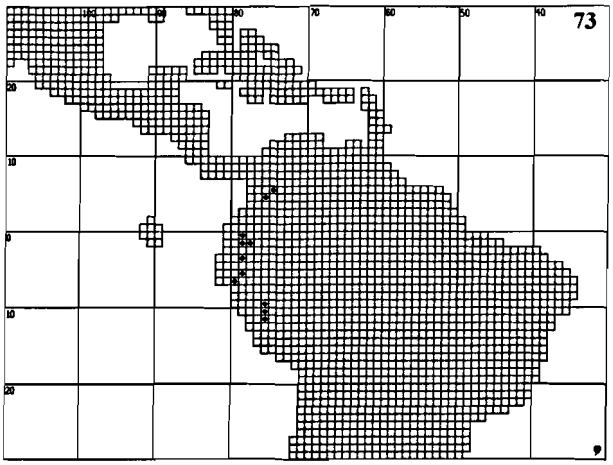


Napeogenes cranto C. Felder & R. Felder, 1865

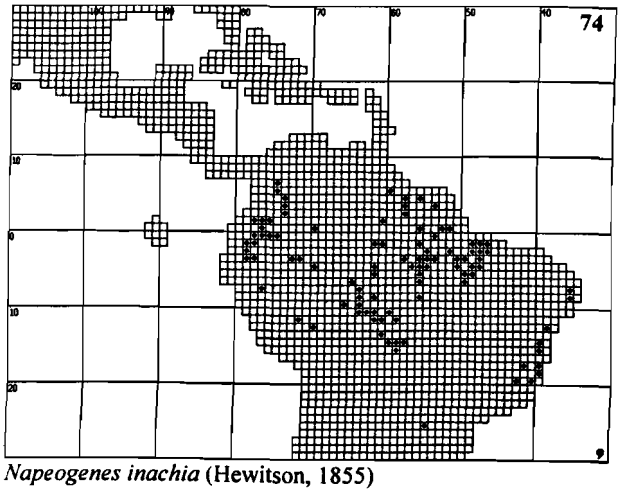


Napeogenes glycera Godman, 1899

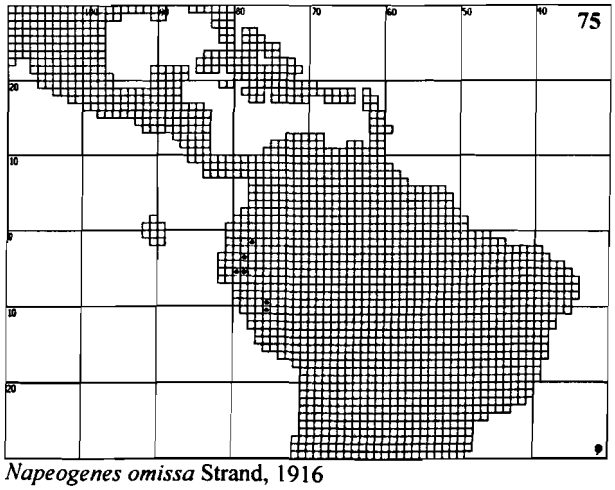
APPENDIX 5.2 - continued



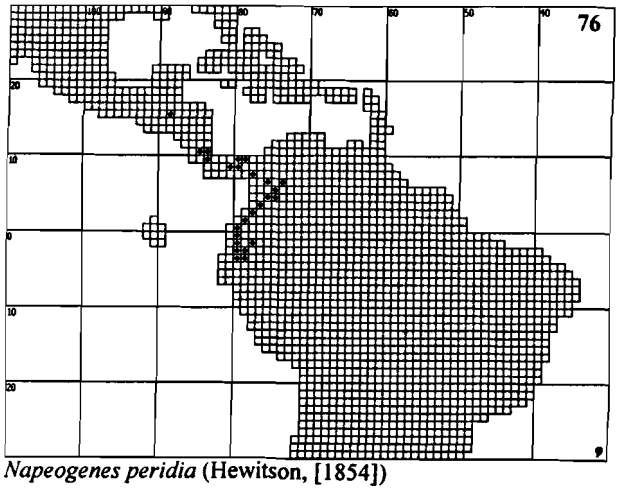
Napeogenes harbona (Hewitson, 1869)



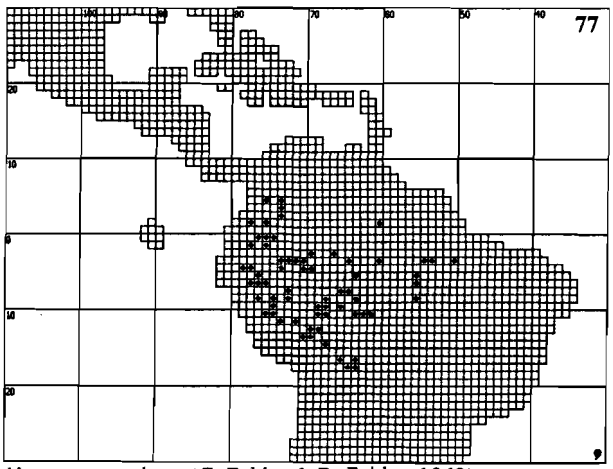
Napeogenes inachia (Hewitson, 1855)



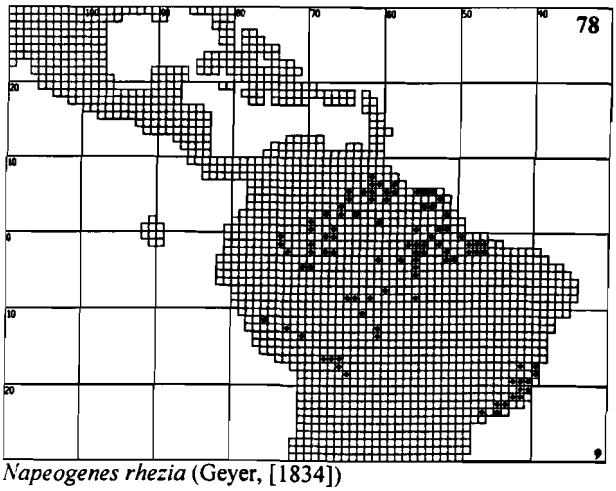
Napeogenes omissa Strand, 1916



Napeogenes peridia (Hewitson, [1854])

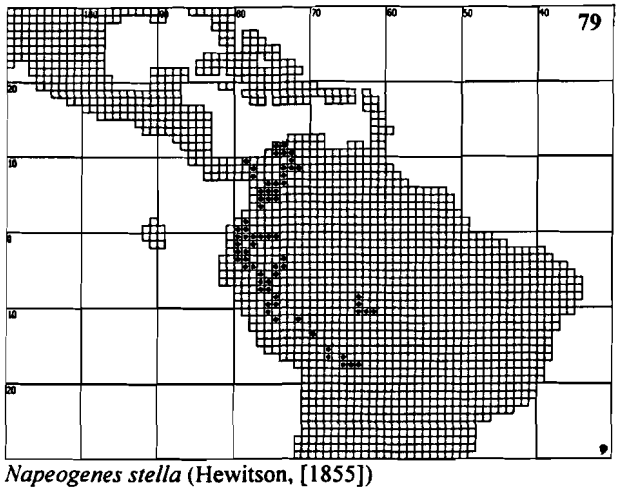


Napeogenes pharo (C. Felder & R. Felder, 1862)

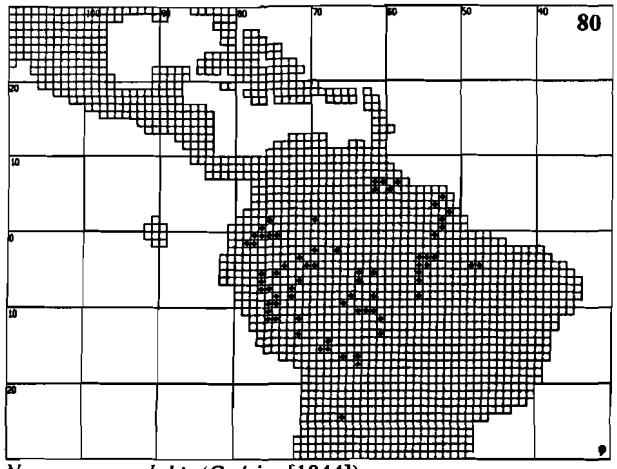


Napeogenes rhezia (Geyer, [1834])

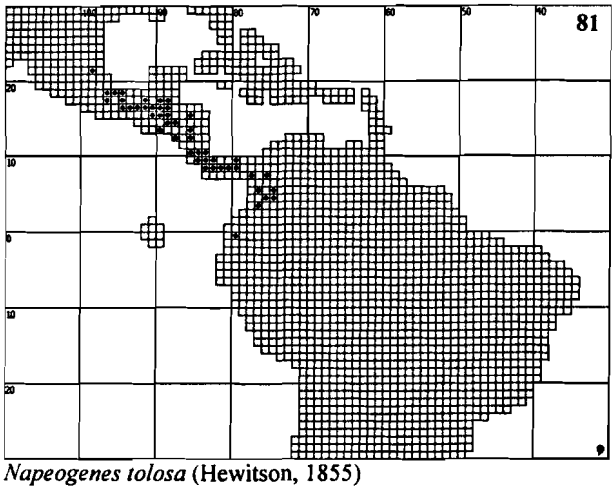
APPENDIX 5.2 - continued



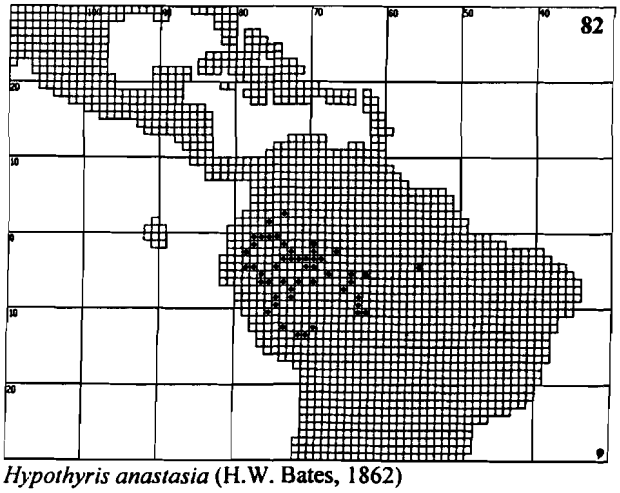
Napeogenes stella (Hewitson, [1855])



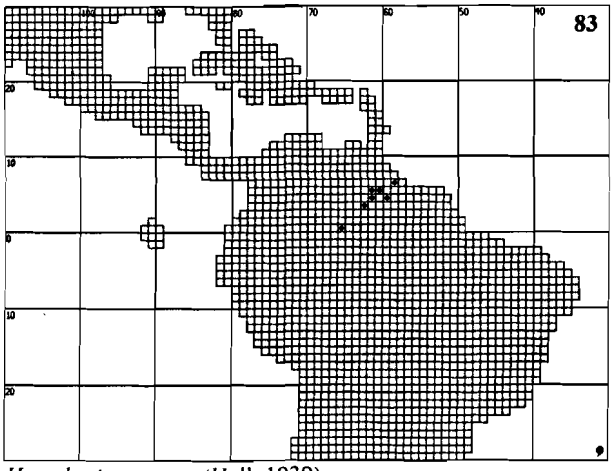
Napeogenes sylphis (Guérin, [1844])



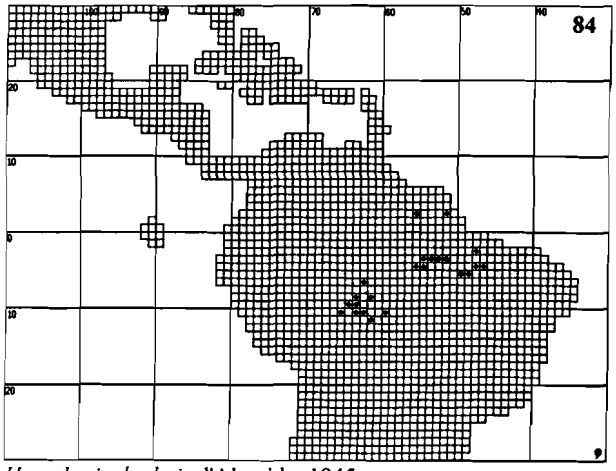
Napeogenes tolosa (Hewitson, 1855)



Hypothyris anastasia (H.W. Bates, 1862)

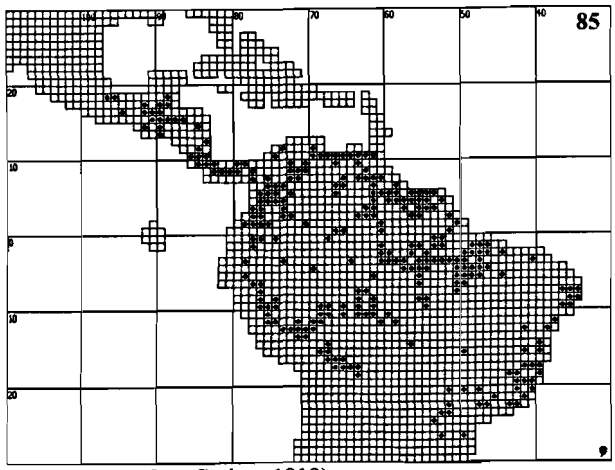


Hypothyris connexa (Hall, 1939)

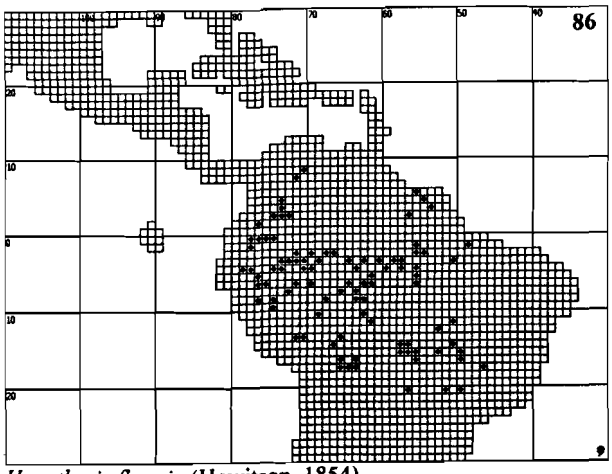


Hypothyris daphnis d'Almeida, 1945

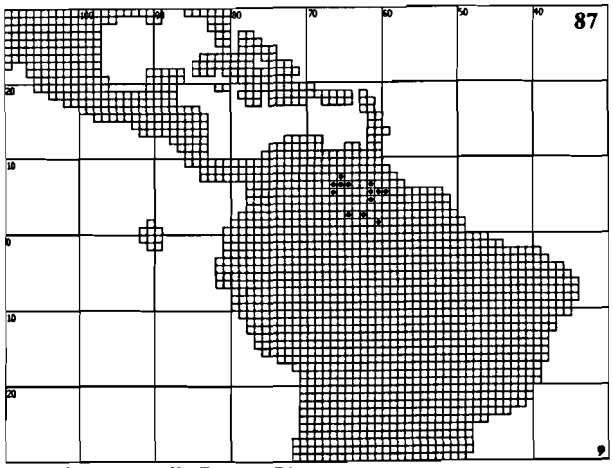
APPENDIX 5.2 - continued



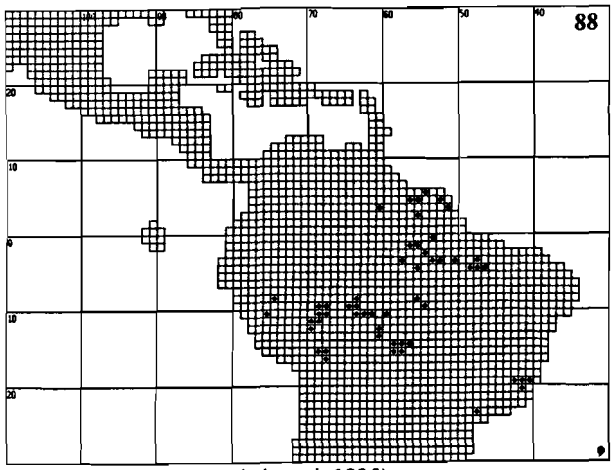
Hypothyris euclea (Godart, 1819)



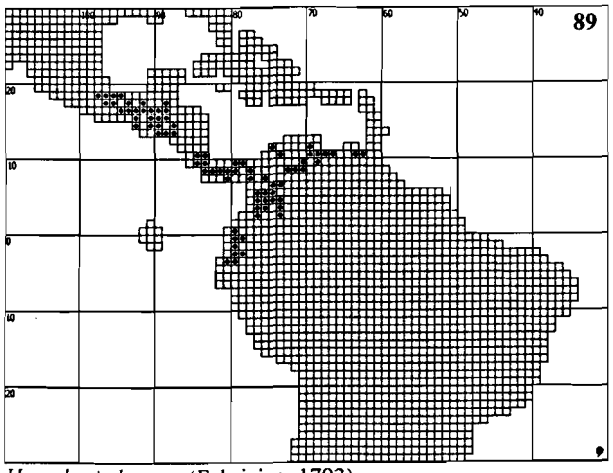
Hypothyris fluonia (Hewitson, 1854)



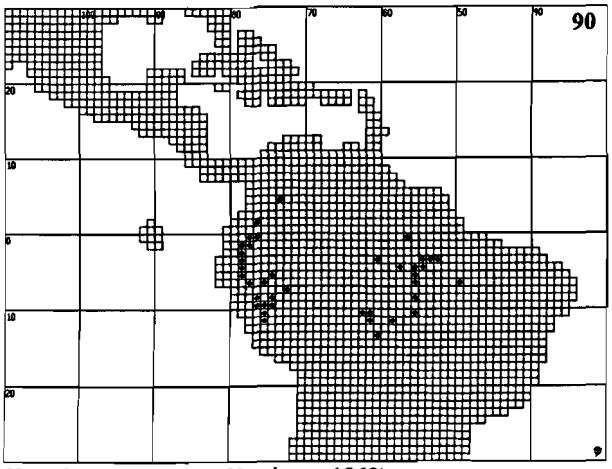
Hypothyris gemella Fox, 1971



Hypothyris leprieuri (Feisthamel, 1835)

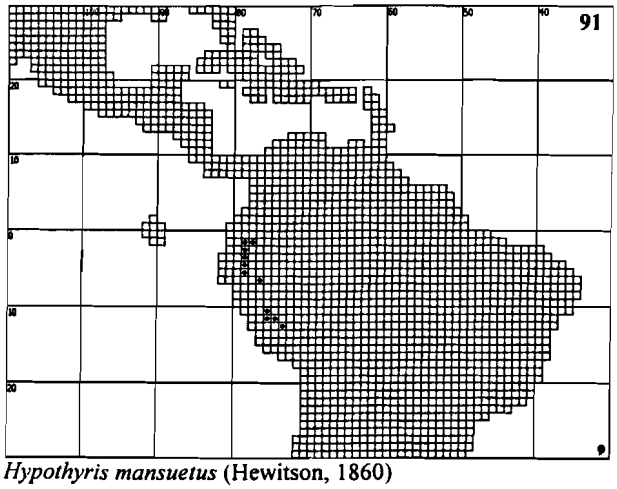


Hypothyris lycaste (Fabricius, 1793)

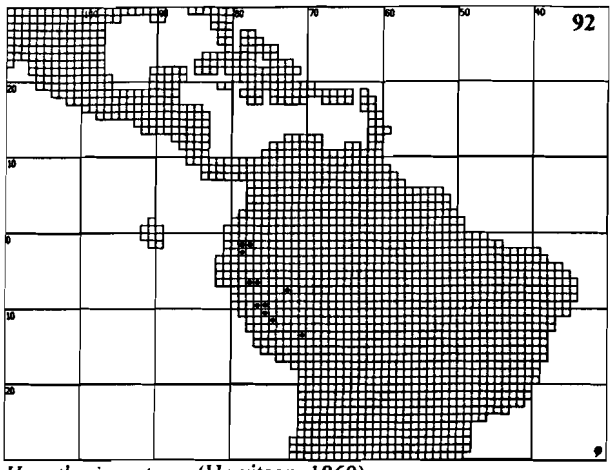


Hypothyris mamercus (Hewitson, 1869)

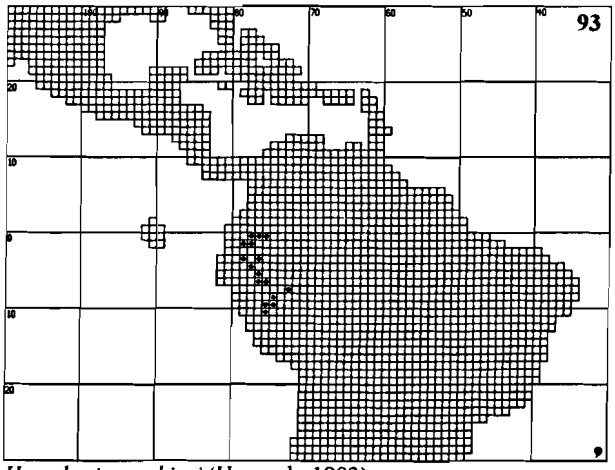
APPENDIX 5.2 - continued



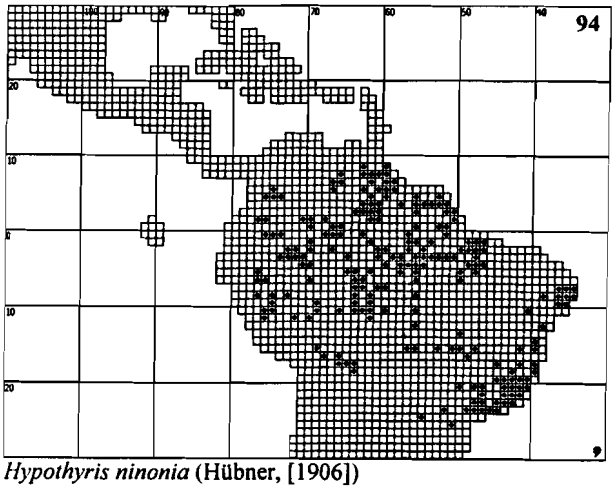
Hypothyris mansuetus (Hewitson, 1860)



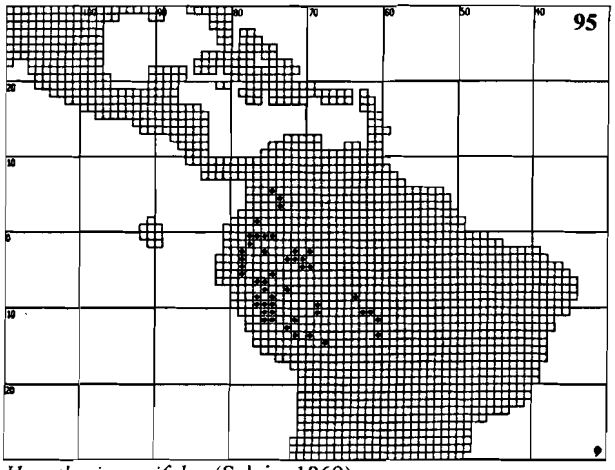
Hypothyris meterus (Hewitson, 1860)



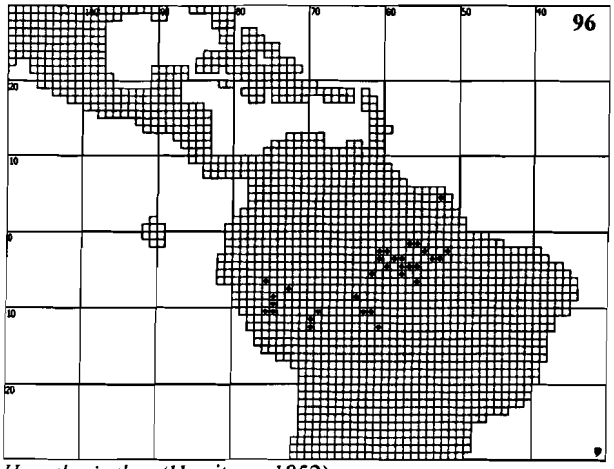
Hypothyris moebiusi (Haensch, 1903)



Hypothyris ninonia (Hübner, [1906])

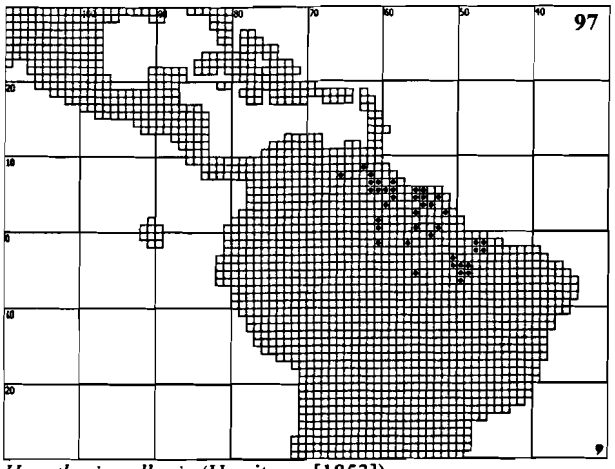


Hypothyris semifulva (Salvin, 1869)

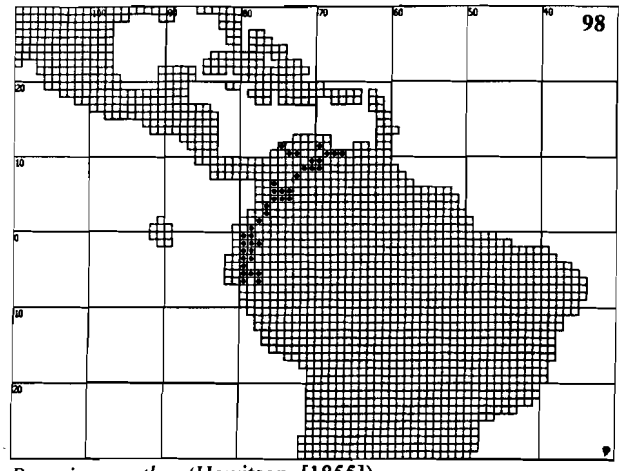


Hypothyris thea (Hewitson, 1852)

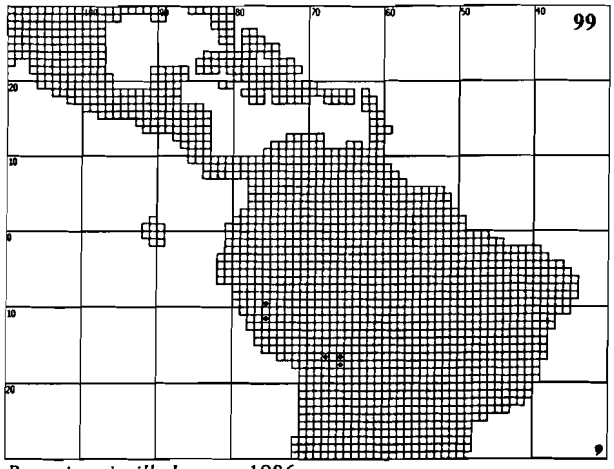
APPENDIX 5.2 - continued



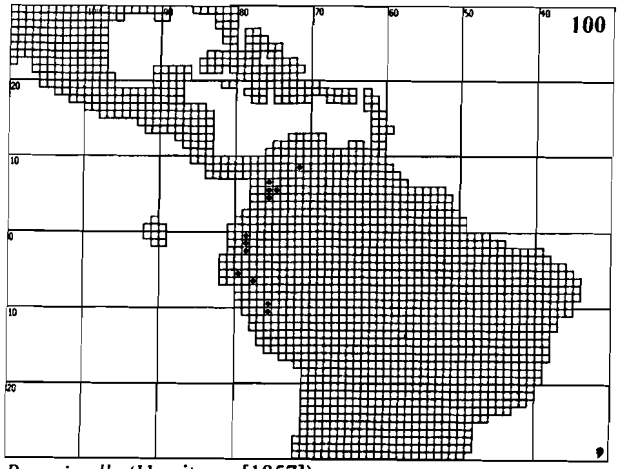
Hypothyris vallonia (Hewitson, [1853])



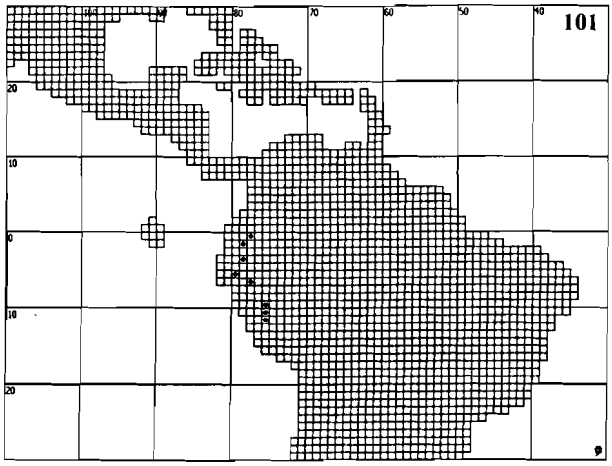
Pagyris cymothoe (Hewitson, [1855])



Pagyris priscilla Lamas, 1986



Pagyris ulla (Hewitson, [1857])



Veladyris pardalis (Salvin, 1869)

APPENDIX 5.3. Computer program written in BASIC programming language which runs the random-draw model discussed in text

```
100 CLS : PRINT "How many areas do you want to simulate"; : INPUT no
200 DIM a(no, 5), b(310)
300 FOR x = 1 TO no
400 PRINT "How many ithomiine species in area"; x; "(maximum 310)"; : INPUT y
500 a(x, 1) = y
600 PRINT "How many 'mapped' species observed in this area"; : INPUT ob
700 a(x, 2) = ob
800 NEXT x
900 REM "p" is the current area
1000 FOR p = 1 TO no
1100 REM "it" is the number of iterations per area
1200 FOR it = 1 TO 10000
1300 REM Generates random list of species for each area, without replacement
1400 FOR y = 1 TO a(p, 1)
1500 RANDOMIZE TIMER
1600 z% = INT(1 + RND * 310)
1700 FOR x = 1 TO a(p, 1)
1800 IF z% = b(x) THEN GOTO 1500
1900 NEXT x
2000 b(y) = z%
2100 NEXT y
2200 REM Counts the number of 'mapped' species after each iteration
2300 wm = 0
2400 FOR x = 1 TO a(p, 1)
2500 IF b(x) > 0 AND b(x) < 102 THEN wm = wm + 1
2600 NEXT x
2700 IF wm = a(p, 2) THEN a(p, 3) = a(p, 3) + 1
```

APPENDIX 5.3 - continued

```
2800 IF wm > a(p, 2) THEN a(p, 4) = a(p, 4) + 1
2900 IF wm < a(p, 2) THEN a(p, 5) = a(p, 5) + 1
3000 REM This loop empties the array "b"
3100 FOR x = 1 TO 310
3200 b(x) = 0
3300 NEXT x
3400 NEXT it
3500 NEXT p
3600 REM Prints out results
3700 CLS
3800 co = 0
3900 FOR x = 1 TO no
4000 PRINT "Area number"; x; "has a total of"; a(x, 1); "ithomiine species"
4100 PRINT "of which"; a(x, 2); "are 'mapped' species. Out of 10000 iterations:"
4200 PRINT a(x, 3); "iterations had an equal number of mapped species"
4300 PRINT a(x, 4); "iterations had a greater number of mapped species, and"
4400 PRINT a(x, 5); "iterations had a lesser number of mapped species."
4500 PRINT "------------------------------------------------------------"
4600 co = co + 1
4700 IF co < 3 THEN GOTO 4900
4800 co = 0: IF INKEY$ = CHR$(27) THEN GOTO 4900 ELSE GOTO 4800
4900 NEXT x
5000 REM Saves results to text file named "randraw.txt"
5100 OPEN "o", #1, "c:\randraw.txt"
5200 FOR x = 1 TO no
5300 PRINT #1, a(x, 1), ",", a(x, 2), ",", a(x, 3), ",", a(x, 4), ",", a(x, 5)
5400 NEXT x
5500 END
```

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