COMPARATIVE ECOLOGY AND MIMETIC RELATIONSHIPS
OF ITHOMIINE BUTTERFLIES IN EASTERN ECUADOR

By

BOYCE ALEXANDER DRUMMOND III

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL
OF THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1976

UNIVERSITY OF FLORIDA

3 1262 08666 406 6

For Nancy,

as she lays aside her net awhile to take up the caduceus

ACKNOWLEDGMENTS

It is my pleasure to thank the members of my committee, Drs. Thomas C. Emmel, Archie Carr, Clifford Johnson, and Thomas Walker, for the guidance and encouragement they have provided throughout my graduate career. I have profited greatly from their respective graduate courses and from the exposure to their divergent, but complementary, approaches to biology. I also thank Drs. John Ewel, Dana Griffin, and Jon Reiskind for helpful discussions and much useful information during the writing of this dissertation.

For the countless ways in which they have assisted in all phases of the research reported here, I profess my deepest appreciation to Dr. Thomas Emmel, chairman of my committee, and Nancy Drummond, my wife and field assistant. Without the benefit of their help, many of the goals of this project could not have been accomplished. To Dr. Emmel, who first introduced me to tropical ecology and kindled my interest in the biology of the Lepidoptera, I am indebted for the constant personal, academic, and financial support he so graciously proffered. My wife, Nancy, whose great enthusiasm for our year of field work in Ecuador was matched only by her unflagging patience during the tedious year and a half that followed in Gainesville, assisted in the collection of specimens and population samples, handled most of the life-history rearings, and aided in the preparation and analysis of the data. For all this and much more I am thankfully beholden.

I am grateful to Dr. William G. D'Arcy, Missouri Botanical Garden, St. Louis, for identifying the solanaceous plants. At the Allyn Museum of Entomology, Sarasota, Florida, Dr. Lee Miller aided in the identification of several butterfly species and Jacqueline Miller kindly identified the Castniidae. I am indebted to Dr. Lincoln Brower, Amherst College, for loaning me a copy of Christine Papageorgis' dissertation, and to F. Martin Brown, Colorado Springs, Colorado, for loaning me one of the few extant copies of d'Almeida's "Mélanges Lépidoptériques." I thank my wife, Nancy, for translating the latter work and other papers from the French. Nancy Drummond also patiently typed and edited early drafts of the manuscript as well as most of the final copy, for which I am extremely grateful. Donna Gillis typed Tables 4 and 5 and the bibliography. The photography staff of the Office of Instructional Resources, University of Florida, prepared Figures 10 through 15. Nancy Drummond kindly drew Figures 33-35 and 46-47 and aided in the preparation of several others.

The year of Ecuadorian field work was made possible only by the aid of a number of helpful persons and organizations in the United States and Ecuador. Dan Doyle of the Miami office of the Summer Institute of Linguistics severed yards of red tape at the Ecuadorian embassy to expedite the issuance of the required visas. Giovanna Holbrook of Holbrook Travel and the staff of JAARS (Jungle Aviation and Radio Service of SIL) kindly arranged the various transfers of our overweight equipment and baggage to, from, and within Ecuador against improbable odds. Ruth and Steve Smith kindly stored our worldly possessions during our fourteen months in Ecuador. The personnel of

the Ecuadorian Branch of the Summer Institute of Linguistics, especially John Lindskoog, Jonathon Johnson, and Don and Helen Johnson, facilitated our transportation in Ecuador and made available housing and supplies at Limoncocha. I am particularly grateful to Wayne and JoAnne Fitch, Jim and Kathie Yost, and Pat Kelley for many personal favors during the course of this research. Special thanks are due Mark and Phyllis Newell for allowing us to live in their spacious house at Limoncocha during the final three months of our stay. I thank Drs. Howard Weems and Robert Woodruff, Department of Entomology, Division of Plant Industry, Florida Department of Agriculture, for providing equipment and supplies. This research was supported in part by a Grant-in-Aid from Sigma Xi.

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Abstract of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of the Requirements
for the degree of Doctor of Philosophy

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By

Boyce Alexander Drummond III.

August, 1976

Chairman: Thomas C. Emmel

Major Department: Zoology

Butterflies of the subfamily Ithomiinae (Lepidoptera, Ithomiidae) are among the most conspicuous and abundant flying insects of neotropical forests, yet they have received little attention from ecologists and their biology is not well known. A comprehensive ecological study of a rich (53 species) ithomiine community (in lowland rainforest at Limoncocha, on the Rio Napo, eastern Ecuador) was combined with an extensive search of the literature to characterize this subfamily in ecological terms.

Ithomiines usually exhibit clumped distribution, even within seemingly homogeneous forests, where their responses to gradients of light and relative humidity result in transient concentrations that crest and ebb through time. Ithomiines are long-lived, with low daily rates of oviposition and adult-financed egg production. The early morning visits of ithomiine males to white flowers fit the syndrome of crepuscular pollination and may represent a coevolved relationship. Females feed on detritus from which they apparently obtain the nitrogen needed for continuous egg production. Courtship behavior is species-specific and involves two categories of mate-locating behavior by males, "display perching" and

"patrol perching." The oviposition strategies of ithomiine females vary greatly and four modes of oviposition behavior are recognized. The adaptive significance of extended copulation in butterflies is discussed.

Local populations of most ithomiine species appear to be narrowly specific in larval foodplant utilization, and the high diversity of the ithomiine community is probably due in large part to the high diversity of the larval foodplants (Solanaceae) in tropical forests. Larval development time depends on the mechanical and chemical characteristics of the foodplant, but the average generation time is about 28 to 30 days. Juvenile ithomiines display great interspecific variation in morphology in all life stages. The similarity of the previously undescribed larva of Melinaea menophilus (Ithomiidae) to larvae of other primitive ithomiines and to larvae of the Danaidae provides new evidence for the relationship between the two families.

A nine-month censusing program at Limoncocha revealed that the ithomiine adult community appears to be quite stable in relative composition of mimetic patterns, age distribution, species diversity (H'), and equitability (J'). Larval foodplants are greatly under-utilized at Limoncocha and intensive parasitism and predation of juvenile stages appear to be controlling the population sizes of most ithomiine species, although the overall abundance of the ithomiine community may be severely depressed by the indiscriminate adult mortality resulting from violent storms and periods of heavy rainfall.

CHAPTER I

INTRODUCTION

Community ecology may be defined as the study of the relationships among a set of coexisting interdependent populations (Price, 1975). Early studies usually concentrated on communities defined largely by spatial constraints, e.g., a field, a rotting log, an algal mat, or any unit that contained several species. More recently, however, segments of a community that contain biologically or evolutionarily closely related species have been employed as a means of studying the ecological relationships of a community. For example, Root (1967) has introduced the concept of the guild, a group of species (i.e., a set of populations) that exploits the same class of environmental resources in a similar manner. A guild, then, contains species that are ecologically similar, but may be taxonomically diverse. Another approach involves the study of a taxonomic segment of a community, or taxocene (Chodorowski, 1959; Hutchinson, 1967), the members of which are likely to be of about the same size, to have similar life histories, and to compete over both evolutionary and ecological time (Deevey, 1969). This combination of characteristics suggests that comparative studies, both among the species within a taxocene and among taxocenes themselves, should be particularly useful in elucidating community structure. Although taxocenes can be defined at several levels, the broader the taxonomic category employed, the less similar the included species will be, and thus the more difficult meaningful comparisons will become. The size and uniformity of the

spatial or environmental dimension of a taxocene is determined by the organisms' size, mobility, and fidelity to particular microhabitats (Hurlbert, 1971).

The present study is an attempt to better understand the butterfly community of a neotropical lowland rainforest through a comparative study of species of the subfamily Ithomiinae (Lepidoptera: Papilionoidea: Ithomiidae), a group of butterflies that closely fits Deevey's description of a taxocene. The ithomiine taxocene is attractive for such a study for several reasons. Although closely related and morphologically similar, ithomiines differ enough in wing pattern, behavior, and reproductive strategy to permit meaningful comparative studies of species that compete over both evolutionary and ecological time. As a group, ithomiines are relatively abundant in neotropical rainforests, and the flight levels of most species make them accessible for detailed study. As adults, they are the most numerous participants in the extensive and widespread mimicry complexes of neotropical forests. As herbivorous immatures, they are known to specialize almost exclusively on a plant taxocene, the Solanaceae, that is notorious for the diversity of its mechanical and chemical anti-herbivore devices. Such a relationship suggests that the study of the Ithomiinae-Solanaceae interface could provide extremely fertile ground in which to cultivate the theories of insect-plant coevolution.

And yet, for all this, the Ithomiinae have received only scant attention from ecologists. In a preliminary study, Gilbert (1969) assessed their suitability for answering certain questions about community ecology. More recently, Young (1972, 1974a,b,c) has published life histories of four species of Ithomiinae from Cuesta Angel, a montane forest

locality in Costa Rica, and thus has laid the foundation for a detailed comparative study there. Pliske (1975a,b,c; Pliske et al., 1976) has begun an investigation into the role of olfactory communication in the behavioral ecology of adult Ithomiinae. In addition, some ecological information may be gleaned from a few scattered observations in the early literature (e.g., Collenette and Talbot, 1928) and from some recent studies of mimicry complexes involving ithomiines (Poole, 1970; Papageorgis, 1974; Brown and Benson, 1974). In spite of these studies, however, the Ithomiinae remain poorly understood ecologically.

Thus, in addition to using the Ithomiinae as a taxocene to approach butterfly community ecology, a main goal of this study is to increase the body of knowledge about the Ithomiinae, both to adequately characterize the subfamily in ecological terms and to determine promising directions for future research.

Study Area

The lowland tropical forests of eastern Ecuador (the Oriente) form the western extremity of that vast sea of tropical vegetation known as Amazonas, or the Amazon Basin. Drained primarily by the Napo and Pastaza Rivers and their numerous tributaries, the Oriente corresponds roughly to the western half of the largest and ecologically most diverse of the several lowland tropical refugia postulated to have harbored tropical forest floral and faunal elements during glacial periods of the Quaternary. Named after the largest river in the Oriente, the Napo Refuge comprised mainly the lowlands of east Ecuador (prior to the political rearrangements of the 1942 Protocolo de Rio de Janeiro which ceded much

of this area to Peru) from the Andes east to the upper Amazon (Haffer, 1974). The evolutionary significance of these Quaternary Refugia will be discussed later in this paper, but it can be noted now that the size and structural diversity of the Napo Refuge was probably responsible in part for the high species richness that occurs in this region at the present. The study area for this research, Limoncocha, in Napo Province, Ecuador, is located within the boundaries of the Napo Refuge.

Limoncocha is the field headquarters for the linguistic, educational, and cultural work in eastern Ecuador of the Summer Institute of Linguistics (known in the United States as the Wycliffe Bible Translators), a nondenominational missionary organization that operates under contract with the Ministry of Education of the Ecuadorian government. Situated at 0° 24' South latitude and 76° 38' West longitude, Limoncocha is located about 210 kilometers almost due east of Quito on the western edge of "Lemon Lake," an oxbow cut-off of the Rio Napo that lies two kilometers to the south. The Limoncocha area is bordered on the west by the Rio Jiveno (see map, Figure 1).

Historical Background

When the Summer Institute of Linguistics (S.I.L.) selected this site in 1957 as a logistic support base for its personnel working with isolated indigenous Indian tribes (Cofan, Secoya-Siona, Shuara=Jivaro, Waodani=Auca, Yumbo) in the Oriente, virgin forest covered the entire area and there were no Indians living in the vicinity, although the remains of pre-colonial villages have since been found on the lake's western edge. Since those humble beginnings, when tools and supplies were flown in by amphibious plane, Limoncocha has grown into a sophisticated

Figure 1. Map of East Ecuador (the Oriente).

settlement, complete with electricity from a diesel-powered generator (operated 0700-2100 daily) and indoor plumbing. The twenty or so missionary families that presently live and work at Limoncocha are supplied by weekly flights of the Institute's own DC-3 which lands on the 1100 meter airstrip completed in the mid-1960s (see map, Figure 2). The only other access to Limoncocha is by canoe from Coca, the terminus of the oil pipeline road built a decade ago by Shell-Texaco to exploit the considerable oil reserves of the Oriente (see map, Figure 1).

During the 1960s, the rapid physical growth of the missionary base at Limoncocha was accompanied by the coalescence of the scattered lowland Quichua (=Yumbo) Indian families of the area into a village just south of the airstrip. As both the village and the missionary settlement grew, increasing demands were made on the surrounding forest, first for lumber and game, and then for cleared land for crops and pasturage. While the entire area within a ten kilometer radius has been heavily hunted and selectively logged, clearing of the land for yuca (=manioc) and banana fields had, until recently, been limited to the area between Limoncocha and the Napo, especially along the "Napo Road" and the lower Rio Jiveno (see map, Figure 2). More recently, however, the Ecuadorian government has initiated a colonization program that offers 50-hectare land grants to "colonistas" who settle in the Oriente, an effort designed to help alleviate the burgeoning overpopulation of the highlands by encouraging eastward migration. The Limoncocha area has many attractions for these colonistas, including two rivers and one lake for fishing, availability of medical and dental care (two Registered Nurses reside at the missionary settlement), and Limoncocha's growing importance as a transportation center. In addition to the Quito-based DC-3, the Institute maintains two Heliocourier aircraft at Limoncocha for shuttling

Figure 2. Map of Limoncocha, Ecuador.

translators to and from tribal areas and for transporting Indians into Limoncocha for various educational programs and for medical care. The synergistic effect of the government's colonization program and Limoncocha's attractiveness as a settlement area presents an ever-increasing demand on the terrestrial and aquatic ecosystems of the area. At the present rate of growth there will be very few--if any--undisturbed forest areas within a 15 kilometer radius of Limoncocha by 1980. Consequently, as the land is cleared or otherwise disturbed, Limoncocha's value as a site for tropical scientific research will continue to diminish proportionately.*

Climatic Description

Weather records (rainfall, maximum and minimum temperature, relative humidity and cloud cover) have been kept by S.I.L. and Ecuadorian military personnel at Limoncocha since 1961. Monthly and yearly means based on the first 14 years (1961-1974) of Limoncocha weather data fall well within the ranges of values given by Richards (1964) as characteristic of lowland tropical rain forests. Such forests are characterized by a high mean annual temperature with little seasonal variance, relatively heavy rainfall in all months of the year, high humidity, low wind velocity except during storms, and frequent cloudiness.

* Prior to this study, Limoncocha had hosted a number of visiting scientists, usually for visits of only one or two weeks. In addition, at least three long-term studies had been conducted at Limoncocha; one on soil composition, one on bird foraging strategy, and a third on army ant behavior.

Mean annual temperature at Limoncocha is 25.2°C , with the range among monthly means less than 2°C . The mean annual maximum temperature is 29.8°C and the mean annual minimum temperature is 20.6°C , a difference of less than 10°C . The mean monthly maximum, mean monthly minimum and mean monthly temperatures are graphed in Figure 3.

The mean total annual rainfall is 3065 millimeters (range: 2600 to 3725 mm). If total annual rainfall is plotted on a yearly basis from 1961 to 1974, the resulting histogram gives some indication that annual rainfall at Limoncocha is increasing (Figure 4). Although this apparent increase may be only a portion of a much longer regional rainfall cycle, or merely chance variation, Emmel (1974) has suggested that the increase may be correlated with the "burning-off" of the new oil wells opened to the northeast of Limoncocha in the early part of this decade. The particulate matter lofted upward in the form of smoke from the burning wells may serve as nuclei for condensation and thus lead to an increase in precipitation. It is true that the mean annual rainfall for the years 1961-1970 (2935 mm) is considerably less than the same statistic for the period after 1970 (3390 mm), but the range of variation during the 14 years of records (1124 mm) is 2.5 times as great as the difference between these two means (456 mm). Several more years of data will be needed to determine if the mean annual rainfall since the burn-off began will stabilize around a new and significantly higher mean.

Although Limoncocha lies almost directly on the equator, where climate is theoretically aseasonal, its weather data tend to support Richards' (1964) statement that "there are probably no land surfaces within the tropics with a completely aseasonal rainfall." Limoncocha's proximity to the equator insures that a substantial amount of rain falls

Figure 3. Mean Monthly Temperatures, Mean Monthly Maximum Temperatures, and Mean Monthly Minimum Temperatures at Limoncocha, Ecuador.

Figure 4. Annual Rainfall at Limoncocha, Ecuador: 1961-1974.

Figure 5. Mean Monthly Rainfall at Limoncocha, Ecuador.

Figure 6. Rainfall at Limoncocha, Ecuador: January 1974 to December 1974.

Figure 7. Percent Rainy Days per Month and Mean Maximum Consecutive Rainless Days per Month at Limoncocha, Ecuador.

Figure 8. Percent Days per Month with Greater Than 50% Cloud Cover at 1300 hours at Limoncocha, Ecuador.

Figure 9. Mean Monthly Percent Relative Humidity at 1300 hours at Limoncocha, Ecuador.

throughout the year, but there are rainfall maxima correlated with those times at which the sun is at its zenith (mid-March and early October at Limoncocha), with corresponding rainfall troughs inbetween. Thus, the rainfall is distributed bimodally, with a broad peak in April-May-June and a sharper peak in October (Figure 5). In spite of the considerable variation in monthly rainfall totals from year to year, most of the 14 years for which data are available show this general pattern. The year of this study, 1974, is an exception because of the unusually high rainfall in July-August-September (Figure 6). Indeed, 1974 had the highest precipitation totals for August and September since record-keeping began.

The average percent rainy days per month (Figure 7) is closely correlated with average monthly rainfall. This suggests that the lower rainfall of drier months is due more to the reduction in the number of days with rain rather than in an overall decrease in the amount of rain per day. Such a pattern allows the accumulation of several consecutive rainless days to occur more often in the drier months, as the histogram in Figure 7 shows.

Likewise, the degree of cloudiness and the percent relative humidity also have a shallow bimodal pattern similar to that of rainfall. Cloud cover, expressed as the percentage of days per month with greater than 4/8 cover at 1300 hours (Figure 8), is quite high, averaging above 70% over the year. Relative humidity measurements are available for 0700, 1300, 1900 hours, but the 0700 readings are always 100% and the 1900 readings are usually 98-100% and never below 95%. The 1300 readings show a very shallow deviation around a yearly mean of nearly 75% (Figure 9).

At Limoncocha, the temperature, rainfall and relative humidity measurements were all taken one meter above the ground in a standard white

weather box located in the open on the airstrip. Comparative measurements made with a sling psychrometer at the same height within mature forest showed that relative humidity at 1300 hours was always substantially higher than that recorded at the weather box. Rarely did the relative humidity in mature forest fall below 85%. Likewise, temperatures in the mature forest at 1300 hours were several degrees cooler than those recorded on the airstrip at the same time.

According to the Holdridge Life Zone System (Holdridge, 1967), the Limoncocha area should be classified as Tropical Moist Forest on the basis of its mean annual temperature (25.2°C) and mean total annual rainfall (3065 mm). Normally, a dry season (i.e., period with soil moisture considerably lower than field capacity) of three or four months would be expected in this life zone with three meters of rain per year. However, the rainfall distribution pattern at Limoncocha is more even than that of the zonal climate, resulting in an "atmospheric association" (Holdridge, 1967). The vegetation in this association is, therefore, more luxuriant than that which would be found in the zonal association (i.e., Tropical Moist Forest).

A calculation of water balance (Table 1) shows that, based on an estimated field capacity of 250 mm, there is an average water surplus of at least 70 mm every month of the year at Limoncocha. Nevertheless, there are occasional months dry enough to produce a water deficit. Significantly, these have occurred only in the "non-rainy" seasons (Aug.-Sept. and Dec.-Jan.-Feb.) and are relatively infrequent (see Table 1). Thus it may be concluded that, except on rare occasions, there is always sufficient water to maintain the soil's field capacity and that the Limoncocha forests are therefore not subject to any prolonged or severe seasonal water deficit.

Table 1. Water Balance Calculation for Limoncocha, Ecuador.

Holdridge Life Zone: Tropical Moist Forest												Elevation: 280 m	
Available Moisture or Field Capacity (FC): 250 mm												R/PET = 2.06	
	MONTH												YEAR
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Mean of Total
Air Temperature C°	25.6	25.8	25.4	25.2	25.0	24.6	24.2	25.0	25.3	25.6	25.7	25.6	25.2
Precipitation (R) mm	216	189	287	304	311	301	276	227	232	283	242	198	3066
Potential Evapo-transpiration (PET) mm	128	118	127	122	125	119	121	125	122	128	124	128	1487
Water Surplus mm	88	71	160	182	186	182	155	102	110	155	118	70	1579
Soil Moisture Change mm	0	0	0	0	0	0	0	0	0	0	0	0	
Moisture available in soil at end of month mm	FC	FC	FC	FC	FC	FC	FC	FC	FC	FC	FC	FC	
Runoff mm	88	71	160	182	186	182	155	102	110	155	118	70	1579
Number of years (out of 14) in which a moisture deficit occurred	2	3	0	0	0	0	0	1	2	0	0	2	

Note: Calculations made according to Tosi method (Holdridge, et al., 1971).

Physical Description

Forest area

Limoncocha is approximately 280 meters above sea level and almost 15 meters above the level of the lake and the two nearby rivers (Rio Napo and Rio Jiveno). All other relief in the area is less than 10 meters. The soils are mostly laterites, covered in forested areas by a layer of humus and decaying organic matter several centimeters thick. Forest soils are always wet and forest trails are muddy year around. During the wetter periods, water may accumulate in poorly drained areas to depths ranging from 2 to 70 cm, with standing water remaining anywhere from two days to two months.

The canopy of the mature forest averages 40 to 50 meters in height, with emergents (e.g., Ceiba) occasionally reaching 70 meters. Undisturbed areas have all the characteristic features associated with climax tropical rain forest: tall, smooth-barked trees with buttressed roots; abundant epiphytes, creepers, and climbers (lianas); a large saprophyte community; a relative openness of the forest understory and a corresponding density of the canopy; a monotony of leaf color (dark green) and leaf form (predominantly elliptical, with an acuminate tip or "drip tip"); a paucity of flowers in the understory; and a high species diversity (i.e., a great number of plant species present in a small area, each represented by only a few individuals).

In the Limoncocha forests palms (Palmae) are quite abundant, especially those known locally as chonta (Iriartea sp.) and chontadura (Bactris gasipus H.B.K.). Natural clearings, from 0.2 to 1.0 or more hectares in size, are an unpredictable but not infrequent occurrence caused by the blow-down of trees. These temporary sunny clearings are

rapidly colonized by various fugitive plant species, especially by members of the genera Eupatorium (Asteraceae), Ochroma (Bombacaceae), Heliotropium (Boraginaceae), Cecropia (Moraceae), Heliconia (Musaceae), and Solanum and Physalis (Solanaceae). These same fugitive elements are also common along the more open forest trails and along the edges of man-made clearings.

Clearings

In 1974, a total of approximately 83 hectares of land at Limoncocha had been cleared by S.I.L. and the local Quichuas. This total may be broken down as follows: airstrip clearing, 20 hectares; missionary settlement, 18 hectares; pasturage, 40 hectares; and Quichua village, 5 hectares (see map, Figure 2). As indicated on the map in Figure 2, there are several areas of secondary or heavily disturbed forest bordering the base, totaling approximately 66 hectares. Since 1974, a great many new clearings have been made along the Napo Road and on both sides of the Rio Jiveno. By early 1976, virtually all of the remaining lands in these areas had been claimed by colonistas (James Yost, personal communication), and thus more clearings can be expected in the future.

The open borders of the grassy airstrip are covered by Ipomoea (Convolvulaceae) and the exposed forest face by the introduced kudzu vine (Pueraria lobata). The pasture blends gradually into the surrounding disturbed forest. Only a few of the original forest trees are still standing in the settlement clearing, which has been heavily planted with fruit trees, including orange, grapefruit, and lemon (Citrus), avocado (Persea), and banana (Musa), and ornamentals, e.g., African oil palm (Elaeis guineensis Jacq.) and Hibiscus.

Trails

There are several forest trails near Limoncocha. Those used in the course of this study are described below (also see map, Figure 2).

Napo Road (NR). This is a broad trail, ten meters wide, that runs south from Limoncocha for three kilometers to the Brazo of the Rio Napo, at a point just east of the mouth of the Rio Jiveno. Numerous side trails branch off to the east and west.

Nature Trail (NT). This trail runs west from the Power House for about 80 meters before it forks into two branches that later reunite to form a large closed loop. The 80-meter stem of the NT passes through second growth forest (see Figure 10). The closed loop occurs in slightly disturbed primary forest (see Figure 11). This two meter-wide trail has been marked with numbered stakes corresponding to points of interest which are explained on a cassette tape (to be played by visitors while walking the trail). Southeast of the NT loop are a series of anastomosing trails less than one meter wide which give access to the NT Study Area (Site 5).

Hunting Trail (HT). This trail begins at the western tip of the NT loop and continues in a broad west-northwest curve. Quite narrow, it is difficult to follow after the first two kilometers.

Logging Trail (LT). Originally a ten meter-wide trail that would accomodate a tractor for the first part of its length, this trail angles NW and roughly parallels the HT. Along it are study sites 1, 2, 3, and 4. In the past, logs were hauled by tractor down this trail to the sawmill located in the Power House building. Greatly overgrown today, the LT fades to less than one meter in width beyond Site 4. A severe storm with localized twisting winds occurred in March 1974, and blew down

several very large trees and numerous smaller ones between Sites 2 and 3. The resulting morass of tangled vines, shrubs, and fallen trees rendered this stretch of the LT nearly impassable. By June 1974, this devastated trail was so choked with new growth that it was never used again as a passage to Site 4.

Cross-Cut Logging Trail (CCLT). A five meter-wide trail first cut in early 1973, this north-south trail links the NT with the LT. After June, 1974, it provided the quickest means of reaching Site 4. Because of its width, this trail receives much sunlight and thus is difficult to keep open. By May 1975, this trail was completely blocked by vines and Heliconia plants and was no longer passable.

Location of study sites

Intensive or long-term studies were conducted at six study-site localities. Site 1, Site 2, Site 3, and Site 4 were located at points along the Logging Trail. Site 5 and Site 6 were in the Nature Trail area (see map, Figure 2).

During this study, Sites 1 and 3 were open sunny areas (see Figure 12) with large numbers of blooming Eupatorium plants that attracted many ithomiines (see Figure 13). Site 2 was a much more shaded spot with several large Heliotropium plants in bloom. Site 4, bisected by the LT (see Figure 14), was a one hectare rectangular plot staked out in relatively undisturbed, mature, but seasonally flooded forest (see Figure 15). Site 5 was a 0.5 hectare plot located in relatively undisturbed, mature, unflooded forest (similar to that shown in Figure 11). Site 6 was a transect 100 meters long and 2 meters wide, located along the closed loop of the Nature Trail (see Figure 11).

Figure 10. Near Beginning of Nature Trail
(stem portion) in Secondary
Forest.

Figure 11. Nature Trail (loop portion) in
Primary Forest, near Study Site 4
(100 m by 2 m transect).

Figure 12. Logging Trail, Study Site 3.

Figure 13. Males of Scada batesi Haensch Feeding at Eupatorium I
Flowers at Study Site 3.

Figure 14. Logging Trail, Study Site 4.

Figure 15. Forest Interior at Study Site 4.

The experiments and observations performed at these study sites are described in the methods section.

The Butterfly Community at Limoncocha, Ecuador

Composition

Along with birds, butterflies are perhaps the most conspicuous of all neotropical animals. This is primarily the result of their diurnal habits, the often brilliant coloration of their wings, and their relative abundance compared to other animal groups in the same region. As is characteristic of many invertebrate taxa in the tropics (Elton, 1973), this abundance of butterflies results not from a few common species each with a large population, but from the presence of a great number of species most of which have a relatively small number of individuals (Ebert, 1969). In short, neotropical butterfly communities usually exhibit high species diversity (sensu Simpson, 1949).

The butterfly community of Limoncocha fits this pattern of diversity quite well. In over twelve months of collecting (two collectors) in the Limoncocha area, about 366 species of butterflies were taken (this does not include the skippers, Superfamily Hesperioidea, of which some 75 species were taken). Based on the number of species represented by only one or two specimens in our collection, I estimate that there are at least another 75 to 100 species that occur in this area, and possibly as many as 150 or more. Thus, the total number of butterfly species at Limoncocha (excluding skippers) is estimated to be between 400 and 500, with 460 as a reasonable figure.

The reasons for the incomplete sampling are several. First, only a small portion of the total time spent in the field was devoted to an active attempt to locate and collect new (i.e., previously untaken) species. Second, nearly all specimens collected were taken in the lower four meters of the forest or in and around clearings. Thus, those species that fly and perch in the mid to upper forest canopy are quite under-represented in the collection as they were caught only when they occasionally strayed into the lower levels of the forest or were attracted to flowering plants in clearings and along trails. Even without the above restrictions, however, the collection of all species of any insect group occurring in any one neotropical locality is exceedingly difficult. Indeed, writing more than one hundred years ago on the low density of most insect populations on the upper Rio Solimoes in Brazil, Bates (1857) concluded that "one year of daily work is scarcely sufficient to get the majority of species in a district of two miles circuit."

Third, some species may be present in an area at a given time, then disappear for a number of months or years, only to reappear at a later date. In this context, however, "disappear" probably has more than one meaning. It could mean that a species is always present in an area, but that its population density becomes so low at certain periods that its presence could only be detected by the collection of an extremely large sample. Or it may mean that the species population becomes locally extinct at times and is re-established only through later immigration. It is most likely that both meanings of the word describe the dynamics of some of the species at Limoncocha.

This same phenomenon of periodic occurrence has been observed in the Limoncocha avifauna. After eight months' study in 1971 and 1972, David Pearson (1972) compiled a species list of all birds occurring within a five kilometer radius of Limoncocha. The list numbered 344. In early 1974 an ornithologist visiting Limoncocha for ten days added over 30 species to the list. Another ornithologist presently studying at Limoncocha has now increased Pearson's original list by over 50 species. Some of these new birds are undoubtedly seasonal migrants that Pearson might have seen had he been at Limoncocha for a full twelve month cycle, and some may be species that were present but so rare in 1971 that he never encountered them, but have since become more common. Still others probably represent species that simply were not present at the time of Pearson's study but have invaded the Limoncocha area since that time.

Similar phenomena are probably influencing the butterfly community. Some of the species taken at Limoncocha only once are undoubtedly mountain forms that apparently strayed or were blown eastward from higher elevations on the eastern slopes of the Andes (e.g., Athyrtis mechanitis salvini Srnka). Also, during short trips to Limoncocha in 1972 and 1973, I have taken a few species that I never saw or collected again during the whole of 1974. Furthermore, some species at Limoncocha (e.g., Helicopis interrupta) have been observed to occur in "blooms," synchronous emergences of large numbers of individuals at seemingly unrelated times of the year, probably triggered by some unique combination of climatic factors. Heinz Ebert (1969), after years of studies on the frequencies and distributions of butterfly populations in Brazil, concluded that

many species of butterflies, especially those of the most numerous families (Hesperiidae, Lycaenidae, and Riodinidae), have populations that are small in size, dispersed widely, and which are not constant in locality, but "migrate" continuously within a great area of favorable habitat, such that local colonies are continually appearing and disappearing.

Thus, just as the scattered distribution of rain forest trees resembles a spatial mosaic (Richards, 1964), so do the temporal vagarities of butterfly abundance resemble a phenological mosaic. Such variability in species composition must always be carefully considered when conducting or evaluating research on tropical butterflies or other insects, and perhaps even birds and mammals. (This phenomenon has long been recognized as characteristic of most tropical forest human populations.)

Ross (1967) has observed that the systematics of the Lepidoptera, especially tropical forms, is in a relatively unstable state. While he was referring primarily to the generic level and below, it is also true that very few students of butterflies agree fully on the number and content of butterfly families. Ehrlich (1958) has published the most recent comprehensive review of the phylogeny and higher classification of the Papilionoidea (i.e., butterflies other than skippers), based on a comparison of a large number of morphological characters. In that paper he recognized only five families of butterflies, the Papilionidae, Pieridae, Nymphalidae, Libytheidae, and Lycaenidae. Several long-standing families were downgraded to the level of subfamily or tribe, including the family Ithomiidae. In spite of this, however, many subsequent workers, especially those who have monographed family-level taxa (e.g., Miller, 1968), have rejected much of this downgrading and have chosen

to retain most of the families familiar to lepidopterists. Following the latter approach in this paper, I recognize nine families of butterflies: the Papilionidae, Pieridae, and Libytheidae, plus four families formed by the separation of Ehrlich's Nymphalidae into the Ithomiidae, Danaidae, Satyridae, and Nymphalidae, and two from the separation of his Lycaenidae into the Riodinidae and Lycaenidae. The number of species collected at Limoncocha in each of these nine families and in the Hesperioidea (skippers) is presented in Figure 16. The number of species estimated to be present in each family (see discussion above) is also indicated in the same figure.

Unfortunately, there are few published summaries of comparable data from other tropical forest localities. Most such faunal lists have been regional in scope, and thus cover a variety of habitat types and a substantial altitudinal range. To provide a rough comparison, however, data from three Brazilian sites have been graphed in Figures 17, 18, and 19. Figures 17 (Eastern Espírito Santo and Southern Bahia; Brown, 1972) and 18 (Eastern Pernambuco; Ebert, 1969) represent regional totals for two areas located in the isolated strip of littoral forest along Brazil's southeastern coast. Figure 19 (Jaru, Rondônia; Brown, 1976b) represents a specific locality in the southwestern Amazonian forest of Brazil.

In general the littoral forests of southeastern Brazil are not so rich in species as are the lowland forests of the Amazon Basin. Indeed, the estimated number of species at the single locality of Limoncocha is greater than that recorded for the entire eastern portion of Pernambuco (Figure 18) and the single locality of Jaru (Figure 19) is estimated to have about the same number of species as do the extensive coastal forests of southern Bahia and Espírito Santo (Figure 17).

Figure 16. Number of Species in each Butterfly Family at Limoncocha, Ecuador.

Dark portion of bar indicates the number of species collected. Light portion of bar indicates the number of additional species estimated to be present.

Figure 17. Number of Species in each Butterfly Family in Eastern Pernambuco, Brazil.

Bars with waved ends indicate the number of species estimated to be present. The number collected was not reported (Brown, 1972).

Figure 18. Number of Species in each Butterfly
Family in Eastern Espírito Santo
and Southern Bahia, Brazil (from
Ebert, 1969).

Figure 19.

Number of Species in each Butterfly
Family at Jaru, Rondonia, Brazil.
Bars with waved ends indicate the
number of species estimated to be
present. The number collected was
not reported (Brown, 1976b).

Interestingly, the butterfly faunas of two coastal regions have a much greater percentage of Hesperioidea (32-36%) than do the Amazonian forest areas (25-26%). The presence of extensive grassland and cerrado areas in the coastal regions probably account for the greater relative number of skipper species in these areas; many skippers specialize on monocotyledonous hosts.

A comparison of the two Amazonian forest localities reveals that the distribution of species among families is quite similar at Limoncocha (Figure 16) and Jaru (Figure 19), although the overall species richness of the Jaru site may be exceptional (with many years of field experience across South America, Brown, 1976b, has called it "...the most exceptional collecting area I have ever seen or imagined"). Thus, I conclude that Amazonian lowland forests may be characterized by a relative distribution of butterfly species among families similar to that shared by Limoncocha and Jaru. The families may be ranked according to the number of species they contain. Beginning with largest, the order is (1) HesperIIDae (Hesperioidea), (2 and 3) Riodinidae and Nymphalidae (very nearly equal, but either family may outnumber the other at a given locality), (4) Lycaenidae, (5) Satyridae, (6) Ithomiidae, (7) Pieridae, (8) Papilionidae, (9) Danaidae, and (10) Libytheidae. The actual number of species present in each family at most lowland Amazonian sites probably varies roughly between the values given for the number of species actually caught at Limoncocha (Figure 16) and the number estimated to occur at Jaru (Figure 19).

A comparison of butterfly faunal lists from various areas in the Neotropics (Table 2) suggests that the Ithomiidae form from 4.5 to 12% of the number of species of Papilionoidea present in a given area.

Table 2. Comparison of the Butterfly Faunas of a Variety of Neotropical Locations.

LOCALITY	Number of Species per Family (Estimated Number of Species given in Parentheses)									
	Pap	Pie	Ith	Dan	Sat	Nym	Lib	Rio	Lyc	Total
1. Limoncocha	10 (12)	24 (27)	53 (53)	4 (4)	39 (55)	91 (102)	0 (0)	90 (120)	55 (90)	366 (463)
2. Sierra de Tuxtla	21	37	20	4	28	112	1	48	88	359
3. Jaru	16	20	56	2	120	154	1	150	70	589
4. Eastern Pernambuco	3	27	15	3	30	82	1	76	101	338
5. Brasília	24	30	29	4	92	141	1	157	(154)	632
6. Belo Horizonte	12 (20)	28 (32)	19 (25)	3 (4)	21 (65)	76 (106)	1 (1)	20 (80)	15 (75)	195 (408)
7. Poças de Caldas	16	35	21	4	41	97	1	47	87	349
8. Espírito Santo	18	44	46	4	92	132	1	(100)	(103)	540
9. Rio de Janeiro	33	44	38	4	63	147	1	115	(153)	598
10. São Paulo	21	44	32	5	65	134	1	93	91	486
										6.6

Table 2 - continued.

Source: Data and reference for each locality are given below.

1. ECUADOR: Napo Province; Limoncocha, on Rio Napo.
Lowland moist forest; 280 m (present paper).
2. MEXICO: State of Veracruz; Sierra de Tuxtla area.
Lower montane rain forest to Elfin woodland; 15-1650 m
(Ross, 1967).
3. BRAZIL: State of Rondônia; Jaru, on Rio Jaru.
Lower montane humid forest; 600 m (Brown, 1976b).
4. BRAZIL: State of Pernambuco; Coastal lowland area.
Lowland monsoon forest; below 1000 m (Ebert, 1969).
5. BRAZIL: State of Minas Gerais; Brasília and vicinity.
Cerrado portion of Planalto: Cerrado and grassland;
600-1300 m (Brown, 1972).
6. BRAZIL: State of Minas Gerais; Belo Horizonte area.
Blend zone: Forest, cerrado, fields; 1500-2000 m
(Brown, 1972).
7. BRAZIL: State of Minas Gerais; Poças de Caldas area.
Primary and secondary forest, open grassland;
1000-1500 m (Ebert, 1969).
8. BRAZIL: States of Espírito Santo and southern Bahia.
Median-littoral humid forest; below 1500 m (Brown, 1972).
9. BRAZIL: State of Rio de Janeiro; Rio de Janeiro and vicinity.
Subtropical humid forest and savanna; 50-1500 m (Brown, 1972).
10. BRAZIL: State of Sao Paulo; eastern area of state.
Littoral tropical and subtropical lowland forest; 100-1000 m
(Ebert, 1969).

Samples from predominantly forested areas, the preferred habitat of ithomiines, have a higher percentage of Ithomiidae than do samples which include cerrado or grasslands. Likewise, the western and southern Amazonian forest areas have the highest percentages of ithomiines, no doubt because these areas, which correspond to the Napo and Rondônia Refuges (Brown, 1976a), were principal centers of geohistorical evolution in the subfamily (Brown, 1972).

The above discussion considers only the number of species present in a given area, and says nothing of the numbers of individuals. Unfortunately, estimates of absolute population size of neotropical butterfly populations in tropical forest areas are practically non-existent. The low density of most species' populations limits the use of the insect ecologist's favorite technique, the capture-mark-recapture sampling series. Until alternative techniques of population size estimation are available, we must be content with estimates of relative abundance, although these are usually severely biased by the investigator's collecting technique, preference for certain taxa, and a tendency to concentrate on unusual or showy species. While techniques to determine the number of butterfly species present in tropical areas have been recently refined (Brown, 1972), little attention has been given to the estimation of absolute population sizes of tropical insects (but see Elton, 1973).

Microhabitat Distribution

Although all of the species of butterflies which occur at Limoncocha are, by definition, inhabitants of lowland tropical rainforest, they differ widely in their preferred microhabitats. Species which are

characteristically found in open fields, and along roads and rivers may be called campestal, while those found predominantly in the forest can be termed sylvestral. Some species are sun-loving (heliophilic), others are shade-loving (scotophilic). Various levels within mature forest, from the lower understory to the upper canopy, contain different, though overlapping, groupings of species.

Of concern to the present work are those species which share the same microhabitats with members of the Ithomiidae, and especially those involved in mimetic relationships with ithomiines. The characteristic habitat, or preferendum, of each butterfly family at Limoncocha may be briefly summarized as follows (all Limoncocha ithomiines and many mimetic species of other families are illustrated in Figures 58-65).

Papilionidae. Most of the larger non-mimetic species are heliophilic, usually flying above the canopy, and thus are most often seen in clearings and along open trails (Papilio) or rivers (Graphium). Mimetic species (Parides, Battus) appear to be rarer in number and are usually found in the mid to upper levels of the forest or along shaded trails.

Pieridae. Most of the Pierinae (except the mimetic genera Archonias, Itaballia, and Perrhybris) and the Coliadinae (except for the fragile Leucidea brephos) are heliophilic and campestal, commonly flying along rivers and open trails or in clearings. The mimetic genera of the Pierinae are chiefly sylvestral, but often wander along the edges of clearings or shaded trails. The six Limoncocha species of Dismorphinae are all mimetic and rarely stray from the forest interior. D. pinthaeus, D. theugenis, D. erythroe, and D. leuconoe are restricted to the lower levels of the understory, while D. orise and D. amphione frequent the mid and upper canopy, respectively.

Ithomiidae. Most species are scotophilic and tightly restricted to the forest understory, although a few are found in the upper levels of the forest. Members of a few genera frequent the sunny edges of clearings (e.g., Ceratinia, Mechanitis) while others (e.g., Melinaea, Tithorea) often fly in the sunlit upper canopy.

Danaidae. The monarch, Danaus plexippus, is campestral, especially common over pastures and large clearings. The mimetic Lycorea ceres is sylvestral and heliophilic, visiting flowers of the upper canopy and forest edges. The clearwing mimic, Ituna lamirus, is a deep forest dweller.

Satyridae. Most species are dark and cryptic in coloration, scotophilic, and occupy only the lower levels of deep forest understory, although some Euptychia are found in second growth or grassy areas as well. The Brassolinae are crepuscular, often flying in banana groves or along open trails. Mimicry is rare.

Nymphalidae. This large family is quite diverse both morphologically and behaviorally. Although most non-mimetic species are heliophilic to some extent and are often found in the sunlit upper canopy, along open trails and rivers, and in clearings, others, e.g. Nessaea regina, are sylvestral. Batesian mimics usually occupy the same microhabitats as their models, e.g., Phyciodes actinote is found in the forest interior, and Anaea (Consul) fabius is found in the upper canopy.

Lycaenidae. This is a large family of generally quite small butterflies, most of which are sylvestral, frequenting sunlit patches in the mid to upper levels of deep forest. Many species are rare, difficult to see, and harder to catch. Mimicry is uncommon.

Riodinidae. Another family of generally small butterflies, the metalmarks are quite similar ecologically to the Lycaenidae. Mimicry is not uncommon, but the mimetic relationships are for the most part poorly understood as they rarely involve classical models. Both species richness and heterogeneity of the Riodinidae is higher than that of the Lycaenidae at Limoncocha, and the range of wing coloration and patterning is astonishing.

Hesperiidae (Hesperioidea). In temperate areas skippers are characteristically campestral, associated with open fields and second growth areas, but in the tropics there are a great many sylvestral species. Some are brightly colored blue or red, but most are of a yellow, brown, or dull orange. Mimicry is rare.

The mimetic associations present at Limoncocha, with special reference to the Ithomiinae, will be discussed in Chapter 7.

The Butterfly Subfamily Ithomiinae

The Ithomiinae have been, and are, largely neglected by students of Exotic Lepidoptera, and one hears as the reason that they are less beautiful than other groups and more difficult. The first answer I will ask you to dismiss from your minds, for it cannot be a well-considered statement by any who make it. As for the latter--the one of difficulty--there is certainly more truth in it, but it is not nearly so great as is often averred, and what difficulty there is should stimulate us to fresh endeavours to overcome it.

--W. J. Kaye (1914)

The stimulation to fresh endeavours has been long in coming. During the first fifty years after Professor Kaye delivered his challenge before a meeting of the South London Entomological and Natural History

Society in 1913, the Ithomiinae were all but ignored except by a very few workers, mostly taxonomists. Only in the last ten years, and particularly in the first half of the present decade, have ecological and behavioral studies been attempted. Since ithomiines are among the most numerous and conspicuous animals in a rapidly disappearing biome, the neotropical rainforest, such attention is long overdue.

The butterfly family Ithomiidae comprises two geographically disjunct subfamilies, the Tellervinae and the Ithomiinae. Containing only the single monotypic genus Tellervo, the Tellervinae are restricted to the insular belt of tropical forests from the Cape York peninsula of Australia north through New Guinea and the Bismark Archipelago, west to Celebes, and east to the Soloman Islands (Common and Waterhouse, 1972). The Ithomiinae are entirely neotropical, ranging from sea level to 3000 meters elevation in the tropical and subtropical portions of Central and South America. Only two species occur in the Antilles, one on Cuba and another on Jamaica and Hispanola (Fox, 1963).

The Ithomiinae have had a nomadic taxonomic history (reviewed in Fox, 1956). Over the past two hundred years they have been shuffled among various family groups, including the Heliconiidae, Nymphalidae, and Danaidae. For most of this century both the Ithomiinae and Tellervinae have been considered part of the Danaidae because that was the arrangement in Seitz's widely distributed The Macrolepidoptera of the World (Seitz, 1924). After considerable morphological and systematic study, Fox (1949, 1956) concluded that the Ithomiidae were worthy of familial rank and called into question their classical association with the Danaidae. He considered the Ithomiidae to be primitive among the

Nymphaloidea, and most closely related to the Satyridae. Gilbert and Ehrlich (1970), however, have reviewed the evidence of the larval, pupal and adult morphology, the foodplant relationships, and the behavioral characteristics of the Ithomiidae and Danaidae and concluded that the two share a much closer relationship than do the Ithomiidae and the Satyridae. Data collected in this study provide further evidence in support of the Ithomiidae-Danaidae relationship.

Since the classic work of Richard Haensch (1903, 1905, 1909), the most active students of the Ithomiinae have been R. Ferreira d'Almeida (see Brown, F., 1975, for a complete bibliography) in Brazil and W. T. M. Forbes (see Fox, 1956, for bibliography) and Richard M. Fox (see Brown, F., 1968, for a complete bibliography) in the United States. Fox began a monographic revision at the family level which was uncompleted at the time of his death in 1968. Of the eight tribes he recognized in the Ithomiinae (Fox, 1949), he completed the revisions of only the first four: Tithoreini (Fox, 1956), Melinaeini (Fox, 1960), Mechanitini (Fox, 1967) and Napeogenini (Fox and Real, 1971). Gerardo Lamas M. (1973) and Herman Real (personal communication) are presently working on the taxonomy of selected genera of the four remaining tribes (Ithomiini, Oleriini, Dircenini, and Godyridini).

The numbers of genera and species contained in the Ithomiinae are far from being decided with certainty. The recent trend in the evolution of the taxonomic study of this subfamily has been a reduction in the number of recognized species. As the biological relationships of many allopatric forms become better known, many of these forms are combined to form wide-ranging, polytypic species, some with a great many

named subspecies. Simultaneously with the reduction in the number of species recognized, there has been a gradual increase in the number of recognized genera as the morphological relationships of greater numbers of species began to be more closely studied. For example, Haensch (1909*), in Seitz's The Macrolepidoptera of the World, listed 883 named forms, most of them treated by him as species, occurring among 33 genera. Since that time the number of recognized genera has been increased by about one-third and the number of recognized species reduced by about one-half. Presently, there are 49 genera recognized in the Ithomiinae and, in spite of the steady stream of descriptions of new species of ithomiines over the past five decades, the number of valid species is probably only about 450.

In Table 3, the eight tribes of the Ithomiinae are listed, and the number of genera and species estimated to occur in each are presented. This table was prepared from the list of genera assigned to each tribe by Fox (1956), modified by the subsequent description of new genera in the subfamily (Fox, 1967; Fox and Real, 1971; Brown and d'Almeida, 1970; Brown et al., 1970; Lamas M., 1973). The numbers of species in the first four tribes are taken from Fox's Monograph. The numbers of species in the remaining four tribes were roughly estimated by applying a formula of reduction to the number of forms listed by Haensch (1909). The

* Although Volume V, The American Rhopalocera, of A. Seitz's The Macrolepidoptera of the World was not published as a unit until 1924, various sections of this work were issued earlier as fascicles. The section on the Danaidae, which included the Ithomiinae, was written by R. Haensch and was first published in 1909.

Table 3. The Number of Genera and Species in the Eight Tribes of the Ithomiinae.

Tribe	Number of Genera	Number of Species*	Number of Named Forms	Ratio Forms/Species
Tithoreini	8	18	63	3.5
Melinaeini	1	17	55	3.2
Mechanitini	6	34	76	2.2
Napeogenini	7	104	236	2.3
Ithomiini	3	(28)	64	(2.3)
Oleriini	4	(51)	117	(2.3)
Dircennini	9	(139)	320	(2.3)
Godyridini	11	(54)	125	(2.3)
Totals	49	(445)	1056	

Source: Data for number of genera from Fox, 1956; Fox, 1967; Fox and Real, 1971; Brown and d'Almeida, 1970; Brown et al., 1970; Lamas M., 1973.

Data for number of species in tribes Tithoreini, Melinaeini, Mechanitini, and Napeogenini from Fox, 1956, 1960, 1967; Fox and Real, 1971.

Data for number of species in the Ithomiini, Oleriini, Dircennini, and Godyridini from Haensch, 1909.

Note: See discussion in text.

* Numbers in parentheses are estimates.

formula was derived as follows. As treated by Fox (1967) the Mechanitini contain 76 named forms divided among 34 species, and the Napeogenini (Fox and Real, 1971) contain 236 named forms divided among 104 species. The ratio of forms to species for the two tribes is thus 2.2 and 2.3 respectively. Applying the figure 2.3 to the number of forms given by Haensch (1909) for each of the four tribes not treated by Fox, we arrive at an approximate number of species per tribe. (The ratios for the Tithoreini and Melinaeini are 3.5 and 3.2, but both of these tribes contain relatively primitive genera, each with a relatively few, widespread, polytypic species. The ratios of the Mechanitini and the Napeogenini are more applicable for comparisons to the remaining four tribes.) This gives a total number of species for the Ithomiinae of approximately 445. Thus, the 53 species at Limoncocha represent a little more than 10% of the total number of ithomiine species, but only about 5% of the total number of named forms (which probably exceeds 1100 today). Of the 49 genera in the subfamily, 24 are represented by species occurring at Limoncocha.

Morphologically, members of the Ithomiinae may be characterized as follows. Adults are generally medium-sized butterflies, although wingspan within the subfamily varies from less than 3 cm to over 10 cm. The forewings are generally long and narrow, but not quite so pronounced in these characteristics as are the wings of the Heliconiinae. Wings may be either opaque (usually some combination of black, brown, orange or yellow) or translucent or transparent, in which case the wing scales are reduced to tiny hairs in the clear areas. Antennae are long (between one half and two-thirds the length of the forewing) and thin, with

a slender, unscaled club. The abdomen is quite long and slender, projecting well beyond the anal margin of the hindwing. All males possess an androconial scent patch located on the dorsal costal margin of the hindwing. The scent patch is accompanied by an androconial brush consisting of a cluster of hair-like scales attached along the posterior margin of the scent patch. Both the scent patch and the androconial brush are normally covered by the overlapping forewing. The androconial scent patch and brush primitively extend the length of the discal cell. They may be separated, however, into a distal portion and a proximal portion so that some species have two androconial patches. Either the distal or proximal androconia may be absent in other species. This costal scent patch is diagnostic of the Ithomiinae (it is not present in the Tellervinae) and, because of its variation, is a useful taxonomic character at the generic level. With the exception of the genus Thyridia, females of the Ithomiinae do not have the androconial patch and brush. The neuration of the hindwing, another generically useful taxonomic character, is nearly always different in the sexes, often markedly so.

A discussion of the ecological requirements and characteristics of the adults, and descriptions of the early stages of the Ithomiinae will be presented in Chapters 3 and 5, respectively.

A list of the 53 species of Ithomiinae collected at Limoncocha during this study is presented in Table 4. The species are arranged by tribe and a subjective estimate of the relative abundance of each at Limoncocha (based on thirteen months' observations) is given in the table. The number of species occurring in each of the five categories of abundance is presented graphically in Figure 20. It is obvious from this

graph that the majority of species at Limoncocha are uncommon or rare. In fact, only about 40% of the species are abundant or common. About 15% of the species are very rare (i.e., no more than 5 specimens were collected in 13 months) which suggests that, in an ecological sense, the effective number of species at Limoncocha may be somewhat less than 53. For example, a single male of Oleria tigilla was collected during a three week visit to Limoncocha in September 1972. This species was therefore expected during the 1973-1974 study period, but, in fact, not a single Limoncocha specimen was taken during this time.

During the course of this study it was possible to make a few brief collecting trips to other lowland forest areas in the Oriente. One-day collections were made at Dureno (275 m), on the Rio Aguarico, and at Veracruz (900 m), just east of Puyo, and several days were spent at Shell (1065 m), on the Rio Pastaza, and at Tiwaeno (410 m), on the Rio Tiwaeno (see map, Figure 1). These supplementary collections revealed that several of the species that fall into the "very rare" category at Limoncocha are much more common in other areas of eastern Ecuador (e.g., Oleria tigilla was found at both Dureno and Tiwaeno). Such species are so indicated in Table 4. Thus it may be concluded that Limoncocha occurs at, or just beyond, the normal distribution of these species at this time. It must be remembered, however, that such species may have been breeding residents of the Limoncocha area in the past, and may be so again in the future (see discussion in previous section of this chapter).

Table 4. Species of Ithomiinae Collected at Limoncocha, Ecuador.

Tribe and Species	Voucher Number	Abundance*	Mean Forewing Length (mm) [†]	Remarks [†]
TITHOREINI				
<u>Athyrtis mechanitis salvini</u> Smka	5002	VR	43.5	1 specimen (05 Jan 74); stray from montane forest to the west
<u>Tithorea harmonia hermiar</u> Godman & Salvin	5037	R	39.0	N = 10♂; 9♀♀
MELINAEINI				
<u>Melinaea egesta egesta</u> Godman & Salvin	5045	VR	37.5	N = 4♂; no ♀♀ taken; nearest population unknown
<u>Melinaea maeonis maeonis</u> Hewitson	5023	U	39.0	N = 12♂; 11♀♀
<u>Melinaea menophilus menophilus</u> (Hewitson)	5024	C	41.0	N = 12♂; 6♀♀
<u>Melinaea mothone mothone</u> (Hewitson)	5025	VR	38.0	N = 4♂; no ♀♀ taken; species more common at Tiwaeno
MECHANITINI				
<u>Forbestra equicola equicoloides</u> (Godman & Salvin)	5005	R	38.5	N = 12♂; no ♀♀ taken
<u>Forbestra truncata juncata</u> (Haensch)	5006	C	33.0	N = 12♂; 12♀♀
<u>Mechanitis egaensis phasianita</u> Haensch	5046	R	34.0	N = 4♂; 2♀♀
<u>Mechanitis lathmia eurydice</u> Haensch	5019	A	33.5	N = 12♂; 12♀♀
<u>Mechanitis lysimnia elisa</u> (Guérin-Ménéville)	5020	A	33.5	N = 12♂; 12♀♀
<u>Mechanitis mazaewa mazaewa</u> Hewitson	5021	C	36.0	N = 12♂; 12♀♀

Table 4 - continued.

Tribe and Species	Voucher Number	Abundance*	Mean Forewing Length (mm) σ	Mean Forewing Length (mm) η	Remarks†
<u>Mechanitis messenoides ballucatus</u> Fox	5022a	R	35.5	38.0	N = 7♂; 5♀♀
<u>Mechanitis m. deceptus</u> Butler	5022b	C	34.5	36.0	N = 12♂; 12♀♀
<u>Mechanitis m. messenoides</u> C. & R. Felder	5022c	C	34.5	37.0	N = 12♂; 12♀♀
<u>Scada batesi</u> Haensch	5035	A	19.0	19.5	N = 12♂; 12♀♀
<u>Scada quotidiana quotidiana</u> Haensch	5044	VR	18.1	--	N = 1 specimen (08 Mar 74); species more common at Tiwaeno
<u>Xanthocleis psidii ino</u> (C. & R. Felder)	5038	U	39.0	39.0	N = 12♂; 2♀♀
NAPEOGENINI					
<u>Hypothyris euclea peruviana</u> (Staudinger)	5012	C	26.5	27.0	N = 12♂; 12♀♀
<u>Hypothyris fluona berna</u> (Haensch)	5013	U	25.5	27.0	N = 12♂; 12♀♀
<u>Hypothyris fulminans satura</u> Haensch	5014	U	29.0	29.5	N = 12♂; 12♀♀
<u>Hypothyris mameucus mameucus</u> (Hewitson)	5042	R	29.5	30.5	N = 7♂; 8♀♀
<u>Hypothyris mansuetus moebiusi</u> (Haensch)	5015	R	31.0	33.5	N = 4♂; 7♀♀
<u>Napeogenes aethra</u> (Hewitson)	5028	R	28.0	28.0	N = 12♂; 12♀♀
<u>Napeogenes apobsoleta</u> Kaye	5026	U	28.0	29.5	N = 12♂; 12♀♀
<u>Napeogenes corena caucayaensis</u> Fox & Real	5027	U	20.0	21.5	N = 12♂; 12♀♀
<u>Napeogenes duesa duesa</u> (Hewitson)	5040	R	24.5	26.0	N = 8♂; 12♀♀
<u>Napeogenes pharo avila</u> Haensch	5029	A	22.0	23.0	N = 12♂; 12♀♀

Table 4 - continued.

Tribe and Species	Voucher Number	Abundance*	Mean Forewing Length (mm) ♂	Mean Forewing Length (mm) ♀	Remarks †
ITHOMIINI					
<u>Ithomia agnosia</u> <u>agnosia</u> Hewitson	5016	A	22.0	22.0	N = 12♂; 12♀♀
<u>Ithomia amarilla</u> Haensch	5017	A	23.0	23.0	N = 12♂; 12♀♀
<u>Ithomia derasa</u> <u>salapia</u> Hewitson	5018	U	24.0	24.0	N = 12♂; 12♀♀
OLERIINI					
<u>Aeria eurimedia</u> <u>nigricola</u> (C & R Felder)	5001	C	23.5	24.0	N = 12♂; 12♀♀
<u>Hyposcada</u> <u>kezia</u> subsp.	5010	U	30.0	31.0	N = 12♂; 12♀♀
<u>Oleria agarista</u> <u>agarista</u> (C. & R. Felder)	5030	A	21.5	23.5	N = 12♂; 12♀♀
<u>Oleria kena</u> <u>ida</u> (Haensch)	5011	C	24.0	25.0	N = 12♂; 12♀♀
<u>Oleria lota</u> <u>lota</u> (Hewitson)	5031	U	19.0	20.5	N = 8♂; 12♀♀
<u>Oleria tigilla</u> (Weymer)	5052	VR	21.5	--	1 specimen (04 SEP 72); species more common at Dureno and Tiwaeno
<u>Oleria</u> species	5048	VR	19.5	20.0	N = 4♂; 3♀♀; species more common at Dureno
<u>Oleria</u> species	5053	U	19.5	21.0	N = 12♂; 12♀♀
DIRENNINI					
<u>Ceratinia poecila</u> <u>poecila</u> (Bates)	5003	A	25.5	25.5	N = 12♂; 12♀♀
<u>Callithomia alexirrhoe</u> aubap.	5041	VR	31.0	32.0	N = 2♂; 2♀♀; nearest population unknown

Table 4 - continued.

Tribe and Species	Voucher Number	Abundance*	Mean Forewing Length (mm) $\frac{\sigma}{\varphi}$	Remarks†
<u>Callithomia epidero</u> (Bates)	5050	R	30.0	N = 6 ♂♂; 7 ♀♀
<u>Dircenna loreta</u> Haensch	5004	R	33.0	N = 5 ♂♂; 11 ♀♀
<u>Pteronymia sparsa</u> Haensch	5034	C	21.0	N = 12 ♂♂; 12 ♀♀
X - 1 (genus and species unknown)	5051	R	20.0	N = 1 ♂; 8 ♀♀
GODYRIDINI				
<u>Dygoris dircenna dircenna</u> (C. & R. Felder)	5049	R	33.5	N = 6 ♂♂; 10 ♀♀
<u>Codyris zavaleta amaretta</u> (Haensch)	5007	A	31.0	N = 12 ♂♂; 12 ♀♀
<u>Heterosais edessa nephele</u> (Bates)	5008	C	28.0	N = 12 ♂♂; 12 ♀♀
<u>Hypoleria chrysodonia</u> (Bates)	5009	C	26.0	N = 12 ♂♂; 12 ♀♀
<u>Hypoleria oriana famina</u> Haensch	5047	VR	24.0	N = 3 ♂♂; species more common at Dureno
<u>Hypoleria orolina</u> (Hewitson)	5039	U	21.0	N = 12 ♂♂; 12 ♀♀
<u>Mcclungia salonia subtilis</u> (Haensch)	5043	R	22.0	N = 12 ♂♂; 4 ♀♀
<u>Pseudoscada egia</u> Hewitson	5032	U	20.5	N = 12 ♂♂; 10 ♀♀
<u>Pseudoscada timna timna</u> (Hewitson)	5033	C	21.0	N = 12 ♂♂; 12 ♀♀
<u>Thyridia confusa psamathe</u> Godman & Salvin	5036	C	44.0	N = 12 ♂♂; 10 ♀♀

Table 4 - continued.

NOTE: See map, Figure 1, for locations of Dureno and Tiwaeno.

*Five classes of abundance are recognized:

A	(Abundant):	Usually more than one dozen caught per day.
C	(Common):	Always part of a day's catch; usually several caught.
U	(Uncommon):	Not surely a part of a day's catch, but regular and expected in three days' collecting.
R	(Rare):	Irregularly caught, but expected in ten days' collecting. Definitely a breeding resident.
VR	(Very Rare):	Less than 5 specimens taken in 13 months' collecting. Probably strays from surrounding areas.

[†]Measured from base to tip of left forewing to the nearest 0.5 mm.

[‡]N = number of specimens measured to obtain mean forewing length.

Figure 20. Relative Abundances of Species of Ithomiinae at Limoncocha, Ecuador.

A = Abundant
C = Common
U = Uncommon
R = Rare
VR = Very rare

The Plant Family Solanaceae

The Solanaceae, or nightshade family, comprises some 80 genera of diverse form (D'Arcy, 1973) and contains approximately 2300 species (Cronquist, 1968). Although the family is strongly centered in tropical America, there are many species of a few genera in Africa, several isolated genera in Australia, and at least a few species in most parts of the world. Endemism is greatest in South America, where there are 38 endemic genera (Lawrence, 1951), of which 14 occur in the temperate portion (D'Arcy, 1973). The Solanaceae have long been included in the Tubiflorae, a large order of some 25 families containing a great number of species (Cronquist, 1968). Recent taxonomists usually subdivide this unwieldy taxon into three orders, the Polemoniales, the Lamiales, and the Scrophulariales. Depending on the cut of the taxonomist's knife, the Solanaceae are usually included in the Polemoniales (Lawrence, 1951; Cronquist, 1968) or the Scrophulariales (Takhtajan, 1969).

Floras treating the Solanaceae of tropical America have been published for most of Central America, including Costa Rica (Standley and Morton, 1937), Guatemala (Gentry and Standley, 1974), and Panama (D'Arcy, 1973), but only one country in South America, Peru (MacBride, 1962; Correll, 1967), has been so treated. Unfortunately there is no Flora of Ecuador, the site of my research, and thus I have used the publications of D'Arcy (1973) and MacBride (1962) to arrive at generic determinations in the field. Dr. D'Arcy has been kind enough to supply the specific determinations of the Ecuadorian solanaceous specimens I have sent to him. There exist a few publications containing information on some of the cultivated species of Solanaceae from the Andean slopes of Columbia,

Ecuador, and Peru, most notably Lawrence (1960), Schultes and Romero-Castaneda (1962), Patino (1962), Jimenez (1966), Pacheco and Jimenez (1968), and Heiser (1968a, b, 1971). D'Arcy (1974) provides a bibliography of some of the more recent literature on Neotropical Solanaceae.

The family is quite diverse morphologically, and includes herbs, shrubs, trees, lianas, and epiphytes. The trunks, petioles, and midribs of Solanaceous plants are often armed with acicular (needle-like) or recurved (hook-like) spines, the latter type being especially common on lianous forms. The leaves may be glabrous but more often are pubescent with simple, dendritic, stellate, scutellate, and/or glandular hairs. Stellate hairs in particular are well developed in the family and quite diverse in form. Some species have tough, coriaceous (leathery) leaves while others have leaves with a waxy cuticle. In short, the family employs a variety of mechanical defenses against herbivory that are developed to a greater or lesser degree among the various genera and species. In addition, secondary plant substances in the form of alkaloids are widely distributed in the Solanaceae (Henry, 1949; Raffauf, 1970; Willaman and Schubert, 1961) and there has been increasing recognition of their possible role as a chemical line of defense against herbivory (Fraenkel, 1959; Ehrlich and Raven, 1964).

Many members of the Solanaceae are of considerable economic importance to man. Indeed, Uphof (1968) lists 92 species from 21 genera as possessing value as agricultural crops, as sources of pharmaceutical chemicals, or as ornamental plants. The fascinating history of man's

encounters with many of these plants has been delightfully related by Charles Heiser (1969). Agricultural crops include the common tomato (Lycopersicon esculentum), the cultivated and Andean potatoes (Solanum tuberosum), peppers (Capsicum, several species), tree-tomato (Cyphomandra crassicaulis), naranjilla or lulo (Solanum quitoense), and eggplant (Solanum melongena), to name a few. Approximately 151 different alkaloids had been isolated from solanaceous plants by 1968 (Raffauf, 1970), many of which have strong narcotic or other physiological properties. Accordingly, a number of solanaceous plants and their alkaloids have medicinal value and thus are economically important to the pharmaceutical industry. For example, belladonna (Atropa belladonna) and Jimson weed (Datura stramonium) contain the alkaloids atropine and scopolamine, respectively. Other drug-producing solanaceous plants are grown for non-medicinal purposes, e.g., the various species of tobacco (Nicotiana) which are important cash crops in many parts of the world. Ornamentals come from many genera in the Solanaceae, especially Petunia, Salpiglossis, Schizanthus, Lycium, Solanum, Streptosolen, Cestrum, Datura, Solandra, Browallia, Nierembergia, and Brunfelsia (Lawrence, 1951).

Of interest to the present study is the fact that nearly all reported foodplants of the larvae of neotropical ithomiine butterflies (Ithomiinae) are in the Solanaceae. This familial-level correlation between the Ithomiinae and the Solanaceae, and the concomitant phytochemical ecology of alkaloid metabolism, have implications to insect-plant coevolution that will be discussed in Chapter 6. With the addition of the information contained in the present study, the number of solanaceous genera on which ithomiine larvae have been reported to feed is raised

to eleven. These eleven genera can be briefly characterized as follows (information from D'Arcy, 1973, and Uphof, 1968, unless otherwise noted).

Brunfelsia. This is a tropical American genus of 25-30 non-herbaceous species, mostly shrubs, with leaves simple, entire, coriaceous to chartaceous, and often glabrate. Several species, e.g., B. calycina var. floribunda, are widely cultivated as ornamentals. In Spanish they are usually known as "galan de noche." The Manaca Raintree, B. hopeana, contains the very poisonous alkaloid manacine, which resembles strychnine in physiological effect. In Brazil, the dried root of this plant is used in the treatment of rheumatism and syphilis.

Capsicum. The pepper genus contains perhaps a dozen species, most of which (and especially C. annuum and C. frutescens) are cultivated throughout the world for their culinary and ornamental fruits. Peppers are annual or short-lived perennial herbs, with leaves simple, entire or weakly toothed, glabrous or pubescent with simple, sometimes glandular hairs.

Cestrum. This is a tropical American genus containing 150-250 species of unarmed shrubs or trees, with leaves simple, entire, mostly glabrous above and variously pubescent beneath, usually with simple or dendritic hairs. Several species are widely cultivated as ornamentals, and a few are used for medicinal purposes on a local basis. One species, C. lanatum, is placed in hens' nests by Mexicans to keep away parasitic arthropods.

Cyphomandra. Occurring mainly in montane South America, Cyphomandra contains about 50-60 species, some of which are used by man for food. The plants are unarmed shrubs, trees, or vines, leaves simple

or compound, entire or lobed, usually glabrous above and pubescent or puberulent below. The tree tomato, C. crassicaulis (= C. betacea), has been cultivated for centuries by Peruvian Indians, and is presently grown for its edible fruit in Australia, New Zealand, and in some parts of South America. C. hartwegii is occasionally cultivated for its edible fruit in Chile, Argentina, Colombia, and Panama, and is known in the latter country as "contra gallinazo" (against chicken-heartedness).

Datura. This infamous genus contains about ten species of unarmed, ephemeral or perennial herbs or shrubs, sometimes with woody trunks, occasionally fetid, leaves simple and entire, repand or variously pinnately lobed or toothed, pubescent with mostly simple, sometimes viscid, hairs. Species of Datura are found in warm temperature regions in both the New and Old Worlds, but Mexico, with eight native species, is probably the center of speciation. The potent alkaloids found in this genus, such as atropine, hyoscyamine, and scopolamine, impart to these plants a variety of drug-related uses, ranging from the treatment of asthma to criminal poisoning. Alkaloids occur in several parts of the plants, but especially in the seeds and leaves.

Juanulloa. This is a little-known genus of about ten species of unarmed shrubs, mostly growing as hemi-epiphytes high in the forest canopy. The leaves are simple, entire, and glabrous to tomentose with dendritic hairs. A few species are cultivated as novelties in temperate greenhouses.

Lycianthes. Closely related to Solanum and often confused with it, Lycianthes contains about 200 species, mostly from tropical America. The genus includes herbs, shrubs, and vines, usually unarmed, the leaves

simple, entire or nearly so, glabrous or pubescent with various types of hairs. One or two species are occasionally grown as ornamentals.

Lycopersicon. Also closely related to Solanum; Lycopersicon is a genus of six species and several varieties centered in the coastal region of western South America. The plants are unarmed, sprawling, ephemeral or perennial herbs with pinnately lobed leaves, pubescent with glandular, aromatic hairs. The cultivated tomato, L. esculentum, is an important vegetable crop in many countries.

Physalis. This genus contains about 90 species, with the greatest number in Mexico, some in Central and South America, and a few in the Old World. These unarmed plants are mostly herbs, rarely shrubs, with leaves simple, entire, shallowly toothed or lobed, pubescent with simple, often glandular or viscid, rarely dendritic hairs. Commonly called ground cherries, several species are cultivated for their fruits which are eaten raw or cooked, or made into preserves (e.g., P. ixocarpa). P. alkekengi is cultivated both as an ornamental and for medicinal purposes.

Solanum. Solanum is one of the largest genera in the plant kingdom. Over 3,500 species have been described, but probably only about 1,400 of these are sound (D'Arcy, 1974). A recent study (D'Arcy, 1972) recognizes 7 subgenera and 50 sections. The morphological diversity of this genus is striking, and includes herbs, shrubs, trees, and lianas, with epiphytic, procumbent, and tuber-bearing species all represented. Plants may be armed or not, glabrous or pubescent with a variety of simple, branched, stellate, or peltate hairs, these often glandular, sometimes accompanied by bristles. Leaves may be simple or compound,

entire, toothed, or variously lobed, sometimes armed. Almost worldwide in distribution, the genus has its greatest number of species in tropical America, but is well represented in temperate America and in Africa. Hybridization and polyploidy are widespread (Heiser, 1969). There are a great many Solanum species of economic importance to man, including agricultural crops, medicinal plants, ornamentals, and noxious weeds. In terms of acreage, tonnage production, market value, and dietary importance, Solanum tuberosum, the cultivated potato, is one of man's most important dicotyledonous crop plants. Other important food plants in this genus include the eggplant (S. melongena), cultivated in various parts of the world, and the lulo, or naranjilla (S. quitoense), of Colombia and Ecuador. Ornamentals include S. wendlandii, S. seaforthianum, S. pseudocapsicum, and many others. S. torvum is cultivated in eastern Europe for its steroid alkaloids. The fruits of S. mammosum and other members of the section Acanthophora (subgenus Leptostemonum) are used in Ecuador and elsewhere for killing roaches, exterminating rats (MacBride, 1962), and for a variety of medicinal purposes. They are perhaps poisonous to mammals, but their armament is sufficient to discourage most grazing animals.

Witheringia. This genus has only recently been clarified as a taxonomic entity (Hunziker, 1969) and includes about 18 species ranging from Mexico to northern South America and perhaps one species in the South Seas. These plants are unarmed, erect herbs or subshrubs, with leaves simple, entire or sinuate, dentate, membranaceous, with simple or dendritic hairs. They have no known economic importance to man.

The examples given above of local uses of solanaceous plants for medicinal and insecticidal purposes attest to the potent nature and widespread occurrence of alkaloids in the family.

During the course of this study, forty-two different plants at Limoncocha were recognized as belonging to the Solanaceae. There are undoubtedly many more Solanaceae present in the area, especially trees and lianas of the upper forest canopy, but recognition of solanaceous plants not in flower or fruit, especially those occurring in the canopy, is quite difficult. A list of these forty-two species, along with the voucher number, estimated abundance, habit, and typical habitat of each one, is given in Table 5. Although there are eleven genera represented, nearly two-thirds (64.3%) of the forty-two species are in the genus Solanum. No other genus has over three species. The eleven genera, and the number of species in each, are: Brunfelsia (1), Capsicum (2), Cestrum (2), Cyphomandra (2), Jaltomata (1), Juanulloa (1), Lycianthes (2-3), Lycopersicon (1), Physalis (2), Solanum (27), Witheringia (1).

Grouped by growth form, the Limoncocha species include eighteen herbs, fourteen shrubs, two trees, and eight lianas. Two of the lianas are epiphytic. In regard to habitat, nineteen species are characteristically found in primary forest and an equal number are characteristically associated with disturbed areas or secondary growth. Four species are entirely domestic. Grouped according to light tolerance, nineteen are found growing in full or partial sun, fourteen occur in areas of open shade, and only nine are found in deeply shaded areas of the forest interior.

Table 5. Species of Solanaceae Collected at Limoncocha, Ecuador.

Scientific Name	Voucher Number	Estimated Abundance†	Habit	Habitat
<u>Brunfelsia</u> sp.	7330	U	Woody shrub; to 2 m, ascending, highly branched.	Deep shade; primary forest understory.
<u>Capsicum annuum</u> L.	7344	D	Herb; to 1.5 m, ascending, heavily branched.	Full sunlight; entirely domestic.
<u>Capsicum frutescens</u> L.	7355	D	Herb; to 1.5 m, ascending, heavily branched.	Full sunlight; entirely domestic.
<u>Cestrum</u> sp. (<u>laenigatum</u> or <u>megaphyllum</u>)	7338	C	Woody shrub or small tree; to 4 m, ascending, heavily branched.	Open shade to partial sun; primary and secondary forest understory.
<u>Solanaceae</u> (probably <u>Cestrum</u>)	7324	R(1)	Woody shrub to small tree; to 12 m, ascending, heavily branched.	Partial sunlight to open shade; second growth areas.
<u>Cyphomandra endopogon</u> Birt.	7348	U	Woody shrub; to 4 m, ascending, moderately branched.	Partial sunlight, edges of clearings and secondary forest.
<u>Cyphomandra hartwegii</u> Benth.	7312	U	Shrub, to 3 m, ascending, lightly branched.	Partial sun to open shade; edges of clearings, along shaded trails.
<u>Jaltomata procumbens</u> (Cav. J. L. Lentry)	7347	C	Herb; to 0.5 m, ascending to decumbent, heavily branched.	Full sunlight; clearings.
<u>Juanulloa</u> sp.	7354	R(1)	Woody lianous shrub; hemiepiphytic.	Partial sunlight; upper canopy of primary forest.
<u>Lycianthes</u> aff. <u>howardiana</u> D'Arcy	7307	A	Liana; unarmed.	Full sunlight; covers canopy of second growth area.

Table 5 - continued.

Scientific Name	Voucher Number	Estimated Abundance	Habit	Habitat
<u>Lycianthes</u> sp. (same as 73077)	7325	R(1)	Liana; unarmed.	Full sunlight; covers canopy of second growth area.
<u>Lycianthes</u> aff. <u>maxonii</u> Standl.	7332	U	Herb; to 1 m, ascending, lightly branched.	Open shade to partial sun; advanced secondary forest.
<u>Lycopersicon</u> <u>esculentum</u> Mill.	7357	D	Herb; to 1.5 m, ascending, heavily branched.	Full sunlight; entirely domestic.
<u>Physalis</u> <u>angulata</u> L.	7343	C	Herb; to 0.8 m, ascending to decumbent, heavily branched.	Full sunlight; clearings and open trails.
<u>Physalis</u> <u>pubescens</u> L.	7321	A	Herb; to 0.8 m, ascending, moderately branched.	Open shade to partial sunlight; edges of clearings and open trails.
<u>Solanum</u> <u>americanum</u> Mill.	7317	A	Herb; to 1 m, decumbent or repent, heavily branched.	Full sunlight; clearings, esp. near dwellings.
<u>Solanum</u> <u>anceps</u> R. + P.	7315	C	Herb; to 1.5 m, ascending, unbranched.	Shade; primary forest, understory.
<u>Solanum</u> aff. <u>antillarum</u> O. E. Schulz	7305	C	Woody shrub; to 4 m, ascending, lightly branched.	Open shade; edges of clearings and sunny trails.
<u>Solanum</u> <u>bicolor</u> Willd.	7316	C	Woody shrub; to 6 m, ascending, heavily branched.	Full to partial sun; edges of clearings and sunny trails.
<u>Solanum</u> <u>coconilla</u> Huber	7301	A	Herb; to 1.5 m, ascending, heavily branched.	Full sunlight; open trails and clearings.
<u>Solanum</u> <u>evolvulifolium</u> Greenm.	7329	R(1)	Lianous; epiphytic, unarmed.	Open shade; mid-canopy of primary forest.
<u>Solanum</u> aff. <u>intermedium</u> Sendt.	7346	U	Woody shrub; to 2 m, ascending, heavily branched.	Open shade; along trails in primary forest.

Table 5 - continued.

Scientific Name	Voucher Number	Estimated Abundance†	Habit	Habitat
<u>Solanum</u> aff. <u>lancaefolium</u> Jacq.	7310	U	Liana; armed.	Shade; advanced second growth and primary forest, middle canopy.
<u>Solanum</u> aff. <u>nudum</u> H.B.K.	7335	U	Shrub; to 3 m, ascending, moderately branched.	Open shade; primary forest understory.
<u>Solanum</u> <u>pectinatum</u> Dun.	7303	C	Herb; to 1.5 m, ascending, heavily branched.	Full sunlight; open trails and clearings.
<u>Solanum</u> <u>quitoense</u> Lam.	7341	D	Herb; to 2 m, ascending, heavily branched.	Full sunlight; entirely domestic.
<u>Solanum</u> aff. <u>schlechtendallianum</u> Walp.	7340	C	Tree; to 9 m, ascending, heavily branched.	Open shade to partial sunlight; along trails in primary forest.
<u>Solanum</u> <u>violaeifolium</u> Schott	7350	A	Herb; to 0.1 m, repent, spreading.	Deep shade; along floor of primary forest.
<u>Solanum</u> (related to <u>americanum</u> Mill.)	7304	A	Herb; to 0.5 m, ascending, lightly branched.	Open shade; edges of clearings and sunny trails.
<u>Solanum</u> (related to <u>lancaefolium</u> Jacq.)	7313	C	Liana; armed.	Shade; primary forest, middle canopy.
<u>Solanum</u> sp.	7306	R(3)	Woody shrub; to 7 m, ascending, unbranched.	Partial sunlight; edges of clearings and sunny trails.
<u>Solanum</u> sp.	7311	U	Liana; armed.	Open shade to partial sun; covers canopy of shaded second growth.
<u>Solanum</u> sp.	7319	A	Herb; to 2 m, ascending, unbranched.	Shade; primary forest, esp. in wet areas.
<u>Solanum</u> sp.	7323	R(1)	Woody shrub; to 7 m, ascending, unbranched.	Full sunlight; open trails and clearings.

Table 5 - continued.

Scientific Name	Voucher Number	Estimated Abundance†	Habit	Habitat
<u>Solanum</u> sp.	7326	C	Tree; to 20 m, unarmed.	Crown usually in upper canopy of mature forest or advanced second growth.
<u>Solanum</u> sp.	7327	A	Shrub; to 1.5 m, ascending, rarely branched.	Deep shade; primary forest understory.
<u>Solanum</u> sp.	7331	U	*Herb (shrub?); to 1.5 m (taller?), ascending, unbranched.	Open shade; primary forest understory.
<u>Solanum</u> sp.	7333	U	*Lianous herb; armed, unbranched.	Open shade to partial sun; along trail in primary forest.
<u>Solanum</u> sp.	7334	C	Herb; to 0.8 m, decumbent, heavily branched.	Full to partial sun; clearings, especially near dwellings.
<u>Solanum</u> sp.	7336	U	Woody shrub or small tree; to 5 m, ascending, heavily branched.	Partial to full sunlight; clearings and open trails, secondary forest.
<u>Witheringia riparia</u> H.B.K.	7328	A	Woody shrub; to 2 m, ascending, moderately branched.	Deep shade; primary forest understory.
<u>Solanaceae</u> (genus unknown)	7353	R(1)	*Herb; to 1.5 m, ascending, lightly branched.	Deep shade; primary forest understory.

†Estimated abundance categories: A - Abundant
C - Common
U - Uncommon

R - Rare (number of specimens at Limoncocha given in parentheses)
D - Domestic (i.e., common in yards and gardens)

*Description based on immature plants.

CHAPTER II

METHODS

Field work at Limoncocha, Ecuador, was conducted from November 1973 to November 1974. Aerial insect nets (American Biological Supply, Baltimore, Maryland) of 18-inch diameter and with standard (3 feet) or adjustable (2 to 12 feet) handles were used for collecting. Captured butterflies were placed in glassine envelopes carried in a small tin attached to the collector's belt. If they were to be released later in capture-mark-recapture experiments, kept for oviposition experiments, or used for dissections, the butterflies were left alive; otherwise, they were killed with a firm pinch at the thorax.

At the beginning of the study a large reference collection of ithomiines and other butterflies was made, and the ithomiines were determined to genus using the key in Fox's (1940) "Generic Review of the Ithomiinae." Each species was given a voucher number and a reference file was maintained so that collected individuals could be readily identified. Nevertheless, the superficial similarity of most Ithomiinae made field identification of the many Limoncocha species difficult. Therefore, a "field guide" or reference notebook was prepared by sealing butterfly wings between sheets of plastic laminate (Full-vu Laminating Film, Cook's Inc., Blackwood, N.J.). For each species of ithomiine, and for each mimicking species of butterfly or diurnal moth, the left forewing, hindwing, and antenna were sealed together with a label to provide a

ready means of comparative identification in the field. The "field guide" worked well and, because it was waterproof, held up admirably throughout the study. After about three or four months of experience in the field it was possible to identify nearly all perched individuals, and most of those in flight, to species without the aid of the field guide. Later in the study the Limoncocha Ithomiinae were determined to species and subspecies by using the keys in Fox's "Monograph of the Ithomiidae" (1956, 1960, 1967, and Fox and Real, 1971) and by comparison with labelled material in the Allyn Museum of Entomology in Sarasota, Florida.

To establish associations between ithomiine species and their foodplants, female butterflies engaged in apparent foodplant searching behavior were followed. If an ithomiine was observed ovipositing, the eggs and the female were brought back to the laboratory for culturing. In addition, plants recognized as solanaceous were thoroughly searched for eggs or larvae, and any immature stages found were collected for culturing. Once foodplant relationships were known or suspected, an attempt was made to induce oviposition by confining a female ithomiine in a screened cage with an appropriate plant or plants. Screened cages of small (15x15x30 cm), medium (50x50x120 cm), and large (3.7x3.7x1.8 m) size were used for these experiments but none provided very satisfactory results.

Early stages of ithomiines were cultured as follows. Each collection of immature stages (set of eggs or larvae from the same female parent) was given a brood number and placed, along with the leaf on which it was found, in an expanded plastic bag (volume approximately 1500 cc). The bags were kept in the laboratory (one room of a small two-room house of wood frame with large screened windows) where lighting and

temperature were similar to the forest understory. After hatching, the larvae were fed as often as necessary (usually once a day) with field-collected leaves from the appropriate foodplant. At the time of feeding, old leaf material and frass were discarded and parasitized or moribund larvae were separated from the rest of the brood. Records of each brood were kept in bound notebooks. Data collected daily included the lateral width of the head capsule (measured to the nearest tenth of a millimeter with a calibrated ocular micrometer in a Bausch and Lomb binocular microscope), the length of the body (measured to the nearest half millimeter with a ruler), the occurrence of ecdysis (verified by the collection of the shed head capsules), and a description of the color and patterning of the integument. Observations on larval feeding and resting behavior were recorded and close-up photographs (using a Pentax 35 mm single lens reflex camera with macro lens and electronic flash) were made of the early stages of most of the species reared.

Cast larval head capsules and pupal cases were preserved dry in labelled pillboxes. Depending on the availability of larval material, an attempt was made to preserve an individual of each larval stadium of each species. Larvae were killed and fixed for 24 hours in a solution of nine parts ethyl alcohol to one part acetic acid. After fixing the larvae were stored in stoppered vials of 95% alcohol. Adults reared in the laboratory were preserved dry in glassine envelopes marked with the appropriate brood number. All preserved specimens are in the author's personal collection.

Solanaceous plants were tentatively identified to genus with the aid of the keys in MacBride (1962) and D'Arcy (1973) and each species was assigned a voucher number for reference. Representative plants of

each species were labelled in the field with the voucher number written on surveyors' tape. Specimens, in flower or fruit if possible, were collected and pressed for future identification by Dr. William D'Arcy. The identified specimens have been deposited in the Missouri Botanical Garden, St. Louis, Missouri. The author has retained a duplicate series for reference.

Surveys were conducted in four different forest areas to determine the number of individuals of each solanaceous species present. The height and number of leaves of each solanaceous plant were recorded. Each plant was carefully searched for ithomiine eggs, larvae, and pupae. The four areas searched were (1) the east half (.25 hectares) of the 0.5 hectare plot at Site 4, (2) the .25 hectare plot at Site 5, (3) a 100 m by 2 m transect along the Nature Trail under closed canopy (Site 6) and (4) a 100 m by 2 m transect along the Logging Trail under open canopy (Site 1).

Behavioral observations on courtship, copulation, oviposition, feeding, etc., were recorded directly into field notebooks. All times of day reported here are Eastern Standard Time. Lack of funding thwarted plans for recording behavioral sequences on 8 mm movie film. Instead, notes, drawings and 35 mm photographs were taken to document ithomiine behaviors. Binoculars were occasionally useful for observing high-flying species. A Bacharach sling psychrometer (Bacharach Instrument Co., Pittsburgh, Pa.) held one meter above the ground was used to record forest temperatures and relative humidities.

All capture-mark-recapture experiments employed the marking technique of Ehrlich and Davidson (1960) so that every collected individual received a different number. Marks were made on the wings with "Sharpie" indelible pens (Sanford Corp., Bellwood, Ill.) of various colors, depending

on the background color of the wing pattern. At the time of marking, each butterfly was handled with stamp-tong style forceps and the following data were recorded: sex, wing condition, number (if previously marked), and forewing length. Any information written on the glassine envelope at the time of collection was also recorded in the record book. Wing condition was scored on the basis of progressive scale loss to provide an estimate of relative age of the butterfly. Seven categories of scale loss were recognized: F+ (teneral or immaculately fresh), F (fresh, no scale loss), F- (almost fresh, some scale loss), I (intermediate scale loss), I- (heavy scale loss, but no fraying of wing margins), W (heavy scale loss, some fraying of wing margins), and W- (heavy scale loss, with tattered and/or stained wings). Wing tears and beak marks are not reliable indicators of age since they may occur at any time during the life of a butterfly and thus were not incorporated in the measurement of wing condition. Forewing length was measured with a ruler to the nearest 0.5 mm from the base of the left forewing (articulation with thorax) to the most distal point on the wing tip.

The capture-mark-recapture experiments in the forest areas (Sites 4 and 5) were conducted by systematically covering the study plots for one hour, collecting all ithomiines and other mimetic Lepidoptera encountered. Individuals seen but not collected (out-of-reach, missed swings of the net, etc.) never exceeded three percent of the total number collected. At the end of the hour's collecting, all specimens were marked and released.

The 0.5 hectare study plot at Site 4 was subdivided into fifty subplots, each marked with a numbered stake in the southwest corner. The number of the plot in which a butterfly was caught was recorded on its glassine envelope and transferred at the end of the hour (during

marking) to the record book. Each butterfly at Site 4 was released in the same subplot where it was caught. Site 5 was not so subdivided and all marked individuals were released in the center of this .25 hectare study plot. Release was effected by holding the butterfly with forceps, lowering the insect onto a wet leaf until it secured a purchase, and waiting until the insect had uncoiled its proboscis and started drinking before releasing the forceps. In this way, the initiation of escape behavior upon release was avoided.

The capture-mark-recapture experiments performed on the ithomiine aggregations at Eupatorium flowers at Sites 1 and 3 involved the same data collection and marking techniques as the forest samples, but the methods of collection and release were different. Beginning shortly after sunrise, all ithomiines and their mimics visiting the flowers were collected at fifteen minute intervals throughout the morning until no more butterflies remained. Between collecting periods, marking and recording were done, and marked butterflies were held in small screen cages. At the completion of the sample, the cage was moved to a central location and the butterflies were allowed to fly away.

Preliminary studies on the reproductive morphology of ithomiines were made during this study, but require further field work for their completion. Female ithomiines of various estimated ages were dissected under the microscope to count the number of eggs and ovarioles present in the reproductive tract. The spermatophores present in the bursa copulatrix were counted to establish the minimum number of times each female had mated. Drawings were made of fully inflated spermatophores. The expanded androconial brushes of adult males were examined under the microscope, drawn and measured, and the density of the androconial scales estimated.

CHAPTER III
ADULT ECOLOGY OF THE ITHOMIINAE

Microhabitat Requirements

All of the ithomiine species at Limoncocha may be classified as sylvestral although some species commonly fly along forest borders and a few (e.g., Mechanitis isthmia) regularly enter clearings. Those individuals that leave the forest interior, however, apparently do so only for specific purposes, e.g., flower feeding (males) or oviposition (females). On numerous sunny days I have watched as an ithomiine strayed into a sun-lit trail or to the edge of a clearing, at which point the butterfly immediately turned back into the deep shade of the understory, usually dropping to a lower vertical level of flight. This behavior has also been noted by other workers (e.g., Young, 1974a), especially for the more scotophilic species, although on cloudy days it may be much less pronounced.

The proximate cause of this behavior is probably the sudden increase in light intensity above a critical level. Although the ultimate causes of this negative phototropism are unknown, there are at least two likely possibilities. One of the prime requirements for good ithomiine habitat is high humidity. Several observers (e.g., Ross, 1967), including myself, have noted that, given an area with a range of dampness, ithomiines are much more likely to be found in the wetter areas, especially along

shaded streams. Those individuals that tolerate higher light intensities are more likely to meet with lower humidities and thus their chances for survival may be diminished by the threat of desiccation.

The ithomiine requirement for forests with relatively high humidities has consequences on a macrohabitat scale as well. In Mato Grosso, Brazil, Collenette and Talbot (1928) described a vegetational "oasis" of large trees shading a relatively open, moist understory in a region otherwise composed of dry scrub forest or bamboo thickets. Within this small area of luxuriant, riparian forest, Collenette discovered large numbers of mimetic butterflies, mostly ithomiines, that were isolated from other such concentrations by several kilometers of surrounding dry forest.

This clumped distribution into "ithomiine pockets," as Brown has termed them (Brown and d'Almeida, 1970), has since been confirmed for ithomiine populations in the median-littoral forests of southeastern Brazil (Brown and d'Almeida, 1970) and suggested for other localities in the Neotropics (Brown, 1972). Ithomiine pockets have also been observed in superficially homogeneous moist forests (Ross, 1967; Brown and Benson, 1974) but here they are likely to be quite unstable and their often close proximity (less than 500 m apart) results in considerable overlap and fusion. Ithomiine pockets in seasonal forests are quite localized during the dry season (but spatially unpredictable from year to year) and high densities of ithomiines may occur (Brown, 1972). During the wet season these pockets become diluted as the butterflies track the expansion of available habitat (Brown, 1972). This expansion and contraction sequence is probably similar (on an ecological rather than a

geological scale) to the expansion and contraction of the neotropical refugia during alternating wet and dry periods of the Quaternary. The temporal and spatial dynamics of these ithomiine pockets have implications for mimicry theory to be discussed in Chapter 7.

A second possible reason for negative phototropism in ithomiines is predator-mediated selection. Many of the clear-wing ithomiine species apparently depend on the dappled lighting and shifting sunspecks against the dark forest floor to conceal or break up their image while flying in the forest understory. Many collectors have referred to the difficulty of following the disembodied spots that represent a clear-wing ithomiine weaving through the forest understory (e.g., Collenette and Talbot, 1928). Such protection is immediately forfeited, however, upon entering the comparative brilliance of an open clearing on a sunny day.

Within the forest, ithomiine species seem to show a preference for a particular light level, as suggested by their fidelity to a given flight level in the understory. In general, the clear-wing species are all found within two meters of the forest floor, while the tiger-patterned ithomiines spend most of their time above the two-meter mark. Ross (1967) found a similar division among the twenty Ithomiinae present in his Sierra de Tuxtla (Mexico) study area. At Limoncocha, however, each species within these two pattern complexes also has a characteristic individual flight stratum, which may be broad or narrow depending on the species. For example, Scada batesi characteristically flies at heights of less than 50 cm, while Godyrus zavaleta is most likely to be found at heights between 1.0 and 2.0 m; all four Melinaea species are rarely found below 5.0 m but may occupy much of the upper canopy region. It

has long been recognized that the light intensity of a tropical forest decreases from the canopy to the floor (Allee, 1926) producing vertical stratification in terms of light (and probably also in terms of humidity). Recent work (Papageorgis, 1974) suggests that this vertical stratification of light intensity is of primary importance in determining the flight levels of different mimetic complexes of butterflies in tropical forests, an hypothesis to be considered in Chapter 7. Further evidence for ithomiine response to light intensity comes from my observations that the perch and flight levels of ithomiines vary depending on the amount of light penetrating a given layer of forest, although this could also be interpreted as a response to changing humidity since relative humidity appears to be tightly correlated with light intensity in the understory. In general, perch heights (and to a lesser extent, flight levels) tend to be lower during periods of high light intensities in the understory. Benson (1967) reported that Mechanitis isthmia (=lycidice) in Costa Rica perch higher in the early morning (ca. 1 m) than they do at midday or during the afternoon (ca. 15 cm), a phenomenon that corresponds with the observations above, although the perch heights are extremely low for Mechanitis. Since Benson's observations were made during the dry season, the relatively low perch heights may indicate a negative response by Mechanitis isthmia to a seasonal decrease in humidity at higher levels in the understory.

The flight of ithomiines is normally slow and graceful, but may become surprisingly rapid and determined if they are violently disturbed. This "escape behavior" usually manifests itself in two ways. Ithomiines that frequent the lower levels (below 3 m) of the forest tend to fly

downward and into thick vegetation when disturbed. Those species characteristic of higher levels usually fly away at the same level of the disturbance or arc upward toward the canopy. Such behavior suggests that the escape reaction may be oriented by either positive or negative phototropism. Flights of males during courtship and of females during oviposition are unique and will be described in Chapter 4.

Activity Patterns

The daily activity pattern for ithomiines appears to be roughly the same for all species observed at Limoncocha. Ithomiines become active at first light and may be seen flying and feeding as early as 0605 h at Limoncocha. The first activity of the day is feeding. Males seek out flowers in open understory, in or along the edges of clearings, or, for those species characteristic of higher flight levels, in the forest canopy. Females are rarely attracted to nectar sources, or at least not to those frequented by males. Instead, they are most often seen feeding on bird droppings and other detritus of the forest interior. Feeding for both sexes may continue intermittently throughout the day in the forest understory, but visits to flowers in clearings by males occur mainly in the early morning and late afternoon (see below).

Courtship and mating begin in mid-morning and usually continue through mid-afternoon. Oviposition occurs predominantly in the afternoon, during which time males may again seek out nectar sources. Unlike most diurnal Lepidoptera (except for the crepuscular Brassoliniæ), ithomiines are generally active until dusk. Some Mechanitis isthmia have been seen

flying in clearings as late as 1815 h, and ovipositing as late as 1835 h (with only faint light on the western horizon) at Limoncocha.

In a very brief study during the dry season in Guanacaste Province, Costa Rica, Benson (1967) found that individuals of Mechanitis isthmia spend on the average only .68 to 3.36% of their time in flight, with the remainder of the time spent perched on leaves (although looked for, no other behaviors were observed). This would be a very low figure (averaging about 21 minutes per 12 h day) for any ithomiine in a wet forest area, especially for a Mechanitis. Although no time budgets of behavior were constructed for any species at Limoncocha, a minimum estimate of the time spent flying by Mechanitis isthmia (and all other Mechanitis) would be two to three times that given by Benson. It is quite possible that Benson's dry-season observations of a very low level of flight activity in the Guanacaste seasonally deciduous forest reflect adaptive behavior in response to the tropical dry season there, when active butterflies would be faced with constant desiccating winds and low humidity levels (T. C. Emmel, pers. comm.). Comparable observations have not been made during the Guanacaste wet season.

Perching Behavior

All ithomiine species at Limoncocha rest (i.e., perch without directed activity) during the day by perching on the upper surfaces of leaves with their wings together over their backs. This is apparently true for ithomiines in general, although Hymenitis (=Greta) diaphane on Jamaica characteristically perches on the underside of leaves (Brown and

Heineman, 1972; Brown, 1973). The exceptional perching behavior of H. diaphane may be unique, since Young (1972), after a detailed study of the natural history of Hymenitis nero in Costa Rica, reported no unusual perching behavior in this congeneric species.

Almost nothing is known about the resting behavior of ithomiines at night. There are a few hints in the literature that roosting aggregations may sometimes form, but these reports are poorly documented. P. L. Guppy (recorded in Poulton, 1931) observed a roost of the black and red Heliconius erato (=hydarus) in Trinidad (several species of Heliconius are known to form gregarious roosts at night; see Turner, 1975) and found that individuals of the tiger ithomiine Tithorea harmonia megara (=megara flavescens) were "not infrequently" perched in close proximity to the Heliconius in the roost. The roost in question was hanging from dried twigs about two meters above St. Ann's River under the shelter of a bamboo thicket. The report implies, but does not state outright, that individuals of both H. erato and T. harmonia, which have quite different patterns of aposematic coloration, returned to the roost on consecutive nights. Faithfulness to a communal roost is now well documented for several species of heliconiines, including H. erato (Turner, 1971; Benson, 1972), but has not been reconfirmed for Tithorea. Turner (1975), however, has recorded the unpublished observation by Vasconcelas Neto and Keith Brown that Tithorea harmonia occurs in roosts of Heliconius erato in Brazil, but the regularity of this association is not known. Guppy also suggested that species in the genus Mechanitis might roost gregariously. And indeed, A. M. Moss (recorded in Poulton, 1933) observed "hundreds" of Mechanitis lysimnia (=nesaea) in Bahia, Brazil,

congregating on shaded leaves in the early afternoon. The observation was made in Sept. 1931, when the species occurred in unusual abundance. Rev. Moss wrote "I did not wait to see, but have no doubt that they spent the night there, sitting in close formation" and that he was "pretty sure" that these large congregations of M. lysimnia included a "sprinkling" of Eueides isabella, a heliconiine of similar mimetic coloration. A third possible example of communal roosting in ithomiines was given by Young (1972) who reported finding "a roost of several adults of clear-wing ithomiines" in Costa Rican lowland forest at 1630 h in August 1969. No other particulars were given so it is not known how many individuals or species the roost included, nor whether the roost remained intact overnight.

No communal roosting was observed at Limoncocha. The few individuals found at night were alone, hanging from the tips of bare twigs. Individuals of several species (e.g., Oleria agarista, Ithomia agnosia) were observed at dusk to inspect potential night perches by fluttering around bare twigs for several minutes before alighting for the night. Perching at the terminus of a bare twig probably reduces the probability that the resting butterfly will be found during the night by nocturnally active arthropod predators, especially patrolling ants and spiders.

Predation and Parasitism

Because members of the Ithomiinae are presumably unpalatable (see Chapter 7), predation of adult ithomiines was a phenomenon I continually watched for, but observed on only four occasions. All four events

involved arthropod predators perched on flowers visited by ithomiines. Oleria agarista fell prey to a crab spider (Thomisidae) on a flower head of Eupatorium sp. (Asteraceae); Forbestra truncata was captured by another species of crab spider when it visited the flowers of Heliotropium sp. (Boraginaceae); Forbestra equicola was captured by a mantid (Mantidae) on Eupatorium sp.; and Ithomia amarilla was captured by another species of mantid on Heliotropium sp. The spiders appeared to liquefy the butterfly body contents in situ by injecting digestive juices in the usual manner before sucking out the tissues. The mantids discarded the wings, legs and antennae and ate only the head, thorax, and abdomen of the butterfly. I once caught a female Godyris zavaleta with a small (3 mm) ant clinging to her proboscis. The ant probably climbed onto the proboscis while the butterfly was feeding on a piece of detritus and would probably have climbed off again during a subsequent feeding period had I not caught the butterfly. But larger ants probably do prey on adult butterflies that perch to feed. Beebe (1955) observed a ponerine ant carrying off an ithomiine that had been feeding on dried fedegoso (Heliotropium indicum) at Simla, Trinidad.

Bronzy Jacamars (Galbula leucogastra, Galbulidae) were observed foraging on over two dozen occasions at Site 4 where ithomiines were abundant. Although these birds were seen to capture and eat one hair-streak butterfly (Lycaenidae), several dragonflies (Odonata) and other non-lepidopterous insects, and to pursue, but not catch, a large brown and white, diurnal castnid moth (Castniidae), they were never seen to chase or capture any ithomiine butterflies or their mimics. Jacamars, however, are frequent predators of butterflies (Collenette and Talbot,

1928), and some of the beak marks (symmetrical, triangular marks or tears of the wings) found on ithomiines collected at this site were long and narrow, suggesting that these jacamars do occasionally capture, and sometimes release, ithomiines. Of the 1108 ithomiines captured during the nine month capture-mark-recapture study at Site 4, beak marks were found on 11 specimens, or about 1.0%. (These beak marks were distributed among 9 of the 41 species collected during the Site 4 study.) Considering the tiger ithomiines and clear-wing ithomiines separately, 9 of the 328 tiger ithomiines (7 of the 19 species) had beak marks (2.7%) and 2 of the 780 clear-wing individuals (2 of the 22 species) had beak marks (0.3%). These figures closely match those of Collenette and Talbot (1928) who present the only published records to date of beak mark frequencies in ithomiines. Collecting in Mato Grosso, Brazil, Collenette and Talbot found 23 individuals out of 1184 in the tiger complex (4 of the 7 species) to have beak marks (1.9%) and 3 individuals out of 499 in the clear-wing complex (2 of the 4 species) to have beak marks (0.6%). Collenette and Talbot also examined 1767 individuals of other butterfly species (excluding small skippers and blues) from the same locality for beak marks and found only 4 (0.23%). Although there are difficulties in interpreting beak mark data (Edmunds, 1974), Carpenter (1941) concluded from Collenette and Talbot's figures that the greater percentage of beak marks among the ithomiines as compared with the non-mimetic sample is evidence for the distastefulness of the Ithomiinae. The individuals with beak marks were interpreted to be butterflies released by birds that found them distasteful. By the same reasoning it could be concluded that the tiger ithomiines, because of their higher beak

mark frequency, are more distasteful than the clear-wing ithomiines. This is to be expected if the clear-wing pattern is to some degree cryptic, as has been suggested by Poole (1970), Papageorgis (1974), and Young (1974a).

During the course of this study several thousand ithomiines were collected or captured for capture-mark-recapture studies, but not a single individual was observed to have a mite attached to its body or wings. Since parasitic mites are not an infrequent occurrence among North American butterflies, I found this absence of external parasites most striking. Perhaps it is related in some way to the presumed distastefulness of the Ithomiinae. Small, colorless mites were found at the base of the proboscis of several ithomiines, however. As these were unattached to the butterfly and were found in the groove formed by the palpi where the coiled proboscis is housed, I assume that the mites are non-parasitic and derive their nourishment from the pollen, nectar, or other fluids that adhere to the surface of the proboscis during feeding.

Food Resources and Feeding Behavior

Like most tropical butterflies, adult ithomiines exploit a diverse array of food sources to meet their nutritional needs. The types of food sources utilized are determined to some extent by the behavioral and ecological characteristics of the subfamily. For instance, I have never observed ithomiines feeding on mammalian dung, vertebrate carcasses, large rotting fruits, urine-soaked mud, or wet sand along river edges, nor do I know of any reports of such behavior in the literature. And

yet all of these have been reported as regular sources of nourishment for a number of butterfly species. One thing that all of these food sources have in common is that they are most likely to occur on the ground, a substrate on which I have never seen an ithomiine perched. Even the ithomiine species that haunt the lowest levels of the forest (e.g., Scada batesi and Oleria lota) have never been observed perched or feeding on the ground, but use instead leaves and twigs, even though the heights of these may be only a few centimeters. Thus it appears that ground level food sources are not normally available to ithomiines because of an innate behavioral avoidance of terra firma as a perching substrate. The reason for this behavior is not known but may be a result of selection to avoid predation by forest floor predators, especially ants and spiders.

In addition, ithomiines seldom feed at food sources above their characteristic flight level, but normally seek nourishment at or below that level. Non-nectar food sources usually occur on leaves or other vegetational structures and include bird and reptile droppings (especially when fresh and moist), rotting flower parts and pieces of decaying fruit that filter down from the canopy, decomposing remains of insects, water (and possibly urine) on the surfaces of leaves, and various other bits of detritus. A striking example of exploitive utilization of an unusual food source in the detritus category is that observed by Brown (1973) in Jamaica. A stream crab had apparently been killed by a bird and dropped onto a leaf where its well decomposed remains were subsequently fed upon by several Hymenitis diaphane. Although most visitors to non-nectar food sources are females, males are not infrequently found feeding

on them as well. Most of these non-nectar sources are probably rich in nitrogenous compounds, some of which may be essential to the longevity and/or the fecundity of ithomiines, a possibility to be considered in the discussion on oviposition.

Locating Food Sources

Ithomiines apparently locate these non-nectar sources by olfaction for I have often observed both sexes, but especially females, flying in a slow, relaxed manner, weaving in and out of vegetation, momentarily attracted to this spot or that. Upon passing an attractive food source, the butterfly circles once or twice and hovers for a few seconds above the item before alighting. The butterfly rarely descends directly on the food item, but usually lands a few centimeters away on the leaf and walks to the food source, all the while gently waving the antennae and slowly flexing the wings through a shallow arc. The proboscis is usually extended before the tarsi or antennae make contact with the food item, and thus a few seconds of probing with the proboscis occurs before the mark is hit and feeding begins.

It is quite possible that ithomiines capitalize on the success of other ithomiines in locating food sources. I have often found two or three, and sometimes four, ithomiines feeding simultaneously at a single food item. Often these groups are of the same species (e.g., three female Godyris zavaleta were found feeding on a bird dropping on a leaf at 1030 h). On several occasions I have watched an ithomine alter its flight when in the vicinity of other, feeding ithomiines and fly toward these perched individuals. Rarely are the first feeders disturbed by

the approach of the new arrival, unless its hovering before landing or probing afterward jostles the others too much. Such incidents suggest that the subsequent visitor may be first attracted to the food source by observing another individual feeding, or perhaps that the sight of the first individual reinforces the olfactory stimulus emanating from the food source. In the uniform greenery of the forest understory, where there are few breezes to aid the diffusion of the odors of these food items, one would expect ithomiines to recognize and be attracted to perched ithomiines if such behavior increased the probability of locating food. Such behavior would be especially advantageous if the potential food items from the canopy usually have a patchy distribution, as many seem to (e.g., synchronous abscission of flower parts; caciques and other birds dropping bits of fruit during gregarious feeding; fecal droppings from flocks of perched vultures, etc.). Similar strategies are apparently employed by butterflies in other feeding situations. For example, Papageorgis (1974) recently demonstrated that flower-feeding mimetic butterflies recognize and are attracted to individuals of like pattern (for reasons independent of sexual approach), which may aid them in finding well-dispersed patches of flowers. Furthermore, it has been shown that the presence of butterflies feeding on damp sand serves as a stimulus to attract conspecifics to the feeding site in the Pieridae (Collenette and Talbot, 1928) and the Papilionidae (Arms et al., 1974).

Flower Feeding

The frequent attraction of ithomiines to small white flowers, especially of the genus Eupatorium and other genera of the Asteraceae

has been reported many times (Muller, 1879; d'Almeida, 1945; Ross, 1967; Gilbert, 1969; Young, 1972; Pliske, 1975b), although flowers of other colors may also be visited. For example, Young (1974a) reported that Oleria zelica pagasa visited red and light yellow flowers of the forest understory in Costa Rica and I have observed several species of ithomiines flocking in great numbers to the pink flowers of coral vine (Antigonon leptopus; Polygonaceae) in western Ecuador. Table 6 summarizes the published records, and those of this study, of flower feeding in the Ithomiinae. Although white is the flower color most commonly visited by ithomiines, the color series pink-to-purple accounts for most of the other records. For example, in his study at Sierra de Tuxtla, Mexico, Ross (1967) found that, of the four species of flowering plants visited by ithomiines, three had white blossoms and the fourth, purple.

At Limoncocha, only one non-white flower was regularly visited by ithomiines. The plant has not yet been identified (voucher number 7339), but the flowers are bright orange, about 3 cm in length, and egg-shaped, with a very small opening at the distal end of the fused corolla. They were visited only by Hyposcada kezia, Oleria agarista, O. lota, and especially by O. kena. Interestingly, all four of these species belong to the Oleriini, which suggests that members of this tribe have an attraction for the flowers of this plant not shared by other ithomiines. The plant rarely grows over 50 cm tall and thus is within the normal flight level of all the Oleriini, but also of Scada batesi, Aeria eurimedia, and several clear-wing species. It is not known why these last named species do not also visit the orange flowers, but the fact that they do not suggests a close, and perhaps, mutualistic, relationship between,

Table 6. Nectar Sources of Ithomiine Butterflies.

PLANT VISITED	COLOR OF FLOWERS	FAMILY	LOCATION	REFERENCE
<u>Oxypetalum</u>	(?)	Asclepiadaceae	Brazil	Brown and d'Almeida, 1970
<u>Ageratum</u> sp.	white (?)	Asteraceae	Costa Rica	W.A. Haber, pers. comm.
<u>Baccharis</u> sp.	white	Asteraceae	Brazil	Muller, 1879
<u>Cilbadium</u> sp.	white	Asteraceae	Costa Rica	Gilbert, 1966
<u>Eupatorium macrophyllum</u>	white	Asteraceae	British Guiana	Kaye, 1906
<u>Eupatorium macrophyllum</u>	purple	Asteraceae	Mexico	Ross, 1967
<u>Eupatorium pittieri</u>	white	Asteraceae	Mexico	Ross, 1967
<u>Eupatorium xestolepis</u>	white	Asteraceae	Venezuela	Pliske, 1975b
<u>Eupatorium</u> sp.	white (?)	Asteraceae	Brazil	d'Almeida, 1945
<u>Eupatorium</u> sp.	white	Asteraceae	Costa Rica	Gilbert, 1969
<u>Eupatorium</u> sp. (I) (7308)	white	Asteraceae	Ecuador	Present study
<u>Eupatorium</u> sp. (II) (7342)	white	Asteraceae	Ecuador	Present study
<u>Mikania</u> sp.	white	Asteraceae	Brazil	Muller, 1879
<u>Veronia</u> sp.	white	Asteraceae	Brazil	Muller, 1879
<u>Heliotropium</u> sp. (I) (7309)	white	Boraginaceae	Ecuador	Present study

Table 6 - continued.

PLANT VISITED	COLOR OF FLOWERS	FAMILY	LOCATION	REFERENCE
<u>Heliotropium</u> sp. (II) (7351)	white	Boraginaceae	Ecuador	Present study
<u>Tournefortia glabra</u>	white	Boraginaceae	Mexico	Ross, 1967
<u>Maranta</u> sp.	lavender	Marantaceae	Ecuador	Present study
unidentified shrub	magenta	Melastomaceae	Ecuador	Present study
<u>Epidendrum paniculatum</u>	white	Orchidaceae	Costa Rica	van der Pijl and Dodson, 1966
unidentified palm	white	Palmae	Costa Rica	Gilbert, 1969
<u>Antigonon leptopus</u>	pink	Polygonaceae	Ecuador	Drummond, unpublished
<u>Genipa</u> sp.	white	Rubiaceae	Costa Rica	Gilbert, 1966
<u>Psychotria guaramalensis</u>	white (?)	Rubiaceae	Venezuela	Pliske, 1975a
<u>Psychotria padifolia</u>	white	Rubiaceae	Mexico	Ross, 1967
unidentified herb (7339)	orange	?	Ecuador	Present study
unidentified liana	red	?	Ecuador	Present study
unidentified plant	light yellow	?	Costa Rica	Young, 1974a
unidentified plant	red	?	Costa Rica	Young, 1974a

these flowers and the Oleriini. The proximate basis for the attractiveness of these flowers may be a spectral sensitivity and preference for the color orange in the Oleriini. This is suggested by the fact that H. kezia and the three Oleria species listed above, but no other ithomiines, were frequently found feeding at the ripe orange fruits of a common species of Araceae. These fruits occur about 40 cm above the forest floor, approximately the same height as the orange flowers (7339). Napeogenes pharo, Godyrus zavaleta, and Hyposcada kezia were occasionally seen at the small reddish flowers of an understory melastomaceous shrub (Melastomaceae), and Melinaea menophilus was once observed feeding at the pendant red inflorescence of an unidentified liana. By far the majority of species and individuals of Limoncocha ithomiines, however, predominantly visit the small white flowers classically associated with the Ithomiinae.

There are five terrestrial plant species (there may be others in the canopy) at Limoncocha with small white flowers, all of which are frequently visited by ithomiines. Two of these are perennial woody shrubs known as heliotrope (Boraginaceae) that have small tubular flowers linearly arranged in a pendant cincinnus. Both species attain a height of about 5 m and are found in open shade or partial sunlight in advanced second growth or along trails in primary forest. Heliotropium I (voucher number 7309) is quite common. Heliotropium II (7351) is a similar species, but the only two specimens known at Limoncocha were found on the base grounds and thus will not be considered in the following discussion. There are two species of composites (Asteraceae), both in the genus Eupatorium. These are "annual" herbs with small, but numerous,

dense flower heads. Eupatorium I (7308), a fugitive species that rapidly colonizes sunny clearings, reaches 1.0 to 1.5 m in height and is often found in large stands of up to a few hundred individuals. Eupatorium II (7342) is found only in the open shade of the forest understory, especially along sun-flecked trails. It normally reaches only 50 cm in height and rarely occurs in patches containing more than a dozen individuals. The fifth species, Maranta I (7322) (Marantaceae), is similar to Eupatorium II in habitat but attains a height of a little over one meter and may occur in large numbers along forest trails. The plant is highly branched and a single individual may simultaneously produce several dozen of the small white to pale lavender flowers. Thus, of the four plant species under consideration, only Eupatorium I is consistently found in open sunny areas that lie outside the normal microhabitat of ithomiines.

Full day observations were made on the three forest species of adult food plants and the results are shown in Figures 21, 22, 23, and 24. Figures 21 and 22 present data from two observation days showing the number of ithomiine species and individuals visiting a patch of eight Heliotropium I plants on the Logging Trail at Site 2. Censuses were performed at 15-minute intervals from 0545 until 1830 h. A number of observations may be made from these data. First, ithomiines begin feeding shortly after dawn, which involves flying and locating a food source under extremely low light intensity. Although the low visibility of the dusk-like early morning in the forest understory was further reduced by the presence of fog, the first ithomiines (male Godyris zavaleta) arrived each morning about 0605 h. Second, the peak of feeding activity occurs early in the day, from 0630 to about 0930 or 1000 h. Third, the feeding

Figure 21. Ithomiline Feeding Activity at Heliotrope 1 Blossoms: June 26, 1974.

Observations were made at Study Site 2 and covered 8 plants with a total of 124 inflorescences.

Figure 22. Ithomiline Feeding Activity at Heliotropium I Blossoms: June 29, 1974.
 Observations were made at Study Site 2 and covered 8 plants with a total of 124 inflorescences.

EXPOSURE OF FLOWERS TO SUN

Figure 23. Ithomiine Feeding Activity at Maranta I Blossoms: July 12, 1974.

Observations were made on the Hunting Trail and covered 10 plants with a total of about 400 inflorescences. Members of the Dismorphinae (Pieridae) regularly visited these flowers also, and data on these species have been included as well.

- //// light rain
- individuals
- species
- flowers in full shade
- ▨ flowers in partial sun
- flowers in full sun

EXPOSURE OF FLOWERS TO SUN

Figure 24. Ithomiine Feeding Activity at Eupatorium II Blossoms: July 12, 1974.

Observations were made on the Hunting Trail and covered 20 plants with a total of about 240 inflorescences.

////// light rain
●—○ individuals
○—○ species
■ flowers in full shade
▨ flowers in partial sun
□ flowers in full sun

EXPOSURE OF FLOWERS TO SUN

activity appears to be correlated with three interdependent environmental factors, namely, temperature, relative humidity, and the exposure of the plants to direct sunlight. As the sun approached and passed through its zenith, the heliotrope plants became exposed to direct sunlight during the early afternoon. As a result, the temperature around the plants went up and the relative humidity dropped, as did the attendance of ithomiines on the heliotrope flowers. After the plants regained the shade in mid to late afternoon, ithomiine attendance at the flowers increased again until darkness fell. On both days Godyris zavaleta males were the last butterflies to abandon the flowers, with the last individuals leaving at 1810 and 1817 h respectively. As in the early morning, this late departure time required flying and navigation in near darkness. Fourth, a light drizzle or gentle rain apparently has very little effect on the feeding activity of ithomiines at heliotrope. This is in strong contrast to the marked depressing effect that rain has on the activities of most other butterflies. Because ithomiines are obviously capable of and well adapted to flying at low light intensities and cooler forest temperatures, and because the forest understory is somewhat protected by the canopy from all but the hardest rains, rainy weather rarely diminishes ithomiine feeding behavior, as my observations on many a soggy occasion will attest.

Figures 23 and 24 report comparable observations for a patch of 10 plants of Maranta I and a patch of 20 plants of Eupatorium II in the forest understory along the Hunting Trail. The patches were about 15 meters apart and the observations on them were made on the same day, again at 15-minute intervals. The Maranta observations (Figure 23) show a pattern of ithomiine activity very similar to that of the heliotrope observations--

an early morning peak unaffected by light rain, followed by a depression in activity in the early afternoon. There was, however, no peak of ithomiine activity at Maranta in late afternoon, such as occurred at the heliotrope flowers. The Eupatorium II observations (Figure 24) reveal that the small amount of ithomiine activity at these flowers occurs during midday and peaks when the flowers are in the sun. Perhaps these understory flowers, normally covered by deep shade near the forest floor, become more attractive during their brief immersion in sunlight. Conclusions are difficult, however, since this graph represents only four ithomiine individuals. The two in the morning were both Oleria agarista and the two in the afternoon were Ithomia amarilla.

Maranta I was the only one of these three forest flowers to consistently attract butterfly species of other families. With the exception of two skipper species (Hesperiidae) and one Eurema sp. (Pieridae), all visitors from other families were members of the genus Dismorphia (Pieridae) and are Batesian mimics of the ithomiine species found on these flowers (i.e., D. pinthaeus mimics Aeria eurimedia, see Figure 58; D. leuconoe mimics Oleria agarista, O. lota, and Oleria IV, see Figure 59). It is interesting that the peaks in Dismorphia feeding activity occur during the troughs of ithomiine activity. Since the ithomiines are active first, and thus would educate any predators in the area to their distastefulness, the Dismorphia, by feeding later in the day, should derive a greater benefit from their mimetic resemblance. The conclusion that the Dismorphia feed later in the day because of a reduced likelihood of predation is probably unwarranted, however, because of the small sample size. The Dismorphia activity pattern could just as easily be due to

environmental factors, e.g., on the observation day the morning rain may have depressed their feeding activity.

Eupatorium I was extremely common at Sites 1 and 3 on the Logging Trail in January 1974 and great numbers of ithomiines were visiting the flowers. Unfortunately, I was not yet able to distinguish among many of the species in the field at this early stage of the research and thus data comparable to that provided for the forest flowers are not available. The pattern of flower visitation was, however, quite similar to that observed for Heliotropium I, although the first individuals arrived at the flowers nearer 0700 than 0600 h, and the peak of activity was between 0800 and 1000 h. The procedure followed was to collect all the individuals present of the species I could identify, mark these, and then release them (see Chapter 2 for details). This was done for the two most common visitors (Scada batesi and Godyris zavaleta) from January 6 to 13 at Site 1 and for the eight clear-wing species (including S. batesi and G. zavaleta) present at Site 3 (see Figures 12 and 13) from January 10-13, 18-20, and on January 28, and February 4. Collections were begun about 0800 and usually by 1100 h all individuals of the species under study had been collected. Once the flowers were free of clear-wing species, only on occasion would another individual of the same pattern be found on the flowers during the next two hours (the flowers were watched during the marking process). In contrast, individuals belonging to species not being collected (these included several species of tiger ithomiines) continued to visit the flowers until 1230 or 1300 h. This circumstantial evidence provides further support for Papageorgis' (1974) suggestion that mimetic flower-feeding butterflies attract other individuals

of like pattern to the food source. A few ithomiines could be found intermittently feeding at the Eupatorium I flowers later in the afternoon, but there was no late afternoon peak of feeding activity such as that observed for Heliotropium I. The lack of midday feeding was probably because the Eupatorium I patches were in full sunlight from about 1000 until about 1500 h. By early afternoon temperatures reached 30-31°C and the relative humidity dropped as low as 60%, environmental conditions apparently intolerable to ithomiines.

Table 7 summarizes the results of these Eupatorium I flower samples for the eight clear-wing ithomiines sampled at Sites 1 and 3 (S. batesi, although it has opaque yellow wings (Figure 13), is considered a member of the clear-wing complex; see Chapter 7). The most striking feature of these samples is the almost complete absence of females, which, for all species combined, account for less than one percent of all individuals collected (N = 736). All-male feeding aggregations are not uncommon in butterflies and have been reported for a number of species in several families (e.g., Bates, 1863; Downes, 1973; Klots, 1951). The significance of the exclusive representation of the male sex in these aggregations remains unknown (Silberglied, 1976), although Wynne-Edwards (1962) considered them to be communal nuptial displays. There is evidence, however, that males of the Ithomiinae and the Danaidae are selectively attracted to certain plants (including the genus Eupatorium) containing pyrrolizidine alkaloids (PA), compounds that they ingest during feeding at the plants and subsequently use as precursors for the manufacture of PA-derived sex pheromones (Pliske, 1975a,c). Many boraginaceous plants, such as

Table 7. Summary of Collections of Ithomiine Butterflies Visiting Eupatorium I flowers at Study Sites 1 and 3 in January 1974.

SPECIES	SITE	D	N	♂♂	♀♀	%♂♂	%♀♀	N _{RL}	N _{RC}	%N _{RC}
<u>Godyris zavaleta</u>	1	7	33	32	1	97.0	3.0	27	2	7.4
<u>Godyris zavaleta</u>	3	8	62	61	1	98.4	1.6	54	9	16.7
<u>Ithomia agnosia</u>	3	8	33	33	0	100	0	27	1	3.7
<u>Ithomia amarilla</u>	3	8	60	59	1	98.3	1.7	48	6	12.5
<u>Ithomia derasa</u>	3	4	8	8	0	100	0	3	1	33.3
<u>Oleria agarista</u>	3	6	24	24	0	100	0	24	0	0
<u>Pseudoscada egla</u>	3	6	23	23	0	100	0	20	5	25.0
<u>Pseudoscada timna</u>	3	8	67	67	0	100	0	55	19	34.5
<u>Scada batesi</u>	1	8	104	103	1	99.0	1.0	80	21	26.3
<u>Scada batesi</u>	3	9	322	322	0	100	0	278	92	33.1

Note: D = Number of sampling days.

N = Total number collected.

N_{RL} = Total number marked and released.

N_{RC} = Number of marked individuals recaptured.

%N_{RC} = Percent of marked individuals recaptured.

heliotrope, also contain pyrrolizidine alkaloids and thus it is interesting that, of a morning sample of ithomiines visiting Heliotropium I, about 90% were males ($N = 36$ for 7 species). Because of the low visitation rates, comparable collections from Maranta I and Eupatorium II are not available, but observations recorded throughout the research period show that both males and females were frequent visitors to these two understory herbs.

Another interesting feature of these samples is the high percentage of recaptures of marked and released butterflies (25.3% of 616 released butterflies for all species combined). Recaptured butterflies, of course, represent individuals that visited the same flower feeding area at least twice, between which times they presumably returned to the surrounding forest for other activities and to pass the night. Some Scada batesi were captured up to four times during the study period at Site 3, with the first and last captures being up to 17 days apart. Whether this is evidence of an ability of ithomiines to learn the location of food sources (as is known for some species of Heliconius; Gilbert, 1975) or merely a testimony of the attractiveness of Eupatorium I to relatively sedentary butterflies is unknown. Although individuals of most species were recaptured only once, the number of multiple recaptures of Scada batesi suggests that the males of this species have a rather restricted home range, whether this be controlled by innate or learned behavior. (At Site 3, 15 S. batesi were recaptured twice, 3 were recaptured three times, and 1 was recaptured four times.)

An attempt was made to estimate the population sizes of S. batesi and G. zavaleta at Sites 1 and 3 by analyzing the capture-mark-recapture

data by the methods of Jolly (1965) and Bailey (1951). Unfortunately, the recapture rates were inconsistent from day to day, ranging up to 90% but with several days of no recaptures. This was partly a result of sample size, for unlike the situation in the forest interior, heavy cloudiness and light rain do depress ithomiine activity at these exposed flower patches, and there were several study days with bad weather. Thus, the extreme unevenness (and occasional absence) of recapture rates precluded the accurate calculation of population sizes, even for the most abundant species, S. batesi. (The standard error for population estimates of S. batesi ranged from 55 to 98% of the estimated population sizes themselves). One basic problem with conducting capture-mark-recapture experiments to estimate population size at flower visitation sites is the lack of random sampling of the population--as evidenced in this case by the heavily male-biased collection. At Sites 1 and 3 it was the Eupatorium flower patch that actually collected the sample; I merely processed it by removing the feeding butterflies from the flowers long enough to mark them.

Coevolution of Ithomiines and White-flowered Plants

Butterflies normally visit brightly colored flowers, especially red and yellow ones (Faegri and van der Pijl, 1966), and have good color vision, including ultraviolet and red (Swihart, 1972). Is there any significance to the fact that the primary nectar sources of ithomiines are small white flowers? The combined facts that (a) ithomiines locate their nectar sources in the dim light of early morning and late afternoon, and (b) that the flowers they visit are white, fit the syndrome (sensu Faegri and van der Pijl, 1966) of

crepuscular pollination and suggest a mutualistic relationship. Crepuscularly pollinated flowers are usually white (Faegri and van der Pijl, 1966), and thus provide high reflectance of available light, facilitating their location by visually oriented pollinators. Because of their frequent and prolonged visits to the flowers of Heliotropium I, Eupatorium I, and Eupatorium II and the relatively infrequent visits to these flowers by other butterflies and insects, it is reasonable to assume that the ithomiines are indeed pollinators (as opposed to mere visitors) and that these plants are specializing in attracting ithomiines. Because ithomiines are denizens of the deep shade of the forest understory, they are, in a sense, physiologically pre-adapted to flying in the dim light and cooler temperatures of the early morning and late afternoon, although this does not explain why their feeding behavior peaks at these times. Gilbert (1969) has suggested that since ithomiine courtship areas (forest understory) and nectar feeding areas (forest edges) are spatially separated, selection should force males to complete their nectar feeding before female emergence in the mornings (before 1000 h for ithomiines). Early morning nectar feeding by males should reduce the time spent feeding during the peak courtship period, 1000-1400 h (presumably, also the period of maximum female sexual receptivity). If there is less than enough nectar available to meet the needs of the male ithomiine community, then competition could force male ithomiines to seek out nectar sources as early as possible to insure the procurement of an adequate allotment before the courtship period begins. It seems unlikely that the emergence time of females plays a significant part in this scenario, however, because it is doubtful that female ithomiines are sexually receptive on

the day of emergence (see Chapter 4). But a receptive female, whether or not she has previously mated (females are known to mate up to six times or more; see Chapter 4), is certainly a limited commodity and it would behoove any male to have established his courtship "display arena" before receptive females become available each day.

Is nectar a limited resource to the male ithomiine community? The nectar sources available to ithomiines at Limoncocha fall into two basic categories: those that occur in shaded areas of primary or secondary forest understory, and those that lie beyond the forest edge in open clearings. Clearly at Limoncocha Eupatorium II, Maranta I, and the orange-flowered plant (7339) are members of the first group, and Eupatorium I is the sole member in the second group. Heliotropium I, although occasionally found in the open, usually occurs along forest borders and in areas of disturbed forest. Since most of the plants at Limoncocha were located in shaded forest, Heliotropium I is included in group one. The shaded nectar sources (group one) are generally of low abundance, but appear to be spatially and phenologically constant over long periods of time. Thus, within the normal microhabitat of ithomiines (shaded understory), nectar sources are locally stable, highly predictable, but of low density. In contrast, the Eupatorium I patches (group two) that occur in sunny clearings are phenologically and spatially unpredictable, but make available large quantities of nectar for short periods of time. It appears that the feeding behavior of male ithomiines at Limoncocha reflects the differences in nectar availability of these two groups.

The location of the shaded nectar sources (group one) near the courtship areas, and their relative stability in place and time, should make

them extremely important feeding areas to ithomiine males, particularly those of scotophilic species. The low abundance of these plants, however, indicates that they are insufficient to satisfy the nectar needs of all males in the surrounding area, especially if those males should attempt to feed simultaneously. Although a maximum of only 21% (26 of 124) of the inflorescences at the Heliotropium I sample area were visited by ithomiines at any one time (see Figures 21 and 22), the small florets (6 to 8 mature florets per inflorescence) were apparently quickly depleted of nectar. After an initial flush of feeding, the effective number of nectar feeding stations (i.e., inflorescences with nectar-filled florets) may have been greatly reduced because the depleted florets passed through a recovery period. Thus, it seems likely that competition at group one plants for nectar procurement prior to courtship could occur, forcing males to visit these nectar sources as early as is physiologically possible, as Gilbert (1969) has suggested. (As discussed above, an alternative or additional explanation for early morning flower visitation by ithomiines is simply that they are avoiding the unfavorable environmental conditions--high temperatures and low humidities--that occur later in the day.)

One would expect, then, that male ithomiines arriving too late to find adequate nectar at the forest flowers (group one) would leave the forest border to seek flowers in the sun. Interesting to this discussion is the fact that the clear-wing ithomiines were found at both groups of flowers while tiger ithomiines were abundant at group two flowers only, and were rarely seen at those of group one (shaded flowers). Perhaps the tigers, with their protective aposematic coloration, their greater

vagility, and their greater tolerance for high light intensities (as evidenced by their higher flight levels in the forest) normally seek nectar sources in the sun (group two flowers). Conversely, the lower flying (and less light tolerant) clear-wings, with their basically cryptic coloration, apparently first seek out nectar sources in the understory shade (group one flowers), leaving the forest to search for group two nectar sources only when those of group one are depleted or too crowded.

Returning to the suggestion made earlier that a mutualistic relationship may exist between certain white-flowered plants and ithomiine pollinators, Pliske (1975b) has presented evidence that at least one plant, Eupatorium xestolepis Robinson in Venezuela, has specialized in attracting male Ithomiinae (and also male moths of the family Ctenuchidae) to pollinate its flowers. The specialization involves ecological adaptations that allow the plant to subsist in the shady microhabitat of its pollinators and the production of a floral fragrance that may contain some of the volatile compounds typically released in dead tissue of PA producing plants that attract male Ithomiinae and Ctenuchidae. Apparently, Eupatorium II at Limoncocha is ecologically quite similar to E. xestolepis, since both have diverged from the common sun-loving habit of most members of the genus (e.g., Eupatorium I) and both attract ithomiines but little else to their flowers. Other Eupatorium and Heliotropium plants are known to be pollinated largely by male ithomiines, danaines, and ctenuchids (Pliske, 1975b) suggesting that mutualistic relationships between male Lepidoptera and these plants may not be infrequent (Pliske, 1975a). Male ithomiines are also known to be the primary pollinators of an orchid, Epidendrum panniculatum L. (van der Pijl and Dodson, 1966; Dodson,

unpublished obs. cited in Pliske, 1975b). Interestingly, this orchid has small white flowers and thus fits the syndrome of early morning ithomiine pollination, although Pliske (1975b) has suggested it may attract ithomiines (and danaines) by mimicking the extra-floral attractant of PA plants.

Ithomiine Attractants

A curious aspect of ithomiine feeding behavior, alluded to above, is the selective attraction of males to the dead plant tissues of Heliotropium indicum Linn. (Boraginaceae), known as Indian heliotrope, or fedegoso (Beebe, 1955). Beebe describes it as "a typical weed, wholly undistinguished, without intensive odor or color." And yet when uprooted, dried, and hung in favorable spots in the forest, it attracts great numbers of ithomiine males, especially clear-wing species, as well as male Danaidae, and both sexes of the moth families Ctenuchidae and Arctiidae. Although Beebe (1955) found few visitors to the dried plant from other insect orders, Moss (1947) and Pliske (1975a) have recorded a great variety of other insects on the plants. The strong attraction of Ithomiinae to dried fedegoso has been exploited by several neotropical collectors (Masters, 1968; Brown and d'Almeida, 1970; Brown, 1972). The evolutionary significance of the attraction of male Ithomiinae to dried H. indicum is difficult to understand since the plant is a native of Asia and has presumably spread to the neotropical region only since the discovery and colonization of the Americas (Beebe, 1955). Also, the attractiveness becomes effective only on the death of the plant and after the consequent desiccation of the foliage (Beebe, 1955).

Heliotropium is one of several genera in the Boraginaceae that, along with certain genera in the families Asteraceae, Leguminosae, and Apocynaceae, produce pyrrolizidine alkaloids (PA) (Bull et al., 1968). As with H. indicum, these other PA producing plants are, under certain conditions, highly attractive to various male Lepidoptera that feed on the surface of the plants (not at the flowers) for long periods of time (Pliske, 1975a). Pliske (1975a) has reviewed the published chemical evidence in light of his own extensive field observations and experiments, and the following scenario unfolds. Male Danaidae possess abdominal hair-pencils that disseminate an aphrodisiac pheromone during courtship. The aphrodisiac component of the pheromone is a dihydropyrrolizidine, produced in the butterfly from chemical precursors acquired during males' visits to PA plants. Likewise, of the Ithomiinae so far analyzed (Ithomia, Pteronymia, Hymenitis), the male hairpencils contain a lactone, derived from PA-side groups and apparently acquired during males' visits to PA-plants (Pliske, 1975b). Pliske (1975c) has suggested that the lactone functions as a male territorial and recognition pheromone (see discussion in Courtship section, Chapter 4). Male ithomiines apparently locate PA-plants by olfactory detection of volatile "esterifying acids" that probably disassociate from the alkaloid ring nucleus in rotting plant tissue. These volatile acids elicit upwind orientation, landing, proboscis extension, and exploration of plant surfaces (Pliske, 1975a). The intact alkaloids serve as phagostimulants inducing prolonged feeding (Pliské et al., 1976). Beebe (1955) observed that the extended feeding at H. indicum exerted a noticeable effect on the reduction of the escape reaction of ithomiines, which "show an obvious reluctance to leave their

repast." A similar "reluctance" was noted in Ithomiinae visiting Eupatorium macrophyllum in British Guiana (Kaye, 1906).

One other curious aspect of ithomiine feeding behavior seems worthy of note. Rene Lichy (1944) recorded that he was "the stupified witness of a remarkable event" when, while collecting with friends in Venezuela, a great number of the clear-wing ithomiine, Hyalyris (=Hypothyris) coeno, converged on the group, perching on their hats, hands, and faces. The three men were smoking, and, after a series of experiments with several lighted cigarettes, became convinced that both males and females of H. coeno were strongly attracted to the tobacco smoke. The butterflies whirled about the "sweet scrolls" of smoke and even extended their proboscises toward the burning tips before the heat drove them back. Lichy stated that he had since repeated the experiment at several other times and places with the same response from both males and females of H. coeno. In Lichy's words:

Was it not for them a reminiscence of their past, a remembrance of the time where they were still only larvae, when, under their primitive form, they ate wild tobacco or several neighboring Solanaceous plants. The odorous waves of the tobacco smoke seemed to them so familiar.

Population Ecology

Spatial Heterogeneity

It has already been mentioned that ithomiines are not randomly distributed throughout the forest understory. Their vertical distribution appears controlled by species-specific preferences for flight and

perch heights and their horizontal or spatial distribution is usually clumped, even within seemingly homogeneous forest. The reasons for the clumped distribution within homogeneous forest are not known. Although moisture and light intensity are probably important, other external factors may also influence ithomiine distributions. The role of internal factors is just now coming under study. Poole (1970), in the study of a Venezuelan mimicry complex dominated by the Ithomiinae, mentioned the possible existence of an "interspecific pheromone used to keep the various Mullerian members of [the mimicry] complex aggregated." W. Haber (pers. comm.) found that male scent scales of Costa Rican Ithomiinae attract males and females of many species and thus may account for aggregations of ithomiines. Apparently contradictory evidence has been published by Pliske (1975c), however, who found that the lactone component of an extract of male ithomiine scent scales is repellent both to conspecific males and males of other lactone-producing species. (For a discussion of scent-scale function and use, see Courtship section, Chapter 4.)

My observations at Limoncocha, although they provide no evidence in favor of ithomiine aggregations being caused or facilitated by male pheromones, would not be incompatible with such an interpretation. But the most likely explanation in my opinion is that the slowly changing constellation of vegetational and environmental characteristics of the forest understory occasionally produces a microhabitat particularly favorable for ithomiines, which then begin to congregate in the area. Pheromones are probably important in determining the nature and extent of activities within the aggregation, but probably do not cause its

formation. It should be noted that the "aggregations" at Limoncocha for the most part cover quite large areas (often several hectares in extent) and are not really comparable to the more tightly clustered groups described by Ross (1967) and Brown and d'Almeida (1970) that occur in drier or seasonal forest areas. Perhaps in these latter areas, where the location of a suitable microhabitat may mean the difference between survival and desiccation, there is stronger selection for a positive behavioral response to an area of pheromone concentration than in areas such as Limoncocha where vast stretches of forest appear to be tolerable, if not preferable, habitat.

Nevertheless, certain areas of the forest at Limoncocha appeared to consistently provide more favorable microhabitat for most species of ithomiines than other areas. One such area was just south of the Nature Trail at Study Site 5 (see Figure 2), set aside early in the research period as an observational area. Within this area of several hectares, there were also regions where certain species of ithomiines could be found with reasonable consistency. For example, the orange-tip clear-wing, Hypoleria chrysodonia, was often seen flying or courting at the fork of the Nature Trail. On any given day this species might be encountered almost anywhere in the NT area, but if I wanted to find H. chrysodonia quickly, the first place I went was to the NT fork, for it was there that I was most likely to find individuals of this species. The same was true for several other small regions in the NT area, each one apparently selectively attractive to one or a small group of species. The most consistent of these associations between regions of the NT area and species of ithomiines are mapped in Figure 25 to provide some

Figure 25. Associations of Species of Ithomlines with Microhabitat Regions of the Nature Trail Observation Area.

idea of the mosaic distribution of species within an area of consistently favorable ithomiine microhabitat. Two of these regions are illustrated photographically in Figures 10 and 11. Figure 10 shows the thick tangle of second growth vegetation near the beginning of the Nature Trail where N. pharo, G. zavaleta, and the three Ithomia species were likely to be found, and Figure 11 shows the portion of the NT just beyond the clearing indicated on the map in Figure 25. (The clearing is visible as a light area in the background of Figure 11.) It is doubtful that individuals show a strong fidelity to these favored regions because the regions appear to be quite small in relation to the probable home range size of most ithomiines.

The Capture-Mark-Recapture Program at Site 4.

On March 5, 1974 a capture-mark-recapture program was begun at Site 4 (see map, Figure 2) which continued until November 12 of the same year. Details of the sampling technique are given in Chapter 2. Site 4 was a 0.5 hectare plot bisected by the Logging Trail (Figure 14) but both "halves" consisted of mature, undisturbed forest (Figure 15). The 0.5 hectare study plot was subdivided into 50 squares, each one approximately 10 meters on a side, and numbered as in Figure 26. The primary objectives of this sampling program were: to estimate the population sizes of as many ithomiine species as possible, to determine the relative abundances of the various species occurring at this particular site, to determine if population sizes or relative abundances of these species changed during the year, and to determine the home ranges of the ithomiines by plotting

Figure 26. Distribution of Captured Ithomine Individuals Among the 50 Subplots at Study Site 4.

their recaptures in the subplots. For reasons given below, only the second and third of these objectives were accomplished with quantifiable results.

The numbers of butterflies caught in each subplot provide further evidence of the nonrandom distribution of ithomiines in seemingly homogeneous forest. When the number of individuals (of all ithomiine species combined) captured in each subplot during the nine month sampling period is mapped (Figure 26), the resulting dispersion of individuals on the grid is far from random. My subjective impression of Site 4 is that the subplots with the highest number of individuals (above 40) all tended to be relatively open between one and three meters above the ground. Subplots 1 through 25 all have low numbers because they were sampled on only the first 7 sampling dates instead of on all 26, as were subplots 26-50. After the cyclonic storm of March 27, 1974, it was no longer possible to collect in subplots 1-25 (see below).

A graph summarizing the results of the sampling program is presented in Figure 27. The number of individuals of the species present on each of the 26 sampling days is given in Figure 28. From March 5 to 9, a sample was collected, marked, and released each day, but by the end of this period it was obvious that the data would be insufficient to calculate population sizes. Out of 246 marked individuals released during those 5 days, only 23, or 9.3%, were recaptured by the sixth sampling date, March 18. As these 23 recaptures were distributed among 30 species, the recapture data for any one species was insignificant for population size analysis. These figures confirmed the impression that discrete populations of ithomiine species do not exist at Limoncocha.

Figure 27. Summary Graph of the 26 Ithomiine Samples Taken at Study Site 4.

Rainfall is given in six-day totals.

●—● individuals

○—○ species

Figure 28. Species and Individuals Present in the 26 Ithomiine Samples Taken at Study Site 4.

Ithomiine species are listed by voucher number in the same order as they appear in Table 4. The dates of the 26 samples may be obtained from Table 8.

STUDY SITE 4 SAMPLE NUMBER

ITHOMINE SPECIES' VOUCHER NUMBERS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
5037																						1		1	2	2
5023		1		1																					1	
5024		1																				1	3		2	
5006	1	2	2	5	2	3	1	1		1	2	3	5	4	1	1				1	2	1	2	3	1	3
5019	1	1		1	2	3				2	2	2	3		5	3					2	2	3	4		3
5020	1				1	2				1	1	1	1	2							1	1	5	2	3	3
5021	2	1		2	3	4				2	2		2	2	1		1				2	3	3	5	2	5
5022	2				1					3											2	3	3	2		2
5035		1	2	2		1		2	3	1	1	1			2	2	1	1							1	1
5012											3				1								1		1	
5013		1		2	1	3					1		2								2	5		1	2	3
5014	1				1								1	1												
5042	1	1										1														
5015	1																							1		1
5028					2					1	1		1										3	1		1
5026		1					2			1	3	1	2		1		1				1	1	1	3	1	4
5027	2		1		1		1					1		1	2	1					1	2	1		1	1
5040					1						1		1					1					1			
5029	5	16	2	4	6	7	8		2	4	5	8	15	8	9	5		3	1	1	9	7	5	1	3	8
5016	3	6	3	6	7	7	16	12	7	4	5	1	3	1	2						2		1			
5017	3	2	4	5	1	6	4	1		2	2	1	2	6	4		1	3	1		1	1	1		1	
5018							1																			
5001					1			1	2	1		1	1				1		1			1		1		
5010	1	1		3	4		2	1			1	2	2	1	2	1	4	1	1	2	1	1	1	2	1	2
5030	10	3	12	7	6	6	7	1	5	2	2	10	2	3	4	3	2	5	3			6		2	6	
5011	2	1		1	2		1					1			4		1							1		1
5031	2			2						1		1		2	1					1			1			
5003	2	4			2	1	3				5		2		1		2	1			1		5			
5041																							1			
5050					1																1				1	
5004		2																			1					
5034		1			1		1				2		2	2	2		1				1			1		
5007	9	4	4	5	6	7	7	2	2	1	7	3	9	9	8	1	3	3		1	2	2	8	17	3	14
5008		1		1	1	3	6			4	4	4	1	1		1						3	6	1		
5009	3			1	1	3						2		4	1	1					1		2	1	2	2
5039		1	2	1			1	1			1	1					1						2	1	1	
5043					2					1	2		3		2										1	
5032	3		3									1					1									
5033	1	1		1		1	2	1		1	8	5	11	7				1			2	2	4		1	
5036						1	1			1	2		3			1						2	1			3

The almost continuous expanse of lush forest in this area, despite the microhabitat heterogeneity described earlier, provide ithomiines with an almost unbroken macrohabitat. The clumped distributions of ithomiines within this macrohabitat do not represent discrete communities and populations, but are merely transient concentrations that crest and ebb erratically through time. The marking program was continued, however, in hopes that there would be sufficient recaptures over the remainder of the year to provide some information on longevity and home-range size. From this point on, a weekly or biweekly sample was taken to provide information on the relative frequencies of ithomiine species and to see if ithomiine abundance varied during the year.

Catastrophic fluctuations

A study of Figure 27 reveals that the one-hour samples normally contained approximately 40-60 individuals and about 20 species, with 74 the maximum number of individuals and 24 the maximum number of species collected during one sample. The periods of strong deviation from this generalized pattern occurred in late March to early April and in mid June to mid July. During these periods the number of individuals collected dropped to about 20 or below and the number of species was less than 10. As all one-hour samples were collected between 1000 and 1200 h on comparably sunny days, and since the low values were consistent for two consecutive samples in the first period and for five consecutive samples in the second, I consider both of these to be actual minima of ithomiine abundance and not merely sample variation or the result of poor collecting weather. Thus, assuming that the pattern in Figure 27 is not the result of chance, what might the causes of this variation be?

The answer could come from one or both of two possible categories of events affecting population sizes: biotic or abiotic factors. During the year I had observed no noticeable changes in the number or quality of ithomiine larval foodplants, nor in any other aspect of the Limoncocha vegetation. The scant data available to me on the predation and parasitism of adults and immature stages suggested no possibilities, so I examined the possible abiotic factors.

The study area at Site 4 periodically flooded, in places up to 80 cm in depth, following periods of heavy rains that apparently brought much more water than the saturated soil and low relief of the area could accomodate. When these periods of flooding are plotted with the ithomiine abundances, as they are at the bottom of Figure 27, it is clear that the first two flooding periods correlate closely with the two largest drops in ithomiine sample size, and that the third occurs at another, but much less dramatic, ithomiine minimum. A close examination of the 1974 rainfall pattern (Figure 6) revealed that in the month before each drop in ithomiine abundance there had been a fairly sharp rise in the amount of rainfall over the preceding month. To better understand the pattern of rainfall distribution, precipitation was grouped into six day totals, instead of monthly totals, and the results were graphed at the top of Figure 27. Now a correlation between rainfall distribution and ithomiine abundance became more easily recognized. Just prior to each flooding period of Site 4 was a six day period of exceptionally high rainfall (over 100 mm), and the longest flooding periods (July and October) each had two such periods. Most dramatic of the three, however, was the first flooding period which literally began overnight after a

spectacular storm struck Limoncocha on the night of March 27. In less than eight hours, 91 mm of rain fell while localized twisting winds felled dozens of trees in the clearings and forests of the Limoncocha area. The next morning, the effects of the storm's violence were everywhere, and the hike to Site 4 from the base, which normally took about 45 minutes, required more than 3 hours. At Site 4 itself I found the entire western half of the one hectare study plot devastated by the felling of two large trees which brought everything else down with them to form an impenetrable tangle of flooded vegetation. Just within the one hectare study plot (the eastern half was flooded but no trees had fallen) I found two dead snakes, a dead porcupine, and numerous dead insects, especially Orthoptera. I have no doubt that the destructive winds, torrential rains, and crushed vegetation took a heavy toll of ithomiine adults and immature stages, and that the low sample sizes of April 2, 9, and 22 reflect this mortality. Although less dramatic, similar storms and torrential rains fell in mid June, early July, and mid October, as my notes and the weather records (and the flooding at Site 4) indicate. It is my interpretation that these intense rain storms were the direct cause of the mortality that resulted in the decreases in ithomiine abundance observed at Site 4. The devastating effects of these rain storms are similar to those attributed to a late snowstorm in a subalpine plant community in Colorado that resulted in the extinction of at least one butterfly population (of the lycaenid, Glaucopsyche lygdamus Dbldy) and severely depressed the populations of many other insects, mammals, and birds (Ehrlich et al., 1972). Tropical rainstorms are also suspected to be a major source of mortality for two species of Parides (Papilionidae) during the wet season in Trinidad (Cook et al., 1971).

Community stability

With the exception of the three depressions in ithomine abundance that appear correlated with storms and intense rainfall, the samples at Site 4 give the impression of a reasonably stable ithomiine community. To provide some other measures of the stability of the community as measured by the similarity of successive samples, certain diversity indices were calculated. Table 8 contains the results of the Shannon-Weaver diversity index (H') and evenness values (J') calculated for each sample at Site 4. Formulae are given at the end of the table and were taken from Poole (1974). Calculations use natural logarithms (base e). The utility of diversity indices, especially those based on information theory (such as H'), has been recently challenged (Hurlburt, 1971), but it is not my intent to imply that they have any intrinsic value as used here. However, they do provide a convenient method of tracking the distribution of individuals among species through time in the sequential samples from Site 4. H' is generally considered to be independent of sample size (Pielou, 1967), although Peet (1974) has shown that, despite being sluggish to changes in sample size, it is not entirely independent of them.

The values of H' at Site 4 vary from 1.476 to 2.951, but only 4 of them are less than 2.000 and 17 are over 2.500, indicating that the H' values are uniformly high. The only comparable figures for Ithomiinae known to me in the literature are those given by Gilbert (1969) for several localities in Costa Rica and for two localities in Brazil calculated on the data of Collenette and Talbot (1928). His figures for three

Table 8. Species Diversity of the Ithomiine Community at Study Site 4.

SAMPLE NUMBER	DATE	N	S	H'	H' _{max}	J'
1	05MAR74	56	22	2.770	3.091	0.896
2	06MAR74	53	22	2.587	3.091	0.837
3	07MAR74	35	10	2.040	2.302	0.886
4	08MAR74	50	18	2.654	2.890	0.918
5	09MAR74	52	21	2.753	3.045	0.904
6	18MAR74	62	19	2.715	2.944	0.922
7	25MAR74	64	17	2.416	2.833	0.853
8	01APR74	22	9	1.604	2.197	0.730 ⁺
9	09APR74	20	6	1.609	1.791	0.898
10	22APR74	35	19	2.797	2.944	0.950
11	29APR74	64	24*	2.951*	3.178*	0.929
12	16MAY74	50	20	2.632	2.996	0.879
13	22MAY74	74*	22	2.709	3.091	0.876
14	30MAY74	55	17	2.534	2.833	0.894
15	04JUN74	53	19	2.664	2.944	0.905
16	14JUN74	20	11	2.194	2.398	0.915
17	21JUN74	20	13	2.415	2.565	0.942
18	28JUN74	19	9	2.004	2.197	0.912
19	05JUL74	7	5 ⁺	1.476 ⁺	1.609 ⁺	0.917
20	11JUL74	6 ⁺	5 ⁺	1.562	1.609 ⁺	0.971*
21	27JUL74	33	18	2.600	2.890	0.900
22	11SEP74	47	21	2.814	3.045	0.924
23	29SEP74	63	24*	2.947	3.178*	0.927
24	12OCT74	52	22	2.545	3.091	0.823
25	23OCT74	37	21	2.864	3.045	0.941
26	12NOV74	59	18	2.570	2.890	0.889

Note:

N = Number of individuals in sample.

S = Number of species in sample.

 $H' = \text{Shannon-Weaver diversity index} = -\sum (n_i/N) \ln(n_i/N)$ $H'_{\max} = \text{Maximum value of } H' \text{ (obtained if all } n_i/N \text{ were equal)}$
 $= \ln(S)$ $J' = \text{Evenness} = H'/H'_{\max}$

*Highest value in series.

+Lowest value in series.

wet forest sites in Costa Rica were

		S	N	H'	J'
La Selva	(75 m)	17	152	1.26	.81
Tilaran	(600 m)	20	50	1.13	.88
San Vito	(1200 m)	.18	94	1.22	.97

and for Collenette and Talbot's data (riparian areas in dry forest)

Serragem	(450 m)	13	1216	.87	.77
Tombador	(450 m)	9	378	.82	.86

Unfortunately, Gilbert did not specify the base of his logarithms and thus, although I suspect he used $\log_{10}$, perhaps it is best to restrict comparisons to the J' values. $J' = H'/H'_{\max}$ and thus provides a measure of the equitability or evenness of the sample by filtering out the contribution of S (number of species) to the index H' . The J' values of the Site 4 samples vary between .730 and .971 with the majority above .900. Thus, most of the time the ithomiine individuals are over 90% as evenly spread among the species as possible. The equitability of the Limoncocha samples most resembles that of the richest area in Costa Rica, San Vito. Interestingly, Gilbert found a nearly linear increase in equitability with altitude, which he attributed to a corresponding increase in diversity in solanaceous larval foodplants with altitude in Costa Rica. It would be most interesting to sample a transect running up the eastern slopes of the Andes in Ecuador, measuring the diversity and equitability of the Ithomiinae and Solanaceae from the lowlands of the Oriente to the upper altitudinal limits of ithomiine distribution.

The equitability values (J') for the Site 4 samples have been plotted in Figure 29. It is interesting that the lowest values occurred in the sample (April 2, 1974) immediately following the March 27 storm, suggesting

Figure 29. Equitability (J') and Quotient of Similarity (QS) Values for the 26 Ithomline Samples Taken at Study Site 4.

that perhaps a few species were less susceptible to the action of the storm than others. The greater survivorship of these species would result in their greater representation in the April 2 sample, thereby lowering the value of J' .

Another statistic calculated to compare the samples taken at Site 4 through time was Sørensen's Quotient of Similarity (QS), also graphed in Figure 29. The formula (from Southwood, 1966) and actual figures are given in Table 9. The Quotient of Similarity compares the species composition of two samples in terms of the number of species shared between them. By comparing Figure 29 with Figure 27, it is readily apparent that QS (Figure 29) varies in much the same way as does N , the sample size (Figure 27). To test this correlation, the regression of QS on N was calculated and the resulting regression line drawn in Figure 30. The correlation coefficient of the regression of QS on N ($r = .874$) was highly significant ($P > .001$, $df = 23$), indicating that about 87% of the variation of QS is accounted for by the size of the sample taken (N). We have already seen that the strongest variations in N appear to be due to "catastrophic" environmental conditions. Thus, when the overall abundance of ithomiines is reduced, the species compositions of consecutive samples taken during this period are apt to be quite different, even though the H' and J' values of consecutive samples may be very similar (e.g., samples 8-9, and samples 17-21 in Table 8 and Figure 29). In other words, small samples may be similar in number of species (S) and the evenness (J') with which the individuals are distributed among the species, but the species composition of the two samples may be entirely different. This may lead to changes in the nature of

Table 9. Similarity of Species Composition Between Consecutive Samples of the Ithomline Community at Study Site 4.

SAMPLE NUMBER	DATE	N	S	J	QS
1	05MAR74	56	22		
2	06MAR74	53	22	13	.591
3	07MAR74	35	10	7	.438
4	08MAR74	50	18	8	.571
5	09MAR74	52	21	13	.667
6	18MAR74	62	19	12	.600
7	25MAR74	64	17	10	.556
8	01APR74	22	9	8	.615
9	09APR74	20	6	4	.533
10	22APR74	35	19	6	.480
11	29APR74	64	24*	17*	.791*
12	16MAY74	50	20	14	.583
13	22MAY74	74*	22	12	.571
14	30MAY74	55	17	14	.718
15	04JUN74	53	19	12	.667
16	14JUN74	20	11	9	.600
17	21JUN74	20	13	4	.333 ⁺
18	28JUN74	19	9	6	.545
19	05JUL74	7	5 ⁺	4	.571
20	11JUL74	6 ⁺	5 ⁺	2 ⁺	.400
21	27JUL74	33	18	2 ⁺	.348
22	11SEP74	47	21	13	.667
23	29SEP74	63	24*	16	.711
24	12OCT74	52	22	14	.609
25	23OCT74	37	21	12	.558
26	12NOV74	59	18	12	.615

Figure 30. Regression of the Quotient of Similarity (QS) on Sample Size (N).

predator-prey relationships. For example, during low ithomiine abundance, a predator may find a sample of ithomiines (i.e., a set of ithomiines flying at a given time in a given place) to be quite different in species composition from one day to the next. If, as is quite likely (see Chapter 7), mimetically similar species of ithomiines are distasteful to varying degrees (i.e., a palatability spectrum exists among species of Ithomiinae), the type of "education" received by a naive predator could vary from day to day, depending on the species composition of the butterfly sample flying during feeding time. A variable education for a predator means a longer period (and more butterflies sampled) to successfully learn to associate an aposematic coloration with distastefulness. Here then may be another explanation for interspecific ithomiine aggregations during periods of low abundance in seemingly homogeneous wet forest--better predator education. If most ithomiines are distasteful but some are either palatable or only slightly unpalatable, it would be selectively advantageous for less palatable individuals to associate with other ithomiines sharing a similar mimetic pattern, if, on the average, those other ithomiines were to a greater degree distasteful.

Further evidence for the stability of the ithomiine community at Site 4 is provided by the measurements of wing condition taken on all individuals as described in Chapter 2. Although wing condition was scored on the basis of seven categories of increasing scale loss as a measure of relative age, the data were lumped into four categories of wing condition for ease of comparison. These four categories are teneral (F+), fresh (F), intermediate (I), and worn (W), and the percentage of individuals (of all species combined) falling into each age class on

each sample day is presented in Figure 31. The first impression given by Figure 31 is of a relatively stable age class distribution for the ithomiine community as a whole, in spite of the fluctuations in community size that occurred during the sampling period (Figure 27). The fluctuations about the nine month averages (10.2% F+, 52.6% F, 26.6% I, and 10.6% W), illustrated on the far right of the graph, are not very great. I had expected a decrease in average wing condition to occur with each catastrophic drop in ithomiine abundance followed by an increase in the proportion of teneral individuals in the next samples as the community recovered. The proportion of worn individuals does not appear to have significantly increased following the storms, however, nor to have been particularly higher during the wettest periods. In fact, the highest proportions of worn individuals occur during peaks of ithomiine abundance (samples 6, 14, 24) suggesting that the increased flying activity that occurs during periods of favorable weather may lead to more rapid scale loss. The proportion of teneral individuals does appear to have been significantly reduced during the low abundance period from mid June to mid July (samples 16-20), however, and may be the result of their vulnerability to hard morning rains that occur soon after emergence. A heavy mortality of late instar larvae or pupae (e.g., by drowning or increased incidence of fungal infection) could also account for the reduced number of teneral individuals. Thus, the relatively even age distribution of the ithomiine community through time indicates that the stormy wet weather that depresses ithomiine abundance does so by causing mortalities among adult butterflies irrespective of age, although teneral individuals may be slightly more affected than those in other age classes.

Figure 31. Age Class Distribution of the Ithomline Community at Study Site 4.

Longevity

Although the overall recapture rate of released butterflies at Site 4 was small (33 recapture events involving 27 individuals out of a total 754 released butterflies, or about 4%), a few of the recaptures provide some insight into the longevity of ithomiines. All of the marked individuals recaptured at Site 4 are listed in Table 10, along with their condition at each capture and the length of time between first and last capture. The number of days (D) between first and last capture can be divided by the number of new age class categories entered by the butterfly since it was marked (Δ). The quotient (D/Δ) provides a crude estimate of the number of days spent in each age class category. Multiplying this times seven (the number of age class categories) we arrive at an estimate of the life span of these individuals. Obviously, a butterfly first caught at the end of one age class and recaptured at the beginning of another age class will tend to overestimate longevity, and vice versa. Also, this method assumes that the amount of time spent in each age class is the same, which is probably not true. For example, Ehrlich and Gilbert (1973) had enough multiple recaptures of Heliconius ethilla on Trinidad to calibrate their measurement of age based on wing-scale loss. They obtained an approximate ratio of 1:3:1.3 for the relative amounts of time spent in the age classes F:I:W. A similar ratio would not be unexpected for ithomiines at Limoncocha if enough data were available, but without it we must be content with the crude estimates given in Table 10. Oleria agarista, for which the most data are available, has life span estimates ranging from 63 to 182 days. The average life span for all eleven individuals of this species comes to nearly 70 days,

Table 10. Estimates of Longevity of Ithomiine Butterflies Based on Recapture Data at Study Site 4.

SPECIES	#	SEX	R _i	D	C _O	C _X	Δ	D/Δ	L= (D/Δ) (7)
<u>Aeria eurimedia</u>	1	♀	2	35	I	W	2	17.5	122.5
<u>Forbestra truncata</u>	6	♂	1	1	F	F-	1	1	7
<u>Godyris zavaleta</u>	10	♂	1	1	I	I-	1	1	7
	13	♂	1	2	F-	F-	0	>2	>14
	25	♀	1	16	I	W	2	8	56
<u>Hyposcada kezia</u>	1	♂	1	1	F	F	0	>1	>7
	3	♀	1	1	I	I	1	1	7
	15	♂	2	29	F	F-	1	29	203
	16	♂	2	37	I	W	2	18.5	129.5
<u>Hypothyris fluona</u>	1	♂	1	3	F	F	0	>1	>7
<u>Ithomia amarilla</u>	4	♂	1	1	F-	F-	0	>1	>7
	9	♂	1	11	F	F-	1	11	77
<u>Napeogenes apobsoleta</u>	1	♀	1	19	I-	I-	0	>19	>133
<u>Napeogenes corena</u>	3	♀	1	2	F+	F-	2	1	7
<u>Napeogenes pharo</u>	23	♀	2	18	F	I	2	9	63
	31	♀	1	10	F	F-	1	10	70
<u>Oleria agarista</u>	11	♀	1	1	F-	F-	0	>1	>7
	13	♀	1	1	F	F	0	>1	>7
	14	♀	1	11	I	I-	1	11	77
	18	♀	2	18	F	I	2	9	63
	23	♂	1	2	F-	F-	0	>2	>14
	26	♂	1	52	F	I	2	26	182
	27	♂	1	1	I	I	0	>1	>7
	31	♀	1	9	I-	W	1	9	63
	47	♀	1	37	F	I	2	18.5	129.5
	52	♀	2	50	F+	I	3	16.7	116.9
	58	♀	1	14	F	F-	1	14	98
	$\bar{x}$							9.9	69.5
<u>Oleria kena</u>	3	♀	1	2	F	F	0	>2	>14

Table 10 - continued.

Note: # = Individual number of marked butterfly.
 R_1 = Number of times the butterfly was recaptured.
 D = Number of days between initial capture and final recapture.
 C_o = Condition of wings at initial capture.
 C_x = Condition of wings at final recapture.
 Δ = Number of units of change in wing condition between initial
 capture and final recapture ($C_o - C_x$).
 D/Δ = Number of days spent in each category of wing condition.
 L = Estimated life span of the individual, assuming that an
 equal number of days was spent in all 7 categories of
 wing condition = $(D/\Delta)(7)$.

or over two months. In fact, nearly all the individuals of all species that have long recapture intervals provide life span estimates of at least two months, and many are considerably longer. For example, a male (# 15) of Hyposcada kezia was first captured in fresh (F) condition, but, nearly a month (29 days) later, was recaptured in fresh-minus (F-) condition. The life span estimate is thus 203 days, or almost 7 months. While this may be an exceptionally long life for an ithomiine, the average life span for most species would appear to be on the order of two to four months. Similar life spans have been reported by Gilbert (unpubl., but cited in Gilbert, 1972) for Ithomia pellucida and Hypothyris euclea in Trinidad, where marking studies indicated these species can live at least four months. The individual with the longest recorded life span in the wild during my study was a male (# 26) of Oleria agarista, first captured on March 8 and recaptured on April 29, 1974. Thus, the recorded life span was 52 days, but this individual had undoubtedly been alive for several days before initial capture (condition F), and probably lived for quite a while after final release (condition I).

A life span measured in months instead of weeks or days is not unexpected in a tropical butterfly, especially for sylvestral species that inhabit the relatively uniform environment of the tropical rain-forest understory. Indeed, Ehrlich and Gilbert (1973) have records of many individuals of Heliconius ethilla living as long as 140 days in the wild and one male, recaptured for the last time 162 days after marking, probably lived a total of 6 months or more. Long life spans have been found for other species of Heliconius (Turner, 1971; Benson, 1972), Marpesia berania (Benson and Emmel, 1973), and in the genus Morpho (Young, 1971).

A life span, however, is not the same as a life expectancy, the latter being greatly influenced by the frequency of catastrophic weather conditions, predation, and other events that place a butterfly's life in jeopardy. Life expectancy is normally calculated from the survivorship term obtained in analyzing recapture data, but, once again, the low recapture rates in any one species population at Limoncocha precluded its calculation. Very few survivorship rates and life expectancy estimates are available for tropical butterflies. Cook et al. (1971) found that both Parides neophilus and P. anchises had life expectancies between 5 and 10 days in Trinidad, although this was considerably shorter than the observed life spans (several weeks to months) of these same species in insectaries. Turner (1971), however, obtained a life expectancy for Heliconius erato in Trinidad of 50 to 100 days. This figure is substantially greater than that recorded for most temperate zone species, the life expectancies of which are generally less than two weeks (Scott, 1973). By comparing the estimated life spans of ithomiines with those established for Heliconius, it can be inferred that most species of ithomiines probably have life expectancies measured in tens or perhaps even scores of days.

CHAPTER IV
REPRODUCTIVE BIOLOGY OF THE ITHOMIINAE

Courtship

Courtship activity of male ithomiine butterflies was observed in 26 of the 53 Limoncocha species, and 139 specific observations of courtship initiation behavior by males are available for analysis. Although field observations were made during all hours of the day (between 0600 and 1900*), male courtship behavior in ithomiines was only observed between 0900 and 1700 h. Courtship activity increases rapidly after 1000 and reaches its peak between 1100 and 1300 h, trailing off gradually over the afternoon, but generally ceasing between 1600 and 1700 h (see Figure 32). Similar peaks in courtship activity for male ithomiines have been recorded by Gilbert (1969) in Costa Rica (1030-1330 h) and Pliske (1975c) in Venezuela (1000-1600 h).

* The number of hours of field observations between 0900 and 1700 outnumbered the number of hours spent between 0600 and 0900, and after 1700, by a factor of three.

Figure 32. Courtship Activity of Male Ithomlines.

Function of Hairpencils in Male Ithomiines

Males of all species of ithomiines have ~~one~~ or two tufts of androconial scales arising from the dorsal surface of the hindwing.* These elongated scales (usually 6 to 8 mm long, but ranging from 4 to 12 mm in length in *Limoncocha* species) are attached to the wing membrane in the anterior portion of the hindwing discal cell, just posterior to the radial sector (Rs) vein (see Figure 33a). These androconial scales are grouped to form a compact bundle or brush, sometimes called a hairpencil (Pliske, 1975c), that normally lies flat against the hindwing, such that the free end points distally. At certain times during courtship (see below), however, these hairpencils may be erected to form a hemispherical splay, such as that shown in Figure 33b. Just anterior to the hairpencil is a region of specialized scales that lacks the normal coloration of the hindwing, having instead a highly reflectant sheen. I suspect that these scales secrete the scent that is disseminated by the hairpencils,

* Curiously, females of some species of the genus Thyridia also have hairpencils, anatomically positioned like those of the males. It is not known if this is an ancestral (Fox, 1940) or a derived (Fox, 1956) condition, although Lamas M. (1973), whose dissertation I have not seen, may have resolved the problem. At Limoncocha, females of Thyridia confusa psamathe were dimorphic for the presence or absence of hairpencils. Of eleven wild-caught females examined, four (36%) had hairpencils and seven did not. Three females reared from the egg stage did not have hairpencils. It is not known if Thyridia females use the hairpencils during courtship, but since all eleven wild-caught females were mated, there is no indication that the presence or absence of hairpencils in female Thyridia affects their mating success.

a

b

Figure 33. Location and Erection of Hairpencils in Male Ithomiines (Napeogenes apobsoleta).

a. Dorsal view of hindwing, showing hairpencil tucked under costal fold of wing.

b. Anterior view of hindwing, showing hairpencil in erected state.

but at present there is no evidence to support or discredit such a suggestion. In some species this region of specialized cells is quite distinct, as in the genus Ithomia in which it is located in an oval cell bounded by the radial sector (Rs) and subcostal (Sc + R₁) veins. In other species the scent-producing scales (assuming for the moment that this is their function) are apparently more widely distributed anterior to the Rs vein (e.g., in the genus Mechanitis). Although the scent-producing function of these surface scales has not been demonstrated, the scent-dissemination function of the hairpencils has long been suspected by early students of the Ithomiinae (Muller, 1877; Kaye, 1914) and recently confirmed by Pliske (1975c).

The scent released by the androconia of male ithomiines was originally thought to have a protective function. Longstaff (1912) described the scent of several Venezuelan clear-wing ithomiines as being "of a disagreeable character, recalling stables or pig-sties" and associated the odor with the hairpencils of the males. Muller (1877) observed that "the Ithomiae (sic) of the Amazon . . . are said to be protected against birds by a disagreeable scent." Muller theorized that if such a scent did indeed emanate from the male hairpencils, the "hundred-fold predominance of the males recorded by Bates, and the entire correspondence between the sexes in pattern and colour" would be explained. Muller reasoned that if a protective odor were confined to the males, an equal sex ratio would provide a predator with an equal chance of associating the ithomiine pattern with either palatable or unpalatable prey. However, if the male were more common, the predator would learn to avoid the ithomiine pattern

on the basis of the more numerous encounters with the protected males. Thus, in Muller's view, female ithomiines are Batesian mimics of their conspecific males, since a close correspondence to the pattern of the more numerous and protected males would confer upon the female a protective resemblance established and maintained by natural selection.

Evidence available at the present, however, strongly suggests that the odors emitted by ithomiine males function primarily as pheromones for intra- and inter-specific communication rather than as a line of olfactory defense (see below; Pliske, 1975c). Yet Muller's hypothesis is of interest in light of the recent suggestion by Birch (1974) that some insect pheromones may have originated as defensive secretions, and, once evolved, became a method of intra-specific communication. If pheromones derived in this manner retained a defensive function as well, their release during courtship and mating might protect the male and female during a time of extreme vulnerability (Birch, 1974). But Muller's argument may be countered on two points. First, the extremely male-biased sex ratio of ithomiines referred to is almost certainly an artifact of collecting technique. It is well known that the majority of individuals in most butterfly collections are males because males are more likely to frequent hilltops, aggregate at flowers or damp soil and in general to haunt those areas most frequented by collectors. This is especially true of ithomiines because males are selectively attracted to certain species of flowering plants (see above; Pliske, 1975a), and such aggregations often form the nucleus of day's collecting. The sex ratio of nearly all butterflies reared to date (including the ithomiines reared in this study) have sex ratios that do not deviate substantially from a

1:1 ratio at eclosion. Furthermore, samples of ithomiines taken in the forest understory at Site 4 have approximately equal sex ratios, although slightly biased in favor of males (see Table 11). The scents of male ithomiines at Limoncocha generally have (to the human nose at least) neutral to slightly agreeable odors (most of the species recall dried hay, musty books, or a faint essence of vanilla). Second, as is described below, the courtship behaviors of male ithomiines involve the use of these androconial scents to attract females and trigger their sexual receptivity, and perhaps also to serve as allomone repellants to conspecific and other ithomiine males (Pliske, 1975c).

Mate-locating Behavior of Male Butterflies

In butterflies, males initiate courtship and locate potential mates by either passive or active means. In passive mate-locating behavior males simply perch and wait for appropriate females to fly by. This behavior has been called "waiting" (Magnus, 1963) and "perching" (Scott, 1972). Active mate-locating behavior involves an active search of the habitat, usually in a stereotyped flight pattern, and has been termed "seeking" (Magnus, 1963) or "patrolling" (Scott, 1972). The location of a potential mate by either method provides a visual stimulus to the male to initiate the next phase of courtship activity, that of pursuit. The visual stimulus may have several components, including color (including ultraviolet), motion, and size of the females, but pattern detail is relatively unimportant (Silberglied, 1976). Considering the vagueness of these three components that elicit pursuit behavior, it is not surprising that the initial approaches of males are often quite indiscriminate

(Silberglied, 1976 and references therein), especially among mimetic species where the difficulty of distinguishing between conspecific males and females is further complicated by the presence of other visually similar species.

This is especially true for the Ithomiinae, nearly all species of which are members of extensive mimicry complexes involving many species. This dilemma was first recognized by Poulton (1907) who concluded that in Mullerian mimics visual stimuli alone would be insufficient to enable males to recognize conspecific females. Brower (1963) suggested that olfaction was the additional mode of communication that allowed these very similar species to determine their correct sexual partners, observing that all members of Mullerian mimicry rings have elaborate scent-disseminating organs of various sorts. Vane-Wright (1972), however, has questioned the universality of this correlation, and Silberglied (1976) has concluded that the courtship of all lepidopterans studied to date involves pheromones at some stage. Both pheromones and visual stimuli are important to successful courtship in ithomiines.

Mate-locating Behavior of Ithomiine Males

A male ithomiine faces the problem of trying to locate a receptive mate out of a relatively large number of visually similar, but mostly inappropriate, individuals. The capture-mark-recapture program at Site 4 revealed that the ithomiine community at Limoncocha has both high diversity (as measured by H') and high equitability or evenness (J'). In other words, a large number of species (often more than twenty) were

usually flying in approximately equal abundance. Because the samples were taken during the peak of courtship activity (indeed, many courting males were caught at Site 4 during sampling) it is reasonable to assume that the composition of the one-hectare plot at Site 4 is representative of that faced by a male ithomiine attempting to locate a receptive, conspecific female. Thus, the chances of a male locating an appropriate mate by flying at random until such an encounter is made are extremely low. The figures in Table 11 show this dramatically. The Probability of Interspecific Encounter (PIE) is a statistic derived by Hurlburt (1971) and based on the premise that each individual in a community can encounter or interact with every other individual in that community, an assumption that seems reasonable for the ithomiine adults flying during the courtship period at Site 4. PIE is expressed as a decimal fraction, ranging from 0 to 1, and thus may be considered (as in Table 11) as the percent probability that two individuals meeting at random will be of different species. The PIE measurements for the Site 4 samples are very high, indicating that most (>90%) encounters between ithomiine individuals will be between members of different species. The Probability of Intraspecific Encounter is simply $1 - \text{PIE}$, and these values are also expressed as percentages in Table 11. To estimate the probability that a male will encounter a conspecific female as the result of a random event, the average proportion of females (for all species combined) for each sample has been multiplied by the Probability of Intraspecific Encounter ($1 - \text{PIE}$). The results range from 1.1 to 14.9%, but the majority of the values are less than 5%. The fact that each species has a characteristic flight level (although this level may be quite broadly defined) improves the

Table 11. Sex Ratio, Probability of Interspecific Encounter (PIE), and Probability of Intraspecific-heterosexual Encounter in the Ithomiine Community at Study Site 4.

SAMPLE NUMBER	DATE	S	♂♂	♀♀	%♀♀	PIE [(Δ_2) x100]	1-PIE [(1- Δ_2) x100]	(1-PIE) x(%♀♀)
1	05MAR74	22	26	30	53.6	93.5	6.5	3.5
2	06MAR74	22	27	26	49.1	89.1	10.9	5.4
3	07MAR74	10	18	17	48.6	85.2	14.8	7.2
4	08MAR74	18	30	20	40.0	86.0	14.0	5.6
5	09MAR74	21	26	26	50.0	93.5	6.5	3.3
6	18MAR74	19	33	29	46.8	93.7	6.3	2.9
7	25MAR74	17	22	42	65.6	89.4	10.6	7.0
8	01APR74	9	11	11	50.0	70.3 ⁺	29.7 [*]	14.9 [*]
9	09APR74	6	5	15	75.0 [*]	81.1	18.9	14.2
10	22APR74	19	24	11	31.4	95.9 [*]	4.1 ⁺	1.3
11	29APR74	24 [*]	42	22	34.4	95.2	4.8	1.7
12	16MAY74	20	27	23	46.0	92.0	8.0	3.7
13	22MAY74	22	53	21	28.4	92.2	7.8	2.2
14	30MAY74	17	35	20	36.4	91.8	8.2	3.0
15	04JUN74	19	35	18	34.0	93.0	7.0	2.4
16	14JUN74	11	12	8	40.0	76.6	22.0	9.0
17	21JUN74	13	9	11	55.0	94.2	5.8	3.2
18	28JUN74	9	13	6	31.6	89.1	10.9	3.4
19	05JUL74	5 ⁺	6	1	14.3 ⁺	85.8	14.2	2.0
20	11JUL74	5 ⁺	3	3	50.0	93.4	6.6	3.3
21	27JUL74	18	25	8	24.2	93.5	6.5	1.6
22	11SEP74	21	20	27	57.4	94.6	5.4	3.1
23	29SEP74	24 [*]	48	15	23.8	95.3	4.7	1.1 ⁺
24	12OCT74	22	28	24	46.2	87.5	12.5	5.8
25	23OCT74	21	16	21	56.8	95.6	4.4	2.5
26	12NOV74	18	32	27	45.8	91.2	8.8	4.0
Totals			626	482				
Overall Sex Ratio			130:100		43.5			

Table 11 - continued.

Note:

S = Number of species in sample.

♂♂ = Number of males of all species in sample.

♀♀ = Number of females of all species in sample.

PIE = Probability of Interspecific Encounter = Δ_2 .

1-PIE = Probability of Intraspecific Encounter = $1-\Delta_2$.

(1-PIE)(% ♀♀) = Probability of Intraspecific-heterosexual
Encounter (i.e., probability that a male of
species A will encounter a female of species
A).

*Highest value in series.

+Lowest value in series.

probability of intraspecific encounter slightly. Nevertheless, it remains evident that an ithomiine male relying solely on chance encounter to locate an appropriate mate will probably squander a lot of time and energy in the process. It is not surprising, then, that most ithomiine males exhibit active, rather than passive, mate-locating behavior.

In none of the 26 species of Limoncocha ithomiines for which observations are available did males use the "seeking" or "patrolling" technique for locating females. Instead, all observed mate-locating behavior involved the use of a perch by males, but not in the sense of simply "waiting" for passing females. Males use their perches in two very different ways, for which I propose the terms "display perching" and "patrol perching." Patrol perching may be considered a special case of "waiting" behavior, but display perching requires a third category of male mate-locating behavior that is perhaps best called "assembling." Both types of behavior have been recently but incompletely described in the literature (Gilbert, 1969; Pliske, 1975c).

Display perching

Gilbert (1969) was apparently the first to record display perching behavior in ithomiines, but unfortunately his observations have never been published. Pliske (1975c) has recently described such behavior for Pteronymia nubivaga and has observed similar behavior in eleven other Venezuelan ithomiine species.

Like most other butterflies at rest, male and female ithomiines normally hold their wings together over their backs when perched on a leaf. In display perching, however, a male ithomiine holds his wings

apart in such a way that the hairpencils are exposed and erected (Figure 34). Gilbert (1969) suggested that the function of this androconial display is to disseminate the male scent and in this way assemble females much in the same way as female moths assemble males. Pliske (1975c) recorded that the wings are held at a 180° angle in Hypothyris and at a $60-120^\circ$ angle for species of the other genera he observed (Pteronymia, Ithomia, Aeria, Hymenitis, Oleria, Prittwitzia, and Tithorea.) Pliske noted that species in the genera Pteronymia, Hymenitis, Ithomia, and Prittwitzia generally perched in open sun where the understory was sparse, but that species of the genera Hypothyris, Oleria, and Aeria were more apt to be found displaying in shady areas. In general, Pliske found that a displaying male ithomiine would fly after many of the butterflies (not just conspecifics) that entered its visual sphere, but that interactions with other species and conspecific males were quickly broken off after only a few seconds. Pursuits of conspecific females lasted much longer, though none were actually observed to lead to copulation. After most pursuits, a male would return to his original perch or an adjacent one.

Patrol perching

At Limoncocha, males of species of the genera Mechanitis, Forbestra, and Thyridia perch on the tips or edges of leaves at heights between one and three meters, usually positioned so that they face an open air space (i.e., an area free of vegetation) of at least one or more cubic meters (Figure 35). If another butterfly (or a falling leaf, or almost any other moving body) penetrates this air space, the perched male flies

Figure 34. Napeogenes apobsoleta in Display Perch Courtship Behavior.

Figure 35. Mechanitis messenoides in Patrol Perch Courtship Behavior.

out and pursues it for an indeterminate distance, the length of which apparently depends on the type and strength of the stimuli provided by the pursued object. Pliske (1975c) also described the mate-locating behavior of two species of Mechanitis (isthmia and polymnia) and of Thyridia (=Methona) confusa. In each of these species the male perches on terminal twigs or leaves with its wings together over its back and, according to Pliske, flies toward any butterfly with its own color pattern. Once again, interspecific or conspecific male encounters were substantially shorter than those involving conspecific females. After most pursuits, males resumed a perch, but not necessarily in the same place from which they flew. Thus, according to Pliske's description, the mate-locating behavior of Mechanitis and Thyridia could be classified as waiting (sensu Magnus, 1963)

Interperch flights

My observations at Limoncocha, however, suggest that both "display perching" and "waiting" in ithomiines are more complex than Pliske's descriptions indicate. In both types of behavior, the perching portion of the behavior is consistently, and more or less regularly, punctuated by "interperch" flights of varying, but usually quite short, duration. The interperch flights of display perches are slow and fluttering and are made at about the same height as the perch. They usually circumscribe an area of about one square meter or less. Most often the butterfly flies a simple loop around such an area and returns to the original perch or one quite nearby at the same height. These flights are usually two to three seconds long and, after landing, the open-wing display is immediately reassumed. Occasionally these flights are slightly longer and

involve a back-and-forth or figure-eight pattern. The fluttery aspect of these interperch flights is unlike any other ithomiine flight behavior, but most closely resembles the pre-oviposition flight characteristic of female ithomiines searching for foodplants. It seems likely that the purpose of this interperch flight is to waft the male scent emanating from the hairpencils into the air space near the perch. The regular pattern and limited extent of these flights serves to concentrate the scent over an area of about one square meter in a layer of air about 10-20 cm thick. (The actual size of the arc circumscribed tends to vary among species but is relatively consistent within any particular species). By distributing his scent within such an air space over a period of several minutes to an hour or more, a male apparently produces an olfactory disc, or courtship arena, with a powerful center that radiates the aphrodisiac pheromone (sensu Butler, 1967) in all directions by diffusion. Presumably, a passing receptive female that detected the odor would respond by orienting so as to fly through the arena and thus into the male's sphere of vision, at which point he would initiate pursuit.

Likewise, the species utilizing the "waiting" perches, or "patrol perches" as I have named them, also have an interperch flight component (patrol) to their behavior. Their interperch flights are stronger and less fluttery, but also circumscribe an area by a looping arc or by some crisscrossing pattern of flight. The area covered, however, is much larger than that of display perchers, and usually encompasses about 10 to 12 square meters. Most of the butterflies that enter this air space at approximately the perch level of the male will stimulate the male to pursuit. The function of the interperch flights is not well understood.

Most probably, they represent "seeking" or "patrolling" mate-locating behavior interspersed among longer stretches of "waiting" or "perching." If this is true, then the appellation "patrol perchers," implying both types of behavior, is appropriate. On two occasions I caught a male T. confusa after observing it for several minutes in patrol perching behavior. When captured, both males were redolent with the musty odor of vanilla, characteristic of this species. It may be, then, that patrol perchers also disseminate their scents during the patrol portion of their mate-locating behavior. A more likely possibility, however, is that both males had recently encountered a female, and that this stimulated the release of their scents (see below) which were still strong at the time of capture.

Species-specific Male Courtship Behaviors

At Limoncocha, display perching behavior in male ithomiines varies consistently from species to species. Pliske (1975c) noted that some species perch in shade while others generally perch in open sun where the understory is sparse. At Limoncocha, male ithomiines of different species not only show preferences in terms of lighting conditions (although none of the species perched in full sun) but also tend to consistently perch at particular levels of the forest understory, although these levels are probably influenced to some extent by light conditions. The fact that males of a given species display at a particular level in the forest is not unexpected since selection should favor males which perch at a level where conspecific females are most likely to be flying. As noted in the previous section, each species of ithomiine at Limoncocha

(for which enough observations are available) has a characteristic flight level in the forest. Although Papageorgis (1974) has shown that members of a particular mimetic subcomplex fly at a given stratum in the forest, it can be predicted that within a given subcomplex, selection will favor flight levels for each species such that the numbers of visually similar but non-conspecific females that fly past a displaying male will be minimized. In other words, we would expect the ithomiine members of a particular mimetic subcomplex to subdivide the flying space of that subcomplex. The preliminary evidence available suggests that this is indeed the case.

In Figure 36, the perch heights of 123 courting male ithomiines are plotted against the time of day that each observation was made. The observations were made throughout the entire study period and represent males from 24 species, including both display perchers and patrol perchers. The histogram in Figure 32, which includes all these observations and more, has already revealed that the peak of courtship activity occurs between 1100 and 1200 h. The scatter diagram of Figure 36 further shows that courtship activity most frequently occurs between 1.5 and 2.5 m above the ground, resulting in a cluster of courtship activity in time and space. By replotting these data for particular mimetic subcomplexes, we can test the hypothesis that the species within a subcomplex are subdividing the available courtship space and time.

In Figure 37, the display perch heights of males of four species of the yellow clear-wing mimetic subcomplex (see Chapter 7) are plotted for three of these species, and they do indeed seem to display at different levels, although there is considerable overlap. Napeogenes pharo displays primarily from 1.7 m to 2.4 m, Godyris zavaleta from 1.0 to

Figure 36. Perch Height versus Time of Day for all Courting Male Ithomiines.

Figure 37. Perch Height versus Time of Day for Display-Perching Male Ithomiines in the Yellow Clearwing Mimetic Subcomplex.

Figure 38. Perch Height versus Time of Day for Display-Perching Male Ithomiines in the Tiger Mimetic Complex.

Figure 39. Perch height versus Time of Day for Patrol-Perching Male Ithomiines in the Tiger Mimetic Complex.

to 1.7 m and Pteronymia sparsa consistently displays at about 0.7 m. There also appears to be some temporal separation in the displays of these three species, although again there is considerable overlap. N. pharo displays primarily between 1000 and 1200, G. zavaleta between 1200 and 1600 and P. sparsa between 1500 and 1600 h. Thus, although there is some overlap both spatially and temporally among these species, the combined effects of time of day and perch height appear to help isolate their courtship behaviors, thereby minimizing the number of interspecific encounters.

Likewise, display perching species with the black-yellow-orange tiger pattern would be expected to show similar separation of courtship activities. Data for six species (31 observations) are plotted in Figure 38, but the resulting pattern is less convincing. Four of the species (Hypothyris euclea, Napeogenes aethra, Napeogenes duessa, and Hyposcada kezia) seem clustered between 1.4 and 2.4 m although there are not enough data points for the last three species to determine if there is any temporal separation. Napeogenes apobsoleta appears to display just above this cluster, and Tithorea harmonia above them all, but these two species show very wide latitude in display perch levels.

A similar graph (Figure 39) has been prepared for six species of patrol perchers bearing the tiger pattern (36 observations). All of these species are in the same tribe (Mechanitini) and five belong to the same genus (Mechanitis), yet there seems to be no observable subdivision of perch height or time and all species exhibit a wide latitude of perch height. These species all perch in more open areas than do display perchers and the pursuit portion of their courtship lasts longer,

often culminating in several minutes of follow-the-leader type flight involving several individuals. The wide amplitude of these flights (1 to 10 m) and their extended length suggest that patrol perchers may rely on the pursuit portion of their courtship for determining conspecifics. Display perchers, on the other hand, perhaps because of the investment of time and energy in establishing a courtship arena, tend to rely on the pre-pursuit phase of courtship to filter out other species.

In addition to differences in display perch location, ithomiine species consistently differ in their posture and behavior during the displays to an extent that suggests that the display pattern is under species-specific genetic control. Table 12 lists the species at Limoncocha that have been observed in display perches and summarizes the postures of all species for which such data is available. There was a small amount of variation in the angle formed by the wings during perch display among a few species, but only G. zavaleta males consistently used a variety of angles (but all between 45° and 90°). The cant of the wings and position of the antennae were remarkably constant within a species. At the tribal level, both the cant of the wings and the angle of the wings (except in the Oleriini) were extremely uniform in expression. There was, however, considerable variation among individuals of all species in the degree to which the hairpencils were displayed during the display perch. The two Ithomia males seen displaying without exposing their hairpencils are probably not typical. Gilbert (1969) illustrated the full hemispherical splay of the hairpencils of I. heraldica during display perching in Costa Rica. Ithomia amarilla (Table 12) exhibited a very curious behavior (wing flutter) unlike any other species

Table 12. Postures of Male Ithomiines During Display Perch Courtship.

TRIBE AND SPECIES	AVG. PERCH HEIGHT (m)	AVG. TIME OF PERCH	ANGLE BETWEEN WINGS	CANT OF WINGS* FORE- WING	HIND- WING	DEGREE OF SPLAY OF EXPOSED HAIRPENCILS	TYPE OF ANTENNAL POSITION†
TITHOREINI							
<u>Tithorea harmonia</u>	6-7	1230	160°	--	--	--	3
NAPEOGENINI							
<u>Hypothyris euclea</u>	1.5	1400	200°	None	None	Tight brush or slightly splayed	1
<u>Hypothyris fulminans</u>	1.0	1530	220°	None	None	Medium splay	1
<u>Napeogenes aethra</u>	1.3	1230	210°	None	None	Medium splay	1
<u>Napeogenes apobsoleta</u>	2.7	1130	180°	None	None	Tight brush or slightly splayed	1
<u>Napeogenes duessa</u>	1.7	1200	190°	None	None	--	1
<u>Napeogenes pharo</u>	2.0	1200	200°	None	None	Full hemisphere	1
ITHOMIINI							
<u>Ithomia amarilla</u>	0.7	1200	Flutter	None	None	Not exposed (1 obs.)	5
<u>Ithomia derasa</u>	1.0	1500	250°	None	Slight	Not exposed (1 obs.)	1
OLERIINI							
<u>Aeria eurimedia</u>	1.3	1200	30°	Strong	Strong	Tight brush	2
<u>Hyposcada kezia</u>	2.0	1230	120°	Strong	Strong	Slightly splayed	--
<u>Oleria agarista</u>	0.3	1130	40°	Strong	Strong	--	--
<u>Oleria kena</u>	0.6	1400	150°	Strong	Strong	Tight brush or hemisphere	5

Table 12 - continued.

TRIBE AND SPECIES	AVG. PERCH HEIGHT	AVG. TIME OF PERCH	ANGLE BETWEEN WINGS	CANT OF WINGS*		DEGREE OF SPLAY OF EXPOSED HAIRPENCILS	TYPE OF ANTENNAL POSITION†
	(m)	FORE- WING		HIND- WING			
DIRCENNINI							
<u>Pteronymia sparsa</u>	0.6	1500	90°	Strong	Strong	Tight brush	5
GODYRIDINI							
<u>Godyris zavaleta</u>	1.3	1400	45-90°	Strong	Strong	Full hemisphere	6
<u>Hypoleria chrysodonia</u>	0.8	1500	50°	Slight	Slight	Tight brush to slight splay	6
<u>Pseudoscada timna</u>	1.3	1630	80°	None	Strong	Tight brush	5

Note: A dash in the body of the table indicates that no observations are available.

*The forewing (FW) and hindwing (HW) of a butterfly normally lie in the same plane. The courtship posture of some ithomiines involves the canting of the FW or HW or both. A canted FW means the costal margin of the FW is angled ventrally relative to the posterior margin. A canted HW means the anal margin of the HW is angled ventrally relative to the costal margin. When both the FW and HW are canted, they form an inverted V.

†Antennal position:

1. Antennae parallel, erect, perpendicular to body axis.
2. Antennae parallel, but pointing anteriorly at a 45°L above horizontal.
3. Antennae forming a 90°L, erect, perpendicular to body axis.
4. Antennae forming a 90°L, pointing anteriorly at a 45°L above horizontal.
5. Antennae forming a 90°L, horizontal, at a 45°L to body axis.
6. Antennae forming a 180°L, horizontal, perpendicular to body axis.

observed. This male, perched in the center of a large Heliconia leaf, was rapidly fluttering his wings from a vertical position to some 10-20° above horizontal. The fluttering continued, with only an occasional split-second stop, for over five minutes before it began to decrease in speed and amplitude and the stops inbetween gained in duration. After ten minutes the stops were much longer than the fluttering periods. Two minutes later the butterfly made a two-second looping flight, then returned to his original perch, and did not display or flutter again.

Perhaps more interesting than the species differences in anatomical orientation are the species differences in flight and perch dynamics. Figure 40 presents a sequence of perches and interperch flights (ethnogram) for a male of each of eight display-perching species. The differences in behavior of these eight species are quite pronounced. The perches and interperch flights of T. harmonia are of approximately equal length. (The relatively long interperch flights of T. harmonia are related to the type of scent dissemination that occurs during them. A male was observed on several occasions to use a 7 m perch on a particular tree at Site 4. After display perching on a favorite leaf, the male fluttered around the tree several times, weaving in and out of the lianous vegetation surrounding the trunk--apparently concentrating his scent--before returning to his original perch.) Hypothyris euclea has a series of short perches broken by relatively longer flights until a very long perch with wing pumping is made. The interperch flights of the remainder of the species vary in length but are shorter than the perches themselves. Not only does each species have a characteristic length of display perch and length of interperch flight, but the species also vary in the

Figure 40. Ethnograms of Eight Species of Display-Perching Ithomiine Males.

Each set of lines per species represents a continuous observation of a single individual.

— perching
~~~~~ flying
~~~~~ flying initiated by a passing butterfly
— wing pumping
— orientation shifts of 90°
— momentary hiatus in observation
— termination of observation

presence and length of wing pumping behavior and in the presence and frequency of body rotations during the display. More detailed observations are planned for the future to collect enough data on these and other species to quantify these apparently species-specific differences in behavior.

Species-specific differences apparently occur in patrol perchers as well. Detailed observations are available for only three species, but all species observed in patrol perching behavior are listed in Table 13, which summarizes their perch postures. Ethnograms similar to those drawn for display-perchers have been constructed for three patrol perchers and are presented in Figure 41. In general, it can be seen that the ratio of the length of the perch to the length of the interperch flight is much greater for patrol perchers than for display perchers (Figure 40). This is to be expected since display perchers must fly relatively often in order to establish a pheromone-saturated display arena.

Figure 41 shows that Mechanitis isthmia and M. messenoides are quite similar in patrol perch behavior, although M. isthmia in general has more frequent interperch flights. Both Mechanitis species tend to assume patrol perches in open areas or along trails, while Thyridia confusa tends to perch in more dense understory. T. confusa also has a characteristic wing flexing behavior in which the wings are lowered slowly until they form an angle of nearly 180° and then are quickly returned to their position over the back. Although Pliske (1975c) observed this same species occasionally perching with wings held open at a 60° angle at Rancho Grande, Venezuela, individuals at Limoncocha were never observed with their wings held open. The hairpencils do not appear to be exposed

Table 13. Postures of Male Ithomiines During Patrol Perch Courtship.

| TRIBE AND SPECIES | AVG.
PERCH
HEIGHT
(m) | AVG.
TIME
OF
PERCH | ANGLE
BETWEEN
WINGS | CANT OF WINGS* | | DEGREE OF SPLAY
OF EXPOSED
HAIRPENCILS | TYPE OF
ANTENNAL
POSITION† |
|-------------------------------|--------------------------------|-----------------------------|---------------------------|----------------|---------------|--|----------------------------------|
| | | | | FORE-
WING | HIND-
WING | | |
| MECHANITINI | | | | | | | |
| <u>Forbestra truncata</u> | 1.2 | 1200 | 0° | None | None | Not exposed | 4 |
| <u>Mechanitis egaensis</u> | 1.0 | 1330 | 0° | None | None | Not exposed | -- |
| <u>Mechanitis isthmia</u> | 1.6 | 1130 | 0° | None | None | Not exposed | 4 |
| <u>Mechanitis lysimnia</u> | 1.5 | 1200 | 0° | None | None | Not exposed | 4 |
| <u>Mechanitis mazaeus</u> | 1.6 | 1200 | 0° | None | None | Not exposed | 4 |
| <u>Mechanitis messenoides</u> | 1.5 | 1130 | 0° | None | None | Not exposed | 4 |
| GODYRIDINI | | | | | | | |
| <u>Thyridia confusa</u> | 2.0 | 1200 | 0° | None | None | Not exposed | 4 |

Note: A dash in the body of the table indicates that no observations are available.

*The forewing (FW) and hindwing (HW) of a butterfly normally lie in the same plane. The courtship posture of some ithomiines involves the canting of the FW or HW or both. A canted FW means the costal margin of the FW is angled ventrally relative to the posterior margin. A canted HW means the anal margin of the HW is angled ventrally relative to the costal margin. When both the FW and HW are canted, they form an inverted V.

- †Antennal position:
1. Antennae parallel, erect, perpendicular to body axis.
 2. Antennae parallel, but pointing anteriorly at a 45°∠ above horizontal.
 3. Antennae forming a 90°∠, erect, perpendicular to body axis.
 4. Antennae forming a 90°∠, pointing anteriorly at a 45°∠ above horizontal.
 5. Antennae forming a 90°∠, horizontal, at a 45°∠ to body axis.
 6. Antennae forming a 180°∠, horizontal, perpendicular to body axis.

Figure 41. Ethnograms of Three Species of Patrol-Perching Ithomiine Males.

Each set of lines per species represents a continuous observation of a single individual.

— perching
 ~~~~~ flying
 o flying initiated by a passing butterfly
 Δ flying initiated by observer's movements
 ● a single flex of the wings, down slowly, up rapidly
 // momentary hiatus in observation
 — termination of observation

Mechanitis
isthmia

Mechanitis
messenoides

Thyridia
confusa

TIME IN SECONDS

during wing flexing, so the function of this behavior remains unknown.

M. isthmia, M. messenoides, and M. mazaeus were also observed to flex their wings occasionally during patrol perching, but it was more frequent and regular in Thyridia confusa.

Pursuit Behavior of Courting Males

Up to this point the discussion of courtship has been concerned only with the mate-locating behavior of male ithomiines. The next step in the courtship sequence is the male's pursuit of the butterfly that--for whatever reason--has flown close by the male's perch and thereby stimulated him to pursuit. Most of the pursuit encounters I observed were between two different species and thus the male's pursuit was rapidly terminated. When initiating pursuit, both display perchers and patrol perchers fly directly and rapidly toward the potential mate (intruder). Upon reaching the intruder, the courting male and the intruder usually "fly around each other" for a few seconds, after which the intruder resumes its normal flight and the male returns to his former perch (if the intruder is of another species) or continues his pursuit (if the intruder is a conspecific female, or sometimes if it is a conspecific male). From this point, display perchers and patrol perchers appear to differ in their pursuit behavior.

A display perch male* that continues the pursuit does so with a unique mode of flight that involves the rapid flutter of the wings through

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* Observations cover Aeria eurimedia, Godyris zavaleta, Hypoleria chrysonia, Hyposcada kezia, Hypothyris euclea, H. fulminans, Ithomia amarilla, I. derasa, Napeogenes aethra, N. apobsoleta, N. duessa, N. pharo, Oleria agarista, O. kena, Pteronymia sparsa, Pseudoscada timna, and Tithorea harmonia.

a shallow arc. He generally flies 15 to 20 cm above the pursued butterfly and about 5 cm behind it. The difference between the fluttery flight of the pursuing male and the normal flight of the pursued butterfly is quite dramatic at this stage, the more so because the pursuing male usually pulses his flight downward every few seconds, coming within 5 cm of the pursued butterfly. I assume the combination of the rapid fluttering of the wings and the pulsating nature of the flight propel the male's aphrodisiac pheromones down over the female. If the pursued butterfly is a male or a nonreceptive female, it generally continues flying in its original direction and may even increase the speed of its flight. A receptive female, however, lands on a leaf with her wings together over her back while the male continues his rapid and pulsating flight above her, gradually lowering himself toward her. Unfortunately, I have never seen an entire courtship carried to completion. Most of the females I have seen land at this point generally fly off again as the male lowers himself over her during the hovering flight. On two occasions, however, a Napeogenes pharo female remained perched while the male landed of the same leaf. As he walked up to her, curling his abdomen forward, she flew away and he resumed pursuit immediately. Apparently this sequence may be repeated several times before copulation is effected.

Pliske (1975c) reported somewhat different sequences for four species (Pteronymia nubivaga, P. beebei, Aeria elodina and Ithomia iphianassa) of display-perching ithomiines in Venezuela. Males of these species fly above and behind females, chasing them with rapid, erratic flight that includes periodic darting pounces toward the females's dorsum. Although no heterosexual encounters were observed to conclusion, Pliske did see the

termination of a male-male encounter between P. nubivaga and Hymenitis andromica at close range. While P. nubivaga was chasing H. andromica, the latter male slowed his flight and canted his hindwings backward displaying the hairpencils, whereupon the pursuing P. nubivaga male ceased the chase and returned to his perch. Pliske (1975c) has presented evidence that a lactone component of the male hairpencil pheromone serves as an allomone repellent to conspecific males and males of other lactone producing species. The lactone (derived from compounds obtained while feeding at PA plants) apparently facilitates male recognition of other males and allows males to terminate male-male intra- and inter-specific courtship pursuits, as described above for P. nubivaga and H. andromica. Even so, physical contact between males may still occur. Pliske (1975c) recorded three instances of male-male contact for T. confusa and one for Ithomia iphianassa. In these curiously violent encounters, a display perching male pounced upon a conspecific male, clutching the intruder with his legs, after which the pair fell to the ground and separated.

Observations at Limoncocha on pursuits by patrol perch males include only Mechanitis isthmia, M. lysimnia, and M. messenoides. Unfortunately, no pursuit encounters were observed for Thyridia confusa. A patrol perch male may maintain pursuit of a co-mimic of another species or of a conspecific male for 30 seconds or more before returning to a perch. For example, I caught the following three pairs of species flying within 10 m of each other within half an hour: Mechanitis messenoides and M. lysimnia, M. lysimnia and M. lysimnia, and M. lysimnia and Napeogenes apobsoleta. All six individuals were males. On several occasions I have

watched as many as ten tiger ithomiines mutually pursuing one another at heights of 5 to 8 meters in a sunspeckled open spot in the forest (Nature Trail). Pursuits of conspecific females by males generally last longer and lead to the next stage in the courtship sequence. On two occasions I watched a courting pair of M. messenoides flying 2-3 m above the ground. In each case the male was flying about 30 cm above and 10 cm behind the female. The male's flight was not as agitated or as fluttery as was the flight observed in display perching males engaged in pursuit, but it did include the pulsing component that periodically brought the male close to the female.

Pliske (1975c) has recorded similar observations on heterosexual encounters for M. isthmia veritabilis and M. polymnia doryssus in Venezuela, although the males he observed had their hairpencils exposed and erected and were flying just in front of the females instead of just behind them. This apparently resulted in an airstream (and, presumably, pheromones) passing down over the female from the male's beating wings. Instead of the pulsing movements I observed, Pliske reported that the males make darting pounces onto the female's dorsum, as did the display perchers he observed. Pliske also found this same darting and pouncing behavior in males of Thyridia confusa psamathe (same as the Limoncocha subspecies), which climaxed in the male clutching the female's head and thorax with his legs. Once this contact was made, the pair either fell to the ground, where copulation was effected, or else the male achieved copulation while the pair was still in the air.

Function of the Display Perch

Pliske (1975c) has suggested that the lactone component of ithomiine hairpencil pheromone functions not only to terminate male-male pursuits as described above, but, when released by display-perching males, also serves as a territorial allomone that repels other males. Pliske reasons that by releasing such an allomone during a display perch, a male ithomiine reduces the probability that another male of any species will enter what I have called the courtship arena. The result, therefore, is that since males are kept out, most of those individuals entering the courtship arena will be females.

As evidence for this interpretation, Pliske cited his findings that the attractiveness of dried Heliotropium indicum baits to male ithomiines was greatly reduced by placing the lactone component of the ithomiine hairpencils in competition with it. Even though this highly artificial experiment provides convincing evidence that the lactone can be repellent to conspecific and other males, there is no evidence that the lactone is being released during the display perch for the purpose of repelling other males. Indeed, Pliske admits he has never observed a male exhibit avoidance behavior upon approaching another male engaged in a display perch.

It seems much more reasonable to me that a male ithomiine in a display perch is releasing a female-attracting or aphrodisiac pheromone for the purpose of "enticing" passing conspecific females into his courtship arena. In this manner the male increases the probability that a butterfly that enters his arena will be a conspecific female--and not just any female, as the male-repellant theory necessitates. Once while watching a

male Godyris zavaleta in a display perch, I saw three different G. zavaleta females enter the male's courtship arena from three different compass directions, two of them apparently changing their course of flight to do so. (G. zavaleta is sexually dimorphic and the sexes are thus easy to distinguish). The male chased all three of them, but, as none of them landed, he returned to his original perch after each encounter. Although such observations imply the existence of a female-assembling function of male display perching, behavioral experiments are needed to determine the exact nature and purpose of this behavior. Perhaps the display-perching male is releasing both the lactone repellent and a female-assembling aphrodisiac simultaneously to maximize his probability of a conspecific heterosexual encounter.

Mating

Because mating butterflies tend to remain motionless, they are not often observed and information concerning the behavior of in copula pairs is scant (Miller and Clench, 1968). During the course of this study, a total of only 18 mated pairs representing 6 species of ithomiines was observed in the field. These observations, grouped according to time of day, are presented as a histogram in Figure 42. The specific time of day and perch height for each pair are given in Table 14.

Based on this small sample, copulation appears to peak between 1200 and 1300 h; just after the peak occurrence of courtship activity at 1100-1200 h (Figure 32). This peak in copulatory activity closely parallels the general pattern of mating times of butterflies of the temperate zone

Figure 42. Mating Activity of Ithomines.

Table 14. Mating Pairs of Ithomiines Observed at Limoncocha.

TRIBE AND SPECIES	DATE	PERCH OF (m)	TIME OF MATING	DURATION OF COPULATION (minutes)	SEX DURING FLIGHT	CONDITION OF ♂	CONDITION OF ♀	REMARKS
MECHANITINI								
<u>Forbestra truncata</u>	12OCT74	1.7	1130	20*	♂	F-	F	♀ held wings open while ♂ flew. Length of flights about 2 m.
	22APR74	1.0	1340	1*	♀	--	--	
	04OCT74	1.0	1240	10*	♀	I	F-	
	24OCT74	1.3	1015	15*	♀	F	F+	
	29APR74	--	1155	1*	--	I	F	
"	12NOV74	--	1230	1*	--	I-	F	
"	12NOV74	--	1300	1*	--	F	F+	
"	29SEP74	2.7	1250	1*	--	I	--	
	06APR74	1.3	1515	1*	--	--	--	
<u>Mechanitis isthmia</u>	03NOV74	1.0	1500	15*	--	--	--	
MECHANITIS lysimnia								
	23OCT74	1.2	1235	5*	--	F	I	♂ uppermost of leaf.
	12NOV74	---	1230	1*	--	I	F+	
	12NOV74	1.7	1135	5*	(♂)	I	I	
OLERIINI								
<u>Oleria agarista</u>	10NOV73	0.5	1200	10*	(♀)	F+	F+	♀ uppermost on leaf.
<u>Oleria kena</u>	24JUN74	0.8	1515	35*	(♂)	F	F	♂ uppermost on leaf.
GODYRIDINI								
<u>Thyridia confusa</u>	29APR74	--	1205	145	--	W	F	Captured at 1205, held in glass- sine envelope; still in copula when released at 1430
	12NOV74	2.4	1120	30*	♂	F-	F-	
	15OCT74	--	1715	--	--	F	I	

* Mating pair separated after capture, sometimes in the net, but usually not until sometime after being placed together in a glassine envelope.

+ Parentheses indicate that the active sex was deduced from the perch orientation, not by the observation of the pair in flight.

(Miller and Clench, 1968). Most of the pairs at Limoncocha were discovered perched at a height compatible with the flight level characteristic of their species (Table 14). Some of the pairs were observed or photographed for a few minutes before being collected and the time that elapsed for each pair before capture is given in Table 14. Because the duration of copulation in most butterflies is measured in hours instead of minutes (Shields and Emmel, 1973), the only time of interest in Table 14 is that of 145 minutes of T. confusa. This pair was caught during a Site 4 sampling period and kept, in copula, in a glassine envelope for over two hours before the two butterflies were marked and released. Even with all this handling they stayed joined and even "feigned death" (see Chapter 7) simultaneously at the time of their release. After marking, I laid the pair on a leaf where the two butterflies remained lying on their sides for over five minutes before flying away together.

Sperm Precedence

Very little work has been done to elucidate the behavior or the mechanics of butterfly copulation, and it remains unknown why in copula pairs remain in such a seemingly vulnerable situation for long periods of time. Because the sperm is transferred to the female in a spermatophore, it has been suggested that the long mating time is necessary for spermatophore formation or transfer (Shields and Emmel, 1973), although Shields (1967) has found that spermatophore transfer can take place in less than ten minutes in at least two species of North American butterflies. Retnakaran (1974) has recently shown that the phenomenon of

sperm precedence in the spruce budworm (Choristoneura fumiferana) depends on the time interval between successive matings. In C. fumiferana, and presumably other lepidoptera, the spermatophore hardens about 30 minutes after transfer to the female. The sperm, however, do not remain in the spermatophore, but migrate from it down the ductus seminalis (and apparently across the oviduct) into the seminal receptacle. If a female C. fumiferana mates a second time before the sperm from the first mating have begun migrating, then the first spermatophore is displaced by the second, and it is only the sperm from the latter that are able to colonize the seminal receptacle. If the second mating occurs after the sperm from the first mating have already migrated and filled the seminal receptacle, then there is apparently no room left in the receptacle for the sperm from the second spermatophore. In this case sperm precedence has occurred and all offspring are fertilized by sperm from the first mating only. If the second mating occurs after the start, but before the completion, of the migration of sperm from the first mating, then some of the sperm from both matings are able to enter the seminal vesicle and subsequently fertilize eggs.

Here, then, is a possible explanation for the long mating times in butterflies. Perhaps the spermatophore is transferred early as Shields' (1967) findings indicate, but if the mechanism of sperm precedence is the same for butterflies as for the spruce budworm, it would behoove the male butterfly to remain in copula with the female until after all his sperm have migrated to the seminal receptacle. By preventing another male from mating with his partner before the transfer of sperm from the spermatophore to the seminal receptacle is completed, he protects his investment by insuring that sperm precedence will operate.

Multiple Matings

While the sperm received from a single mating are apparently enough to fertilize all the eggs of a female butterfly in the temperate zone (Labine, 1966), they may be inadequate to fertilize all the eggs of a tropical female butterfly--not because of insufficient numbers, but because of insufficient life span. Female Heliconius, and presumably female ithomiines, may live for several months over which time they lay eggs at a low (by temperate standards), but consistent daily rate (Crane, 1955; Ehrlich and Gilbert, 1973; Gilbert, 1972). If sperm are able to survive in the seminal receptacle for only a few days, but the female lays eggs over a period of several weeks or longer, she may require multiple inseminations. This seems to be the case for most ithomiines because females often mate several times. Preliminary dissections have revealed that the majority of wild-caught females (except for very fresh (F+) ones) have mated at least twice, and many have mated three to five times. One fresh (F-) female of Hypothyris mamercus was found to be carrying six spermatophores. By contrast, the average number of matings per mated female in most temperate zone butterflies appears to be between one and two (Scott, 1972). It is doubtful that female ithomiines would engage in so many mating sequences if they did not derive some selective benefit from doing so. If it is true that sperm held in the seminal receptacle have a short life span, then one benefit becomes obvious. It is also possible that multiple mating serves a nutritive function, allowing the female to lay more eggs. Proteinaceous components of the spermatophores may be broken down by proteolytic enzymes supplying

the female with amino acids available for egg production (Scott, 1972). Male ithomiines are apparently reproductively active throughout most of their long life span as well. Of the 15 males found in copula for which wing condition was recorded, over 50% (8) were either intermediate (I) or worn (W). Many of the males observed in display perch courtship were also intermediate or worn in condition. T. C. Emmel (personal communication) has found spermatogenesis proceeding in male ithomiines of all ages. Males of Heliconius ethilla up to 4 months old have been shown to successfully participate in courtship and mating that resulted in normal adult offspring (Ehrlich and Gilbert, 1973).

Some male butterflies are known to form a sphragis or plug during copulation that blocks the female's ostium bursae after mating, preventing other males from inseminating her. Sphragis were not found in any Limoncocha ithomiines, but in T. confusa the neck (elongated portion) of the spermatophore consistently protruded about 5 mm beyond the ostium bursae of mated females. In addition, a dried mucous-like substance was usually present on the chitinous genital plate of mated females, although never of an amount or nature to form a sphragis. These preliminary observations suggest that the postcopulatory position of the spermatophore in T. confusa females may thwart a subsequent mating attempt by a second male for at least a few hours or days after an insemination. The position of the spermatophore neck does not totally prevent rematings, however, as evidenced by a dissected female (I) found to be carrying six spermatophores. The occurrence of a large sphragis in females is usually associated with a lack of elaborate courtship in conspecific males, many of which "capture" females instead

of courting them (Scott, 1972). Although the plugging effect of the spermatophore neck in T. confusa females is apparently not great, it is interesting that Pliske (1975c) has described "mating by capture" in this species in Venezuela (see above). The presence of hairpencils on some T. confusa females (see above) adds another curious, and unsolved, dimension to the reproductive biology of this species.

Preliminary observations on spermatophore morphology revealed that spermatophore shapes, especially of the neck portion, are quite diverse among Limoncocha species of Ithomiinae. Within a species, however, the shapes are consistent, and the neck, whether straight, curved, or curly-cued, is apparently of the proper length and configuration to end just opposite the ductus seminalis. Detailed studies of spermatophore formation and morphology and of the mechanics of sperm transfer are planned for the Ithomiinae.

Carrying Pair Behavior

Although normally motionless, mating butterflies will sometimes fly if disturbed by wind, other butterflies, collectors, etc., and Miller and Clench (1968) have pointed out the regularity within taxonomic groups of the sex which is the active partner during flight. For instance, in the Danaidae, it is always the male of a copulating pair that flies, carrying the female in tandem. In the Nymphalidae, females predominate as the active sex, but in some species, either sex may take the lead. These are the two families most closely related to the Ithomiidae and thus it would be of interest to see if the latter show any regularity

in carrying pair behavior. Unfortunately, there appear to be no published behavioral data on mating pairs of ithomiines despite exhaustive reviews of the literature (Scott, 1972; Shields and Emmel, 1973). About half of the 18 ithomiine pairs I saw in copula were observed to fly, usually because I disturbed them while moving closer for observations. The generally slow and labored flights of these pairs were always for short distances (rarely more than 2 m), and usually to perches of heights about the same level as the original. Because of the great similarity between the sexes of most ithomiines it was difficult to determine the active partner of a flying pair, but I was able to do so for four of the nine observed pairs of Forbestra truncata. In two pairs the female flew carrying the male behind; in the other two, it was the male that flew with the female in tandem. These observations parallel those of F. M. Brown (cited in Miller and Clench, 1968) on Speyeria nokomis nokomis (Edwards) in Colorado. Of the several pairs Brown observed, the male took the lead in some and the female in others. One of the F. truncata pairs (1040 h in Table 14) was photographed in flight and the resulting slide shows that the tandem female was holding her wings open at a 180° angle while the male flew. This would seem to assist the male in flight by providing increased lift, but whether this is the normal wing orientation of the tandem partner in flying mated pairs is not known. For one of the pairs of T. confusa it was definitely established that the male flew with the female in tandem. In this case the male (Left FW = 47.5 mm) was slightly larger than the female (LFW = 46.0 mm). In the one case for which wing length was recorded in F. truncata, however, the smaller male (LFW = 32.5 mm) carried the larger female (35.0 mm).

For three other pairs, the active sex has been deduced from the orientation of the butterflies during perching. In one pair each of Oleria kēna and M. lysimnia, the male was uppermost on a near vertical leaf. Assuming that the pair flew to the perch, it seems likely that the male was the active partner. The pair of Oleria agarista was first observed with the female clinging to a leaf and the male dangling below, unsupported except for the attachment to the female's abdomen. After a minute or two, the female walked forward on the leaf and the male was able to gain purchase on the leaf and climb up beside the female. After this, the pair shifted positions until they faced in opposite directions, the normal posture of all ithomiine mated pairs observed. Again, the most likely interpretation is that the individual uppermost on the leaf (female) was the active partner.

Thus, the carrying pair behavior of the Ithomiinae, based on the few examples given here, most closely approximates the observations available for temperate zone Nymphalidae, in which either sex may be the active partner (Miller and Clench, 1968).

Oviposition

The third component of reproductive behavior in butterflies is the laying of eggs by mated females. Like courtship and mating, oviposition in ithomiines may occur over much of the day but is characterized by a period of peak activity. Figure 43 summarizes the 46 observed oviposition events for which time of day was recorded. These observations, which

Figure 43. Oviposition Activity of Female Ithomiines.

cover 22 species, occurred mostly in the afternoon and reveal a peak of activity between 1400 and 1500 h. Thus, the daily sequence of events in the reproductive activity of the ithomiine community parallels that which occurs in the life of an individual female; first courtship, followed by mating, and finally oviposition. This diel sequence is illustrated graphically in Figure 44, in which the number of observations of courtship, mating, and oviposition during each hour of the day is expressed as a percentage of the total number of observations of that behavior. From this graph it is seen that the peak periods of activity for courtship, mating, and oviposition behavior represent about 35, 40 and 25% respectively of the daily totals.

The reasons for an afternoon peak in oviposition activity are not clear. Since the number of days that a female engages in mating is relatively small compared to the number of days over which she lays eggs, it seems unlikely that afternoon oviposition represents a delay caused by prior mating activity. Perhaps it represents a delay resulting from morning feeding activity. As mentioned earlier, female ithomiines derive most of their nourishment from detritus-type food items (e.g., bird droppings, falling pieces of fruit, etc.) which usually become available in the morning as a result of early feeding activity by birds. Another possibility is that, for unknown reasons, the afternoon is a better, or safer, time for laying eggs. That the afternoon may be a safer time for oviposition is suggested by the behavior of females of the genus Mechanitis. Female M. isthmia, M. lysimnia, and M. messenoides predominately oviposit on solanaceous plants characteristic of sunny second growth areas (see

Figure 44. Summary of Ithomiine Reproductive Activities.

○	Courtship	N = 130 observations (26 species).
□	Mating	N = 18 observations (6 species).
△	Oviposition	N = 46 observations (22 species).

Tables 18 and 5). Searching for a suitable larval foodplant on which to lay eggs thus brings a female out of the forest shade and into the open, where the likelihood of predation may be higher than in the forest. Perhaps by ovipositing in the late afternoon (most of the records after 1500 in Figure 43 are for species of Mechanitis), Mechanitis females avoid a morning peak of avian predation. For whatever the reason, M. isthmia females carry this late afternoon oviposition to the extreme. I observed several females of this species initiating oviposition after 1700 h, and one (described earlier) began as late as 1810 h.

Oviposition Strategies

The distribution of a female's reproductive effort over space and time, or oviposition strategy, is the product of many interacting ecological and evolutionary factors. Labine (1966), in one of the first comprehensive discussions of oviposition strategy, outlined the major components of variation in oviposition patterns of butterflies.

1. Number of eggs laid during female's lifetime
2. Egg size
3. Onset of oviposition
4. Rate of oviposition
5. Cluster size

The first two components define the total reproductive effort of a female butterfly, while the last three are concerned with the distribution of the effort over space and time. The degree to which these five

parameters vary among butterfly species is very great, and is influenced by the interaction of many selective forces, including parasitism, predation, competition, and the range of mechanical and chemical defenses employed by potential larval foodplants. In addition to the parameters listed by Labine, then, the study of oviposition strategies should include: (6) the number of foodplants utilized by a species population in a given locality (i.e., the degree of foodplant specificity), (7) the location of the eggs on the foodplant, (8) the behavioral sequence that establishes the identity and suitability of the foodplant and leads to placement of the eggs on the plant, and (9) the genetic and environmental controls of foodplant tolerances in larvae and adult females.

A thorough understanding of the ecological and evolutionary consequences of the oviposition strategies employed by the Ithomiinae, which show considerable variation in most of the parameters listed above, must wait the collection of much more detailed information. There is, however, enough available data to provide estimates of the ranges of variation of many oviposition parameters and to formulate some tentative generalities. All of the published information known to me plus the data obtained during the present study has been summarized in Table 15 and will form the basis of the following discussion.

The total number of eggs laid in a lifetime by a female ithomiine is not known for any species. In the absence of observations on oviposition rates of ithomiine females over long periods of time, such as those obtained for Heliconius in insectaries (Crane, 1955), we must turn

Table 15. Summary of Oviposition Parameters for Ithomiine Butterflies.

TRIBE AND SPECIES	EGG SIZE (mm ³)	MEAN CLUSTER SIZE (N)	RANGE OF CLUSTER SIZE	LOCATION OF IMMATURES ON LEAF* EGGS LARVAE	MODE OF OVI- POSITION SEQUENCE†	# OF FOOD- PLANTS UTILIZED	LOCALITY‡	SOURCE
TITHOREINI								
<u>Tithorea harmonia megara</u> (Latrielle)	--	1		V [V]	--	1	TR	9
MELINAEINI								
<u>Melinaea menophilus menophilus</u> (Hewitson)	0.98	1		V V	C	1	EC(1)	1
MECHANITINI								
<u>Forbestra truncata</u> <u>juntana</u> (Haensch)	0.83	5(7)	4-9	D V	A	1	EC(1)	1
<u>Mechanitis isthmia eurydice</u> Haensch	--	~40(1)	--	D V (G)	--	--	PR(1)	7
<u>Mechanitis isthmia eurydice</u> Haensch	0.67	31(54)	10-59	D V (G)	A	5	EC(1)	1
<u>Mechanitis isthmia isthmia</u> Bates	--	--	[40-60]	D V (G)	A	1	CR(1)	8
<u>Mechanitis isthmia isthmia</u> <u>veritabilis</u> Butler	--	--	12-25	D [V](G)	A	--	TR	9
<u>Mechanitis lysimnia elisa</u> (Guér.-Mén.)	0.67	9(13)	3-21	D V (G)	A	3	EC(1)	1
<u>Mechanitis lysimnia lysimnia</u> (Fabricius)	--	--	10-20	D V (G)	--	[>1]	BR(1)	3
<u>Mechanitis mazaeus mazaeus</u> Hewitson	0.73	23(4)	10-33	D V (G)	A	1	EC(1)	1
<u>Mechanitis menapis mantineus</u> Hewitson	0.66	1		D V (G)	A	--	EC(2)	2
<u>Mechanitis menapis satura</u> Godman	--	--	[40-60]	V V [G]	--	1	CR(3)	8
<u>Mechanitis messenoides</u> C. & R. Felder	0.92	8(6)	6-12	D V (G)	A	2	EC(1)	1
<u>Mechanitis polymnia doryssus</u> Bates	--	--	[40-60]	D V [G]	[A]	2	CR(3)	8
<u>Mechanitis polymnia polymnia</u> (Linné)	--	ca. 25	--	D V (G)	A	1	SU	10

Table 15 - continued.

TRIBE AND SPECIES	EGG SIZE (mm ³)	MEAN CLUSTER SIZE (N)	RANGE OF CLUSTER SIZE	LOCATION OF IMMATURES ON LEAF*	MODE OF ♀ OVI- POSITION SEQUENCE†	# OF FOOD- PLANTS UTILIZED	LOCALITY ‡	SOURCE
<u>Scada batesi</u> Haensch	0.33	1		V V	[C or D]	1	EC(1)	1
<u>Xanthocleis paidii</u> ino (C. & R. Felder)	0.23	1		V V	B	1	EC(1)	1
NAPEOGENINI								
<u>Hypothyris daeta</u> (Boisduval)	--	1		V V	D	1	BR(1)	3,4
<u>Hypothyris euclea leucania</u> (Bates)	[0.15- 0.50]	75 120	--	V V (G) V V (G)	[C or D] [C or D]	1 1	CR(2) CR(3)	8 8
<u>Hypothyris euclea peruviana</u> (Staudinger)	0.13	1		V V	C	1	EC(1)	1
<u>Hypothyris fluona berna</u> (Haensch)	0.32	1		V V	[C or D]	1	EC(1)	1
<u>Hypothyris fulminans satura</u> Haensch	0.37	1		V V	D	1	EC(1)	1
<u>Napeogenes corena caucayaensis</u> Fox & Real	0.20	1		V V	[C or D]	1	EC(1)	1
<u>Napeogenes pharo avila</u> Haensch	0.21	1		V V	C	1	EC(1)	1
<u>Placidula euryanassa</u> C. & R. Felder	--	100(1)	--	V [V][G]	[C or D]	1	BR(1)	3,4
ITHOMIINI								
<u>Ithomia agnosia agnosia</u> Hewitson	0.20	1		V V	C	1	EC(1)	1
<u>Ithomia amarilla</u> Haensch	0.46	1		V V	[C or D]	1	EC(1)	1
<u>Ithomia derasa travella</u> Haensch	0.27	1		V V	[C or D]	1	EC(1)	1
<u>Ithomia drymo</u> Hübner	--	1		V V	D	1	BR(1)	3

Table 15 - continued.

TRIBE AND SPECIES	EGG SIZE (mm)	MEAN CLUSTER SIZE (N)	RANGE OF CLUSTER SIZE	LOCATION OF IMMATURES ON LEAF*	MODE OF 9 OVI- POSITION SEQUENCE†	# OF FOOD- PLANTS UTILIZED	LOCALITY‡	SOURCE
OLERIINI								
<u>Hypocada virginiana</u> <u>evanides</u> Haensch	[.5-1.5]	1		--	--	--	CR(2)	8
<u>Oleria agariata</u> <u>agariata</u> (C. & R. Felder)	0.66	1		V V	C	4	EC(1)	1
<u>Oleria zelica</u> <u>pagasa</u> (Druce)	1.15	1		V V	C	1	CR(4)	13
DIRCENNINI								
<u>Ceratinia poecila</u> <u>poecila</u> (Bates)	0.14	1		V V	C	1	EC(1)	1
<u>Ceraticscada canaria</u> <u>Brown & d'Almeida</u>	0.20	1		V V	--	1	BR(3)	6
<u>Dircenna klugi</u> (Geyer)	~0.15	1		--	--	2	CR(3)	8
<u>Dircenna loreta</u> <u>Haensch</u>	0.15	1		V V	C	1	EC(1)	1
<u>Dircenna olyras</u> <u>lonera</u> <u>Butler & Druce</u>	~0.15	1		--	--	1	CR(3)	8
<u>Dircenna relata</u> <u>Butler & Druce</u>	0.20	--	1-14	V V	D	1	CR(5)	12
<u>Episcada clausina</u> (Hewitson)	--	~17	--	V V	--	sev.	BR(1)	3
<u>Prittwitzia hymenaea</u> (Prittwitz)	--	1		V V	--	[1]	BR(1)	3
<u>Pteronymia eurites</u> <u>Cramer</u>	--	1		V V	--	sev.	BR(1)	3
<u>Pteronymia notilla</u> <u>Butler & Druce</u>	0.94	1	1-3	V V	[C or D]	2	CR(4)	14
<u>Pteronymia sparsa</u> <u>Haensch</u>	0.16	1		V V	C	1	EC(1)	1
<u>Pteronymia sylvo</u> <u>Hübner</u>	--	1		V V	--	sev.	BR(1)	3
X-1 (genus and species unknown) (5051)	--	1		V V	--	1	EC(1)	1

Table 15 - continued.

TRIBE AND SPECIES	EGG SIZE (mm)	MEAN CLUSTER SIZE (N)	RANGE OF CLUSTER SIZE	LOCATION OF IMMATURES ON LEAF*	MODE OF ♀ OVI- POSITION SEQUENCE†	# OF FOOD- PLANTS UTILIZED	LOCALITY‡	SOURCE
GODYRIDINI								
<u>Epityches eupompe</u> Hübner	--	1		V V	--	1	BR(1)	3,4
<u>Godyris zavaleta amaretta</u> (Haensch)	0.15	1		V V	B	2	EC(1)	1
<u>Godyris zavaleta caesiopicta</u> (Niepelt)	--	1		V V	B	1	CR(4)	15
<u>Heterosais edessa nephele</u> (Bates)	0.23	1		V V	--	1	EC(1)	1
<u>Heterosais edessa nephele</u> (Bates)	--	1		V V	--	1	BR(1)	3
<u>Hymenitis nero</u> (Hewitson)	0.29	1		D D	A	1	CR(4)	11
<u>Hypoleria ocalea</u> (Hewitson)	--	1		V V	--	--	TR	9
<u>Hypoleria oreas</u> Weymer	--	1		V V	--	1	BR(1)	3
<u>Hypoleria orolina</u> (Hewitson)	--	--		-- V	--	1	EC(1)	1
<u>Mcclungia salonia</u> (Hewitson)	0.23	1		V V	--	1	BR(2)	5
<u>Pseudoscada timna</u> (Hewitson)	0.19	1		V V	B	1	EC(1)	1
<u>Thyridia confusa psamathe</u> Godman & Salvin	3.08	1		V V	[B]	1	EC(1)	1

- Source:
1. Present study
  2. Drummond, unpublished
  3. d'Almeida, 1922
  4. d'Almeida, 1938
  5. d'Almeida, 1944
  6. Brown and d'Almeida, 1970
  7. Fox, 1967
  8. Gilbert, 1969
  9. Guppy, 1904
  10. Sepp, 1828
  11. Young, 1972
  12. Young, 1973
  13. Young, 1974a
  14. Young, 1974b
  15. Young, 1974c

Table 15 - continued.

Note: Figures or characters in [brackets] are inferred from incomplete data.

LARVAE: [G] means larvae are probably gregarious, but author did not so state.

MODE OF OVIPOSITION SEQUENCE: [A] means that "A" is the probable mode of oviposition. [C or D] means that the mode of oviposition is definitely not A or B, but that the date are insufficient to distinguish between C and D.

NUMBER OF FOODPLANTS UTILIZED: Refers to the number known to be utilized at one locality.

*D - Dorsal surface of leaf. V - Ventral surface of leaf. (G) - Larvae are gregarious.

+A - ♀ lands on dorsal surface of leaf, lays eggs on dorsal surface of leaf.

B - ♀ lands on dorsal surface of leaf, lays eggs on ventral surface of leaf by curling abdomen under.

C - ♀ lands on dorsal surface of leaf, then flies to and lands on ventral surface of leaf and lays eggs.

D - ♀ lands on ventral surface of leaf, lays eggs on ventral surface of leaf.

†LOCALITY: Unnumbered localities indicate that no specific locations within the country were given in the source publication.

BR: Brazil

(1) Presumably southern Brazil, especially state of Rio de Janeiro (precise localities not given).

(2) States of São Paulo, Goiás, southern Minas Gerais (precise localities not given).

(3) Espírito Santo, Serra da Mantiqueira (near Santa Teresa).

CR: Costa Rica

(1) Guanacaste Prov., Finca La Pacifica (5.5 km NW Cañas), 45 m elev.

(2) Heredia Prov., Finca La Selva (5 km SE Puerto Viejo), 105 m elev.

(3) Puntarenas Prov., Finca Las Cruces (7.8 km S San Vito), 1210 m elev.

(4) Heredia Prov., Cuesta Angel (7 km SW Cariblanco), 950 m elev.

(5) San Jose Prov., Bajo la Hondura (on the Rio Clara), 900 m elev.

EC: Ecuador

(1) Napo Prov., Limóncocha (on the Rio Napo), 280 m elev.

(2) Pichincha Prov., Tinalandia (10 km E Sta. Domingo), 680 m elev.

PR: Peru

(1) Huánuco Prov., Tingo Maria.

SU: Surinam

TR: Trinidad

to egg cluster sizes or the number of eggs carried by wild-caught females as estimates of the egg-producing capabilities of ithomiines. The largest egg clusters known for ithomiines are those reported for Hypothyris euclea in Costa Rica (mean cluster size of 75 or 120, depending on the locality) by Gilbert (1969) and for Placidula euryanassa in Brazil (about 100) by d'Almeida (1922). The largest egg cluster found at Limoncocha was laid by Mechanitis isthmia and contained 59 eggs. This number is probably near the upper limit of egg cluster size for this species population, which has an average cluster size of 31 ($N = 54$), because dissections of over a dozen females showed that most of them were carrying between 30 and 40 eggs, with the maximum number being 52. These females also carried numerous immature eggs in their ovarioles and it is likely that they lay several egg clusters during a life time. Dissections of females of other ithomiine species revealed that the number of mature eggs carried at one time can be quite high. For example, a fresh (F-) Dircenna loreta was found to be carrying 181 mature eggs (but very few immature ones) and an intermediate condition (I) Hypothyris mansuetus was found to be carrying 478 mature eggs (but no immature eggs). Of course, without a consideration of egg size, the number of eggs produced does not accurately measure the reproductive effort. Not surprisingly, the eggs of D. loreta and H. mansuetus are quite small (see Table 15; H. mansuetus eggs = 0.20 mm^3). Thyridia confusa has the largest known eggs (3.08 mm^3) of any ithomiine, and the one female (I) that was dissected had 21 eggs in her abdomen. The approximate egg volumes carried by these three females are thus 27 mm^3 for D. loreta,

96 mm³ for H. mansuetus, and 63 mm³ for T. confusa. Similarly a M. isthmia with 50 mature eggs would be carrying about 34 mm³. These figures, of course, are based on small sample sizes, and represent only the egg volume carried at one time. Without knowledge of the total number of eggs produced, a comparison of reproductive effort among ithomiines is premature. Labine's (1966) discussion assumed that the cost of producing a given volume of eggs, regardless of egg size, was constant. There may, however, be differential physiological costs involved in producing 100 mm³ of very small eggs compared to producing 100 mm³ of large eggs (e.g., the ratio of shell material to internal contents may be substantially greater under the former strategy). Therefore, a thorough consideration of reproductive effort in butterflies should include not only total egg number and egg size, but also the metabolic expense associated with producing eggs of a certain size or shape.

Among the ithomiine species listed in Table 15, egg size varies by a factor of 24 from the largest (T. confusa) to the smallest (H. euclea). To better appreciate the nature of this variation, egg volume was plotted against the mean forewing length of females in Figure 45. This graph shows that, for ithomiines as a group, there is no strong correlation between egg size and the size of adult females. The data points in Figure 45 were plotted using different symbols for each ithomiine tribe, however, and some interesting taxonomic correlations resulted.

First, in the Tribes Napeogenini, Ithomiini, Dircennini, and Godyridini, most species have an egg size between .15 and .35 mm³. [There

Figure 45. Egg Volume versus Female Forewing Length.

is, however, one significant exception to the pattern in the Dircennini, Pteronymia notilla (0.94 mm^3), and in the Godyridini, Thyridia confusa (3.08 mm^3), and a lesser deviant in the Ithomiini, Ithomia amarilla (0.46 mm^3)]. Second, in the Mechanitini, the four Mechanitis species and Forbestra truncata are relatively similar in egg size and wing length, while Xanthocleis psidii departs from the pattern with an unexpectedly small egg. Scada batesi, another member of the Mechanitini, is the smallest ithomiine represented, but nevertheless has an egg size larger than most members of the first four tribes discussed above. Third, the most interesting pattern is that shown by the Oleriini, which, when compared to the other tribes, has an extremely large egg for the size of the female. The Oleriini species show a sharp increase in egg volume with body size, suggesting that selection has tended to maximize egg size in this group. By contrast, there appears to be selection for a relatively small egg (independent of adult size) in species belonging to the first four tribes discussed (Napeogenini, Ithomiini, Dircennini, and Godyridini). The extreme departures in egg size from the tribal means shown by T. confusa, P. notilla, and X. psidii probably represent adaptations to unique situations where selection has favored very different oviposition strategies. Until these species are better known biologically, the significances of their aberrant oviposition patterns will remain unknown. Unfortunately, data on the Melinaeini and Tithoreini are too meager to drawn any general conclusions.

The reproductive effort (total number of eggs laid multiplied by egg size) of butterflies is nutritionally financed by feeding--either in the larval stage, the adult stage, or both. Labine (1966), in her

study of the nymphalid Euphydryas editha in California, found that females emerge as heavy-bodied adults with large numbers of eggs already mature in their oviducts, proving that the bulk of the reproductive effort in this species is financed by larval feeding. By contrast, females in the neotropical genus Heliconius rarely lay eggs during the first few days of life and probably have no mature eggs at the time of eclosion (Gilbert, 1972). In Heliconius, then, adult females must obtain most of the nutrients required to manufacture the eggs. The situation in ithomiines appears to be the same as that in Heliconius. Dissections of wild-caught adult females of several species showed that very fresh (F+) specimens were rarely mated and carried no mature eggs ($N = 8^*$). Further evidence for adult financing of egg production in ithomiines comes from reared virgin females that were fed sugar water after eclosion and then dissected at various ages. The following females showed no sign of egg production (time after emergence in parentheses): Ceratinia poecila (13 hours), Napeogenes pharo (1 day), Mechanitis isthmia (1 hour; 3 days), and M. lysimnia (1 day). Older reared females did show evidence of egg production. A seven-day-old

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*The following wild-caught females were dissected and found to have no mature or immature eggs (only thin oviducts and yellow supporting tubules were present): 1 Godyrus zavaleta (F+), 1 Hypoleria chrysodonia (F+), 2 Napeogenes apobsoleta (F+), 1 N. pharo (F), 1 Oleria agarista (F), 1 Oleria lota (F+), 1 Scada batesi (F). G. zavaleta, N. pharo, and S. batesi each carried one spermatophore, but the remainder of these females were unmated.

Mechanitis lysimnia female had many tiny (less than 0.1 mm diameter) embryonic eggs in her oviducts, but no mature or immature eggs were present. Two reared M. messenoides females were kept alive for 21 days before dissection. One contained 10 mature and 9 immature eggs; the other carried 3 mature and 12 immature eggs. Both females also had numerous tiny embryonic eggs.

These preliminary results indicate that ithomiine females emerge with no mature eggs in their oviducts and must pass through a period of at least several days of egg production before oviposition can begin. Although mating can occur before egg production has begun (as in the females of G. zavaleta, N. pharo and S. batesi cited above), it appears that many females are not sexually receptive on the day of emergence and may not become receptive until after egg production is under way. Judging from the data on reared Mechanitis, it probably takes females two weeks to produce mature eggs if they are limited to a sugar-water diet as these were. A source of nitrogenous compounds is probably essential to the longevity and continued egg production of ithomiines just as has been shown to be true for Heliconius. Gilbert (1972) has demonstrated that many Heliconius females obtain amino acids and proteins by gathering and digesting pollen on their proboscises and use these nitrogenous compounds in the manufacture of eggs. Females without access to pollen sources lay fewer eggs than those that can obtain pollen (Gilbert, 1972). Female ithomiines probably obtain many of the amino acids and proteins needed for their egg production from bird droppings and other nitrogen-rich detritus on which they feed

(and perhaps also from decomposing spermatophores; see above). If the two M. messenoides females I kept for 21 days on only sugar water had had access to fresh bird droppings as well, perhaps their rate of egg production would have significantly increased. Male ithomiines probably obtain the amino acids needed for a long life span from the nectar of the flowers they visit, for Baker and Baker (1973) have recently shown that flowers visited and pollinated by butterflies have nectars with high concentrations of several different amino acids.

Returning to Table 15, it is clear that the majority of ithomiines lay their eggs singly, just as do the majority of all butterfly species (Labine, 1966). The major exception to this is the genus Mechanitis, most species of which lay clusters of eggs ranging in size from 3 or 4 to nearly 60. M. isthmia and M. mazaesus seldom lay egg clusters of less than 10 eggs, while M. lysimnia and M. messenoides rarely lay clusters containing over 10 eggs. The eggs laid by M. isthmia, M. mazaesus and M. messenoides are tightly clustered and evenly spaced, while those of M. lysimnia and the closely related Forbestra truncata are more widely spaced in a loose cluster. There are no other species at Limoncocha that lay egg clusters, but large egg clusters have been reported for Hypothyris euclea in Costa Rica (Gilbert, 1969), and for Placidula eurynassa and Episcada clausina in Brazil (d'Almeida, 1922).

Although egg cluster size appears to be constant within a species population (as at Limoncocha), some widespread species may have very different oviposition strategies at different localities. For example, Hypothyris euclea, an extremely widespread and usually

abundant ithomiine, lays large egg clusters in Costa Rica (subspecies leucania) but deposits eggs singly at Limoncocha (subspecies peruviana). It is interesting that H. euclea appears to be much less common at Limoncocha than has been reported for Costa Rica (Gilbert, 1969), Trinidad (Barcant, 1971), and Brazil (Brown and Benson, 1974), although the egg cluster size in the latter two areas is not known. Another case of subspecific populations differing in oviposition strategy is that of Mechanitis menapis, which in Costa Rica (subspecies satura) apparently lays clusters of eggs on the ventral surface of the foodplant leaves (Gilbert, 1969), but in western Ecuador (subspecies mantineus) lays single eggs on the dorsal surface of the foodplant leaves (Drummond, unpublished). Two other published reports suggest the occurrence of variation in oviposition behavior within a species, but these appear to contain incorrect information.*

Egg clustering in ithomiines is clearly correlated with larval gregariousness, although a few species (such as Forbestra truncata) that lay small, loose clusters have non-gregarious larvae (Table 15).

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*Young (1972) mentioned that M. isthmia lays egg clusters on the ventral surfaces of leaves in Costa Rica (subspecies isthmia), but this is undoubtedly an erroneous statement since Gilbert (1969) clearly reports that the egg clusters of M. i. isthmia are laid on the dorsal surface, just as they are at Limoncocha (subspecies eurydice) and in western Ecuador (subspecies chimbarazona) (Roy McDiarmid, color transparency). Young mentions in the same paper that Godyris zavaleta caesiopicta in Costa Rica lays "loose clusters of eggs on the ventral leaf surface of Solanum hispidum," but, in his life history of this butterfly, Young (1974c) states that "the eggs are laid singly" and that the female he observed "never laid more than one egg on a leaf."

Egg clustering is apparently not closely correlated with the position of the eggs on the leaf, although most species that lay clusters do so on the dorsal leaf surface. With the exception of M. menapis satura in Costa Rica, all observed Mechanitis species deposit their eggs on the dorsal leaf surface, as does the closely related F. truncata. The other two species in the Mechanitini for which records are available (S. batesi and X. psidii) lay single eggs on the ventral leaf surface. Outside the Mechanitini, only one ithomiine species, Hymenitis nero in Costa Rica, has been recorded to lay its eggs on the dorsal leaf surface (Young, 1972). H. nero is even more exceptional in that it is the only ithomiine in which the larvae are known to feed and rest on the dorsal surface of the foodplant leaves.

Modes of Oviposition Behavior

In all ithomiine species studied so far, females lay their eggs on either the upper or lower surfaces of a foodplant leaf, and rarely, if ever, on petioles, stems, fruits, or flowers of the larval foodplant. Eggs are generally laid on mature rather than young leaves (Young, 1972, 1974c; present study), suggesting that there may be chemical changes with age in foodplant leaves, rendering older leaves more attractive. The behavioral sequences leading to foodplant recognition by female ithomiines are not well understood, and the chemical and/or mechanical stimuli that elicit these behaviors are as yet unknown.

In attempting to locate a larval foodplant, females characteristically fly slowly and evenly through the forest understory, weaving in and

Figure 46. Modes of Oviposition Behavior.

- a. Mode A. Female lands on dorsal surface of leaf, lays eggs on dorsal surface of leaf.
- b. Mode B. Female lands on dorsal surface of leaf, lays eggs on ventral surface of leaf by curling abdomen under.
- c. Mode C. Female lands on dorsal surface of leaf, then flies to and lands on ventral surface of leaf and lays eggs.
- d. Mode D. Female lands on ventral surface of leaf, lays eggs on ventral surface of leaf.

a

b

c

d

out of vegetation, but rarely stopping to perch. Once a foodplant has been located, presumably by olfaction, the female generally flies around or near the plant for some time (from several seconds to a few minutes) before landing on a leaf. My observations at Limoncocha have resulted in the identification of at least four distinct behavioral sequences (modes) leading to leaf selection and egg deposition. In Table 15 these have been designated Modes A, B, C, and D. These modes, illustrated in Figure 46, describe behavioral sequences that begin after the adult female has located the larval foodplant. Mode A results in eggs being laid on the dorsal leaf surface of the larval foodplant. Modes B, C, and D all lead to egg deposition on the ventral leaf surface. Other modes of oviposition behavior may exist in the Ithomiinae, but only the four described below were observed at Limoncocha.

Mode A (Figure 46a; description based on Mechanitis isthmia). Only Forbestra truncata and species in the genus Mechanitis were observed to use this mode of oviposition at Limoncocha. The female generally spends a relatively long time circling and "inspecting" the foodplant before alighting, which may happen several times before an egg is laid. Some females may hover above a leaf for several seconds before descending to perch. After landing, usually near the center or toward the tip of the leaf, the female remains motionless for a moment or two, and sometimes for several minutes, before the abdomen is lowered to the leaf and the first egg is laid. If the species lays single eggs, as does M. menapis mantineus in western Ecuador, the female flies off immediately after raising the tip of her abdomen from the leaf. If several eggs

are laid, the female stays motionless for several seconds before lowering her abdomen again. In M. isthmia the time elapsing between the deposition of one egg and the next decreases as time passes. In species that lay tight egg clusters (M. isthmia, M. mazaesus, and M. mesenoides), the female palpates with the tip of her abdomen to find the last egg in a row so as to lay the next one adjacent to it. After completing a "row" (the width of which is apparently determined by the distance a stationary female can angle her abdomen in either direction from an anterior-posterior axis), the female moves forward slightly and lays another row, and the sequence continues until the egg cluster is complete. It is not known how "completeness" is determined, but it may simply be the result of the number of mature eggs present in the female's abdomen.

Mode B (Figure 46b; description based on Godyrus zavaleta). As in Mode A, females using Mode B land on the dorsal surface of a leaf, but usually with much less time spent "inspecting" the plant in flight before landing. Shortly after landing, the abdomen is curled over the edge and up under the leaf, the female adjusting her position to maximize the distance she can reach under the leaf with her abdomen. All species observed with this behavior at Limoncocha utilized foodplants with relatively small leaves, so that little body adjustment was needed. Oviposition takes place along the side of the leaf and rarely at the tip or near the base. All species known to display this behavior lay single eggs and females fly from the plant almost immediately after the egg is laid. An interesting outcome of this behavior is that the eggs of a given species are nearly always found at the same distance from the leaf

margin. At Limoncocha, I became aware of this because I routinely drew the location on the leaf of each egg I collected, and very early made an association between the mode of oviposition (B) observed in Godyris zavaleta and the distance of her eggs from the leaf margin. Therefore, when I found a consistent marginal distance in placement of eggs of Thyridia confusa and Xanthocleis psidii, I predicted that both species would use Mode B oviposition behavior. I was fortunate enough to subsequently observe oviposition by a Xanthocleis female and the prediction was fulfilled. Although I have never observed oviposition in T. confusa, the prediction of Mode B is strongly supported by the consistent 10 mm distance of the eggs of this species from the foodplant leaf margin.

Mode C (Figure 46c; description based on Ceratinia poecila). Once again, the female lands on the dorsal leaf surface, usually after much flying about the foodplant, but with little or no prior inspection of the particular leaf on which she perches. Several leaves may be visited in quick succession before a suitable one is found. If the leaf is inappropriate she stays but a second before flying on. If the leaf is correct she stays only a little longer (perhaps two seconds) before flying slightly upward in a hovering flight, and then down and around to the underside where she lands on the ventral surface. After landing, the abdomen is slowly raised to the leaf and a single egg is laid. Immediately following the release of the egg, she flies off to repeat the sequence, usually on another leaf of the same plant.

Mode D (Figure 46d; description based on Hypothyris fulminans). This is the only mode in which the female first lands on the underside

of the leaf, and she does so after hovering around, and especially under, the leaf for some time. Only one egg is laid, after which the female immediately flies off, usually to repeat the sequence on another leaf of the same plant.

Obviously, Mode A is used exclusively by species that lay eggs on the dorsal leaf surface. This includes most of those that lay eggs in clusters. Unfortunately, it is not known what mode is used by species that lay clusters on the ventral surfaces of leaves, but Mode B can probably be ruled out because of the physical difficulty of laying a great many eggs in a tight cluster on the underside of the leaf while curling the abdomen around from the dorsal surface. Of the remaining two observed modes, C and D, I suspect the latter, for reasons given below.

Based on my observations at Limoncocha, Mode C is clearly the most inefficient. On numerous occasions I have watched a female of Ceratinia poecila or Ithomia agnosia land on the dorsal surface of a leaf of the correct foodplant, then leave the leaf to fly to the underside, only to land on a leaf of another, usually unrelated, plant and lay her egg there. The females that landed on the underside of an inappropriate leaf, after first perching on the dorsal surface of a correct leaf, always proceeded to lay an egg, never correcting their mistake. It seems apparent that the stimulus eliciting egg-laying behavior is received during the perch on the upperside of the leaf. Once the female leaves the upperside of the leaf, she will lay her egg on the next "underside" she encounters, even if it be an incorrect one that happens to block

her short flight to the underside of the correct leaf. This explains why I suspect that species which lay egg clusters on the underside of a leaf employ Mode D (or some other, as yet unobserved, mode), because the chance for error in Mode C appears too great to risk a large batch of eggs. Interestingly, Hypothyris euclea, which lays single eggs at Limoncocha (subspecies peruviana), uses Mode C. Since the same species lays large egg clusters on the underside of the foodplant leaves in Costa Rica (subspecies leucania), it would be nice to know if the subspecies there follows the prediction that Mode D should be used.

Both Modes B and D should provide less chance for error than Mode C, but they may still allow mistakes to be made. It is not surprising then that the "safest" of the four Modes (A) is utilized by most of the clustering species (Mechanitini). Since single egg deposition on the ventral surfaces of leaves is the most widespread condition in ithomiines, it is probably also the ancestral condition. If, for unknown reasons, selection should favor an oviposition strategy utilizing egg clusters in certain species of ithomiines, one would expect concomitant selection to minimize egg placement mistakes. Perhaps the switch to the dorsal surface of the foodplant leaf in the egg-clustering species of the Mechanitini is the result of just such a selective process.

Gilbert (1969) suggested that the dorsal position of egg clusters of M. isthmia facilitated their relocation by the female if she were disturbed during oviposition, implying that there is a critical minimum cluster size. I could not elicit such relocation behavior in females of this species at Limoncocha (N = 2), and since the egg clusters of M.

isthmia were quite variable in size, ranging from 10 to 59 eggs, there is no evidence for egg cluster relocation behavior at Limoncocha.

Foodplant Specificity

The relationship of foodplant specificity to oviposition strategy in the Ithomiinae while undoubtedly important, is unclear at present. At Limoncocha, most of the species in the genus Mechanitis have broad foodplant tolerances, and considerable overlap in foodplant use as well (see Chapter 6). Most of the foodplants utilized by Mechanitis are fugitive or weedy species that colonize open areas and are thus patchily distributed both spatially and temporally. Perhaps the strategy of egg clustering permits better exploitation of these isolated patches when they are found. For example, because of this patchy distribution, Mechanitis females may spend proportionally more time flying in search of foodplants than species that utilize forest plants. As a result, energetic constraints may favor the deposition of eggs in clusters in most Mechanitis species. Also, if larval predators are more common in open areas than in forest situations, the larval gregariousness made possible by egg clustering might have a defensive function resulting in higher progeny survival rates than would be provided by single egg deposition (see Chapter 5).

Wiklund (1974) has raised the question of how the suitability of various plant species as food for the larvae is interrelated with the oviposition preferences of the adults. Three possible alternative explanations were identified: (1) the larval food is somehow remembered by

the adult female and predisposes her to lay eggs on the same plant species as that upon which she fed as a larva (Hopkins' host selection principle), (2) the larval foodplant suitability and the adult ovipositing preferences are determined by the same gene complex, and (3) the larval foodplant suitability and the adult oviposition preferences are determined by different gene complexes. Based on his elegant experiments with Papilio machaon L. in Sweden and a review of the literature, Wiklund (1974) disproved the first possibility (at least for P. machaon) and concluded that the third possibility, separate genetic control of foodplant tolerance in larval feeding and female oviposition behavior, was the most likely. Part of the argument against the second possibility (a single controlling gene complex) was based on numerous observations of larvae successfully feeding on plants never oviposited upon by adults of the species, and of adults ovipositing on plants on which their larvae were unable to complete development. A few preliminary observations are available on the foodplant tolerances of ithomiine larvae (Chapter 6), but controlled experiments on larval feeding preferences and adult oviposition preferences of the Ithomiinae are clearly needed.

CHAPTER V
COMPARATIVE LIFE HISTORIES OF THE ITHOMIINAE

The complete metamorphosis of a butterfly involves four life stages: egg, larva, pupa, and adult. The bias shown by lepidopterists in studying one of these stages to the near exclusion of the other three has led to the accumulation of a tremendous body of knowledge about the adult stage. By comparison, very little information is available concerning immature stages of butterflies. The preoccupation with adult butterflies has less to do with the importance of the imago as the stage of reproduction and genetic recombination than with the comparative ease with which adult butterflies may be collected, preserved, identified, and, of course, admired in display cabinets. The present study reflects this same bias, for immature stages of ithomiines are indeed difficult to work with, but I have attempted to reduce the imbalance somewhat by initiating a study of the life histories of the Ithomiinae at Limon-cocha.

Although butterfly eggs and pupae are usually regarded merely as vessels of cellular reorganization and the larva as little more than an efficient feeding machine, all four stages carry a suite of adaptations that represent a series of selective compromises made in response to the matrix of environmental variables to which the organism has been exposed. The sum of these adaptive responses accumulated over

evolutionary time constitutes a life history strategy (Wilbur et al., 1974), similar in concept to the strategy of oviposition discussed earlier. The study of adaptations at the life history level has received a growing attention recently and has as its objectives: (1) to explain the diversity of observable life history patterns in terms of a minimum number of selective pressures, and (2) to identify those areas in need of more detailed examination and experimentation (Wilbur et al., 1974).

Although knowledge of life histories of ithomiines is minimal at present, it is already clear that the unit of study for ithomiine life history phenomena must be the local or subspecific population and not the species. The variability in oviposition strategies among conspecific subspecies of wide-ranging species has already been discussed. It will be seen below that foodplant specificity and the length of developmental time may also be quite different among conspecific subspecies. Perhaps the two most fruitful lines of research into ithomiine life history phenomena will be the comparative life history strategies of (1) subspecific populations of wide-ranging species and (2) all the species present in a given area. The present research is an attempt to lay the foundation for a study of the latter type.

Immature Stages

The information available on immature stages of ithomiines comes from the studies of a very few researchers. Brief descriptions, and occasionally illustrations, of eggs, larvae, and pupae may be found in

several older works (Muller, 1886; Guppy, 1894; Haensch, 1909; Fountaine, 1913; Kaye, 1914; d'Almeida, 1938) and a few more recent ones (Costa Lima, 1950; Fox, 1967; Gilbert and Ehrlich, 1970; Rathcke and Poole, 1975; Brown, 1976b)*. Reasonably complete life histories for 19 species have been published: 1 by Moreira (1881); 12 by d'Almeida (1922, 1938, 1944), one of which duplicates that of Moreira; 1 by Brown and d'Almeida (1970); and 5 by Young (1972, 1973, 1974a,b,c). The papers by the latter two authors illustrate all life stages photographically. In addition, A. M. Young and W. A. Haber (pers. comm.) have life histories of several Costa Rican Ithomiinae in manuscript. During the Ecuadorian research reported here, life histories of 18 species of Limoncocha ithomiines were obtained, as well as information on some of the life stages of 8 more species. These observations, however, cover less than half of the 53 Ithomiinae known from Limoncocha. Furthermore, the total number of detailed studies made to date represent less than 10% of the species in the subfamily. Clearly, much more work must be done before the first objective of life history studies, that of explaining life history pattern diversity in terms of a minimum number of selective pressures, can be realized. The data summarized here, however, should do much toward meeting the second objective, that of identifying those areas in need of more detailed examination and experimentation.

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* Descriptions of immature stages of Tellervo zoilus (Tellervinae) are given in Barrett and Burns (1951), Common (1964), McCubbin (1971), and Common and Waterhouse (1972), the latter work containing a photograph of a larva.

Figure 47. Illustrations of Some Eggs, Larvae, and Pupae of Ithomiines.

Eggs (17.5 x life size)

- a. Mechanitis messenoides C. & R. Felder
- b. Thyridia confusa psamathe Godman & Salvin
- c. Godyris zavaleta amaretta (Haensch)
- d. Ceratinia poecila poecila (Bates)
- e. Xanthocleis psidii ino (C. & R. Felder)

Larvae (2 x life size)

- f. Mechanitis isthmia eurydice Haensch
- g. Forbestra truncata juntana (Haensch)
- h. Ceratinia poecila poecila (Bates)
- i. Dircenna relata Butler & Druce (Drawn from Young, 1973)
- j. Melinaea menophilus menophilus (Hewitson)

Pupae (2 x life size)

- k. Xanthocleis psidii ino (C. & R. Felder)
- l. Ceratinia poecila poecila (Bates)
- m. Ithomia amarilla Haensch
- n. Melinaea menophilus menophilus (Hewitson)
- o. Thyridia confusa psamathe Godman & Salvin

a

b

c

d

e

f

g

h

i

j

k

l

m

n

o

The following discussion makes no attempt to present detailed accounts of the morphology of the early stages of the Ithomiinae but simply tries to give some indication of the range of morphological variability within the subfamily, and to discuss those aspects of the information available on immature stages most relevant to this analysis of ithomiine community ecology.

Eggs

Egg size in terms of volume was presented earlier for many species in Table 15. The majority of ithomiine eggs are basically ovoid in shape, but the ratio of length to width varies considerably from a little over 2:1 for the spindle-shaped eggs of Mechanitis to about 1:1 for the nearly spherical eggs of Xanthocleis and several other genera (Figure 47). At Limoncocha, there are at least two exceptions to the ovoid shape, Godyris zavaleta (Figure 47c) and Heterosais edessa. Both species have eggs in the shape of a truncated cone. Eggs of most ithomiines are either white, pale yellow or cream in color. Because of their small size and ventral position on the leaf, yellow and cream-colored eggs are difficult to see. On the other hand, the large white eggs of Mechanitis, Forbestra, Oleria, and Thyridia are much more conspicuous, especially those of the first two genera, which are laid in clusters on the dorsal leaf surface. The eggs of all species examined have a series of vertical ridges, variable in number within predictable limits. In most species, these vertical ridges are traversed by faint horizontal ribbing, forming a grid of shallow depressions on the surface of the

egg. Eggs are cemented to the leaf surface during oviposition in the usual way, but on foodplant leaves with a thick covering of stellate hairs, the eggs may be less securely anchored in the tomentum.

The incubation period is usually five or six days, and rarely exceeds a week. Just prior to hatching, the eggs turn slightly darker, especially at the upper end where the mandibles undergo sclerotization. Most eggs kept in the laboratory, especially clusters of Mechanitis eggs, tended to hatch in the late afternoon or early evening. Such timing may be a protective adaptation that helps prevent larval desiccation, since most Mechanitis eggs are positioned dorsally on the leaf and the foodplants often grow in open sun.

Larvae

Upon hatching, larvae of most species consume from 50 to 100% of the egg casing before feeding on the leaf tissue. Most species also consume the larval skin following ecdysis. All ithomiine species reared to date have five larval instars, but the time spent in the larval period varies considerably, from as short as 11 days to nearly a month (see Table 16). The first and last instars are generally the longest, the fifth including an active prepupal stage that lasts about a day. The beginning of the prepupal stage is marked by the termination of feeding which leads to a change in color at least partially due to the expulsion of the gut contents. The prepupa may wander a considerable distance from the foodplant before pupation begins. The behaviors of solitary and gregarious larvae differ substantially and will be treated separately below.

Solitary larvae, with one exception (Young, 1972), feed and rest on the underside of the foodplant leaves. Feeding may be initiated anywhere on the ventral surface, but the larva rarely begins at the edge of the leaf. The most common feeding pattern in solitary larvae is that of scraping away the leaf tissue from the underside, thereby leaving only the upper cuticle and major veins of the leaf intact. Most larval feeding appears to occur in the daylight hours. When not feeding, most larvae rest in a J-position, with the head curled around to face posteriorly. The wide-spread occurrence of this resting position among solitary ithomiine larvae of many species suggests that it may be a selectively advantageous behavior, possibly with a defensive function. Such a resting position allows the head quick access to the mid-dorsal region of the body, where the larva's mandibles or regurgitated gut contents may provide a means of defense against the oviposition attempts of parasitic wasps and flies.

Most solitary larvae appear to be cryptic in coloration and pattern, physical attributes which correlate well with their behavioral preferences for positions on the ventral surfaces of the foodplant leaves. The single known exception to the ventral position of ithomiine larvae on leaves, Hymenitis nero in Costa Rica, achieves crypsis by curling the edges of its leaf (holding them in place with spun silk) to form a shallow cradle in which it rests (Young, 1972). In at least two species of ithomiine, Episcada clausina in Brazil (d'Almeida, 1922) and Godyris zavaleta caesiopicta in Costa Rica (Young, 1974c), late instar larvae live hidden between foodplant leaves bound together with silk thread.

Interestingly, the larvae of both these ithomiines have fine, nearly transparent skin, a trait shared with the larvae of some skippers (Hesperiidae) that also construct similar leaf shelters.

Young (1974a,c) has described the behavior of solitary larvae of two species of ithomiines, which, when artificially placed with other, conspecific larvae on the same leaf, reacted with apparent agonistic behavior. This suggests that the solitary habit of these larvae, originating in the single egg deposition by the female parent, may be maintained by selection for agonistic behavior.

Gregarious larvae are synchronous in their feeding and resting behavior. Gregarious larvae feed at the edge of a leaf (on the underside), usually lined up in rows facing outward. During resting periods, the larvae retreat en masse inward on the leaf to a silken mat constructed soon after hatching. The coloration of Mechanitis larvae, the only genus having gregarious larvae at Limoncocha, appears to be neither aposematic nor strongly cryptic. Their position on the undersides of leaves and their generally light color (dingy white tinged with yellow) combine to make them fairly inconspicuous, however.

The gregarious larvae of M. isthmia, M. lysimnia, M. mazaesus, and M. messenoides all engage in a behavior that results in the expulsion of frass from the leaf occupied by the brood. Upon encountering a fecal pellet, a larva grasps it with its mandibles and raises its head a centimeter or so above the leaf before releasing the pellet. Since the larvae live on the undersides of leaves, the raising of the head lowers the pellet relative to the leaf and the pellet falls free. Gregarious larvae in humid conditions are notoriously susceptible to fungal and viral

infections (e.g., Drummond et al, 1970), and thus by removing frass from the leaf surface before it accumulates, the larvae reduce the probability that infectious micro-organisms will become established in the colony.

Ithomiine larvae described to date appear to be of three basic morphological types (Figure 47). Larvae of the first type, characterized by eight pairs of stubby lateral protuberances, have been called "cogwheel" caterpillars (Fox, 1967). The cogwheel type is apparently limited to the Mechanitini and may be characteristic of all members of the tribe, although the larvae of Sais and Scada have never been described. Larvae of the genus Mechanitis (Figure 47f) have relatively long, tapering lateral protuberances, while the larvae of the closely related genera Forbestra (Figure 47g) and Xanthocleis have rather stubby lateral protuberances.

The second type of larval morphology lacks any protuberances and is usually smooth, but often has a "corrugated" effect (Brown and d'Almeida, 1970), in which the apparent number of segments of the body is substantially greater than the actual number, an appearance caused by several indented annulations per segment. All of the larvae reared at Limoncocha in tribes other than the Mechanitini and Melinaeini were basically of this type. For example, Figure 47h shows the basically smooth larvae of Ceratinia poecila, while Figure 47i illustrates a larva of Dircenna relata (Young, 1973) in which the setae are well-developed.

The third morphological type of ithomiine larvae, one that is remarkably similar to larvae of the danaid genus Lycorea (see illustration in Guppy, 1904), bears a pair of very long flexible protuberances

(the "Scherndornen" of Muller, 1886) extending from the dorsal surface of the second thoracic segment. Although the only species reared at Limoncocha that has this larval type is Melinaea menophilus (Figure 47j), larvae of Tithorea harmonia megara on Trinidad (Guppy, 1894; 1904), Tithorea tarricina duenna Bates in Costa Rica (Fountaine, 1913), and Aeria elara (and other Aeria species) in Brazil (Brown, 1976b) all have been reported to have similar larvae. The close morphological resemblance between larvae of Tithorea and Lycorea has been cited by Gilbert and Ehrlich (1970) as evidence for the close relationship between the Ithomiinae and the Danainae. The discovery made during this work that a Melinaea species has the same larval type provides further evidence for such a taxonomic association. It is also of interest that the larva of Tellervo zoilus gelo (Tellervinae) (figured on Plate 18 in Common and Waterhouse, 1972) is of this larval type, although the flexible protuberances appear to be on the third thoracic segment instead of the second. The foodplants utilized by these species are also important in sorting out the taxonomic affinities of the Ithomiinae and will be discussed in Chapter 6.

Pupae

The prepupae of most ithomiine species apparently leave the food-plant in their wandering search for a pupation site, for pupae are rarely found on the larval foodplant (Young, 1972; Brown and d'Almeida, 1970; present study). For example, Beutelspacher (1972) reported finding a pupa of Melinaea imitata Bates in a leaf of an epiphytic bromeliad in Veracruz, Mexico. This observation is of interest because larvae of

M. imitata, like those of M. menophilus at Limoncocha, probably feed on a species of Juanulloa, an epiphytic genus in the Solanaceae. The prepupa of M. imitata apparently wandered from its epiphytic foodplant and ended up in a bromeliad on the same or an adjacent tree. Further evidence for prepupal wandering is provided by Mechanitis larvae reared on foodplants growing in the large (3.7x3.7x1.8 m) screened insectory at Limoncocha; these invariably pupated on the roof of the enclosure or on the uppermost leaves of the tallest plants available. This circumstance suggests that these larvae seek relatively distant and high pupation sites in the wild. A few species, however, appear to occasionally utilize the foodplant as a pupation site. Young (1974b) has reported that pupae of Pteronymia notilla are often found suspended from the ventral midribs of foodplant leaves, and at least one species, Episcada clausina in Brazil, regularly pupates on the foodplant. As mentioned earlier, the larvae of the latter species live between two leaves bound together with silk. It is within this larva-constructed shelter that pupation normally occurs (d'Almeida, 1922). I have observed a similar situation at Limoncocha where a field-collected fifth instar larva of Dircenna loreta bound the two curled edges of a food-leaf together with silk to form a shelter in which pupation occurred. Although I never found any pupae on their foodplants in the field at Limoncocha (see Chapter 6), many pupae of Thyridia confusa were found on their larval foodplant in Puyo, Ecuador in August, 1974. In the gardens of the Hotel Turingia, a hedge row of the ornamental shrub, Brunfelsia calycina var. floribunda, supported a large population of eggs, larvae, and pupae of this species.

Pupal morphology varies quite a bit in the Ithomiinae and some examples are given in Figure 47. The pupae of Xanthocleis (Figure 47k), Mechanitis, and Forbestra (Mechanitini) are all of a similar elongate shape and a brilliant metallic appearance of burnished silver when mature. Many of the compact pupae of species in the Dircennini (e.g., Figure 47l) have gold and silver patches but are not uniformly metallic like those of the Mechanitini. Metallic markings in pupae of the other tribes appear to be rare. Both the yellow pupa of M. menophilus (Figure 47n) and the milky white pupa of Thyridia confusa (47o) are streaked with black markings when mature, but differ radically in shape. The Ithomiinae share with the Danaidae the trait of pupal rigidity (Muller, 1886), further advancing the argument in favor of a close relationship between the two groups (Gilbert and Ehrlich, 1970).

Generation Time

The available data on developmental times of ithomiine life stages are presented in Table 16. At least partial data are available for 42 species, and the total generation time has been computed for 32 species. Unfortunately, many of these generation times are only estimates, because the eggs were collected in the field and the times given for egg development reflect only the time since harvesting and bear no predictable relationship to the time elapsed since oviposition. This is especially true for many of d'Almeida's (1922) life histories and also for several of mine. Such times are placed in brackets in the table. Another difficulty in comparing the generation times given in Table 16 is the

Table 16. Summary of Developmental Times of Ithomiine Butterflies.

TRIBE AND SPECIES	DEVELOPMENT TIME IN DAYS				N	LENGTH OF MATURE LARVA IN mm	FOODPLANT	LOCALITY*	SOURCE
	EGG	LARVA		TOTAL					
		LARVA	PUPA						
MELINAEINI									
<u>Melinaea menophilus menophilus</u> (Hewitson)	4	16	[7]	[27]	1	30	<u>Juanulloa</u> sp. (7354)	EC(1)	1
MECHANITINI									
<u>Forbestra truncata juntana</u> (Haensch)	5	11	8	24	5	24	<u>Solanum anceps</u>	EC(1)	1
<u>Mechanitis isthmia eurydice</u> Haensch	7	14	7	28	88	29	<u>S. coconilla</u> (unspined)	EC(1)	1
	7	15	7	29	74	27	<u>S. coconilla</u> (spined)	EC(1)	1
	7	18-23	7	32-37	34	25-29	<u>Solanum quitoense</u>	EC(1)	1
	7	--	7	--	16	30	<u>Solanum</u> sp. (7334)	EC(1)	1
	[7]	16	7	30	7	22	<u>Lycopersicon esculentum</u>	EC(1)	1
<u>Mechanitis lysimnia elisa</u> (Guér.-Mén.)	7	15	7	29	130	27	Avg. over all 5 plants	EC(1)	1
	[5]	22	7	34	1	--	<u>Solanum pectinatum</u>	EC(1)	1
	5	12	7	24	6	22	<u>Solanum</u> sp. (7304)	EC(1)	1
	5	13	7	25	15	22	<u>Solanum</u> sp. (7334)	EC(1)	1
	5	13	7	25	22	22	Avg. over all 3 plants	EC(1)	1
<u>Mechanitis lysimnia lysimnia</u> (Fabricius)	[7]	18	10	[35]	51	31	<u>Solanum arrebenta</u>	BR(1)	3
<u>Mechanitis mazaesus mazaesus</u> Hewitson	[8]	17	8	[33]	20	30	<u>Solanum</u> sp. (7333)	EC(1)	1
<u>Mechanitis menapis mantineus</u> Hewitson	5	15	9	29	3	23	<u>Solanum mammosum</u>	EC(2)	2
<u>Mechanitis messenoidea</u> C. & R. Felder	8	15	7	30	15	29	<u>S. coconilla</u> (unspined)	EC(1)	1
<u>Scada batesi</u> Haensch	6	--	--	--	2	--	<u>Solanum</u> sp. (7331)	EC(1)	1
<u>Xanthocleis psidii ino</u> (C. & R. Felder)	[5]	--	7	--	3	40	<u>Cyphomandra hartwegii</u>	EC(1)	1

Table 16 - continued.

TRIBE AND SPECIES	DEVELOPMENT TIME IN DAYS			N	LENGTH OF MATURE LARVA IN mm	FOODPLANT	LOCALITY*	SOURCE
	EGG	LARVA	PUPA					
NAPEOGENINI								
<u>Hypothyris daeta</u> (Boisduval)	[5]	17	8	[30]	3	23	<u>Solanum argenteum</u>	BR(1) 3
<u>Hypothyris euclea peruviana</u> (Staudinger)	[5]	17	7	[29]	1	18	<u>Solanum bicolor</u>	EC(1) 1
<u>Hypothyris fluona berna</u> (Haensch)	7	14	7	28	1	18	<u>Solanum sp. (7311)</u>	EC(1) 1
<u>Hypothyris fulminans satura</u> Haensch	[5]	22	8	[35]	3	22	<u>Solanum sp. (7340)</u>	EC(1) 1
<u>Napeogenes corena cauayaensis</u> Fox & Real	[3]	--	--	--	3	--	<u>Lycianthes sp. (7325)</u>	EC(1) 1
<u>Napeogenea pharo avila</u> Haensch	[4]	--	6	--	5	--	<u>Lycianthes sp. (7307)</u>	EC(1) 1
<u>Placidula euryanassa</u> C. & R. Felder	--	--	15-16	--	--	30	<u>Datura arborea</u>	BR(1) 3,4
ITHOMIINI								
<u>Ithomia agnosia agnosia</u> Hewitson	4	--	6	--	2	15	<u>Physalis pubescens</u>	EC(1) 1
<u>Ithomia amarilla</u> Haensch	[4]	17	7	[28]	1	22	<u>Solanum sp. (7327)</u>	EC(1) 1
<u>Ithomia derasa salapia</u> Hewitson	[5]	20	7	[32]	3	--	<u>Physalis angulata</u>	EC(1) 1
<u>Ithomia drymo</u> Hübner	[2]	16	9	[27]	1	20	<u>Solanaceae</u>	BR(1) 3
OLERIINI								
<u>Oleria agarista agarista</u> (C. & R. Felder)	4	13	7	24	1	19	<u>Solanum sp. (7319)</u>	EC(1) 1
	4	17	6	27	1	19	<u>Solanum sp. (7310)</u>	EC(1) 1
	[4]	13	[6]	[23]	1	18	<u>Solanum evolvulifolium</u>	EC(1) 1
	4	14	6	24	2	17	<u>Lycianthes sp. (7332)</u>	EC(1) 1
	4	14	6	24	5	18	<u>Avg. on all 4 plants</u>	EC(1) 1

Table 16 - continued.

TRIBE AND SPECIES	DEVELOPMENT TIME IN DAYS				N	LENGTH OF MATURE LARVA IN mm	FOODPLANT	LOCALITY*	SOURCE	
	EGG	LARVA		PUPA						TOTAL
<u>Oleria zelica pagasa</u> (Druce)	6	19	10	35	8	21	<u>Solanum evolvulifolium</u>	CR(4)	9	
DIRCENNINI										
<u>Ceratinia poecila poecila</u> (Bates)	8	14	7	29	7	20	<u>Solanum</u> sp. (7305)	EC(1)	1	
<u>Ceratiscada canaria</u> Brown and d'Almeida	9-10	17	6-8	32-35	4?	20	<u>Solanum caavurana</u>	BR(3)	6	
<u>Dircenna relata</u> Butler and Druce	5	14	6	25	34	24	<u>Solanum hispidum</u>	CR(5)	8	
<u>Episcada clausina</u> (Hewitson)	[1]	20	6-10	[27-31]	4	17	<u>Solanaceae</u>	BR(1)	3	
<u>Prittwitzia hymenaea</u> (Prittwitz)	[1]	12	9	[22]	1	24	<u>Solanaceae</u>	BR(1)	3	
<u>Pteronymia euritea</u> Cramer	[7]	19-29	10-12	[38-46]	6	20	<u>Solanaceae</u>	BR(1)	3	
<u>Pteronymia notilla</u> Butler & Druce	5	18	7	30	20	22	<u>Cestrum megalophyllum</u>	CR(4)	10	
<u>Pteronymia sparsa</u> Haensch	[5]	16	7	[28]	3	18	<u>Solanum</u> sp. (7335)	EC(1)	1	
<u>Pteronymia sylvo</u> Hübner	[2]	25	10	[37]	2	20	<u>Solanum argenteum</u>	BR(1)	3	
X-1 (genus and species unknown)	[5]	--	7	--	1	20	<u>Solanum</u> sp. (7336)	EC(1)	1	
GODYRIDINI										
<u>Epityches eupompe</u> Hübner	[5]	14	8	[27]	1	26	<u>Solanaceae</u>	BR(1)	3,4	
<u>Godyria zavaleta amaretta</u> (Haensch)	[5]	19	9	[33]	1	22	<u>Cestrum</u> sp. (7338)	EC(1)	1	
<u>Godyria zavaleta caesiopicta</u> (Niepelt)	6	15	12	33	6	26	<u>Solanum brenesii</u>	CR(4)	11	
<u>Heterosais edessa nephele</u> (Bates)	4	--	--	--	2	--	<u>Cestrum</u> (?) sp. (7324)	EC(1)	1	
<u>Heterosais edessa nephele</u> (Bates)	[5]	17	12	[34]	4	19	<u>Solanaceae</u>	BR(1)	3	

Table 16 - continued.

TRIBE AND SPECIES	DEVELOPMENT TIME IN DAYS				N	LENGTH OF MATURE LARVA IN mm	FOODPLANT	LOCALITY*	SOURCE
	EGG	LARVA	PUPA	TOTAL					
<u>Hymenitis nero</u> (Hewitson)	4	15	11	30	18	21	<u>Cestrum standleyi</u>	CR(4)	7
<u>Hypoleria oreas</u> Weymer	[5]	16-20	8	[29-33]	3	23	<u>Solanaceae</u>	BR(1)	3
<u>Mcclungia salonina</u> (Hewitson)	[5]	15	8	[28]	3	22	<u>Solanaceae</u>	BR(2)	5
<u>Pseudoscada timna</u> (Hewitson)	5	--	--	--	2	--	<u>Cestrum</u> (?) sp. (7324)	EC(1)	1
<u>Thyridia confusa</u> psamathe Godman & Salvin	[5]	28	--	--	1	45	<u>Brumfelsia</u> sp. (7330)	EC(1)	1
Source:									
1. Present study	5. d'Almeida, 1944								
2. Drummond, unpublished	6. Brown and d'Almeida, 1970								
3. d'Almeida, 1922	7. Young, 1972								
4. d'Almeida, 1938	8. Young, 1973								
	9. Young, 1974a								
	10. Young, 1974b								
	11. Young, 1974c								

Note: Figures in [brackets] are minimum observed times (eggs were often collected in the field and thus the actual date of oviposition was unknown; occasionally, the actual emergence date of a pupa was missed).

N = the minimum number of individuals on which developmental data was based (time estimates for some life stages were based on more individuals than others).

*LOCALITY: Unnumbered localities indicate that no specific locations within the country were given in the source publication.

BR: Brazil (1) Presumably southern Brazil, especially state of Rio de Janeiro (precise localities not given).
(2) States of São Paulo, Goiás, southern Minas Gerais (precise localities not given).
(3) Espírito Santo, Serra da Mantiqueira (near Santa Teresa).

CR: Costa Rica (1) Guanacaste Prov., Finca La Pacifica (5.5 km NW Cañas), 45 m elev.
(2) Heredia Prov., Finca La Selva (5 km SE Puerto Biejo), 105 m elev.
(3) Puntarenas Prov., Finca Las Cruces (7.8 km S San Vito), 1210 m elev.
(4) Heredia Prov., Cuesta Angel (7 km SW Cariblanco), 950 m elev.
(5) San Jose Prov., Bajo la Hondura (on the Rio Clara), 900 m elev.

EC: Ecuador (1) Napo Prov., Limoncocha (on the Rio Napo), 280 m elev.
(2) Pichincha Prov., Tinalandia (10 km E Sta. Domingo), 680 m elev.

apparent lack of uniformity in rearing conditions. While the species at Limoncocha were reared under relatively uniform conditions, as were those in Costa Rica (Young, 1972, 1973, 1974a,b,c), little is known about the methods used by d'Almeida (1922, 1938, 1944) and other authors.

The variation in larval development within some of the species reared by d'Almeida (1922) suggests to me (based on broods at Limoncocha that gave similar results) that the availability of fresh foodplant was not uniform throughout the rearing procedure. Such problems will, of course, tend to overestimate generation times by prolonging larval development.

The generation times given for Limoncocha species in Table 16 are averages of the number of individuals reared on a single plant species. The variation in developmental times among individuals or broods of the same species reared on a particular foodplant was usually quite small. Only when the variation exceeded two days for any one stage within a single brood (as in Mechanitis isthmia on Solanum quitoense) was this variability entered in the table. Broods that experienced a lack of food during the rearing period were not used in calculating the averages. A few Limoncocha species regularly utilize more than one foodplant and, for these, the developmental time required on each foodplant is presented in Table 16 along with the developmental time averaged over all the foodplants.

The degree of accuracy of the generation times given in Table 16 depends on how many of the three immature stages for which accurate data was gathered. For 14 species, accurate measurements of all three immature stages (egg, larva, pupa) are available, resulting in very reliable generation times for these species. For an additional 18 species

the data on the larval and pupal stages are accurate, but egg developmental times are not, since the eggs were collected in the field. Of these 18, however, the egg developmental times given for 14 species are within the range of values of the other species in the same tribe, and thus may be considered reasonable, albeit minimal, estimates of egg developmental times. The total generation times given for these 14 species, then, are probably quite close to the true values. Of the remaining 4 species, for which the egg development times listed are only one or two days (being the time between field collection and hatching), reasonable estimates of total generation time may be made by selecting the minimum accurate egg development time from the same tribe. In two species the pupal stage was not accurately measured, although the 7 day minimum for Melinaea menophilus is probably a reasonable estimate. For Thyridia confusa, there is no information on pupal developmental time, but a minimum estimate of at least 8 days may be assumed, this being the shortest pupal developmental time recorded in the Godyridini. Application of these estimation procedures augments the complete data to yield a total of 34 accurate measurements or reasonable estimates of generation times covering 32 species of ithomiines (2 subspecies of M. lysimnia and of G. zavaleta are included).

These data have been plotted graphically in Figure 48, in which the species have been grouped by tribal affinities. The range between the shortest and longest generation times is about 20 days, with Oleria agarista (Limoncocha) completing development in only 24 days, while Pteronymia euritea in Brazil and Thyridia confusa (Limoncocha) both require a little over 40 days (see Table 16). Thus, the range in

Figure 48. Generation Times of 34 Species of Ithomiinae.

Circles represent observed generation times. Squares represent calculated estimates of generation times (see text). Solid symbols indicate Limoncocha species.

length of total developmental time among species in the lowland forests of Limoncocha is as great as that recorded to date for all Ithomiinae so studied. Considering all species listed in Table 16, the range in development times for the egg stage is 4 to 10 days, the range in larval development times is 11 to 28 days, and the range in pupal development times is about 6 to 12 days (although d'Almeida, 1922, recorded 15-16 days for Placidula euryanassa).

Although these data represent only a fraction of the species in the Ithomiinae, they provide enough information to make a tentative comparison of development times among tribes and among certain genera. In Figure 49 the data for the species in each tribe have been averaged to provide a mean developmental time for the egg, larval, and pupal stages of each tribe. The tribal averages for each of these stages have been added together to obtain a mean tribal generation time. Unfortunately, no data is available for the Tithoreini, and the Melinaeini is represented only by M. menophilus, but several species contributed to the means of the other tribes (see Figure 48). Figure 49 reveals that the average total generation time for each of the seven tribes studied is just over 4 weeks, or approximately 30 days, with a range of 27 to 32 days. Since many of the Tithoreini species are relatively large butterflies and inhabit the cool mid to upper elevational slopes of the eastern Andes, it can be predicted that they will have comparatively long generation times. The mean generation time for the Tithoreini will probably exceed that of the Godyridini, which has the longest generation time of the other seven tribes.

Figure 49. Comparative Developmental Times Among Ithomine Tribes.

The comparison of the tribal averages of the three immature stages (Figure 49) shows that the shortest egg development times (4 and 4.3 days) are found in the Melinaeini and Ithomiini, and the longest (6.9 days) in the Dircennini. For the larval stage, the Mechanitini has the shortest developmental average (14.3 days) while the Ithomiini average (17.7 days) is just slightly longer than those of most of the remaining tribes. Average pupal development times are about 7-7.5 days in the Melinaeini, Mechanitini and Napeogenini, but range from 8 to 9.7 days among the Oleriini, Dircennini and Godyridini (9.7 days). Thus, the range in mean generation times among all tribes is matched by the range in variation among each of the three life stages as well. No single stage accounts for most of the observed variation in generation time.

To see if the variability in egg size and mature larval size (Table 16) is correlated with the development times of these stages, the graphs in Figures 50 and 51 were constructed. There seems to be no correlation between egg volume and egg development time (Figure 50), and only a slight correlation between larval length at maturity and the length of larval development (Figure 51). When the sizes of these two stages are plotted against total generation time (Figures 52 and 53), a similar pattern results. Figure 52 shows that there is apparently no correlation between egg volume and total developmental time. More likely, egg size is a response to the requirement for a newly hatched larva of a certain minimum size, perhaps related to the need for larval mandibles of a minimum size to successfully initiate feeding on that species' foodplant. Figure 53 shows a definite, but not very strong,

Figure 50. Egg Volume versus Egg Development Time..

Figure 51. Mature Larval Length versus Larval Development Time.

Figure 52. Egg Volume versus Generation Time.

Figure 53. Mature Larval Length versus Generation Time.

correlation between the size of the mature larva and the total generation time. The fact that this correlation is more pronounced than that of Figure 51 (mature larval size and larval development time) is probably due to a relatively long pupal development time in species with large mature larvae (Table 16).

Three ithomiine species at Limoncocha were reared on several different larval foodplants and the developmental times for these species (Mechanitis isthmia, M. lysimnia, and Oleria agarista) on each foodplant are given in Table 16. All of these foodplants were utilized in the wild by the ithomiine species which were reared on them, but some were more frequently used than others. The variability in developmental times resulting from feeding on different foodplants was manifested only in the larval stage. The developmental times of the eggs and pupae (with one possible exception in O. agarista) were species-specific regardless of the foodplant. In each of the two Mechanitis species, the most commonly used foodplant resulted in the shortest generation time. For M. isthmia, this was Solanum coconilla, which, however, is dimorphic for the presence or absence of acicular spines on the stems, petioles, midrib, and most of the leaf veins. It was no surprise that larval development took slightly longer on the spined form (15 days) than on the unspined morph (14 days), but it is perhaps premature to ascribe the differences in developmental time solely to an impediment to feeding caused by the presence of the spines since nothing is known of the chemical defenses of the two morphs. Nevertheless, a similar correlation between mechanical defenses of foodplant leaves and longer larval development time occurred in M. lysimnia and O. agarista and on two other foodplants used by M. isthmia, S. quitoense and L. esculentum.

Solanum quitoense is not native to the Limoncocha area, but a few introduced plants grew on the missionary base. Although lacking spines and trichomes, the leaves and stems of S. quitoense are densely pubescent with stellate hairs. Two egg clusters of M. isthmia were found on this species and reared to maturity. The larvae raised on S. quitoense required 18 to 23 days to mature, however, instead of the usual 14 required on S. coconilla. The added development time probably reflects a detrimental effect on larval feeding ability, especially of the earlier instars, caused by the stellate pubescence, much of which was left uneaten by later instars. Larval development also took longer on the cultivated tomato (L. esculentum), on which M. isthmia females occasionally laid clusters of eggs (16 days required as compared to the normal 14 days). L. esculentum lacks spines and trichomes but is well endowed with glandular hairs.

The principal foodplant used by M. lysimnia is Solanum sp. (7304), and the larval development time on this plant (12 days) was slightly shorter than on Solanum sp. (7334) (13 days). Both of these plants, however, gave considerably shorter larval development times than Solanum pectinatum (22 days). Solanum spp. 7304 and 7334 are soft-leaved, unarmed, glabrous plants. By contrast, S. pectinatum has a dense covering of stellate and glandular hairs on all vegetative parts of the plant and extremely sharp acicular spines on the stems, petioles, and leaf veins, making it one of the most well-armed solanaceous plants at Limoncocha. These mechanical defenses were almost surely responsible in large part for the long larval development time on S. pectinatum.

Oleria agarista utilizes four foodplants at Limoncocha. Although it is not possible to say which of these is most frequently used, Solanum sp. (7319) is the most abundant. Three of the plants are entirely unarmed and the leaves appear to be glabrous. These three gave similar larval development times of 13 to 14 days. The fourth plant (Solanum sp., 7310), however, is heavily armed with recurved spines on the midrib, trichomes on the leaf veins, and is heavily tomentous with stellate hairs. Not unpredictably, this plant resulted in a larval development period of 17 days, 3 to 4 days longer than those of the other three foodplants.

It appears, therefore, that even though a solanaceous plant may be acceptable as a larval food source for ithomiines, the mechanical defenses employed by the plant can result in considerable lengthening of the larval development time, thereby prolonging the exposure of the immature stages to parasitism and predation. Chemical defenses, in the form of toxic alkaloids, may also significantly affect the developmental time of ithomiine larvae. Some of the "foodplants" on which ithomiine females occasionally oviposit may even prove lethal to the resulting larvae, depending on the efficacy of the plant's mechanical and chemical defenses, and the tolerances of the larvae (see Chapter 6).

Parasitism and Predation

The data presented in Chapter 4 indicated that the ithomiine community at Limoncocha (or at least that portion of it sampled at Site 4) achieves a relatively stable existence for most of the year as measured by the

relative abundances, diversity, and comparative sample sizes throughout the year. Catastrophic weather conditions appear to depress the overall abundance of ithomiines at various times during the year but this mortality appears to be rather equally distributed among age classes and species of the community. The recovery shown by the community to these acute depressions in abundance appears to return the community to approximately its former level of diversity and abundance. Thus, the ithomiine community at Limoncocha gives the impression of compositional and numerical stability occasionally, and perhaps regularly, depressed by adverse weather conditions. There are no seasonal or other periodic population explosions of ithomiine species such as those recorded by Brown and Benson (1974) and Brown (1976b) in the seasonal forests of Brazil. In addition, the relatively even distribution of a female's reproductive effort over time, and the resulting overlapping of two or more generations, certainly must contribute to the stability of species populations by dampening the effect of cyclic predation and parasitism so well known in the population biology of temperate insects.

The abundance of ithomiines at Limoncocha, although periodically and strongly affected by environmental conditions, does not appear to be regulated by them. Censuses of forest and second growth areas at Limoncocha reveal very low densities of ithomiine juvenile stages and a great under-utilization of available foodplant tissue (Chapter 6). Thus, it is highly unlikely that low availability of larval foodplant is limiting the population of any Limoncocha ithomiine. It is possible that adult nectar sources, and possibly detritus food sources as well, may be somewhat limiting (Chapter 3). As will be discussed below, there

appears to be a high juvenile mortality of ithomiines at Limoncocha, apparently the result of intense parasitism and predation by other insects. This high juvenile mortality, coupled with the low daily reproductive rate of most ithomiines, appears to be the controlling factor in setting the levels of abundance of Limoncocha Ithomiinae.

Parasitism

Based on field collections of immature stages at Limoncocha, it appears that parasitism of eggs makes a greater contribution to ithomiine juvenile mortality than does larval parasitism. This may be partly a result of the small sample size of field collected larvae, but one important factor may be a great reduction in the number of larvae available for parasitism caused by the prior action of egg parasites and larval predators. Table 17 summarizes the parasitism data for immature stages of Limoncocha ithomiines collected in the field. These data underestimate the rates of parasitism, however, because, by collecting these juvenile forms before they had completed their life stage, a sample was chosen that had been exposed to parasites for less than the normal time. Even so, the rates of egg parasitism appear to be high for many species, ranging up to 60% in Hypothyris fulminans and Ceratinia poecila, species for which relatively large samples were taken. Curiously, egg parasitism is not equally distributed among species, many of which (e.g., Napeogenes pharo) appear to be virtually free of parasitism. Such observations imply either that egg parasites (mostly species of braconid and trichogrammatid wasps) are very host-specific, or that the

Table 17. Parasitism of Field-collected Ithomiine Eggs and Larvae.

TRIBE AND SPECIES	NUMBER OF EGGS		NUMBER OF EGGS OR EGG CLUSTERS		PERCENT PARASITISM*	NUMBER OF LARVAE OR LARVAL BROODS ⁺		PERCENT PARASITISM
	OF EGGS	OR EGG CLUSTERS*	OF EGGS OR EGG CLUSTERS	PARASITIZED*		OF LARVAE OR LARVAL BROODS	PARASITIZED ⁺	
MECHANITINI								
<u>Forbestra truncata</u>	6c		1c		16.7	4b	2b	50.0
<u>Mechanitis isthmia</u>	46c		9c		19.6	5b	0	0
<u>Mechanitis lysimnia</u>	10c		0		0	1	0	0
<u>Mechanitis mazaeus</u>	4c		0		0	1b	0	0
<u>Mechanitis messenoides</u>	4c		1c		25.0	4	1	25.0
<u>Mechanitis</u> sp. on 7326	1c		1c		100.0	--	--	--
<u>Mechanitis</u> spp. on 7334	7c		0		0	1b	0	0
<u>Mechanitis</u> sp. on 7313	2c		0		0	--	--	--
<u>Scada batesi</u>	2		0		0	0	0	0
<u>Xanthocleis psidii</u>	15		0		0	3	0	0
NAPEOGENINI								
<u>Hypothyris euclea</u>	12		3		25.0	3	0	0
<u>Hypothyris fluona</u>	7		1		14.3	6	0	0
<u>Hypothyris fulminans</u>	41		25		61.0	1	0	0
<u>Napeogenes corena</u>	4		0		0	--	--	--
<u>Napeogenes pharo</u>	33		0		0	10	0	0

Table 17 - continued.

TRIBE AND SPECIES	NUMBER OF EGGS OR EGG CLUSTERS*	NUMBER OF EGGS OR EGG CLUSTERS PARASITIZED*	PERCENT PARASITISM	NUMBER OF LARVAE OR LARVAL BROODS+	NUMBER OF LARVAE OR LARVAL BROODS PARASITIZED+	PERCENT PARASITISM
ITHOMIINI						
<u>Ithomia agnosia</u>	17	3	17.6	17	0	0
<u>Ithomia amarilla</u>	3	1	33.3	2	0	0
<u>Ithomia derasa</u>	10	0	0	15	0	0
OLERIINI						
<u>Oleria agarista</u>	16	2	12.5	24	0	0
DIRCENNINI						
<u>Ceratinia poecila</u>	59	35	59.3	27	0	0
<u>Dircenna loreta</u>	2	0	0	2	0	0
<u>Pteronymia sparsa</u>	24	7	29.2	1	0	0
GODYRIDINI						
<u>Godyris zavaleta</u>	4	0	0	3	0	0
<u>Heterosais edessa</u>	5	0	0	1	0	0
<u>Hypoleria orolina</u>	--	--	--	6	0	0
<u>Thyridia confusa</u>	15	2	13.3	5	0	0

Table 17 - continued.

TRIBE AND SPECIES	NUMBER OF EGGS OR EGG CLUSTERS *	NUMBER OF EGGS OR EGG CLUSTERS PARASITIZED *	PERCENT PARASITISM	NUMBER OF LARVAE OR LARVAL BROODS PARASITIZED ⁺	PERCENT PARASITISM
	NUMBER OF EGGS OR EGG CLUSTERS	NUMBER OF LARVAE OR LARVAL BROODS ⁺	PERCENT PARASITISM	NUMBER OF LARVAE OR LARVAL BROODS	PERCENT PARASITIZED ⁺
UNKNOWN SPECIES					
Species on Sol. 7328	2	0	0	1	0
Species on Sol. 7346	3	1	33.3	--	--

* Egg clusters are indicated by the letter c (98-100% of all eggs in a parasitized cluster were parasitized).

⁺ Larval broods are indicated by the letter b (100% of all larvae in a larval brood were parasitized).

eggs of some ithomiine species are much more vulnerable than others. The rates of parasitism of egg clusters in the Mechanitini are lower than those for the single eggs for species in other tribes, but the actual number of parasitized eggs found in the Mechanitini exceeded the number found in other tribes, because nearly all of the eggs in a parasitized egg mass were parasitized. The parasite female is obviously very efficient in her oviposition behavior.

Larval parasites were found in only two ithomiine species, Forbestra truncata and Mechanitis lysimnia. Two broods of F. truncata, one of four larvae and another of five larvae, were completely parasitized by a species of braconid wasp (Hymenoptera: Braconidae). Each brood contained larvae of equal age (fourth instar; presumably from eggs laid by the same female) scattered over the five or six leaves of the foodplant. The fact that all larvae on the plant were parasitized suggests that the female parasite can either recognize the larval foodplant, which she subsequently searches thoroughly, or after a chance encounter with one larva she adjusts her searching behavior to include all the leaves in the vicinity of the one on which she encountered the first larva. Of four mature larvae of M. lysimnia collected in pairs on two foodplants, only one was parasitized. The parasite was a tachinid fly (Diptera: Tachinidae) and, unlike the braconids on F. truncata, emerged from the chrysalis rather than the mature larva.

Predation

Although circumstantial evidence indicates that predators take a heavy toll of ithomiine larvae, predation of immature stages was actually

observed on only three occasions. A second instar larva of Oleria agarista was once found (1630 h) impaled on the proboscis of a small (5 mm) yellow reduviid nymph (Hemiptera: Reduviidae) that was walking on the underside of a leaf of the larval foodplant (Solanum sp., 7319). On another occasion (1500 h), several dozen small black Crematogaster ants (Hymenoptera: Formicidae) were observed crawling over a cluster of Mechanitis isthmia eggs on Solanum coconilla. A closer inspection revealed that several of the eggs had been badly damaged by the ants, many of which were carrying away bits of egg material in their mandibles. A second example of egg predation occurred when a cluster of ten Mechanitis mazaesus eggs was discovered in the process of hatching in the late afternoon. At the time of discovery, six of the eggs had hatched but the larvae were not present on the plant and the empty egg shells had not been devoured. Since the larvae in the other four eggs of the cluster were just emerging, it is most likely that the first six larvae had been predated just before I arrived. No pupal predation was observed, but an emerging adult of Ceratinia poecila, while in the process of abandoning the pupal shell, fell prey to a spider that was inside the rearing cage in which the larva had been placed prior to pupation. Although an artificial situation, this incident illustrates the vulnerability of teneral adults during the period before their wings harden. (Freshly emerged adults can fly within 45 to 60 minutes after emergence, but, in the laboratory at least, they often remain suspended from the pupal shell for several hours before first taking flight).

Ants and other social insects are undoubtedly responsible for a great deal of larval predation. Small Solanopsis ants construct nests

among the fruits of Solanum coconilla and along the stems, leaves, fruits, and flowers of several other solanaceous plants, which they patrol incessantly at Limoncocha. The much larger Ectatoma and Paraponera ants also patrol many solanaceous plants, and probably take many larvae. The swarm raids of Eciton burchelli and foraging columns of other army ants are frequent events of the Limoncocha understory. Social wasps are probably also important predators of ithomiine larvae and may account for the wholesale disappearance of broods of Mechanitis isthmia known to take place in just a few hours. For example, a Solanum coconilla plant cultivated behind our house at Limoncocha attracted the attention of numerous ovipositing M. isthmia females, and some of the egg clusters were kept under close observation. One cluster of 50 eggs hatched on the evening of the sixth day after oviposition. By noon of the seventh day, 48 of the original 50 were left. On the eighth day 45 larvae were present, on the ninth day 44, and by the afternoon of the tenth, all the larvae (second instar) were gone. Another egg cluster laid under similar circumstances suffered a similar fate. Of the 32 eggs originally laid, only 24 were present on the fourth day and these all hatched on day seven. By noon of the eighth day, 20 larvae were left, on the ninth day only 4 larvae were present, all of which were gone by noon of the tenth day. The plant on which these larvae occurred was large and healthy and plenty of leaf material was available, so lack of food was not responsible for this disappearance. The disappearance of only one or two larvae at a time is probably due to solitary patrolling ants or assassin bugs, but the sudden disappearance of large numbers of larvae may have been the result of social wasps finding the brood and

recruiting other individuals. Swarm raids of army ants could presumably have the same effect but none occurred in the area during the observations described above.

The shelters constructed by late instar larvae of Hymenitis nero and Episcada clausina probably do not prevent predation by large ants, but may significantly reduce the probability of wasp predation, and perhaps of parasitism as well. The gregarious larvae of Mechanitis engage in synchronous head jerking behavior when disturbed, much as do the gregarious larvae of many other species (e.g., Drummond et al., 1970). This behavior, combined with the expulsion of the larval gut contents may be effective in deterring some insect predators and parasites. The ability of larvae to suspend themselves below a leaf on a silk thread has been described for all instars of Hypothyris euclea (Gilbert, 1969) and for the first two instars of the larvae of Hymenitis nero (Young, 1972). This "drop-off" behavior presumably reduces predation by ants, which elicit the behavior by walking on the dorsal leaf surface. The "drop-off" behavior does not occur when other insects walk on the leaf and it cannot be elicited mechanically (Gilbert, 1969; Young, 1972). "Drop-off" behavior or suspension by silk threads under other circumstances was never observed in any larvae of Limoncocha ithomiines.

Eggs and young larvae may also occasionally fall prey to cannibalism by their own species. I once placed several large leaves of Solanum coconilla in a plastic bag containing a nine-day old brood of fourth instar M. isthmia larvae. One of the leaves had a cluster of 25 M. isthmia eggs on it. Within a few hours this leaf--and the eggs on

it--had been devoured by the M. isthmia larvae. As there was plenty of other leaf tissue left, the eggs were apparently eaten inadvertently as a consequence of being on the leaf chosen by the older larvae. Selection should favor oviposition behavior in female M. isthmia that minimizes the chances of such occurrences. This may be another reason for the preference shown by ovipositing M. isthmia females for well-isolated foodplants (see Chapter 6).

CHAPTER VI
THE ITHOMIINAE-SOLANACEAE INTERFACE

In their review of the larval foodplant relationships of the butterflies, Ehrlich and Raven (1964) concluded that the plant-herbivore "interface" may be the major zone of interaction responsible for generating terrestrial organic diversity. These authors proposed an evolutionary sequence progressing by stepwise adaptive responses between plants and herbivores. Recognizing that the adaptive responses of the species in one trophic level affected the fitness of the species in the other, they termed this process "coevolution." Secondary plant compounds, such as the alkaloids occurring in the Solanaceae, were recognized as being of primary importance in this evolutionary sequence. Plant groups that developed, by mutation or recombination, effective chemical deterrents to herbivores, evolved and diversified under the protection of this biochemical shield. Several major groups of plants have apparently evolved in this way, including the Solanaceae, which are not well represented among larval foodplants of the Lepidoptera (Ehrlich and Raven, 1964). The alkaloid barrier erected by the Solanaceae, however, was breached by early ithomiine stock, which subsequently entered a new "adaptive zone." Relatively free from the competition of other herbivores, and possessing the basic physiological ability to tolerate solanaceous alkaloids, this ancestral stock was able to diversify rapidly on the closely related species of the Solanaceae.

In addition to tolerating or detoxifying the potent alkaloids in solanaceous plants, it is generally assumed that many ithomiines actually sequester these poisonous compounds, which in turn make them unpalatable to vertebrate predators. Although the extensive participation of the Ithomiinae in mimicry complexes provides circumstantial evidence for their distastefulness, little empirical evidence exists (see Chapter 7).

Plant Defenses and Larval Adaptations

The considerable mechanical and chemical defenses of the Solanaceae were briefly characterized in Chapter 1. Among mechanical devices, particular attention was given to spines, trichomes, and various glandular and stellate hairs, although leaf toughness may also be important in affecting herbivory rates. Despite the demonstrated presence of a great number and variety of alkaloids in solanaceous plants, almost nothing is known about the effects of these compounds on the growth rates or viability of ithomiine or other lepidopterous larvae. The phytochemical ecology of ithomiine butterflies and their solanaceous foodplants is completely unstudied, but promises to be one of the most exciting and rewarding avenues of investigation into the coevolution of insect-plant relationships.

The data presented in Chapter 5 demonstrated that, among Limoncocha ithomiines that utilize more than one species of foodplant, larval development took considerably longer on solanaceous species that were armed (with spines and/or stellate or glandular pubescence) than on those

plants which lacked such mechanical defenses. Lack of chemical knowledge of these plants should temper the conclusion to be drawn from these data, but it seems quite likely that the mechanical devices of some solanaceous plants can have an adverse effect on ithomiine larval feeding efficiency.

The question has been recently raised as to the possibility of "absolute" plant defenses that could prevent larval feeding completely. Gilbert (1971) described one such deterrent, hooked trichomes, on Passiflora adenopoda. Species in the genus Passiflora serve as larval food-plants for Heliconius butterflies, but the widespread P. adenopoda is apparently immune to Heliconius herbivory as a result of the selective effect of the hooked trichomes. Gilbert (1971) suggests that the highly specific nature of these trichomes (they are not known to affect other groups of herbivores) indicates that they were evolved after the chemical defenses of the plant, which presumably act in a more general manner by excluding large classes of herbivores. Once most herbivores have been "filtered out" by chemical deterrents, Gilbert reasons, mechanical defenses specific for the remaining herbivores are selected for.

Rathcke and Poole (1975) recently suggested that the gregarious larvae of Mechanitis isthmia avoid the detrimental effects of spines on Solanum hirtum by spinning a silk webbing over the tops of the spines. Since silk production is nearly universal in lepidopterous larvae, they reasoned that the trichome-avoidance strategy used by M. isthmia should be available to Heliconius as well.

It is doubtful that there are any "absolute" defenses or responses in the "coevolutionary race" between insects and plants. What may appear

as an "absolute" now probably represents only a "step" in the Ehrlich and Raven (1964) sequence. Only by studying all the factors that affect the relationship between ithomiine larvae (e.g., mandible strength, assimilation efficiencies, microsomal oxidases in the midgut and other detoxification systems, etc.) and their foodplants (mechanical and chemical characteristics of different parts of the plant at different ages, nutritional content of leaves, etc.) will a full understanding of the coevolutionary steps that have led to the present situation be gained.

Larval Foodplant Relationships of the Ithomiinae

An attempt was made during this study to collect all the published records of larval foodplants for the Ithomiinae. The results of this literature research, combined with the larval foodplant information obtained during my Ecuadorian field work, are presented in Table 18. All eight tribes of the Ithomiinae are represented by these records, which include at least preliminary information on 71 species and subspecies in 26 genera.

Interpretations or conclusions drawn from the material in Table 18 must be made with caution, however, because, in the attempt to be all-inclusive, many vague and poorly documented records were included. Since some ithomiines are known to feed on Apocynaceae (see Table 18) and Gesneriaceae (W. A. Haber, pers. comm.), even records that merely state the family of the ithomiine foodplant have been included in Table 18. There is no way to check the accuracy of such records, however, since

Table 18. Larval Foodplant Records for the Ithomiidae.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER) *	FAMILY	LOCALITY†	SOURCE
TELLERVINAE				
TELLERVININI				
<u>Tellervo zoilus</u> <u>zollus</u> (Fabricius)	"a creeper, prob. <u>Aristolochia</u> ".	Aristol.	NG(1)	7
<u>Tellervo zoilus</u> <u>gelo</u> Waterhouse & Lyell	<u>Aristolochia</u> sp.	Aristol.	AU(1)	14
<u>Tellervo zoilus</u> <u>zollus</u> (Fabricius)	<u>Parsonia velutina</u>	Apocyn.	AU(2)	14, 17 27, 28
ITHOMIINAE				
TITHOREINI				
<u>Tithorea harmonia</u> <u>megara</u> (Latreille)	<u>Echites</u> sp.	Apocyn.	TR	6, 25
<u>Tithorea harmonia</u> <u>salvadores</u> Staudinger	<u>Mesechites trifida</u> Jacq.	Apocyn.	TR	22
<u>Tithorea tarracina</u> <u>pinthias</u> Godman & Salvin	<u>Urechites karwinsky</u> Mueller	Apocyn.	ES	18
	"large thick-leaved creeper" (<u>Echites</u> ?)	Apocyn. (?)	CR(6)	19, 22
MELINAEINI				
<u>Melinaea menophilus</u> <u>menophilus</u> (Hewitson)	<u>Juanulloa</u> sp. (7354)	Solan.	EC(1)	1
MECHANITINI				
<u>Forbestra truncata</u> <u>juntana</u> (Haensch)	<u>Solanum anceps</u> R. & P. (7315)	Solan.	EC(1)	1

Table 18 - continued.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY†	SOURCE
	"arrebenta-cavallo" [<u>Solanum arrebenta</u>]	Solan.	BR(7)	15
	"coirana" [prob. <u>Cestrum nocturnum</u>]	Solan.	BR(7)	15
	"fumo branco"	Solan.	BR(7)	15
	"Maria branca"	Solan.	BR(7)	15
	"joa manso"	Solan.	BR(7)	15
	"manaca" [<u>Brunfelsia hopeana</u> Benth.]	Solan.	BR(7)	15
	"trombeteira" [<u>Datura arborea</u> L.]	Solan.	BR(7)	15
<u>Mechanitis mazaeus</u> <u>mazaeus</u> Hewitson	<u>Solanum</u> sp. (7333)	Solan.	EC(1)	1
<u>Mechanitis menapis</u> <u>mantineus</u> Hewitson	<u>Solanum mammosum</u> L.	Solan.	EC(2)	2
	<u>Solanum quitoense</u> Lam.	Solan.	EC(2)	2
<u>Mechanitis menapis</u> <u>saturata</u> Godman	<u>Solanum</u> near <u>aculeatissimum</u> (#16)	Solan.	GR(3)	21
<u>Mechanitis messenoides</u> C. & R. Felder	<u>Solanum coconilla</u> Huber (7301)	Solan.	EC(1)	1
	<u>Solanum pectinatum</u> Dun. (7303)	Solan.	EC(1)	1
<u>Mechanitis messenoides</u> <u>deceptus</u> Butler	<u>Solanum quitoense</u> Lam.	Solan.	EC(3)	2
<u>Mechanitis polymnia</u> <u>doryssus</u> Bates	<u>Solanum</u> sp. (near <u>rugosum</u>) (#12)	Solan.	CR(3)	21
	<u>Solanum rugosum</u> Dun. (#7)	Solan.	CR(2)	21
<u>Mechanitis polymnia</u> <u>polymnia</u> (L.)	<u>Solanum aculeatissimum</u> Jacq.	Solan.	SU	32
<u>Mechanitis</u> sp.	<u>Solanum</u> sp. (7326)	Solan.	EC(1)	1
<u>Mechanitis</u> sp.	<u>Solanum</u> sp. (rel. <u>lancaeifolium</u>) (7313)	Solan.	EC(1)	1
<u>Scada batesi</u> Haenach	<u>Solanum</u> (?) (7331)	Solan.	EC(1)	1
<u>Xanthocleis aedesia</u> <u>aedesia</u> (Dblidy & Hewit.)	<u>Cyphomandra crassicaulis</u> (Ortega)	Solan.	VZ(2)	20
<u>Xanthocleis psidii</u> L.	"manaca" [<u>Brunfelsia hopeana</u> Benth.]	Solan.	BR	16
<u>Xanthocleis psidii</u> Ino (C. & R. Felder)	<u>Cyphomandra hartwegii</u> Benth. (7312)	Solan.	EC(1)	1

Table 18 - continued.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY†	SOURCE
NAPEOGENINI				
<u>Hypothyris daeta</u> (Boisduval)	<u>Solanum argenteum</u>	Solan.	BR(1)	3, 15
<u>Hypothyris euclea laphria</u> (Dblly)	"bushy Solanaceae"	Solan.	BR(8)	13
<u>Hypothyris euclea leucania</u> (Bates)	<u>Solanum rugosum</u> (#7)	Solan.	CR(2)	21
	<u>Solanum</u> sp. (near <u>rugosum</u>) (#12)	Solan.	CR(3)	21
<u>Hypothyris euclea peruviana</u> (Staudinger)	<u>Solanum bicolor</u> Willd. (7316)	Solan.	EC(1)	1
<u>Hypothyris fluona berna</u> (Haensch)	<u>Solanum</u> sp. (prob. aff. <u>lanceaefolium</u>) (7311)	Solan.	EC(1)	1
<u>Hypothyris fulminans satura</u> Haensch	<u>Solanum</u> (aff. <u>schlechtendallianum</u>) (7340)	Solan.	EC(1)	1
<u>Napeogenes corena caucayaensis</u> Fox & Real	<u>Lycianthes</u> sp. (7325)	Solan.	EC(1)	1
<u>Napeogenes pharo avila</u> Haensch	<u>Lycianthes</u> (aff. <u>howardiana</u> D'Arcy) (7307)	Solan.	EC(1)	1
<u>Placidula euryanassa</u> C. & R. Felder	"trombeteira" [<u>Datura arborea</u> L.]	Solan.	BR(1)	3, 4, 15
	<u>Cyphomandra crassicaulis</u> (Ortega)	Solan.	BR(4)	8
	<u>Datura arborea</u> L.	Solan.	BR(4)	8
	<u>Datura suaveolens</u> Humb. & Bonpl.	Solan.	BR(4)	8
ITHOMIINI				
<u>Ithomia agnosia agnosia</u> Hewitson	<u>Physalis pubescens</u> L. (7321)	Solan.	EC(1)	1
<u>Ithomia amarilla</u> Haensch	<u>Solanum</u> sp. (7327)	Solan.	EC(1)	1
<u>Ithomia derasa salapia</u> Hewitson	<u>Physalis angulata</u> L. (7343)	Solan.	EC(1)	1
<u>Ithomia diasia hippocrenis</u> Bates	<u>Lycianthes</u> sp. (#6)	Solan.	CR(2)	21
<u>Ithomia drymo Hübner</u>	"Solaneé"	Solan.	BR(1)	3
	<u>Cestrum nocturnum</u> L.	Solan.	BR(4)	8
	<u>Cestrum parqui</u> L'Herit.	Solan.	BR(4)	8

Table 18 - continued.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY†	SOURCE
<u>Ithomia heraldica</u> <u>heraldica</u> Bates	<u>Capsicum</u> (?) sp. (#18)	Solan.	CR(3)	21
<u>Ithomia patilla</u> <u>patilla</u> Hewitson	<u>Capsicum</u> <u>tetramericum</u> (#24)	Solan.	CR(3)	21
OLERIINI				
<u>Aeria elara</u> (Hewitson)	"apocynaceous vine"	Apocyn.	BR(9)	11
<u>Aeria eurimedia</u> <u>agna</u> (Godman & Salvin)	<u>Echites</u> sp.	Apocyn.	TR	24
<u>Oleria agarista</u> <u>agarista</u> (C. & R. Felder)	<u>Lycianthes</u> (aff. <u>maxonii</u> Standl.) (7332)	Solan.	EC(1)	1
	<u>Solanum</u> <u>evolvulifolium</u> Greenm. (7329)	Solan.	EC(1)	1
	<u>Solanum</u> (aff. <u>lancaeifolium</u> Jacq.) (7310)	Solan.	EQ(1)	1
	<u>Solanum</u> sp. (7319)	Solan.	EC(1)	1
<u>Oleria zelica</u> <u>pagasa</u> (Druce)	<u>Solanum</u> <u>evolvulifolium</u> Greenm.	Solan.	CR(4)	35
DIRCENNINI				
<u>Ceratinia poecila</u> <u>poecila</u> (Bates)	<u>Solanum</u> (aff. <u>antillarum</u> Schulz) (7305)	Solan.	EC(1)	1
<u>Ceratiscada canaria</u> Brown & d'Almeida	<u>Solanum</u> <u>caavurana</u> Vell.	Solan.	BR(3)	12
<u>Dircenna dero</u> Hubner	<u>Brunfelsia</u> <u>calycina</u> var. <u>floribunda</u> Hort.	Solan.	UR(1)	10
	<u>Brunfelsia</u> <u>hopeana</u> Benth.	Solan.	BR(4)	8
	<u>Solanum</u> <u>auriculatum</u> Ait.	Solan.	BR(4)	8
	<u>Solanum</u> <u>sisymbriifolium</u> Lam.	Solan.	BR(4)	8
	<u>Solanum</u> <u>auriculatum</u> Ait.	Solan.	BR(5)	9
<u>Dircenna euchytna</u> C. & R. Felder	<u>Solanum</u> (near <u>ochraceo-ferrugineum</u> (Dun.)) (#10)	Solan.	CR(2)	21
<u>Dircenna klugii</u> (Geyer)	<u>Solanum</u> <u>lancaeifolium</u> Jacq. (#9)	Solan.	CR(3)	21
	<u>Solanum</u> sp. (near <u>rugosum</u>) (#12)	Solan.	CR(3)	21
<u>Dircenna olyraa</u> <u>lonera</u> Butler & Druce	<u>Cyphomandra</u> <u>hr-twegii</u> (Miers) (#14)	Solan.	CR(3)	21

Table 18 - continued.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY*	SOURCE
<u>Dircenna</u> <u>relata</u> Butler & Druce	<u>Solanum hispidum</u> Pers.	Solan.	CR(5)	34
	<u>Solanum</u> sp. (near <u>rugosum</u>) (#12)	Solan.	CR(3)	21
	<u>Solanum</u> sp. (#22)	Solan.	CR(3)	21
	<u>Solanum</u> sp. (#23)	Solan.	CR(3)	21
<u>Episcada</u> <u>clausina</u> <u>striposita</u> Haensch	"plusieurs Solanées"	Solan.	BR(1)	3
	<u>Capsicum</u> sp.	Solan.	BR(10)	12
<u>Prittwitzia</u> <u>hymenaea</u> (Prittwitz)	"d'une Solanée"	Solan.	BR(1)	3
	<u>Brunfelsia</u> <u>hopeana</u> Benth.	Solan.	BR(4)	8
	<u>Cestrum</u> <u>nocturnum</u> L.	Solan.	BR(4)	8
	<u>Cestrum</u> <u>parqui</u> L'Herit.	Solan.	BR(4)	8
	<u>Solanum</u> <u>sisymbriifolium</u> Lam	Solan.	BR(4)	8
	<u>Solanum</u> <u>sisymbriifolium</u> Lam.	Solan.	BR(5)	9
	<u>Brunfelsia</u> <u>calycina</u> var. <u>floribunda</u> Hort.	Solan.	UR(1)	10
	<u>Cestrum</u> <u>nocturnum</u> L.	Solan.	UR(1)	10
	<u>Cestrum</u> <u>parqui</u> L'Herit.	Solan.	UR(1)	10
<u>Pteronymia</u> <u>euritea</u> Cramer	"plusieurs Solanées"	Solan.	BR(1)	3
<u>Pteronymia</u> <u>notilla</u> Butler & Druce	<u>Solanum</u> <u>roblense</u> (#4)	Solan.	CR(3)	21
	<u>Cestrum</u> <u>megalophyllum</u> Dun.	Solan.	CR(4)	36
	<u>Capsicum</u> sp.	Solan.	CR(4)	36
<u>Pteronymia</u> <u>sparsa</u> Haensch	<u>Solanum</u> (aff. <u>nudum</u> H.B.K.) (7335)	Solan.	EC(1)	1
<u>Pteronymia</u> <u>sylvo</u> (Hübner)	<u>Solanum</u> <u>argenteum</u>	Solan.	BR(1)	3, 15
	other Solanaceae	Solan.	BR(1)	3, 15
X-1 (5051)	<u>Solanum</u> sp. (7336)	Solan.	EC(1)	1

Table 18 - continued.

TRIBE AND SPECIES	FOOD PLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY†	SOURCE
GODYRIDINI				
<u>Epityches eupompe</u> Hübner	"una Solanée"	Solan.	BR(1)	3, 4
	<u>Witheringia</u> sp.	Solan.	BR(1)	15, 30
	<u>Cestrum nocturnum</u> L.	Solan.	BR(4)	8
	<u>Cestrum parqui</u> L'Herit.	Solan.	BR(4)	8
	<u>Cestrum nocturnum</u> L.	Solan.	UR(1)	10
	<u>Cestrum parqui</u> L'Herit.	Solan.	UR(1)	10
	<u>Cestrum</u> sp. (7338)	Solan.	EC(1)	1
	<u>Solanaceae</u> (prob. <u>Cestrum</u> sp.) (7324)	Solan.	EC(1)	1
<u>Godyris zavaleta amaretta</u> (Haensch)	<u>Solanum brenesii</u> Morton & Standley	Solan.	CR(4)	37
<u>Godyris zavaleta caesiopicta</u> (Niepett)	<u>Solanaceae</u> (#13)	Solan.	CR(3)	21
<u>Godyris zygia</u> Godman & Salvin	<u>Solanaceae</u> (prob. <u>Cestrum</u> sp.) (7324)	Solan.	EC(1)	1
<u>Heterosais edessa nephele</u> (Bates)	"une Solanée"	Solan.	BR(1)	3
	"Solanaceae" (#13)	Solan.	CR(3)	21
<u>Hymenitis andromica</u> <u>lyra</u> Salvin	<u>Cestrum</u> sp.	Solan.	CU	23
<u>Hymenitis cubana</u> Herrich-Schäffer	<u>Cestrum standleyi</u> Morton	Solan.	CR(4)	33
<u>Hymenitis nero</u> (Hewitson)	<u>Cestrum latifolium</u> Lam.	Solan.	TR	6
<u>Hypoleria ocales</u> (Hewitson)	"une Solanée"	Solan.	BR(1)	3
<u>Hypoleria oreas</u> Weymer	<u>Solanaceae</u> (7353)	Solan.	EC(1)	1
<u>Hypoleria orolina</u> (Hewitson)	<u>Solanaceae</u>	Solan.	BR(11)	5
<u>Macclungia salonina</u> (Hewitson)	<u>Solanaceae</u> (prob. <u>Cestrum</u>) (7324)	Solan.	EC(1)	1
<u>Pseudoscada timna</u> <u>timna</u> (Hewitson)	<u>Brunfelsia</u> sp. (7330)	Solan.	EC(1)	1
<u>Thyridia confusa</u> <u>psamathe</u> Godman & Salvin	<u>Brunfelsia calycina</u> var. <u>floribunda</u> Hort.	Solan.	EC(3)	2

Table 18 - continued.

TRIBE AND SPECIES	FOODPLANT (VOUCHER NUMBER)*	FAMILY	LOCALITY ⁺	SOURCE
<u>Thyridia</u> <u>themisto</u> Hubner				
	<u>Brunfelsia</u> sp.	Solan.	BR(6)	15
	"jasmín serra"	Solan.	BR(6)	15
	"primavera"	Solan.	BR(6)	15
	<u>Brunfelsia</u> <u>hopeana</u> Benth.	Solan.	BR	16
	<u>Brunfelsia</u> <u>hopeana</u> Benth.	Solan.	BR(4)	8
	<u>Solanum</u> <u>auriculatum</u> Ait.	Solan.	BR(5)	9
	<u>Brunfelsia</u> <u>calycina</u> var. <u>floribunda</u> Hort.	Solan.	UR(1)	10
UNKNOWN SPECIES				
(immature stages not raised to adult)	<u>Witheringia</u> <u>riparia</u> H.B.K. (7328)	Solan.	EC(1)	1
(immature stages not raised to adult)	<u>Solanum</u> aff. <u>intermedium</u> Sendt. (7346)	Solan.	EC(1)	1
Source:				
1. Present study	14. Common & Waterhouse, 1972	26. Kaye, 1921		
2. Drummond, unpublished	15. Costa-Lima, 1936	27. McGubbin, 1971		
3. d'Almeida, 1922	16. Costa-Lima, 1950	28. Manski, 1960		
4. d'Almeida, 1938	17. D'Abreu, 1971	29. Moreira, 1881		
5. d'Almeida, 1944	18. Edgar et al., 1974	30. Muller, 1886		
6. Barcant, 1970	19. Fountaina, 1913	31. Rathcke & Poole, 1975		
7. Barrett & Burns, 1951	20. Fox, 1967	32. Sepp, 1828		
8. Biezanko, 1960a	21. Gilbert, 1969	33. Young, 1972		
9. Biezanko, 1960b	22. Gilbert & Ehrlich, 1970	34. Young, 1973		
10. Biezanko et al., 1957	23. Gundlach, 1881	35. Young, 1974a		
11. Brown, 1976b	24. Guppy, 1894	36. Young, 1974b		
12. Brown & d'Almeida, 1970	25. Guppy, 1904	37. Young, 1974c		
13. Brown & Benson, 1974				

Table 18 - continued.

* Common names are those given by the authors cited. Scientific names in [brackets] following a common name have been added by the present author where possible. Several scientific names given in the literature have been changed or modified to conform with recent taxonomic treatment (D'Arcy, 1973).

†LOCALITY: Unnumbered localities indicate that no specific locations within the country were given in the source publication.

AU: Australia	(1) Queensland, Claudie River, Cape York Peninsula.
	(2) Queensland, Cairns.
BR: Brazil	(1) Presumably southern Brazil, especially state of Rio de Janeiro (precise localities not given).
	(2) States of São Paulo, Goiás, southern Minas Gerais (precise localities not given).
	(3) Espírito Santo, Serra da Mantiqueira (near Santa Teresa).
	(4) Sueste, Rio Grande do Sul.
	(5) Zona Missioneira, Rio Grande do Sul.
	(6) Ceara (Dias da Rocha), Rio de Janeiro, São Paulo, Santa Catharina.
	(7) Minas Gerais, Belo Horizonte.
	(8) Espírito Santo, Linhares.
	(9) Goiás, Gojas Velho and Aragarcus.
	(10) Rio de Janeiro, Xerem.
	(11) Minas Gerais (precise locality not given).
CR: Costa Rica	(1) Guanacaste Prov., Finca La Pacifica (5.5 km NW Cañas), 45 m elev.
	(2) Heredia Prov., Finca La Selva (5 km SE Puerto Viejo), 105 m elev.
	(3) Puntarenas Prov., Finca Las Cruces (7.8 km S San Vito), 950 m elev.
	(4) Heredia Prov., Cuesta Angel (7 km SW Cariblanco), 950 m elev.
	(5) San Jose Prov., Bajo la Hondura (on the Rio Clara), 900 m elev.
	(6) Limon Prov., Guapiles.
CU: Cuba	
EC: Ecuador	(1) Napo Prov., Limoncocha (on the Rio Napo), 280 m elev.
	(2) Pichincha Prov., Tinalandia (10 km E Santo Domingo), 680 m elev.
	(3) Pastaza Prov., Puyo, 1000 m elev.
ES: El Salvador	
NG: New Guinea	(1) Papuan Region.
PR: Peru	(1) Huanuco Prov., Tingo Maria.
SU: Surinam	
TR: Trinidad	
UR: Uruguay	(1) Paysandú and Colonia
VZ: Venezuela	(1) Rancho Grande Exp. Sta., near Maracay.
	(2) El Valle, Sucre.

no specific plant names are given. It may be tempting to entomologists to simply list the family name normally associated with the Ithomiinae, rather than determine the true identity of the foodplant by consulting a botanist or an appropriate botanical text.

In one publication (Costa Lima, 1936) foodplants of Brazilian ithomiines were listed by common names (in Portuguese) rather than by their Latin counterparts. By comparing these common names with those given in other papers that also included the scientific names, a few of these plants have been identified. In all cases where only common names of plants were given, these have been entered in Table 18, followed by my ad hoc determination of the Latin name in brackets.

Another source of error in these data may be the mis-association of ithomiines with foodplants. For example, Gilbert (1969) presented 18 associations between Costa Rican ithomiines and solanaceous plants, but because of the limited field time available, he was able to verify only 5 of these by rearing the immatures to the adult stage. The remainder of the associations were made by comparing the size and shape of eggs found on solanaceous plants with eggs dissected from female ithomiines. Although Gilbert claimed it was possible in most cases to match the eggs with great certainty, the associations remain unverified by actual rearings.

Many of the Limoncocha Solanaceae submitted to Dr. D'Arcy for determination have not yet been completely identified, owing to the scarcity of Ecuadorian Solanaceae in museum collections and the primitive state of the taxonomy of Amazonian Solanaceae. As a result, many species have so far been identified only to genus, although for some, the nearest

relative or affinity can be given in Tables 5 and 18. In addition, the plant names given by some authors (e.g., Rathcke and Poole, 1975; Gilbert, 1969; d'Almeida, 1922) were apparently not verified by botanists, and in view of the many mis-identifications and lengthy synonymies in the history of the Solanaceae (D'Arcy, 1973), further caution is needed when using these names.

Patterns of Foodplant Utilization

Not surprisingly, perhaps, many of the foodplant records in Table 18, especially those from Brazil, are of common garden plants, often grown as crops (e.g., Lycopersicon esculentum and Cyphomandra crassicaulis) or ornamentals (e.g., Brunfelsia hopeana, B. calycina, Datura arborea). Undoubtedly, most of these occur in a semi-wild state as well, especially in clearings and along roadsides, areas frequently visited by collectors. Only in the three studies that have focused on the foodplant relationships of a forest community of ithomiines (Gilbert, 1969; Young, 1972, 1973, 1974a,b,c; present study) have non-cultivated Solanaceae been well-represented in the larval foodplant records. The Brazilian records, if considered alone, would probably present an extremely biased picture of foodplant utilization of the Ithomiinae by overemphasizing the ithomiine species with broad foodplant tolerances and high vagility (e.g., Mechanitis lysimnia, Prittwitzia hymenaea, Thyridia themisto). A meaningful understanding of the foodplant relationships of the Ithomiinae and of the coevolutionary pathways that led to the present relationships await more detailed studies of natural communities.

Despite these difficulties, however, it is of interest to attempt to summarize the foodplant data presently available for the Ithomiinae.

The tiered histogram in Figure 54 provides a broad overview of these data at the tribal level. Ithomiinae have been reported feeding on eleven solanaceous genera, but, not unexpectedly, over half of the foodplant records involve species of the extremely large genus Solanum. The scarcity of foodplant records in some tribes (e.g., Tithoreini and Melinaeini) makes generalizations or tribal comparisons difficult, but it is apparent that the Mechanitini and Dircennini display the broadest patterns of foodplant utilization. These two tribes have been reported from six and five genera of Solanaceae, respectively, including at least four subgenera of Solanum. In the Mechanitini this pattern is mirrored by the broad foodplant utilization of many Mechanitis species. Fox (1967) has pointed out the extreme intraspecific variability in color pattern of many species in the genus Mechanitis and suggested that these "plastic species" have apparently developed genetic traits that enable them to evolve rapidly and to take advantage of the ecological rearrangement of tropical forests that attended the cyclic glaciation of the northern hemisphere. As the tropical forest refugia expanded in the interglacial periods, one consequence of the renewed sympatry of these partially differentiated species and subspecies would be a "genetic revolution" (Mayr, 1954) resulting from population hybridizations. The recombinations resulting from such hybridizations could alter the gene complexes controlling foodplant specificity and result in broader foodplant tolerances in both ovipositing females and larvae. Broad foodplant tolerances could be selectively advantageous to individuals in populations expanding their range beyond that of their original foodplants.

Figure 54. Larval Foodplant Relationships of Ithomiine Tribes.

Scale at left indicates the number of butterfly-foodplant relationships reported for each combination of ithomiine tribe and solanaceous genus.

At present, the Tithoreini have been reported feeding only on Apocynaceae and the Melinaeini only on Juanulloa. The other six ithomiine tribes have all been reported on at least three solanaceous genera. Only the genus Solanum has been reported among the foodplants of all six of these tribes, although Cestrum has been reported for four of them. Undoubtedly, however, the eleven genera reported here and also many others in the Solanaceae will become better represented among the ithomiine tribes as the foodplants of more species are discovered.

It was possible to place most of the identified Solanum species in the appropriate subgenus. So far, six of the seven subgenera of this large genus have been reported as ithomiine foodplants. Somewhat surprisingly, the subgenus Leptostemonum, containing many heavily spined or otherwise armed species (D'Arcy, 1973), is the best represented. Many of these are weedy species, however, and are thus more likely to be encountered by entomologists, which may explain their strong representation among reported foodplants.

The only published records of ithomiines feeding of non-solanaceous plants are those for Tithorea (Tithoreini) and Aeria (Oleriini) feeding on Apocynaceae, although the records for Aeria are poorly documented. At least one species of Apocynaceae (Parsonia velutina) has been reported as a foodplant of Tellervo zoilus (Tellervinae) in Australia (see Table 18) raising the possibility that the original foodplants of primitive Ithomiidae were in the Apocynaceae and that the switch to the Solanaceae occurred later in the evolution of the group. The close relationship between the Ithomiidae and the Danaidae (Gilbert and Ehrlich, 1970) discussed

earlier is further supported by the fact that Tellervo has the same food-plant affinities as the Danaidae, Asclepiadaceae and Apocynaceae.

The importance of the Apocynaceae in the repertoire of larval foodplants of primitive Ithomiinae (namely, Tithorea) has been recently discussed by Edgar et al. (1974). These authors suggested that the ancestral larval foodplants of the Ithomiidae (presumably Apocynaceae) contained both pyrrolizidine alkaloids (PA), which provided male ithomiines with the precursors for sex pheromone manufacture (see Chapter 4), and cardiac glycosides, which rendered both sexes unpalatable. After the switch to the Solanaceae, a family that lacks PAs, adult male ithomiines began visiting flowers of PA-containing plants (Asteraceae, Boraginaceae) to obtain the compounds needed for the manufacture of sex pheromones essential to successful courtship. Presumably, the toxic alkaloids in the Solanaceae allowed the continuance of the unpalatability previously provided by the Apocynaceous cardenolides. This is a tenuous theory, however, erected by analogy to a coevolutionary sequence proposed for the Danaidae and their larval foodplants, and because of the established presence of a dihydropyrrolizine in Urechites karwinsky, the larval foodplant of Tithorea harmonia salvadores in El Salvador.

Foodplant Specificity of Limoncocha Ithomiines

The foodplant relationships of the ithomiines studied at Limoncocha are presented diagrammatically in Figure 55. Of the 53 Ithomiinae recorded from Limoncocha, foodplants were found for 27, although two of these ithomiines remain unidentified since they were not raised through to the adult stage. One of the five species of Mechanitis occasionally ,

Figure 55. Larval Foodplants of Limoncocha Ithomiinae.

laid small clusters of eggs on Solanum sp. 7313, but, as explained below, the larvae were unable to feed on the leaves of this plant and thus it is not known which Mechanitis species laid the eggs. (Mechanitis eggs are not consistently different enough in size or shape to allow their identification.) Of the 42 species of solanaceous plants found at Limoncocha, 33 were utilized by at least one ithomiine species. As stated earlier, however, many more species of Solanaceae undoubtedly exist at Limoncocha and thus it is not possible to say what percentage of the solanaceous flora at Limoncocha is utilized by the Ithomiinae. In addition, the fact that no early stages were found on ten of the solanaceous plants observed at Limoncocha (despite repeated searches of most of these) does not eliminate the possibility that they serve as ithomiine foodplants. The low densities of immature stages of most ithomiine species (see next section) make their discovery difficult. For example, Witheringia riparia was searched repeatedly for a period of over four months before eggs and larvae were found on the leaves (unfortunately, these immatures did not survive to maturity).

Based on the information gathered to date at Limoncocha, the great majority of ithomiines in this community lay their eggs and complete their life cycle on a single foodplant (Figure 56). In other words, the ithomiine community at Limoncocha exhibits high foodplant specificity. Only five species of ithomiines (19%) were found to utilize more than one foodplant (Figure 56), and three of these were in the genus Mechanitis (Figure 55). Likewise, the degree of overlap in foodplant utilization by ithomiines is quite low, with 85% of the solanaceous hosts supporting only one species of ithomiine (Figure 57).

Figure 56. Numbers of Solanaceous Foodplants Utilized by Species of Ithomiinae at Limoncocha.

Figure 57. Numbers of Ithomiinae Supported by Species of Solanaceae at Limoncocha.

Similar patterns of high foodplant specificity have been found in the ithomiine communities studied in Costa Rica by Gilbert (1969) at La Selva (5 of 5 species utilized one foodplant) and San Vito (9 of 11 species utilized one foodplant) and by Young (1972, 1974a,b,c) at Cuesta Angel (3 of 4 species utilized one foodplant). Such high foodplant specificity exhibited by Ithomiinae in Costa Rica and Ecuador suggests that the diversity of the family Solanaceae has influenced the diversity of the Ithomiinae by providing a vast array of potential foodplants on which ithomiines have specialized.

Although members of the Solanaceae share a basic chemical similarity, the alkaloid content of each species is probably qualitatively and quantitatively unique. Likewise, the Ithomiinae share a physiological ability to metabolize solanaceous tissues, but the specific chemical composition of the larval foodplant probably requires a corresponding enzymatic specificity on the part of the butterfly utilizing it. As selection favors increased efficiency on a particular foodplant (e.g., due to the advantage of reducing generation time to reduce rates of juvenile parasitism and predation), the increasing physiological specialization on the part of the butterfly gradually narrows its foodplant tolerance. The exact nature and degree of this specialization and its consequences have not been investigated for any ithomiine, although such studies are clearly needed. A few preliminary observations on the larval tolerances of Mechanitis isthmia were made during this study, however.

Briefly summarized, the M. isthmia feeding experiments led to two conclusions. First, freshly hatched (naive) M. isthmia larvae will feed and develop on any foodplant normally oviposited on by females of this

species, regardless of the foodplant chosen for oviposition by their own female parent. Second, if the larvae first feed on one foodplant and are later transferred to another, they will rarely feed on the second plant and almost never complete development. Thus the broad larval tolerances to foodplants exhibited by M. isthmia are characteristic only of naive larvae.

Freshly hatched M. isthmia larvae were also placed on two solanaceous plants fed upon by other Limoncocha Mechanitis but not used by M. isthmia. Sixteen M. isthmia larvae placed on Solanum sp. 7333 (the foodplant of M. mazaeus) fed and developed normally through second instar (lack of available food ended the experiment here). Fifty-two M. isthmia larvae (in three groups) placed on Solanum pectinatum (a foodplant of M. lysimnia and M. messenoides) failed to complete the first instar, apparently unable to cope with the plant's dense stellate and glandular pubescence in which the larvae appeared to founder. This paralleled the experience of newly hatched larvae of an unknown Mechanitis species that laid two egg clusters on Solanum sp. 7313, on which the larvae were unable to complete the first instar, apparently because of the trichomes and dense stellate pubescence. Thus, it appears that mechanical, as well as chemical, defenses of plants require specialized adaptations on the part of the larvae that are able to successfully utilize them as foodplants.

Utilization of Larval Foodplants at Limoncocha

The great under-utilization of solanaceous leaf tissue by Limoncocha ithomiines was alluded to in Chapter 5, and the low densities of immature

stages were attributed to high levels of parasitism (especially of eggs) and predation (especially of larvae) acting on relatively low daily rates of ithomiine reproduction.

To quantify the low densities of juvenile ithomiines, and to provide some estimates of the abundances of solanaceous foodplants, vegetational surveys were conducted in areas of both primary and secondary forests as described in Chapter 2. The results of these surveys are given in Tables 19 through 23. The surveys at the two .25 hectare primary forest plots, Site 4 (Table 19) and Site 5 (Table 20), will be considered first (see map, Figure 2).

The number of solanaceous plants present at Site 4 (Table 19) was exceedingly low, there being only 16 individuals of 4 species, for a density of 64 plants per hectare. By contrast, Site 5 (Table 20) had 8 species and 224 individual plants, for a density of 896 plants per hectare. The most probable reason for the vegetational difference in the two sites was the periodic flooding that occurred at Site 4 (see Chapter 3). Indeed, six of the plants at Site 4 (two Lycianthes, two Solanum sp. 7319, and two Solanum sp. 7327) were growing not from the ground but were rooted in the decaying trunks of fallen trees so that their root systems, located at least 80 cm above the ground, were thus free from flooding. All the remaining plants were growing in the subplots that experienced little or no flooding. The forest of the NT observation area (Site 5) does not flood, however, and the solanaceous plants at this site were greater in number and were distributed throughout the plot.

Table 19. Numbers of Solanaceous Plants and Ithomine Immatures at Site 4.

	NUMBER OF PLANTS PRESENT	AVERAGE HEIGHT OF PLANT (m)	TOTAL NUMBER OF LEAVES	AVERAGE NUMBER OF LEAVES PER PLANT	NUMBER OF EGGS PRESENT	NUMBER OF LARVAE PRESENT	NUMBER OF IMMATURES PER LEAF
<u>Brunfelsia</u> sp. (7330)	7	1.0	395	56.4	0	0	0
<u>Lycianthes</u> sp. (7307)	2	1.2	78	39.0	0	0	0
<u>Solanum</u> sp. (7319)	2	0.8	27	13.5	0	0	0
<u>Solanum</u> sp. (7327)	5	0.9	59	11.8	0	0	0
Totals (4 species)	16		559		0	0	0

Table 20. Numbers of Solanaceous Plants and Ithomiine Immatures at Site 5.

	NUMBER OF PLANTS PRESENT	AVERAGE HEIGHT OF PLANT (m)	TOTAL NUMBER OF LEAVES	AVERAGE NUMBER OF LEAVES PER PLANT	NUMBER OF EGGS PRESENT	NUMBER OF LARVAE PRESENT	NUMBER OF IMMATURES PER LEAF
<u>Cestrum</u> sp. (7338)	1	0.3	10	--	0	0	0
<u>Solanum</u> sp. (7313)	2	1.4	42	21.0	0	0	0
<u>Solanum</u> sp. (7327)	171	0.6	1629	9.5	5	3	0.005
<u>Solanum</u> sp. (7331)	1	0.3	2	--	0	0	0
<u>Solanum</u> sp. (7335)	3	0.3	58	19.3	0	0	0
<u>Solanum</u> sp. (7346)	5	1.5	161	32.2	0	0	0
<u>Witheringia</u> <u>riparia</u>	35	0.6	996	28.5	2	1	0.003
<u>Solanaceae</u> sp. (7353)	1	1.1	9	--	5	4	1.000
Totals (9 species)	224		2935		12	8	0.007

Table 21. Numbers of Solanaceous Plants and Ithomiine Immatures at Site 1.

	NUMBER OF PLANTS PRESENT	AVERAGE HEIGHT OF PLANT (m)	TOTAL NUMBER OF LEAVES	AVERAGE NUMBER OF LEAVES PER PLANT	NUMBER OF EGGS PRESENT	NUMBER OF LARVAE PRESENT	NUMBER OF IMMATURES PER LEAF
<u>Lycianthes</u> sp. (7307)	1	--	72	--	0	0	0
<u>Solanum anceps</u>	1	0.6	6	--	0	0	0
<u>Solanum coconilla</u>	68	0.7	719	10.6	61	0	0.085
<u>Solanum</u> sp. (7305)	1	2.0	21	--	25	16	1.952
<u>Solanum</u> sp. (7319)	4	0.7	30	7.5	0	0	0
Totals (5 species)	75		848		86	16	0.120

Table 22. Numbers of Solanaceous Plants and Ithomine Immatures at Site 6.

	NUMBER OF PLANTS PRESENT	AVERAGE HEIGHT OF PLANT (m)	TOTAL NUMBER OF LEAVES	AVERAGE NUMBER OF LEAVES PER PLANT	NUMBER OF EGGS PRESENT	NUMBER OF LARVAE PRESENT	NUMBER OF IMMATURES PER LEAF
<u>Brunfelsia</u> sp. (7330)	3	0.6	122	40.7	0	0	0
<u>Cestrum</u> sp. (7338)	1	6.1	940	--	4	2	0.006
<u>Cestrum</u> (?) sp. (7324)	1	0.2	7	--	0	0	0
<u>Cyphomandra hartwegii</u>	1	1.2	8	--	0	0	0
<u>Lycianthes</u> sp. (7307)	4	0.8	217	54.3	3	0	0.014
<u>Solanum anceps</u>	2	0.8	18	9.0	1	0	0.056
<u>Solanum</u> sp. (7305)	1	3.6	134	--	5	0	0.037
<u>Solanum</u> sp. (7310)	1	0.5	24	--	0	0	0
<u>Solanum</u> sp. (7311)	4	0.3	34	8.5	0	0	0
<u>Solanum</u> sp. (7313)	1	0.2	7	--	0	0	0
<u>Solanum</u> sp. (7319)	18	0.8	103	5.7	6	6	0.117
<u>Solanum</u> sp. (7326)	1	0.3	4	--	0	0	0
<u>Solanum</u> sp. (7327)	40	0.6	377	9.4	0	1	0.003
<u>Solanum</u> sp. (7331)	9	0.2	78	8.7	1	0	0.013
<u>Solanum</u> sp. (7335)	17	1.3	1911	112.4	21	4	0.013
<u>Solanum</u> sp. (7336)	4	0.8	49	12.3	0	3	0.061
<u>Solanum</u> sp. (7340)	1	1.1	17	--	12	0	0.706
<u>Witheringia riparia</u>	52	0.5	895	17.2	0	0	0
Totals (18 species)	161		4945		53	16	0.014

Table 23. Summary of Foodplant and Juvenile Ithomiine Densities.

SURVEY SITE	NUMBER OF PLANT SPECIES IN SAMPLE	ESTIMATED NUMBERS OF INDIVIDUALS PER HECTARE				TOTAL IMMATURES
		PLANTS	LEAVES	EGGS	LARVAE	
Site 4	4	64	2,236	0	0	0
Site 5	9	896	11,740	48	32	80
Site 1	5	3,750	42,400	4,300	800	5,100
Site 6	18	8,050	247,250	2,650	800	3,450

There were no juvenile ithomiines present at Site 4 on the day of the census, although larvae of Thyridia confusa had been collected there (on Brunfelsia sp. 7330) on previous occasions. At Site 5, the density of immatures was 48 eggs and 32 larvae per hectare (these figures being quadruple the amounts actually found on the .25 hectare survey plot). The density per plant was about .09, but the number of immatures per leaf was .007. The two most abundant plants, Solanum sp. 7327 and Witheringia riparia, are quite similar morphologically and occurred together in large stands in favorable spots of the forest. Nevertheless, the densities of ithomiine immatures on these plants were still quite low.

The two 100 m by 2 m transects made along the Logging Trail (in full sun) at Site 1 (Table 21) and along the Nature Trail (in open shade) at Site 6 (Table 22) revealed much higher densities of ithomiine immatures. At Site 1, most of these immatures were Mechanitis isthmia eggs (61 distributed among three clusters) which were found in an extensive stand of the foodplant (S. coconilla) that dominated the area. A much greater diversity of solanaceous plants was found in the shaded Site 6 transect, although, as was Site 5, this area was dominated by Solanum sp. 7327 and Witheringia riparia. The densities of ithomiine immatures at the two secondary forest sites were 4300 eggs and 800 larvae per hectare at Site 1, and 2650 eggs and 800 larvae per hectare at Site 6. The distribution of these juvenile ithomiines, however, was strongly clumped both among and within species. Table 23 summarizes the densities of the foodplants and the ithomiine immatures at each of the four survey sites in terms of the number of individuals per hectare.

The fact that only three clusters of M. isthmia eggs were found in the large stand of S. coconilla (68 plants) at Site 1 may be the result of a tendency, mentioned earlier, of M. isthmia females to seek out isolated foodplants for oviposition. An explanation offered for this behavior in Chapter 5 was the possibility that egg cannibalism by older larvae might select for females which lay eggs on well-isolated plants where other larvae might less likely be present. Ant predation may be another factor favoring this ovipositing behavior. Nearly all plants in the S. coconilla stand at Site 1 supported large colonies of Solanopsis ants that nested among the clusters of fruit. Although ant densities were not quantified, such colonies on S. coconilla appeared to be smaller in size and less frequent in occurrence on single, isolated plants than on plants in large stands. Thus, it appears possible that the egg and early instar larval predation (Chapter 5) associated with large ant colonies on clustered S. coconilla may have been a factor selecting for searching behavior in ovipositing M. isthmia females that favors isolated instead of clustered foodplants.

CHAPTER VII

THE MIMETIC RELATIONSHIPS OF THE ITHOMIINAE

There are hardly any species of Ithomiines that are not roughly, but very often most exactly, copied by Ithomiine species of other genera.

--W. J. Kaye (1914)

Kaye's succinct observation readily explains why the Ithomiinae have been able to simultaneously produce headaches in taxonomists and delight in students of mimicry. The extensive participation of ithomiines in mimicry complexes has long been recognized and, indeed, the original formulations of Batesian Mimicry (Bates, 1862) and Mullerian Mimicry (Muller, 1879), were based on neotropical mimetic complexes involving ithomiines.

The literature on mimicry in butterflies is voluminous and has been summarized several times, most recently by Papageorgis (1974). Mimicry theory and considerations of the mimicry complexes entered by all members of the Ithomiinae are beyond the scope of this chapter. The purposes of the following discussion are (1) to characterize the mimicry complexes at Limoncocha in which ithomiines participate, (2) to review the evidence available concerning the palatability of ithomiines, and (3) to examine the consequences to mimicry of some aspects of ithomiine community ecology.

The Mimetic Subcomplexes at Limoncocha

As stated earlier (Chapter 1), ithomiines may be generally classified as belonging to one of two classes of wing pattern and coloration--those with part or most of the wings transparent or apparently so (Transparent Complex) and those with opaque wings, usually with some combination of black, orange, and yellow coloration (Tiger Complex). These two mimetic complexes, the Transparent Complex and the Tiger Complex, are the largest of the five mimetic associations occurring at Limoncocha and are the only two in which ithomiines participate. The other three mimicry complexes are the Orange Complex (red-orange wings with black borders), the Blue Complex (blue basal areas on black wings, with yellow forewing markings), and the Red Complex (red basal areas on black wings, with yellow forewing markings). These three complexes consist largely of species of Heliconiinae, but include some Batesian mimics (mostly butterflies) and some Mullerian mimics (mostly diurnal moths). All five complexes coexist throughout most of Amazonian South America and were recently studied in Peru by Papageorgis (1974, 1975), whose terminology for these complexes is followed here.

Papageorgis found that each of these mimicry complexes occupied a different vertical stratum of the forest at her study sites in Peru. At the site most comparable to Limoncocha (Rio Llullapichis), the complexes were segregated in the following manner: the Transparent Complex flew between ground level and 2 m, the Tiger Complex flew between 1.5 and 12 m, the Red Complex flew between 5 and 17 m, the Blue Complex flew between 15 and 25 m, and the Orange Complex flew above the canopy.

The degree of overlap between adjacent groups was in all cases rather low. My observations on the relative flying heights of the mimicry complexes at Limoncocha, although not quantified, agree fairly well with those of Papageorgis (1974). For example, the flying height separation between the transparent and tiger ithomiines was previously discussed in Chapter 3. Papageorgis' (1974) study was primarily addressed to the apparent contradiction posed by the presence of several mimicry complexes at a single locality. Classical Mullerian theory predicts that all protected species (and thus Batesian mimics as well) should converge on a single warning pattern. Papageorgis observed that the light conditions within the forest provide a varying background against which a butterfly will be seen by a predator. She concluded that the different colorations of the mimicry complexes in the different strata of the forest perform a dual purpose--warning coloration when the butterfly is perched and crypsis during flight. The cryptic effect of the clear-wing ithomiine pattern during flight was discussed in Chapter 3, but Papageorgis' arguments are less convincing for the Tiger Complex.

Since ithomiines participate in only two mimicry complexes at Limoncocha, the remainder of this chapter will be restricted to the Transparent Complex and the Tiger Complex, both of which may be further subdivided into subcomplexes.

Transparent Mimetic Complex

There are 49 species and subspecies of Lepidoptera in the Limoncocha Transparent Complex (Figures 58-61), which comprises five families of butterflies and three families of moths. By comparison Papageorgis (1974)

Figure 58.

Transparent Mimetic Complex: Yellow Opaque Subcomplex and Orange-Tip Subcomplex.

All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Yellow Opaque Subcomplex

Aeria eurimedia
nigricola (C & R Felder) ♀
(ITHOMIINAE)

Itaballia pisonis
subsp. ♀
(PIERIDAE)

Hypoleria chrysodonia
(Bates) ♂
(ITHOMIINAE)

Dismorphia erythroe
Bates ♂
(PIERIDAE)

Scada batesi
Haensch ♂
(ITHOMIINAE)

Dismorphia pinthaeus
amelina Hopffer ♂
(PIERIDAE)

Hypoleria orolina
(Hewitson) ♂
(ITHOMIINAE)

Ithomels corena
Felder ♂
(RIODINIDAE)

Hyphilaria nicias
(Stoll) ♀
(RIODINIDAE)

Pseudoscada egla
Hewitson ♂
(ITHOMIINAE)

Scada batesi
Haensch ♂
(ITHOMIINAE)

Dismorphia theugenis
Doubleday ♂
(PIERIDAE)

Scada quotidiana
quotidiana Haensch ♂
(ITHOMIINAE)

Hyalurga near fenestra
Linnaeus (14009) ♀
(PERICOPIDAE)

Napeogenes corena
caucayaensis Fox & Real ♀
(ITHOMIINAE)

Figure 59. Transparent Mimetic Complex: White Subcomplex.

All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

<u>Oleria kena</u> <u>ida</u> (Haensch) ♂ (ITHOMIINAE)	<u>Dismorphia leuconoe</u> <u>melanoides</u> Röber ♂ (PIERIDAE)	<u>Teratophthalma phelina</u> (C & R Felder) ♂ (RIODINIDAE)	<u>Heterosais edessa</u> <u>nephele</u> (Bates) ♀ (ITHOMIINAE)
<u>Oleria agarista</u> (C & R Felder) ♀ (ITHOMIINAE)	<u>Dismorphia leuconoe</u> <u>melanoides</u> Röber ♀ (PIERIDAE)	<u>Teratophthalma phelina</u> (C & R Felder) ♀ (RIODINIDAE)	<u>Hypoleria oriana</u> <u>famina</u> Haensch ♂ (ITHOMIINAE)
<u>Oleria tiggilla</u> (Weymer) ♂ (ITHOMIINAE)	<u>Oleria lotta</u> <u>lotta</u> (Hewitson) ♂ (ITHOMIINAE)	<u>Phyciodes nauplia</u> <u>plagiata</u> Röber ♂ (NYMPHALIDAE)	<u>Ithomia agnosia</u> <u>agnosia</u> Hewitson ♀ (ITHOMIINAE)
<u>Oleria sp.</u> (5053) ♂ (ITHOMIINAE)	<u>Oleria sp.</u> (5048) ♂ (ITHOMIINAE)	<u>Sylepta sp.</u> (14006) ♂ (PYRALIDAE)	<u>Pseudoscada timna</u> <u>timna</u> (Hewitson) ♂ (ITHOMIINAE)
<u>Hyalurga near leucophaea</u> <u>Walker</u> (14003) ♂ (PERICOPIDAE)	<u>Moth species</u> (14004) ♂	<u>Moth species</u> (14007) ♀	

Figure 60. Transparent Mimetic Complex: Yellow Clear-wing Subcomplex.
 All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

<u>Dircenna loreta</u> Haensch ♀ (ITHOMIINAE)	<u>Callithomia epidero</u> (Bates) ♂ (ITHOMIINAE)	<u>Napeogenes pharo</u> avila Haensch ♀ (ITHOMIINAE)
<u>Godyris zavaleta</u> amaretta (Haensch) ♂ (ITHOMIINAE)	<u>Ithomia amarilla</u> Haensch ♀ (ITHOMIINAE)	X-1 (5051) ♀. (ITHOMIINAE)
<u>Godyris zavaleta</u> amaretta (Haensch) ♀ (ITHOMIINAE)	<u>Ithomia derasa</u> salapia Hewitson ♂ (ITHOMIINAE)	<u>Mcclungia salonina</u> subtilis (Haensch) ♂ (ITHOMIINAE)
<u>Dygoris dircenna</u> dircenna (C & R Felder) (ITHOMIINAE) (not pictured)	<u>Pteronymia sparsa</u> Haensch ♀ (ITHOMIINAE)	<u>Phyciodes sp.</u> (9059) ♀ (NYMPHALIDAE)

Figure 61. Transparent Mimetic Complex: Large Clear-wing Subcomplex.

All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Thyridia confusa
psamathe Godman & Salvin ♂
 (ITHOMIINAE)

Ituna lamirus
lamirus (Latreille) ♀
 (DANAIDAE)

Xanthocleis psidii
ino (C & R Felder) ♀
 (ITHOMIINAE)

Castnia (Cabirrus) linus
Cramer ♀
 (CASTNIIIDAE)

Dismorphia orise
denigrata Rosenberg & Talbot ♀
 (PIERIDAE)

Dysschema heliconides
Swainson (14001) ♂
 (PERICOPIDAE)

Pericopsis near nigrivenata
Hering (14005) ♀
 (PERICOPIDAE)

found 33 species in the Transparent Complex at Rio Llullapichis, the richest of her three Peruvian study sites. At least five relatively discrete subcomplexes occur at Limoncocha, including one (Orange-Tip Subcomplex) that is endemic to the region. The other four are similar in composition to those in Peru (at Rio Llullapichis) illustrated by Papageorgis (1975).

Transparency in the wings of butterflies and other Lepidoptera has been achieved in various ways, involving both structural and pigmental modifications of the wing scales (Poulton, 1898; Kaye, 1905; Punnett, 1915). The scales of ithomiines are basically of two types, one long and narrow and the other broad and short, placed alternately on the wing membrane. In the transparent areas of the wings of most ithomiines, the long narrow scales have become no more than tiny hairs standing up away from the wing membrane. Likewise, the broader scales are greatly reduced in size, and altered from a fan shape to the appearance of the letter Y (Kaye, 1914). The following descriptions should be read while consulting the appropriate figures.

Yellow Opaque Subcomplex (Figure 58). The seven species in this subcomplex have light yellow wings outlined with black, and a strong black forewing bar. The name of this subcomplex may be slightly misleading, since its ithomiine members have translucent and even partially transparent wings. The diffuse yellow pigment of the wings, however, produces an appearance of opacity, and indeed, the Batesian members of the subcomplex are truly opaque. Two species, Scada quotidiana and Dismorphia theugenis are exceedingly rare (only one specimen of each taken at Limoncocha) and probably occur only occasionally at Limoncocha.

Scada quotidiana is more common south and west of Limoncocha (e.g., Tiwaeno; see map, Figure 1). Both Scada quotidiana and S. batesi are dimorphic for the presence or absence of the hindwing crossbar (shown on one of the specimens of S. batesi in Figure 58). The hindwing bar is always present in a third species, S. ethica, that occurs along the foothills of the Andes in Ecuador (Fox, 1967). Scada batesi, extending from central Colombia to southern Peru, enjoys the greatest geographical range of the three species, and one would predict that the hindwing bar would be more common in the zone of sympatry with S. ethica than elsewhere, as this would enhance the effect of the Mullerian mimicry. Since Limoncocha occurs at the northern edge of this zone of sympatry, it may be of interest to record the frequency of the hindwing bar in this area. The proportion of individuals with the hindwing bar in the all-male samples collected on Eupatorium I flowers at Study Site 1 and 2 was 9.18% (N = 425). I predict that the frequency of the hindwing bar should decrease northward from Limoncocha (where S. ethica does not occur), and increase southward from Limoncocha to just beyond the Peruvian border, which marks the extent of the range of the monomorphic S. ethica.

Orange-Tip Subcomplex (Figure 58). Geographically, this is perhaps the most restricted of the South American mimicry subcomplexes in which ithomiines participate. Found along the Rio Napo and Rio Putamayo drainages of east Ecuador, southern Colombia, and northeastern Peru into the western Amazonas region of Brazil, this subcomplex includes a number of other species not represented at Limoncocha (Haensch, 1909). As the name implies, the light-colored patch near the tip of the forewing is

orange, of a deep fulvous hue. The transparent wings are outlined with a dark brown band and the wing veins, even of the two of the Batesian mimics (Dismorphia erythroe and Ithomeis corena), are dark brown.

White Subcomplex (Figure 59). In terms of the number of species involved (17), this is the most extensive of the transparent subcomplexes at Limoncocha, and could actually be subdivided further, For example, the four ithomiines in the righthand column of Figure 59 differ from the others in having larger transparent areas of the wing. They are, in fact, very similar to the Orange-Tip subcomplex except that, instead of a patch of orange near the forewing tip, they have a streak of white scaling. The remaining species in this complex (three lefthand columns of Figure 59) have broader wing borders, often with a trace of orange that may be slightly expanded to form a very small patch near the forewing tip. In addition, the transparent area of the forewing is broken up into a number of small hyaline patches, and the hindwing is suffused with white scaling that obscures most of the veins. Like the Yellow Opaque and Orange-Tip Subcomplexes, the numbers of the White Subcomplex are generally found within one meter of the forest floor.

Yellow Clear-wing Subcomplex (Figure 60). The transparent wings of the ten ithomiine members of this subcomplex are lightly tinted with yellow scaling and are bordered with dark brown. All species have a partial or complete forewing bar and two, Callithomia epidero and Dygoris dircenna (not pictured), have a hindwing bar across the end of the discal cell. As mentioned earlier, Godyris zavaleta is sexually dimorphic, the female with dark scaling at the bases of the wings and brighter yellow scaling in the transparent areas. The only non-ithomiine

member of the subcomplex, an unidentified Phyciodes, was very rare (only one specimen taken). The Yellow Clear-wing Subcomplex, occupying a slightly higher flight stratum than the first three subcomplexes, generally flies one to two meters above the forest floor.

Large Clear-wing Subcomplex (Figure 61). The large size and bold black wing borders of these species make this subcomplex distinctive in appearance. The hyaline areas of the wing are tinted a light yellow, and are crossed by two or three bars on the forewing and one on the hindwing. The close pattern mimicry exhibited within this subgroup even extends to the enlarged yellow club at the tip of the antennae. Three of the species in this group are exceedingly rare at Limoncocha. Only one individual each of Dismorphia orise and Ituna lamirus, and two of Castnia linus, were collected during the year-long study. By comparison, the two pericopid moths and the two ithomiines were relatively common. The flight level occupied by this sub-complex (1.5 to 3 m above the ground) is above those of the other groups in the Transparent Complex.

Tiger Mimetic Complex

There are 42 species and subspecies of Lepidoptera in the Limoncocha Tiger Complex (Figures 62-65), which comprises four families of butterflies and two families of moths. At the Rio Llullapichis site studied by Papageorgis (1974), the Tiger Complex contained 31 species. The Tiger Complex does not subdivide as neatly as does the Transparent Complex, although four overlapping patterns may be distinguished at Limoncocha on the basis of flight level and the distribution of the yellow and black pigment.

Figure 62. Tiger Mimetic Complex: Yellow, Orange and Black Understory Subcomplex.
 All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Mechanitis isthmia
eurydice Haensch ♀
 (ITHOMIINAE)

Hypothyris euclea
peruviana (Staudinger) ♂
 (ITHOMIINAE)

Stalachtis calliope
 (Linnaeus) ♂
 (RIODINIDAE)

Ceratinia poecila
poecila (Bates) ♂
 (ITHOMIINAE)

Mechanitis lysimnia
elisa (Guérin-Ménéville) ♀
 (ITHOMIINAE)

Napeogenes duessa
duessa (Hewitson) ♂
 (ITHOMIINAE)

Phyciodes pelonia
pelonia Hewitson ♂
 (NYMPHALIDAE)

Napeogenes apobsoleta
Kaye ♀
 (ITHOMIINAE)

Forbestra truncata
juntana (Haensch) ♂
 (ITHOMIINAE)

Phyciodes pelonia
pelonia Hewitson ♀
 (NYMPHALIDAE)

Hypothyris fulminans
satura Haensch ♀
 (ITHOMIINAE)

Hypothyris fluona
berna (Haensch) ♀
 (ITHOMIINAE)

Callithomia alexirrhoe
 subsp. ♂
 (ITHOMIINAE)

Hyposcada kezia
 subsp. ♀
 (ITHOMIINAE)

Chlosyne sp.
 (9052) ♀
 (NYMPHALIDAE)

Napeogenes aethra
 (Hewitson) ♂
 (ITHOMIINAE)

Figure 63. Tiger Mimetic Complex: Yellow-Bar Canopy Subcomplex.

All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Melinaea menophilus
menophilus (Hewitson) ♂
(ITHOMIINAE)

Heliconius numata
near euphrasius Weymer ♀
(NYMPHALIDAE)

Hypothyris mansuetus
moebiusi (Haensch) ♀
(ITHOMIINAE)

Melinaea egesta
egesta Godman & Salvin ♂
(ITHOMIINAE)

Pericopis near bivittata
Walker (14002) ♀
(PERICOPIDAE)

Mechanitis messenoides
messenoides C & R Felder ♂
(ITHOMIINAE)

Mechanitis mazaesus
mazaesus Hewitson ♀
(ITHOMIINAE)

Mechanitis messenoides
near ballucatus Fox ♂
(ITHOMIINAE)

Castnia (Duboisualia)
cononia cononioides ♂
Strand
(CASTNIIIDAE)

Hypothyris mamecus
mamecus (Hewitson) ♀
(ITHOMIINAE)

Perrhybris pyrrha
pyrrha (Fabricius) ♀
(PIERIDAE)

Anaea (Consul) fabius
quadridentatus (Butler) ♂
(NYMPHALIDAE)

Figure 64. Tiger Mimetic Complex: Yellow-Spot Canopy Subcomplex.
 All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Tithorea harmonia
hermias Godman & Salvin ♀
 (ITHOMIINAE)

Dismorphia amphione
descrepans Butler ♂
 (PIERIDAE)

Dismorphia amphione
descrepans Butler ♀
 (PIERIDAE)

Melinaea maeonis
maeonis Hewitson ♀
 (ITHOMIINAE)

Heliconius pardalinus
orteguaza Brown ♀
 (NYMPHALIDAE)

Anaea (Consul) fabius
tithoreides (Butler) ♀
 (NYMPHALIDAE)

Heliconius numata
near superioris Butler ♂
 (NYMPHALIDAE)

Forbestra equicola
equicoloides (Godman & Salvin) ♂
 (ITHOMIINAE)

Eueides isabella
(Cramer) ♀
 (NYMPHALIDAE)

Lycorea ceres
pales C & R Felder ♀
 (DANAIDAE)

Figure 65. Tiger Mimetic Complex: Orange and Black Subcomplex.

All illustrations are life size. The configuration of the names given below corresponds to that of the illustrations.

Melinaea mothone
mothone (Hewitson) ♂
(ITHOMIINAE)

Heliconius numata
aristione (Hewitson) ♂
(NYMPHALIDAE)

Mechanitis messenoides
deceptus Butler ♀
(ITHOMIINAE)

Mechanitis egaensis
phasianita Haensch ♂
(ITHOMIINAE)

Mechanitis mazaesus
mazaesus Hewitson ♀
(ITHOMIINAE)

Lycorea pasinuntia
concolor Staudinger ♂
(DANAIDAE)

Athyrtis mechanitis
salvini Srnka ♂
(ITHOMIINAE)

Yellow, Orange, and Black Understory Subcomplex (Figure 62). The members of this complex, which includes most of the smaller tiger species, are found primarily in the forest understory, usually from about 1.5 or 2 m to 7 m. By contrast, the members of the remaining three tiger subcomplexes are rarely found below 4 or 5 m and usually occur in the mid to upper canopy. With sixteen species, this is the largest of the four tiger complexes but also the least consistent in pattern. In general, the hindwing and base of the forewing are orange with black spots or lines, while the distal half of the forewing is black with yellow markings. In Figure 62, those species in which the hindwing black bar tends toward enlargement to form a black patch represent transitional forms that also have characteristics of the Yellow-Bar Canopy Subcomplex (Figure 63). These transitional forms include the closely matched species, Napeogenes duessa and N. apobsoleta (center of Figure 62) and the Chlosyne Batesian mimic (lower right of Figure 62). Two other species included in Figure 62, Hyposcada kezia and Stalactis calliope, are similar to each other (both lack any yellow markings and have white spots in the black forewing tips) but do not closely match the other members of the subcomplex. Interestingly, H. kezia is consistently found at heights of 1 to 2 m, considerably below most of the other members of the subcomplex, and the three specimens of S. calliope collected during the study were also taken at this height. Three members of this subcomplex, Mechanitis isthmia, M. lysimnia, and Ceratinia poecila are regular visitors to forest edges and clearings but the remainder of the species rarely leave the forest interior.

Yellow-Bar Canopy Subcomplex (Figure 63). This subcomplex is characterized by a large black patch on the hindwing and a strong yellow median bar on the forewing. The forewing tip is black and the lighter areas of the hindwing and the base of the forewing are orange. Once again, a few species are transitional. For example, Melinaea egesta has an extra yellow bar at the tip of the forewing making it look similar to the Yellow-Spot Subcomplex (Figure 64) but has the black hindwing patch characteristic of the Yellow-Bar Subcomplex. The rather tattered Castnia cononia was the only specimen taken of this species.

Yellow-Spot Canopy Subcomplex (Figure 64). The members of this subcomplex are similar in size and flying range (upper canopy) to those of the Yellow-Bar Subcomplex, but lack the large black disc on the hindwing, and have broken or spotted bars in the distal half of the forewing instead of a single intact yellow bar. Dismorphia amphione is a member of this group and illustrates the incredible ability of this pierid genus of Batesian mimics to mimic not only the divergent color patterns of different mimetic complexes (see also Dismorphia species in Figures 58, 59, 60, and 61) but also the flight characteristics of its models.

Orange and Black Subcomplex (Figure 65). As the name implies, there is no yellow coloring in this group, only orange and black. Otherwise, it is quite similar to the Yellow-Bar Subcomplex, since the groups share the large black hindwing disc and the black forewing tip. Two butterflies included in Figure 65, Lycorea pasinuntia and Athyrtis mechanitis are probably not residents at Limoncocha, as their lack of

conformity to any of the tiger subcomplexes suggests. Both specimens illustrated are the only individuals of the two species collected at Limoncocha, and probably represent strays from outlying populations to the southwest (see Chapter 1). Like the Yellow-Bar and Yellow-Spot Subcomplexes, the Orange and Black Subcomplex inhabits the upper canopy, although the Mechanitis species are frequently encountered in the understory.

Polymorphic Mimetic Species

With the exception of the sexual dimorphism of Godyris zavaleta (Figure 60) and the hindwing bar polymorphism of Scada batesi (Figure 58), members of the Transparent Complex exhibit very few clear-cut pattern polymorphisms. The Tiger Complex, however, has several, involving both Batesian and Mullerian mimic species.

The familiar case of sex-limited mimetic polymorphism of a Batesian mimic is exhibited by the pierid, Perrhybris pyrrha, in which the female (Figure 63) is mimetic but the male (white with black markings) is not. Minor pattern differences occur between the sexes (both of which are mimetic) of Phyciodes pelonia (Figure 62) and of Dismorphia amphione (Figure 64). Two subspecific forms of Anaea fabius, a Batesian mimic in the Nymphalidae, occur at Limoncocha. These two forms clearly illustrate the pattern differences described earlier that exist between the Yellow-Bar Canopy Subcomplex (subspecies quadridentatus, Figure 63) and the Yellow-Spot Canopy Subcomplex (subspecies tithoreides, Figure 64).

Among Mullerian mimics, the most dramatic polymorphism is that of the three forms of Heliconius numata, each of which closely mimics a different species of Melinaea (H. n. near euphrasius mimics M. menophilus, Figure 63; H. n. near superioris mimics M. maeonis, Figure 64; and H. n. aristione mimics M. mothone, Figure 65). Similar mimetic pairs of Melinaea species and H. numata mimics in Brazil have been described by Brown and Benson (1974), and their theory of the adaptive polymorphism of Heliconius numata will be discussed in the last section of this chapter.

Among tiger ithomiines, there are two polymorphic species whose forms participate in different mimetic subcomplexes. Both Mechanitis mazaesus and M. messenoides have an all orange and black form (Figure 65) and a form with a yellow median bar on the forewing (Figure 63). Mullerian Mimicry theory, of course, predicts that pattern-stabilizing selection should keep all Mullerian species monomorphic and converged on a single warning pattern. Papageorgis' (1974) theory as to why several mimetic complexes exist at a single locality has already been discussed, but the cases just described refer to polymorphic species participating in different subcomplexes of the same (Tiger) mimetic complex. Why do these species not conform to theory at Limoncocha?

The answer apparently lies in the geographic distribution of mimetic patterns, and the relationship of this distribution to the Quaternary tropical forest refugia mentioned earlier, a subject of growing interest (Brown et al., 1974; Brown, 1976a). Anaea fabius (Batesian mimic); Mechanitis mazaesus, M. messenoides, and Heliconius numata (Mullerian mimics) are all widespread species with numerous subspecies, each with

a different mimetic pattern depending of the geographic location and the historical events that occurred at the sites of the nearest neotropical refugia. Limoncocha appears to lie at a confluence of adjacent mimetic patterns. Along the eastern foothills of the Andes in Ecuador, Peru, and Bolivia, the Orange and Black Subcomplex is well developed, but in upper Amazonia (between Manaus and Iquitos) tiger patterns with much yellow mottling of the forewing occur (Moulton, 1909). Thus in the western Amazon basin there is an increasing representation of orange and black to the west and south and an increasing representation of yellow and loss of black to the north and east (Moulton, 1909; Papageorgis, 1975). The most recent map of proposed Quaternary Refugia for butterflies (Brown, 1976a) places Limoncocha near the western edge of the large Napo Refuge, but under the influence of the Abitagua Refuge to the west and the Loreto Refuge to the southeast (in northwest Peru). Thus, many of the polymorphic forms present at Limoncocha may actually result from the overlapping of parapatric subspecific populations, e.g., the three "subspecies" of Mechanitis messenoides (Table 4; Figures 63 and 65), and the three "subspecies" of Heliconius numata (Figures 63, 64, and 65) present at Limoncocha. The fact that the forms of these two species appear to segregate in the Limoncocha populations with few intermediates suggests that the patterns of these subspecies are under the genetic control of a single gene (supergene). By contrast, the two forms of Mechanitis mazaesus shown in Figures 63 and 65 represent the ends of a continuum of pattern variation that occurs in the Limoncocha populations of this species.

Ithomiine Participation in Limoncocha Mimicry Complexes

Table 24 summarizes the taxonomic representation of the 53 ithomiine species in the 9 mimetic subcomplexes at Limoncocha. The species are equally divided between the Transparent and Tiger Complexes, but, within the former, most species and genera occur in either the White or Yellow Clear-wing Subcomplexes. In the Tiger Complex, the great majority of the genera and species are found in the Yellow, Orange, and Black Understory Subcomplex and the Yellow-Bar Canopy Subcomplex. While species in a particular genus may participate in as many as three different mimetic subcomplexes, all of these tend to be in one or the other of the two main complexes. Indeed, only 2 genera, Napeogenes and Callithomia, of the 25 genera at Limoncocha have species occurring in both the Transparent and Tiger Complexes. Of the remaining 23 genera, 8 are exclusively transparent and 15 are exclusively tiger in pattern. Half of the eight tribes include both transparent and tiger species. Two tribes, Ithomiini and Godyridini, are exclusively transparent, and two others, Tithoreini and Melinaeini, are exclusively tiger in pattern. It must be remembered that these comparisons and restrictions are applicable only at Limoncocha, and may not reflect the true extent of the participation of these genera and tribes in mimicry complexes throughout South America. For example, there are several clear-wing species in the Tribe Tithoreini (Fox, 1956).

Evidence for Unpalatability in the Ithomiinae

Although members of the Ithomiinae have long been considered distasteful (Bates, 1862; Muller, 1879; Kaye, 1914), the evidence for their unpalatability is almost entirely circumstantial. Kaye (1914) reviewed some of this circumstantial evidence and concluded that the sum total of proof by inference was large enough to warrant considering the Ithomiinae as a protected group. He noted further, however, that the degree of distastefulness probably varies greatly among different genera.

Circumstantial Evidence

Abundance. Bates (1862) and numerous later observers (e.g., Collenette and Talbot, 1928) have reported that the Ithomiinae are nearly always exceedingly numerous and occur where insectivorous birds abound. This is certainly true in the forest understory at Limoncocha, where the Ithomiinae are very abundant in comparison with other butterfly groups, and insectivorous birds are common (Pearson, 1972).

Slow flight. Part of the seeming abundance of ithomiines may be more apparent than real, owing to their slow, conspicuous flight. It is well known that butterflies frequenting open areas (e.g., Pieridae, Nymphalidae) often have strong and rapid flight, which is apparently their only means of defense against birds if attacked in flight. Because of the much slower flight of ithomiines (and other protected groups, such as the Heliconiinae, Acraeinae, and Danainae), it has been assumed that most rely on distastefulness as a defense (Kaye, 1914).

Wing marks. Kaye (1914) argued that notches taken out of the wings occurred less often in the Ithomiinae as compared to the Nymphalidae and Satyridae, suggesting that, despite their slow conspicuous flight, ithomiines are less susceptible to attack. The beak mark frequencies (beak marks are not the same as notches) presented by Collenette and Talbot (1928) were used by Carpenter (1941) to demonstrate that ithomiines are more often released by birds after capture, presumably because of the butterflies' distastefulness (Chapter 3).

Tenacity of life. Longstaff (1908) characterized the Ithomiinae as being "tenacious of life," referring to their relative success (as compared to other butterfly groups) at surviving rough handling by collectors, and, presumably, by other predators. Strong tenacity of life is considered a trait of distasteful butterflies (Kaye, 1914), but the character also seems to be correlated with body size. The larger ithomiines at Limoncocha (Yellow-Bar and Yellow-Spot Canopy Subcomplexes, Orange and Black Subcomplex, and Large Clear-wing Subcomplex) are much hardier than the smaller members of the subfamily.

Coloration. In addition to slow flight and tenacity of life, another character traditionally associated with distasteful butterflies is a similar coloration on both the dorsal and ventral surfaces of the wings (Kaye, 1914), a trait held by most ithomiines. Papageorgis (1974), however, concluded that the patterns of members of the Transparent and Tiger Mimicry Complexes are not aposematic per se, but provide a warning stimulus only through their great repetition, and perform a second function by conferring flight crypticity.

Strong scent. Although Longstaff (1908, 1912) has referred to the strong and occasionally unpleasant scent of some ithomiines, most of the species at Limoncocha emitted a faint but neutral or slightly pleasant odor. The possibility that sexual pheromones may have originated as protective odors was considered in Chapter 4.

Feigning death. As Gilbert and Ehrlich (1970) noted, death feigning is a behavioral trait exhibited by many Ithomiinae and some distasteful Danaidae (e.g., Lycorea ceres). The death feigning of an in copula pair of Thyridia confusa was described in Chapter 4, and similar instances of individuals remaining motionless in the net after capture occurred for most species at Limoncocha, but was more common among the larger tiger-patterned species. Death-feigning upon release after marking (placing the individual on a leaf) was much less common than playing dead in the net. The shock of an encounter with another object (e.g., the wall of an insect net or the beak of a bird) while flying apparently provides the stimulus initiating this behavior.

Models. Since the time of Bates, many lepidopterists have commented on the great number of species from several generally palatable families that have converged on the patterns of the Ithomiinae. This phenomenon is well illustrated in the mimicry subcomplexes at Limoncocha (Figures 58-65) in which species from the Pieridae, Nymphalidae, and Riodinidae--all presumably palatable--have converged in pattern and behavior to mimic ithomiines. It is presumed that these palatable (Batesian) mimics would only derive benefit from such a convergence if the Ithomiinae were unpalatable and thus protected from predation.

Foodplants. The early generalization that the larval foodplants of ithomiines belong to the Solanaceae (Muller, 1879), interpreted against the background of the longstanding notoriety concerning the poisonous qualities of this plant family (Heiser, 1969), reinforced the belief that ithomiines are unpalatable and suggested that ithomiines derive their distastefulness from these plants during the larval stage. Despite the vast numbers of alkaloids known to occur in solanaceous plants (Chapter 1) and the sophisticated biochemical techniques available to identify these compounds, I know of only one published report of an alkaloid analysis being performed on any life stage of an ithomiine. Rothschild (1973) reported that an adult of Mechanitis polymnia polymnia (L.) was found to be lacking solanaceous alkaloids, although the larval foodplant and locality of capture of the analyzed specimens were both unknown. Chemical analyses of all life stages of ithomiine butterflies and of their larval foodplants are clearly needed.

It appears then, that the circumstantial evidence presently available concerning the unpalatability of the Ithomiinae is ambiguous, but, in the aggregate, tends to support Kaye's (1914) conclusion that ithomiines are a protected group.

Direct Evidence

Feeding experiments. Although often cited as direct evidence for the unpalatability of the Ithomiinae to vertebrate predators, Brower and Brower's (1964) study in Trinidad tested the palatability of only one species of ithomiine, the clear-wing Ithomia drymo pellucida, on

only one species of bird, the North American Blue Jay (Cyanocitta cristata bromia Oberholser), imported from Massachusetts. As Fox (1967) has noted, these experiments tell us nothing about the feeding habits of the potential avian predators of ithomiines nor of the relative palatabilities of ithomiines belonging to different mimetic complexes and subcomplexes. These experiments do, however, strongly suggest that at least some ithomiines may be unpalatable to some birds at some times. To determine the extent of this unpalatability among taxonomic and mimetic groups of ithomiines will require carefully controlled feeding experiments involving natural potential predators. If performed in conjunction with the chemical experiments described above, such experiments should lead to a clearer understanding of the various roles played by ithomiines in the Batesian-Mullerian milieu.

Some Mimetic Consequences of Ithomiine Ecology

The diversity and equitability values calculated on the Site 4 ithomiine samples (Chapter 3) revealed that the ithomiine community at Limoncocha appears to be relatively stable in character through time, and only occasionally depressed in abundance by adverse weather conditions. During the periods of low abundance, however, the similarity in species composition between successive samples (as measured by the Quotient of Similarity) dropped, suggesting that, if ithomiines are indeed variable in palatability (see above), different assemblages of individuals during these periods may provide naive predators with different learning experiences regarding the palatability of the color

pattern, depending on the species composition of the assemblage (Chapter 3). The question then arises as to the stability of the relative abundances of the mimicry complexes and subcomplexes at Limoncocha.

To determine if the relative abundances of the various mimetic subcomplexes vary during the year, the Site 4 data were re-analyzed on the basis of color pattern. The results are given in Figures 66 through 68. In Figure 66 the number of ithomiine individuals present in each of the subcomplexes of the Transparent Mimetic Complex on the 26 sample days at Site 4 is graphed (mimetic individuals of other lepidopteran families are indicated separately). Likewise, the number of ithomiine individuals present in each of the subcomplexes of the Tiger Complex is given in Figure 67. These data are summarized in Figure 68, which presents the total number of individuals and species in the Transparent and Tiger Complexes present at Site 4 during the sampling period.

These figures show that all nine subgroups of both mimetic complexes varied in approximately the same manner throughout the year, paralleling the variation in total ithomiine abundance as given in Figure 27. The one possible exception to this pattern is the slight increase in abundance of the Yellow Opaque Subcomplex in early April (Figure 66a). From the point of view of a predator, then, the relative frequencies of the various mimetic complexes vary but little, even though the variation in overall ithomiine abundance may be substantial.

Brown and Benson (1974) have shown that the ithomiine pockets in southeastern Brazil are spatially and temporally unstable, and that the

Figure 66. Abundances of Transparent Mimetic Subcomplexes at Study Site 4.

- a. Yellow Opaque Subcomplex
- b. Orange-Tip Subcomplex
- c. White Subcomplex
- d. Yellow Clear-wing Subcomplex
- e. Large Clear-wing Subcomplex.

Figure 67. Abundances of Tiger Mimetic Subcomplexes at Study Site 4.

- a. Black, Yellow, and Orange Understory Subcomplex
- b. Yellow-Bar Canopy Subcomplex
- c. Yellow-Spot Canopy Subcomplex.
- d. Orange and Black Subcomplex

Figure 68. Summary of the Abundances of the Transparent and Tiger Mimetic Complexes at Study Site 4.

a. Transparent Complex

●—● individuals

○—○ species

b. Tiger Complex

●—● individuals

○—○ species

great differences in the relative abundances of the species in these pockets over time result in corresponding changes in the relative abundances of the mimetic color patterns as well. Polymorphic populations of Heliconius numata occur in the same areas, although this species is much less abundant than its demographically unstable ithomiine co-mimics. In an attempt to explain the polymorphism of Heliconius numata, these authors proposed that this distasteful Mullerian mimic is acting numerically in a pseudo-Batesian fashion. In other words, the various H. numata morphs are maintained in the population because the changing character of the dominant mimetic pattern (of the more abundant ithomiine co-mimics) favors different H. numata morphs at different times of the year.

Such an explanation for the presence of the three morphs of Heliconius numata at Limoncocha appears unlikely, however, since the relative abundances of the three mimetic subcomplexes in which they participate appear to be fairly stable through time (Figure 67b,c, and d). (Unfortunately, the sample sizes for these three mimetic subcomplexes are small because the members of these subcomplexes spend most of their time in the mid to upper canopy, while the samples themselves were collected only in the lower four meters of the understory.) It seems more probable that the polymorphism of H. numata at Limoncocha is the result of a confluence of different mimetic patterns, each one favored in an adjacent geographical area.

CHAPTER VIII

CONCLUSIONS

Butterflies of the subfamily Ithomiinae are among the most conspicuous and abundant flying insects of the lowland tropical forests of eastern Ecuador. They are sensitive to microhabitat differences within seemingly homogeneous forest, apparently responding to gradients of light and relative humidity, resulting in a clumped distribution of adults. Capture-mark-recapture experiments reveal that ithomiines appear to have much larger home ranges than previously believed and that the clumped distributions of ithomiines within the continuously forested lowlands of the upper Amazon basin do not represent discrete communities and populations, but merely transient concentrations that crest and ebb erratically through time.

Ithomiines, active from dawn until dusk, are able to fly and navigate in near darkness. Feeding activity occurs primarily in the early morning and late afternoon. The early morning visitation to white flowers by males fits the syndrome of crepuscular pollination, and adaptations of the butterflies and some of the adult foodplants suggest a coevolved relationship. Females forage within the forest understory for bits of detritus that may provide the nitrogenous compounds needed for egg production and/or longevity. Both males feeding at flowers and females feeding at detritus appear to act as

stimuli attracting other ithomiines to the food sources, behavior which may aid the exploitation of food sources patchily distributed in space and time.

Reproductive activities of ithomiines occur mostly during the middle of the day. Courting males are most active in late morning, and mating activity peaks between 1200-1300 h. Oviposition occurs throughout the afternoon and may occur as late as 1800 h, but peaks between 1400-1500 h. Male ithomiines face the difficulty of locating a mate among a large number of similarly colored species and exhibit two types of mate-locating behavior. "Display perching" males hold their wings open at a species-specific angle and display the hindwing hair-pencils. Short interperch flights between perches tend to concentrate the males' aphrodisiac pheromone in a broad disc that presumably lures females into the male's sphere of vision, at which point male pursuit is initiated. The sequence of perches and interperch flights and the postures of displaying males indicate that this courtship behavior is under species-specific genetic control. "Patrol perching" males perch with their wings together and make periodic interperch flights that patrol an area of several square meters. Almost any moving body within the patrolled area will elicit pursuit behavior by the male. As in most butterflies, copulation probably lasts several hours, and it is proposed that the long length of copulation in butterflies is an adaptive behavior of the male to insure that sperm precedence, rather than sperm displacement, occurs if the female mates again soon (females are known to mate up to 6 times). Oviposition strategies among ithomiines vary greatly with regard to egg volume, onset of oviposition, clutch size,

and probably in daily fecundity. Egg manufacture is financed by the adult stage, not the larva. Four modes of oviposition behavior, each defining the sequence of events after the location of the larval food-plant and before the laying of the eggs, are described. It is proposed that the switch from laying single eggs (ancestral condition) to laying egg clusters was accompanied by selection favoring oviposition on the dorsal leaf surface to minimize mistakes in egg placement.

Juvenile ithomiines display great variation in morphology in all life stages. Of particular importance is the discovery that the larva of Melinaea menophilus bears a strong resemblance to larvae of the primitive ithomiine genus Tithorea, and to larvae of Lycorea and other Danaidae, providing further evidence for the close relationship between the Ithomiidae and Danaidae.

The generation time for most ithomiines is approximately 28 to 30 days. Larval development takes considerably longer on foodplants with well-armed leaves than on unarmed plants. Chemical differences in foodplants probably also affect the length of the larval feeding period. Larval feeding on the ventral surfaces of leaves is almost universal among ithomiines. Parasitism and predation take an extremely high toll of juvenile stages of ithomiines. The combined effects of this high juvenile mortality and the low daily reproductive rate of most adult females result in an extreme under-utilization of foodplant tissue.

Although parasitism and predation of juvenile stages, and not foodplant availability, appear to regulate the size of ithomiine populations, adult mortality from severe storms and periods of heavy rainfall can severely depress the abundances of most ithomiine

species. In spite of these periodic depressions in abundance, however, the ithomiine community at Limoncocha (as measured by the samples collected at Site 4) appears to be quite stable in relative composition of mimetic patterns, age distribution, species diversity (H'), and equitability (J').

This high species diversity results in part from the large number of species (53) present in the Limoncocha ithomiine taxocene. The sympatric occurrence of a large number of closely related ithomiine species at Limoncocha is probably a reflection of the large number of potential larval foodplants in the Solanaceae available in the same area. Local populations of most ithomiine species appear to be highly specific in foodplant utilization, rarely developing on more than one foodplant. The foodplants utilized by subspecific populations of widely distributed species, however, may be different, resulting in broad foodplant associations at the species level. The primary exceptions to foodplant specificity within populations appear to be wide-ranging, vagile, species that develop on fugitive, or second-growth, Solanaceae.

The participation of ithomiines in mimicry complexes is extensive. The ithomiine species at Limoncocha are approximately equally divided between the Transparent Complex (with 5 subcomplexes) and the Tiger Complex (with 4 subcomplexes). Most ithomiines are probably unpalatable to some degree, but it is likely that, as a group, there exists a broad palatability spectrum among ithomiine species.

There are many promising areas for future research in ithomiine ecology, and several of these have been mentioned in the text. The most interesting areas in my opinion include (1) the role of chemical

and mechanical defenses of larval foodplants in determining the food-plant utilization of the Ithomiinae, (2) the foodplant tolerances of larvae and ovipositing females, (3) the contributions of nectar and detritus food sources to longevity and fecundity in ithomiines, (4) the significance of multiple matings of ithomiine females and the mechanics of sperm transfer from copulation to oviposition, (5) behavioral studies of male courtship behavior with experiments designed to delimit the function of the male hairpencils and pheromones, (6) palatability experiments offering adult and immature ithomiines to natural potential predators to determine the nature of the palatability spectrum, and (7) chemical analyses of ithomiines and their foodplants to determine the basis for any observed ithomiine unpalatability and to define the phytochemical ecology of the Ithomiinae-Solanaceae interface.

REFERENCES

- Allee, W. C. 1926. Measurement of environmental factors in the tropical rain forest of Panama. *Ecology* 7: 273-301.
- d'Almeida, R. F. 1922. *Mélanges lépidoptérologiques. Etudes sur les lépidoptères du Bresil.* Berlin. 226 pp. (Mimeo)
- d'Almeida, R. F. 1938. Estudo sobre tres generos de sub-familia Ithomiinae. *Mem. Inst. Oswaldo Cruz.* 33: 381-394.
- d'Almeida, R. F. 1944. Estudos biologicos sobre alguns Lepidopteros do Brasil. *Arq. Zool. Est. São Paulo.* 4: 33-72.
- d'Almeida, R. F. 1945. Revisão do genero Xanthocleis Boisd., 1870. *Arq. Zool. Est. São Paulo.* 4: 97-112.
- Arms, K., P. Feeny, and R. C. Lederhouse. 1974. Sodium: stimulus for puddling behavior by tiger swallowtail butterflies, Papilio glaucus. *Science* 185: 372-374.
- Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. *Biometrika* 38: 293-306.
- Baker, H. G., and I. Baker. 1973. Amino-acids in nectar and their evolutionary significance. *Nature* 241: 543-545.
- Barcant, M. 1970. Butterflies of Trinidad and Tobago. Collins, London. 314 pp.
- Barrett, C., and A. N. Burns. 1951. Butterflies of Australia and New Guinea. N. H. Seward Pty. LTD. Melbourne. 187 pp.
- Bates, H. W. 1857. Proceedings of natural-history collectors in foreign countries. *Zoologist* 15: 5659.
- Bates, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. *Lepidoptera: Heliconidae.* *Trans. Linn. Soc.* 23: 495-566.
- Bates, H. W. 1863. The Naturalist of the River Amazons. Univ. of California Press, Berkeley. 1962 reprint. 465 pp.
- Beebe, W. 1955. Two little-known selective insect attractants. *Zoologica* 40: 27-32.
- Benson, W. W. 1967. Studies on the ecology of Ithomiinae and Heliconiinae in Costa Rica. Mimeo Research Report. OTS, Ciudad Universitaria, Costa Rica. Feb.-March.

- Benson, W. W. 1972. Natural selection for Mullerian mimicry in Heliconius erato in Costa Rica. *Science* 176: 936-939.
- Benson, W. W., and T. C. Emmel. 1973. Demography of gregariously roosting populations of the Nymphaline butterfly Marpesia berania in Costa Rica. *Ecology* 54: 326-335.
- Beutelspacher, C. R. 1972. Some observations on the Lepidoptera of bromeliads. *J. Lep. Soc.* 26: 133-137.
- Biezanko, C. M. 1960a. Danaidae et Ithomiidae da Zona Sueste do Rio Grande do Sul. *Arquivos de Entomologia* (Inst. Agron. do Sul, Escola de Agron. Eliseu Maciel, Pelotas, Rio Grande do Sul, Brasil). III. Serie A: 1-6.
- Biezanko, C. M. 1960b. Danaidae et Ithomiidae da Zona Missioneira do Rio Grande do Sul. *Arquivos de Entomologia* (Inst. Agron. do Sul, Escola de Agron. Eliseu Maciel, Pelotas, Rio Grande do Sul, Brasil). III. Serie B: 1-6.
- Biezanko, C. M. de, A. Ruffinelli, and C. S. Carbonell. 1957. Lepidoptera del Uruguay; Lista anotada de especies. *Revista de la Facultad de Agronomia, Montevideo, Uruguay*, No. 46, 152 pp.
- Birch, M. C. 1974. Aphrodisiac pheromones in insects. In M. C. Birch, ed., Pheromones. North-Holland, Amsterdam, pp. 115-134.
- Brower, L. P. 1963. The evolution of sex-limited mimicry in butterflies. *Proc. 16th Intern. Cong. Zool.* 4: 173-179.
- Brower L. P., and J. V. Z. Brower. 1964. Birds, butterflies, and plant poisons: A study in ecological chemistry. *Zoologica* 49: 137-159.
- Brown, F. M. 1968. Richard Middleton Fox. *J. Lep. Soc.* 22: 192-195.
- Brown, F. M. 1975. An annotated entomological bibliography of Romualdo Ferreira d'Almeida (1891-1969). *J. Lep. Soc.* 29: 40-51.
- Brown, F. M., and B. Heineman. 1972. Jamaica and Its Butterflies. E. W. Classey Ltd., London. 478 pp.
- Brown, K. S. 1972. Maximizing daily butterfly counts. *J. Lep. Soc.* 26: 183-196.
- Brown, K. S. 1973. A portfolio of neotropical Lepidopterology. Private pamphlet printed by the author. Rio de Janeiro, Brazil. 28 pp.
- Brown, K. S. 1976a. Geographical patterns of evolution in Neotropical Lepidoptera. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae). *J. Entomology, Series B*, 44: 201-242.

- Brown, K. S. 1976b. The 1975 Field Season Summary, Zone 10, South America. News of the Lep. Soc., 1976, No. 2 (15 May 1976).
- Brown, K. S., and R. F. D'Almeida. 1970. The Ithomiinae of Brazil (Lepidoptera: Nymphalidae). II. A new genus and species of Ithomiinae, with comments on the tribe Dircennini d'Almeida. Trans. Amer. Ent. Soc. 96: 1-17.
- Brown, K. S., and W. W. Benson. 1974. Adaptive polymorphism associated with multiple Mullerian mimicry in Heliconius numata (Lepid. Nymph.). Biotropica 6: 205-228.
- Brown, K. S., O. H. H. Mickle, and H. Ebert. 1970. Os Ithomiinae do Brasil. I. Prittwitzia g. n. para Ithomyia hymenaea Prittwitz e suas subspecies. Rev. Brasil Biol. 30: 269-273.
- Brown, K. S., P. M. Sheppard, and J. R. G. Turner. 1974. Quaternary refugia in tropical America: evidence from race formation in Heliconius butterflies. Proc. Roy. Soc. Lond. (B) 187: 369-378.
- Bull, L. B., C. J. Culvenor, and A. T. Dick. 1968. The Pyrrolizidine Alkaloids. North-Holland, Amsterdam. 293 pp.
- Butler, C. G. 1967. Insect pheromones. Biol. Rev. 42: 42-87.
- Carpenter, G. D. H. 1941. The relative frequency of beak-marks on butterflies of different edibility to birds. Proc. Zool. Soc. Lond. (A) 111: 223-230.
- Chodorowski, A. 1959. Ecological differentiation of turbellarians in Harsz-Lake. Polsk. Archwm. Hydrobiol. 6: 33-73.
- Collenette, C. L. and G. Talbot. 1928. Observations on the bionomics of the Lepidoptera of Mato Grosso, Brazil. Trans. Roy. Ent. Soc. Lond. 76: 391-416.
- Common, I. F. B. 1964. Australian Butterflies. Jacaranda Press. 131 pp.
- Common, I. F. B., and D. F. Waterhouse. 1972. Butterflies of Australia. Angus and Robertson, Sydney. 498 pp.
- Cook, L. M., K. Frank, and L. P. Brower. 1971. Experiments on the demography of tropical butterflies. I. Survival rate and density in two species of Parides. Biotropica 3: 17-20.
- Correll, D. S. 1967. Solanaceae (Juss.) Lindl. Key to Section Neolycopersicon and Section Tuberarium. In "Flora of Peru," Publication 1015, Bot. Ser., Field Mus. of Nat. Hist., Vol. 13, Part V-B, No. 2: 271-458.
- Costa-Lima, A. da. 1936. Terceiro Catalogo dos Insectos que Vivem nas Plants do Brasil. Rio de Janeiro. 469 pp.

- Costa-Lima, A. da. 1950. Insetos do Brasil. Tomo 6, Lepidopteros, Parte 2. Escola Nacional de Agronomia, Serie Didatica, No. 8. 420 pp.
- Crane, J. 1955. Imaginal behaviour of a Trinidad butterfly, Heliconius erato hydara Hewitson, with special reference to the social use of colour. *Zoologica* 40: 167-196.
- Cronquist, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston. 396 pp.
- D'Abrera, B. 1971. Butterflies of the Australian Region. Lansdowne, Melbourne. 415 pp.
- D'Arcy, W. G. 1972. Solanaceae studies II: typification of subdivisions of Solanum. *Ann. Missouri Bot. Gard.* 59: 262-278.
- D'Arcy, W. G. 1973 (1974). Flora of Panama. Part IX. Family 170. Solanaceae. *Ann. Missouri Bot. Gard.* 60: 573-780.
- D'Arcy, W. G. 1974. Solanum and its close relatives in Florida. *Ann. Missouri Bot. Gard.* 61: 819-867.
- Deevey, E. S. 1969. Coaxing history to conduct experiments. *Bioscience* 19: 40-43.
- Downes, J. A. 1973. Lepidoptera feeding at puddle-margins, dung and carrion. *J. Lep. Soc.* 27: 89-99.
- Drummond, B. A., III, G. L. Bush, and T. C. Emmel. 1970. The biology and laboratory culture of Chlosyne lacinia Geyer (Nymphalidae). *J. Lep. Soc.* 14: 135-142.
- Ebert, H. 1969. On the frequency of butterflies in Eastern Brazil, with a list of the butterfly fauna of Poços de Caldas, Minas Gerais. *J. Lep. Soc.* 23, Supplement 3: 48 pp.
- Edgar, J. A., C. C. J. Culvenor, and T. E. Pliske. 1974. Co-evolution of danaid butterflies and their host-plants. *Nature* 250: 646-648.
- Edmunds, M. 1974. Significance of beak marks on butterfly wings. *Oikos* 25: 117-118.
- Ehrlich, P. R. 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Univ. of Kansas Sci. Bull.* 39: 305-370.
- Ehrlich, P. R., D. E. Breedlove, P. F. Brussard, and M. A. Sharp. 1972. Weather and the "regulation" of subalpine populations. *Ecology* 35: 243-247.
- Ehrlich, P. R., and S. E. Davidson. 1960. Techniques for capture-recapture studies of Lepidoptera populations. *J. Lep. Soc.* 14: 227-229.

- Ehrlich, P. R., and L. E. Gilbert. 1973. Population structure and dynamics of the tropical butterfly Heliconius ethilla. Biotropica 5: 69-82.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586-608.
- Elton, C. S. 1973. The structure of invertebrate populations inside neotropical rain forest. J. Anim. Ecol. 42: 55-104.
- Emmel, T. C. 1974. Rainfall in the Amazon Basin (Letter). Science 183: 257-258.
- Faegri, K., and L. van der Pijl. 1966. The Principles of Pollination Ecology. Pergamon Press, Oxford. 248 pp.
- Fountaine, M. E. 1913. Five months butterfly collecting in Costa Rica in the summer of 1911. Entomologist 46: 189-194, 214-219.
- Fox, R. M. 1940. A generic review of the Ithomiinae (Lepidoptera: Nymphalidae). Trans. Amer. Ent. Soc. 66: 161-207.
- Fox, R. M. 1949. The evolution and systematics of the Ithomiidae (Lepidoptera). Univ. of Pitt. Bull 45: 1-12.
- Fox, R. M. 1956. A monograph of the Ithomiidae (Lepidoptera), Part I. Bull. Amer. Mus. Nat. Hist. 111: 76 pp.
- Fox, R. M. 1960. A monograph of the Ithomiidae (Lepidoptera), Part II. Trans. Amer. Ent. Soc. 86: 109-171.
- Fox, R. M. 1963 (1964). Affinities and distribution of Antillean Ithomiidae. J. Res. Lep. 2: 173-184.
- Fox, R. M. 1967. A monograph of the Ithomiidae (Lepidoptera), Part III. Tribe Mechanitini Fox. Amer. Ent. Soc., Mem. 22: 200 pp.
- Fox, R. M., and H. G. Real. 1971. A monograph of the Ithomiidae (Lepidoptera), Part IV. The tribe Napeogenini Fox. Amer. Ent. Inst., Mem. 15: 368 pp.
- Fraenkel, G. S. 1959. The *raison de'etre* of secondary plant substances. Science 129: 1466-1470.
- Gentry, J. L., Jr., and P. Standley. 1974. Solanaceae. In "Flora of Guatemala." Fieldiana: Bot. 24: 1-151.
- Gilbert, L. E. 1966. The effects of meteorological factors on butterfly flight activity. Mimeo Research Report. OTS, Ciudad Universitaria, Costa Rica. July-Aug.
- Gilbert, L. E. 1969. Some aspects of the ecology and community structure of ithomid butterflies in Costa Rica. Mimeo Research Report. OTS, Ciudad Universitaria, Costa Rica. July-Aug.

- Gilbert, L. E. 1971. Butterfly-plant coevolution: Has Passiflora adenopoda won the selectional race with Heliconiine butterflies? *Science* 172: 585-586.
- Gilbert, L. E. 1972. Pollen feeding and reproductive biology of Heliconius butterflies. *Proc. Nat. Acad. Sci.* 69: 1403-1407.
- Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. In Coevolution of Animals and Plants, L. E. and P. Raven (eds.), pp. 210-240, Univ. Texas Press, Austin. 246 pp.
- Gilbert, L. E., and P. R. Ehrlich. 1970. The affinities of the Ithomiinae and the Satyrinae (Nymphalidae). *J. Lep. Soc.* 24: 297-300.
- Gundlach, J. 1881. Contribucion á la entomologia Cubana. Havana.
- Guppy, J. L. 1894. Notes on Trinidad butterflies. *J. Trinidad Field Nat. Club* 2: 170-174.
- Guppy, J. L. 1904. Notes on the habits and early stages of some Trinidad butterflies. *Trans. Ent. Soc. London* 52: 225-228.
- Haensch, R. 1903. Kurzer Bericht über die entomolg. Ergebnisse meiner Ecuador-Reise. Die Ithomiinen meiner Ecuador-Reise. *Berliner Ent. Zeitschr.* 48: 149-214.
- Haensch, R. 1905. Neue sudamerikanische Ithomiinae meiner Sammlung. *Berliner Ent. Zeitschr.* 50: 142-182.
- Haensch, R. 1909. Familie: Danaidae. In Seitz, A., *Die Gross-Schmetterlinge der Erde*. Stuttgart, Vol. 5, pp. 113-171. pls. 31-41.
- Haffer, Jurgen. 1974. Avian speciation in tropical South America. Pub. Nuttall Ornith. Club., No. 14. 390 pp.
- Heiser, C. B. 1968a. The prehistoric cultivated plants of Colombia with particular reference to the lulo (Solanum quitoëense). XXXVII Congreso Internacional de Americanistas, Republica Argentina, 1966, Actas y Memorias, Vol. 2: 535-545.
- Heiser, C. B. 1968b. Some Ecuadorian and Columbian solanums with edible fruits. *Ciencia y Naturaleza (Quito)* 11: 3-9.
- Heiser, C. B. 1969. Nightshades: The Paradoxical Plants. W. H. Freeman and Co., San Francisco. 200 pp.
- Heiser, C. B. 1971 (1972). Notes on some species of Solanum (Sect. Leptostemonum) in Latin America. *Baileya* 18: 59-65.
- Henry, T. A. 1949. (4th ed.) The Plant Alkaloids. The Blaikston Co., New York. 804 pp.

- Holdridge, L. R. 1967. Life Zone Ecology. (Rev. Ed.). Tropical Science Center, San Jose, Costa Rica. 206 pp.
- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, J. A. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones. A Pilot Study. Pergamon Press, Oxford. 747 pp.
- Hunziker, A. T. 1969. Estudios sobre Solanaceae 5. *Kurzia* 5: 101-179.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52: 577-586.
- Hutchinson, E. H. 1967. A Treatise on Limnology. Vol. II. John Wiley and Sons, New York. 1115 pp.
- Jimenez, J. A. 1966. La naranjilla. Ministerio de Agricultura y Ganaderia. Puyo, Ecuador.
- Jolly, G. M. 1965. Explicit estimates from capture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.
- Kaye, W. J. 1905. Transparency in the wings of Lepidoptera. *The Ent. Rec. and J. of Var.* 17: 83-86, 115-121.
- Kaye, W. J. 1906. Notes on the dominant Mullerian group of butterflies from the Potaro district of British Guiana. *Trans. Ent. Soc. London* 53: 411-435.
- Kaye, W. J. 1914. The Ithomiinae. *Proc. So. Lond. Ent. and Nat. Hist. Soc.* 1913-1914: 38-48.
- Kaye, W. J. 1921. A catalogue of the Trinidad Lepidoptera Rhopalocera. *Mem. Dept. Agr. Trinidad and Tobago* 2: 1-163.
- Klots, A. B. 1951. A Field Guide to the Butterflies of North America, East of the Great Plains. Houghton Mifflin Co., Boston. 349 pp.
- Labine, P. A. 1966. The population biology of the butterfly, Euphydryas editha. IV. Sperm precedence—A preliminary report. *Evolution* 20: 580-586.
- Lamas Muller, G. 1973. Taxonomia e evolucao dos generos Ituna Doubleday (Danainae) e Paititia, gen. n., Thyridia Hübner e Methona Doubleday (Ithomiinae) (Lepidoptera, Nymphalidae). D.Sc. Thesis to the Departamento do Zoologia, Instituto de Biociencias, Universidade de São Paulo, pp. vii, 1-225.
- Lawrence, G. H. M. 1951. Taxonomy of Vascular Plants. The Macmillan Company, New York. 823 pp.
- Lawrence, G. H. M. 1960. The cultivated species of Solanum. *Baileya* 8: 21-35.

- Lichy, R. 1944. Documents pour servir à l'étude des lépidoptères du Vénézuéla. Bol. Acad. Cien. Fis. Matem. Nat. 24: 13-27.
- Longstaff, G. B. 1908. Bionomic notes on butterflies. Trans. Ent. Soc. Lond. 1908: 607-662.
- Longstaff, G. B. 1912. Butterfly-Hunting in Many Lands. Longmans, Green, and Co., London. 729 pp.
- MacBride, J. F. 1962. Solanaceae (Juss.) Lindl. In "Flora of Peru." Publication 951, Bot. Ser., Field Mus. Nat. Hist., Vol. 13, Part V-B, No. 1: 1-267.
- Magnus, D. B. E. 1963. Sex limited mimicry II--Visual selection in the mate choice of butterflies. Proc. 16th Intern. Cong. Zool. 4: 179-183.
- Manski, M. J. 1960. Foodplants of some Queensland Lepidoptera. Qd. Nat. 16: 68-73.
- Masters, J. H. 1968. Collecting Ithomiidae with heliotrope. J. Lep. Soc. 22: 108-110.
- Mayr, E. 1954. Change of genetic environment and evolution. In J. Huxley, A. C. Hardy, and E. B. Ford, eds., Evolution as a Process. Allen and Unwin, London, pp. 157-180.
- McCubbin, C. 1971. Australian Butterflies. Thomas Nelson, Melbourne. 206 pp.
- Miller, L. D. 1968. The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). Amer. Ent. Soc., Mem. 24: 174 pp.
- Miller, L. D., and H. K. Clench. 1968. Some aspects of mating behavior in butterflies. J. Lep. Soc. 22: 125-132.
- Moreira, N. 1881. Metamorphose de uma Heliconia. Arch. Mus. Rio de Janeiro 4: 1-13.
- Moss, A. M. 1947. Notes on the Syntomidae of Para, with special reference to wasp mimicry and fedegoso, Heliotropium indicum (Boraginaceae), as an attractant. Entomologist 80: 30-35.
- Moulton, J. C. 1909. On some of the principal mimetic (Mullerian) combinations of tropical American butterflies. Trans. Ent. Soc. Lond. 56: 585-606.
- Muller, F. 1877. On hair-tufts, felted patches, and similar structures on the wings of male lepidoptera. Jenaische Zeitschrift fur Naturwissenschaft, XI (New Series, IV.): 99-114. Trans. in Longstaff, G. B. 1912. Butterfly-Hunting in Many Lands. Longmans, Green, and Co., London, pp. 604-619.

- Muller, F. 1879. Ituna and Thyridia: a remarkable case of mimicry in butterflies. Proc. Roy. Ent. Soc. Lond. 1879: xx-xxix. Trans. by R. Meldola from "Kosmos," May, 1879, p. 100.
- Muller, W. 1886. Sudamerikanische Nymphalidenraupen. Zool. Jahrb. 1: i-x, 1-225.
- Pacheco, R., and J. Jimenez. ca. 1968. El cultivo de la naranjilla en el Ecuador. Ministerio de Agricultura y Ganaderia. Quito, Ecuador.
- Papageorgis, C. 1974. The adaptive significance of wing coloration in neotropical butterflies. Ph.D. dissertation, Princeton University. 196 pp.
- Papageorgis, C. 1975. Mimicry in neotropical butterflies. Amer. Sci. 63: 522-532.
- Patino, V. M. 1962. Edible fruits of Solanum in South American historic and geographic references. Bot. Mus. Leaf. (Harvard U.) 19: 215-234.
- Pearson, D. L. 1972. The birds of Limoncocha. Instituto Linguistico de Verano, Quito. 13 pp.
- Peet, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. and Syst. 5: 285-307.
- Pielou, E. C. 1967. The use of information theory in the study of the diversity of biological populations. Proc. Berkeley Symp. Math. Stat. Prob., 5th, 4: 163-177.
- Pliske, T. E. 1975a. Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. Environ. Ent. 4: 455-473.
- Pliske, T. E. 1975b. Pollination of pyrrolizidine alkaloid-containing plants by male Lepidoptera. Environ. Ent. 4: 474-479.
- Pliske, T. E. 1975c. Courtship behavior and use of chemical communication by males of certain species of Ithomiine butterflies (Nymphalidae: Lepidoptera). Ann. Ent. Soc. Amer. 68: 935-942.
- Pliske, T. E., J. A. Edgar, and C. C. J. Culvenor. 1976. The chemical basis of attraction of ithomine butterflies to plants containing pyrrolizidine alkaloids. J. Chem. Ecol. (in press).
- Poole, R. W. 1970. Habitat preferences of some species of a Mullerian-mimicry complex in Northern Venezuela, and their effects on evolution of mimic-wing pattern. J. N. Y. Ent. Soc. 78: 121-129.
- Poole, R. W. 1974. An Introduction to Quantitative Ecology. McGraw-Hill, Series in Population Biology, New York. 532 pp.

- Poulton, E. B. 1898. Essays on evolution. J. Linn. Soc. (1898): 558-612.
- Poulton, E. B. 1907. The significance of some secondary sexual characters in butterflies. Proc. Roy. Ent. Soc. Lond. (1907): xl-xliii.
- Poulton, E. B. 1931. The gregarious sleeping habits of a heliconian and ithomiine butterfly in Trinidad, observed by P. Lechmere Guppy. Proc. Ent. Soc. Lond. 6: 68-69.
- Poulton, E. B. 1933. The gregarious resting habits of dananine butterflies in Australia: also of heliconine and ithomiine butterflies in Tropical America. Proc. Ent. Soc. Lond. 7: 64-67.
- Price, P. W. 1975. Insect Ecology. John Wiley and Sons, New York. 514 pp.
- Punnett, R. C. 1915. Mimicry in Butterflies. Cambridge Univ. Press, Cambridge. 188 pp.
- Raffauf, R. F. 1970. A Handbook of Alkaloids and Alkaloid-Containing Plants. Wiley-Interscience, New York. Unpaginated.
- Rathcke, B. J., and R. W. Poole. 1975. Coevolutionary race continues: Butterfly larval adaptation to plant trichomes. Science 187: 175-176.
- Retnakaran, A. 1974. The mechanisms of sperm precedence in the spruce budworm, Choristoneura fumiferana (Lepidoptera: Tortricidae). Can. Ent. 106: 1189-1194.
- Richards, P. W. 1964. (2nd ed.) The Tropical Rain Forest. Cambridge Univ. Press, London. 450 pp.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37: 317-350.
- Ross, G. N. 1967. A distributional study of the butterflies of the Sierra de Tuxtla in Veracruz, Mexico. Ph.D. dissertation, Louisiana State University. 266 pp.
- Rothschild, M. 1973. Secondary plant substances and warning colouration in insects. In Insect/Plant Relationships. H. F. Van Emden (ed.), pp. 59-83, Blackwell Scientific Publications, Oxford. 215 pp.
- Schultes, R. E., and R. Romero-Castaneda. 1962. Edible fruits of Solanum in Colombia. Bot. Mus. Leaf. (Harvard U.) 19: 235-286.
- Scott, J. A. 1972 (1973). Mating of butterflies. J. Res. Lep. 11: 99-127.
- Scott, J. A. 1973 (1974). Lifespan of butterflies. J. Res. Lep. 12: 225-230.

- Seitz, A. (ed.) 1924. The Macrolepidoptera of the World. Vol. 5. The American Rhopalocera. Alfred Kernan Verlag, Stuttgart. 1139 pp.
- Sepp, J. 1828-1855. Surinaamsche Vlinders. 3 vols. (usually bound as one). Amsterdam.
- Shields, O. 1967. Hilltopping: an ecological study of summit congregation behavior of butterflies on a southern California hill. *J. Res. Lep.* 6: 69-178.
- Shields, O., and J. F. Emmel. 1973. A review of carrying pair behavior and mating times in butterflies. *J. Res. Lep.* 12: 25-64.
- Silberglied, R. E. 1976. Communication in the Lepidoptera. In Animal Communication (2nd ed.), T. A. Sebeok, ed. Indiana Univ. Press, Bloomington. (in press).
- Simpson, E. H. 1949. Measurement of diversity. *Nature* 163: 688.
- Southwood, T. R. E. 1966. Ecological Methods, With Particular Reference to the Study of Insect Populations. Methuen and Co., London. 391 pp.
- Standley, P. C., and C. V. Morton. 1937. Solanaceae. In "Flora of Costa Rica." *Field Mus. Nat. Hist. Bot.* 18: 1035-1099.
- Swihart, S. L. 1972. The neural basis of colour vision in the butterfly, Heliconius erato. *J. Insect Physiol.* 18: 1015-1025.
- Takhtajan, A. 1969. Flowering Plants: Origin and Dispersal. Smith. Inst. Press, Washington, D.C. 310 pp.
- Turner, J. R. G. 1971. Experiments on the demography of tropical butterflies. II. Longevity and home-range behaviour in Heliconius erato. *Biotropica* 3: 21-31.
- Turner, J. R. G. 1975. Communal roosting in relation to warning colour in two Heliconiine butterflies (Nymphalidae). *J. Lep. Soc.* 29: 221-226.
- Uphof, J. C. T. 1968 (2nd ed.) Dictionary of Economic Plants. J. Cramer, Lehre, Germany. 591 pp.
- van der Pijl, L., and C. H. Dodson. 1966. Orchid Flowers: Their Pollination and Evolution. Univ. Miami Press, Coral Gables. 214 pp.
- Vane-Wright, R. I. 1972. Pre-courtship activity and a new scent organ in butterflies. *Nature* 239: 338-340.
- Wiklund, C. 1974. Oviposition preferences in Papilio machaon in relation to the host plants of the larvae. *Ent. exp. appl.* 17: 189-198.

- Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resources availability in life history evolution. *Amer. Nat.* 108: 805-817.
- Willaman, J. J., and B. G. Schubert. 1961. Alkaloid Bearing Plants and Their Contained Alkaloids. U.S.D.A. Agric. Res. Serv. Tech. Bull. No. 1234. Govt. Printing Office, Washington, D.C. 287 pp.
- Wynne-Edwards, V. C. 1962. Animal Dispersion in Relation to Social Behaviour. Hafner Publ. Co., New York. 653 pp.
- Young, A. M. 1971. Notes on gregarious roosting in tropical butterflies of the genus Morpho. *J. Lep. Soc.* 25: 223-234.
- Young, A. M. 1972. On the life cycle and natural history of Hymenitis nero (Lepidoptera: Ithomiinae) in Costa Rica. *Psyche* 79: 284-294.
- Young, A. M. 1973. The life cycle of Dircenna relata (Ithomiidae) in Costa Rica. *J. Lep. Soc.* 27: 258-267.
- Young, A. M. 1974a. A natural historical account of Oleria zelica pagasa (Lepidoptera: Nymphalidae: Ithomiinae) in a Costa Rican Mountain Rain Forest. *Studies Neotrop. Fauna* 9: 123-140.
- Young, A. M. 1974b. Notes on the biology of Pteronymia notilla (Ithomiidae) in a Costa Rican mountain forest. *J. Lep. Soc.* 28: 257-268.
- Young, A. M. 1974c. On the biology of Godyris zavaleta caesiopicta (Lepidoptera: Nymphalidae: Ithomiinae). *Ent. News* 85: 227-238.

BIOGRAPHICAL SKETCH

Boyce Alexander Drummond III was born 28 February 1946 in Denison, Texas. He received his primary and secondary education in the public schools of Arkadelphia, Arkansas. From 1964 until 1967 he attended Henderson State College, from which he graduated with a Bachelor of Science Cum Laude in biology. In 1967 he began graduate study in the Department of Zoology of the University of Texas at Austin, where he held a position of Research Scientist Assistant. After serving in the United States Army as a member of the Fourth U.S. Army Band in San Antonio, Texas, from 1968 until 1971, he graduated with a Master of Arts in zoology from the University of Texas at Austin in 1971. He entered the Department of Zoology of the University of Florida in the fall of 1971 and has since pursued studies leading to the degree of Doctor of Philosophy. During this time he has held positions in the Department of Zoology as a graduate fellow, a graduate teaching assistant, and a graduate research assistant.

Mr. Drummond is married to the former Nancy Jean Price of Fort Smith, Arkansas, who is presently studying for the degree of Doctor of Medicine in the University of Florida's College of Medicine. He is a Research Associate of the Florida State Collection of Arthropods, Florida Department of Agriculture, and a member of the American Association for the Advancement of Science, the Society for the Study of Evolution, the Entomological Society of America, the Lepidopterists' Society, Sigma Xi, and Alpha Chi.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas C. Emmel, Chairman
Professor and Chairman of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Archie F. Carr
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F. Clifford Johnson
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas J. Walker
Professor of Entomology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1976

Dean, Graduate School