DIVERSITY AND ECOLOGY OF THE LEPIDOPTERA IN THE GALAPAGOS ISLANDS, ECUADOR

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Dissertation

Submitted in Partial Fulfilment of Requirements for the Degree of Doctor of Philosophy in Biology, Cardiff University, University of Wales

Cardiff, July 2006

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This thesis is dedicated to my wife Valentina Cruz Bedón

"..The natural history of these [Galapagos] islands is eminently curious, and well deserves attention. Most of the organic productions are aboriginal creations, found nowhere else; there is even a difference between the inhabitants of different islands; yet all show a marked relationship with those of America, though separated from the continent by an open space of ocean, between 500 and 600 miles in width. The archipelago is a little world within itself, or rather a satellite attached to America, whence it has derived a few stray colonists, and has received the general character of its indigenous productions. Considering the small size of these islands, we feel the more astonished at the number of their aboriginal beings, and the boundaries of most of the lava-streams still distinct, we are led to believe that within a period, geologically recent, the unbroken ocean was here spread out. Hence, both in space and time, we seem to be brought somewhere near to that great fact - that mystery of mysteries – the first appearance of new beings on this earth."

C. Darwin, 1845, *Voyage of the Beagle.*

".. Notwithstanding the fact that the flora and fauna of the Galapagos are fairly well known, there still remains an immense field for further investigation there, and the only manner in which a satisfying knowledge of the natural history of these interesting islands could be obtained, would be by residing in the archipelago for several years, and studying the fauna in all its relations in a most thorough and systematic manner.."

(F. X. Williams, 1911)

Summary

In this thesis the diversity and ecology of the Lepidoptera fauna of the Galapagos Islands, Ecuador are investigated. The study covers aspects of Lepidoptera diversity, their interactions with host plant and their seasonality.

Diversity: The Galapagos Lepidoptera fauna is characterized by low diversification, a high level of endemism and prolonged geographic isolation. To date, 313 species of Lepidoptera are known to occur on the Archipelago and 64% of the native component of this fauna is endemic. Humans have introduced 62 species accidentally to the Islands. All Galapagos Lepidoptera are of American origin except the few introduced Old World species that are nearly cosmopolitan.

Host plant relationships: Host plant data covering 155 species Galapagos species are reviewed, and new records of larvae of 113 species collected in the study area are presented. Most of the species are herbivores (272), with a few detritivores (13) and carnivores (3). Plants of the families Leguminosae and Asteraceae are the most common hosts for Galapagos species. Monophagy at the plant family level appears to be widespread in Galapagos Lepidoptera.

Seasonality: The phenology of adult Sphingidae was studied at one locality in the arid zone of the southern slope of Santa Cruz Island, Galapagos for a period of 28 months (April 1999 - August 2001). A total of 14 species, representing eight genera, was recorded during this study period. Sphingidae moths were more abundant in the wet season (December-May) with peaks occurring mid season. The number of specimens recorded decreased in the dry season (June-November) with the lowest numbers found in August. The seasonality and temporal stability (in terms of species diversity, population abundance and niche breadth) of this community is analysed.

Resumen

En esta tesis la diversidad y ecología de la fauna de Lepidoptera de las Islas Galápagos, Ecuador fue investigada. El estudio cubre aspectos de la diversidad, la interacción con las plantas huéspedes y la estacionalidad de las especies.

<u>Diversidad</u>: La fauna de Lepidopteros es caracterizada por una baja diversificación, el alto nivel de endemismo y el prolongado aislamiento geográfico. Un total de 313 especies de Lepidoptera son conocidas que ocurren en el Archipiélago y 64% de las especies nativas son endémicas. Los humanos han introducido 62 especies accidentalmente a las islas. Todos los Lepidoptera de Galápagos son de origen americano excepto unas pocas especies del viejo mundo que también son cosmopolitas.

<u>Plantas huéspedes</u>: Las plantas huéspedes de 155 especies fueron revisadas, y nuevos registros de larvas que se alimentan de plantas son presentadas para 113 especies de Lepidoptera colectadas en el área de estudio. La mayoría de las especies son herbívoras (272) y unas pocas detritivoras (13) y carnívoras (3). Plantas de las familias Leguminosae y Asteraceae son los hospederos más comunes de las especies de Galápagos. Monofagia al nivel de familia de planta parece ser bien representado en los Lepidoptera de Galápagos.

<u>Estacionalidad</u>: La fenología de adultos de Sphingidae fue estudiada en una localidad de la zona árida en el lado sur de la isla Santa Cruz durante 28 meses sucesivos (Abril 1999 - Agosto 2001). Un total de 14 especies, representando a ocho géneros, fueron registradas durantes el periodo de estudio. Sphingidae fueron más abundantes en la temporada húmeda (Diciembre-Mayo) con picos en la mitad de la estación, El número de especimenes registrados disminuyó en la temporada seca (Junio-Noviembre) con la menor abundancia en Agosto. La estacionalidad y la estabilidad temporal (en términos de diversidad de especies, abundancia poblacional y amplitud de nicho) de esta comunidad fueron estudiadas.

Acknowledgments

This thesis would not have been possible without the help of many people and institutions.

Special thanks go to the Galapagos National Park Service and Charles Darwin Research Station (CDRS), and their staff for their kind support during these years. Financial support for this research has been partially supported by an UK Government Darwin Initiative for a Survival of Species Project: Terrestrial Invertebrate Biodiversity in Galapagos (Ecuador): training and collection rehabilitation. Support has also been provided by the Charles Darwin Foundation through numerous small grants. The Galapagos Conservation Trust (London) has supported my work in many ways. They have followed my research with enthusiasm and have given me much logistical support and funds for my visits to The Natural History Museum London, UK (NHM-London).

To my thesis advisors Drs Hefin Jones (Cardiff University) and Mike Wilson (National Museum and Art Galleries of Wales), for their excellent guidance and help during the different phases of this project. A special thank to my colleague Dr Bernard Landry from the Museum d'histoire naturelle, Geneva, Switzerland for his constant encouragement and inestimable friendship.

I had the pleasure of participating in field trips in the Galapagos with three enthusiastic people: Drs Stewart B. Peck (Carleton University, Ottawa, Canada), Charlie V. Covell Jr. (McGuire Research Center for Lepidoptera Research and Insect Conservation, Florida, USA) and William Conner (Wake Forest University, North Carolina, USA). I benefited from interesting discussions about Galapagos insects, and their experiences as very capable scientists.

I am also grateful to Mr. Martin Honey and Dr Malcolm Scoble (NHM-London), Drs Leon Baert, Konjev Desender and Peter Verdick (Royal Institute of Natural Sciences, Brussels, Belgium), and Norman Penny (California Academy of Sciences (CAS), San Francisco, USA). They were very helpful and made my work on the collections under their care enjoyable. I am especially grateful to Zoran and Leonor Stjepic, and

Barbara West, for hospitality and logistical help during my visit to NHM-London and CAS.

Many thanks to all my colleagues in the department of Terrestrial Invertebrates (CDRS): Alejandro Mieles, Germania Estevez, Charlotte Causton, Ana Maria Ortega, Henry Herrera, Piedad Lincango, Helmuth Rogg, Ruth Boada and my field assistant Novarino Castillo; for their company and friendship through the years. Galapagos botanists have lent great assistance. I am especially indebted to Alan Tye, Heinke Jäger, Patricia Jaramillo and Ivan Aldáz for their identification of plants, and general botanical information. My sincere gratitude to Washington Llerena and Solanda Rea for helping with thesis illustrations and meteorological data.

A number of people commented upon earlier versions of this thesis. I would like to thank especially Chris Buddenhagen, Charlotte Causton, Helmuth Rogg and Bernard Landry for reading draft chapters.

Finally, I wish to thanks to my family: my mother for her exemplar life and support even when all my hopes to have a decent life as a biologist were lost. "Gracias mami". To my son Claudio Alejandro, and most of all to my wife Valentina Cruz Bedon for introducing me to the wonderful paradise of the Galapagos Islands, and for their love and company in life.

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Chapter 1

1. General Introduction

1. 1 THE GALAPAGOS ISLANDS

1.1.1. Geography and Geology

The Galapagos Islands (Fig. 1.1) are one of the most isolated oceanic archipelagos in the world. They are located 960 km off the West Coast of South America and lie on the equator. The Archipelago is part of the Republic of Ecuador and has a total land surface of 7856 km^2 (Wiggins & Porter 1971). The islands are volcanic in origin and are an aggregate of 19 major islands (over 1km^2), with 108 islets and rocks of different sizes (Snell *et al.* 1995). Isabela Island is the largest and highest, with an area of 4588 km^2 and a maximum altitude of just over 1700m. The next largest islands, in descending order, are Santa Cruz (904 km^2), Fernandina (635 km^2), Santiago (572 km^2), San Cristobal (552 km^2), Floreana (171 km^2) and Marchena (130 km^2). San Cristobal Island has a permanent freshwater lake, El Junco, as well as a permanent freshwater stream.

The archipelago is one of the most volcanically active areas in the world (McBirney & Aoki 1966). Large eruptions have been described several times (Beebe 1926; Colinvaux *et al.* 1968; Simkin 1977). Relatively recent eruptions have occurred on Isabela (in 1979, 1982, 1998, 2003 and 2005) and Fernandina (in 1978, 1984, 1988, 1991, 1995 and 2005). Less obvious signs of volcanic activity, such as earthquakes or the presence of volcanic gas-emitting holes (fumaroles), are widespread in the Archipelago. The Islands are located on a submarine platform on the Nazca seafloor crustal plate. The plate is presently moving at a rate of about 3.4 - 7cm a year to the east and south towards, and being subducted under, the western South American crustal plate (Cox 1983). Recent investigations have, however, determined that the Nazca plate has in fact, been moving to the northeast at 5.4cm a year; the adjoining Cocos plate has also moving to the northeast at 11.9cm a year (Mann 1995). The Islands themselves have been formed on the seafloor by a “hot spot” rising from the Earth’s mantle. This hot spot may have originated some 80 or 90 million years (myr) ago (Duncan & Hargraves 1984) and some rock from this time may now form part of the seafloor of the Caribbean and igneous terrains in Costa Rica (Hauff *et al.* 1997). The presence of the hot spot and the moving of the crustal plates have resulted in islands of different ages. The south eastern islands appear to be the oldest whereas the northern and western islands are the youngest. Age estimations of the extant islands are variable: K-Ar radiometry and marine fossils indicate that the maximum age of the oldest, exposed land is of the order of 3 - 4 myr (Geist *et al.* 1985; Hickman & Lipps 1985), whereas different geological plate motion models set a maximum age of emergence of the extant islands in the range of 4.5 - 6.3 myr, depending on the velocity of the Nazca plate (55mm yr^{-1} and 37mm yr^{-1}, respectively) (White *et al.* 1993; Geist 1996). It is likely that there were other islands present to the east of the islands visible today that were raised above sea level 10 - 18 myr ago, but have subsequently sunk through a process of subsidence (Christie *et al.* 1992). Terrestrial colonization has probably occurred during the last 3 - 6 myr of the present islands´ existence.

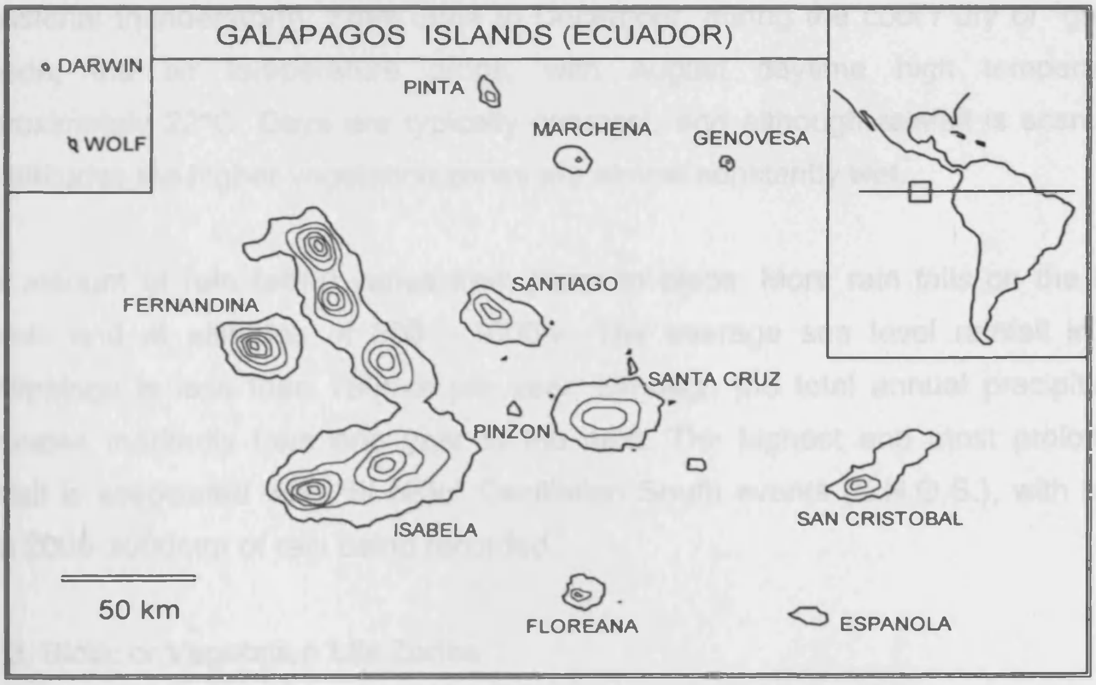


Figure 1.1. Map of the Galapagos Islands and their location to the mainland (inset).

The Galapagos volcanoes are shield-shaped with gentle lower slopes, a steep upper slope and a central cone. Volcanoes of relatively recent origin, such as Fernandina, and the five volcanoes of Isabela each have a giant crater, the so-called caldera. On the older islands, San Cristobal and Santa Cruz, for example, the caldera has disappeared due to erosion and is consequently less evident. Pleistocene climatic changes have also had their impact on the Islands. The Islands, especially in the central part of the Archipelago, were originally somewhat closer to each other than they are now (Geist 1996). The large islands have always remained separated from each other even when sea levels were 100m or lower during the full-glacial episodes (Peck 2001).

1.1.2. Climate

The climate of Galapagos is extremely arid compared to most tropical archipelagos. The Archipelago lies at the edge of the Central Pacific dry zone weather region and shows a remarkably seasonal, but highly unpredictable, climatic pattern. The year is divided into two main seasons (Fig. 1.2). From January to May, also known as the warm / wet season, the air temperature is warm with an average daytime high of about 29°C. During this period the climate is generally sunny, except for the occasional thunderstorm. From June to December, during the cool / dry or "garua" season, the air temperature drops, with August daytime high temperature approximately 22°C. Days are typically overcast, and although rainfall is scarce at low altitudes the higher vegetation zones are almost constantly wet.

The amount of rain falling varies from place to place. More rain falls on the high islands and at altitudes of 800 - 1000m. The average sea level rainfall in the Archipelago is less than 750mm per year, although the total annual precipitation fluctuates markedly from one year to the next. The highest and most prolonged rainfall is associated with "El Niño" Oscillation South events (E.N.O.S.), with more than 2000-3000mm of rain being recorded.

1.1.3. Biotic or Vegetation Life Zones

Santa Cruz, as well as the other six major islands, has six major vegetation zones. These vegetation zones are defined by precipitation and temperature gradients, which are controlled by island elevation and wind direction (Fig. 1.3). The first zone is the littoral zone (Fig. 1.4a), a narrow coastal belt, which varies in composition from lava boulders to sandy beaches. The composition of vegetation in this zone depends strongly on the plants' abilities to tolerate salt. Common plants include *Avicennia germinans* (Verbenaceae), *Batis maritima* (Batidaceae), *Conocarpus erectus* (Combretaceae), *Cryptocarpus pyriformis* (Nyctaginaceae), *Ipomoea pes-caprae* (Convolvulaceae) and *Heliotropium curassavicum* (Boraginaceae).

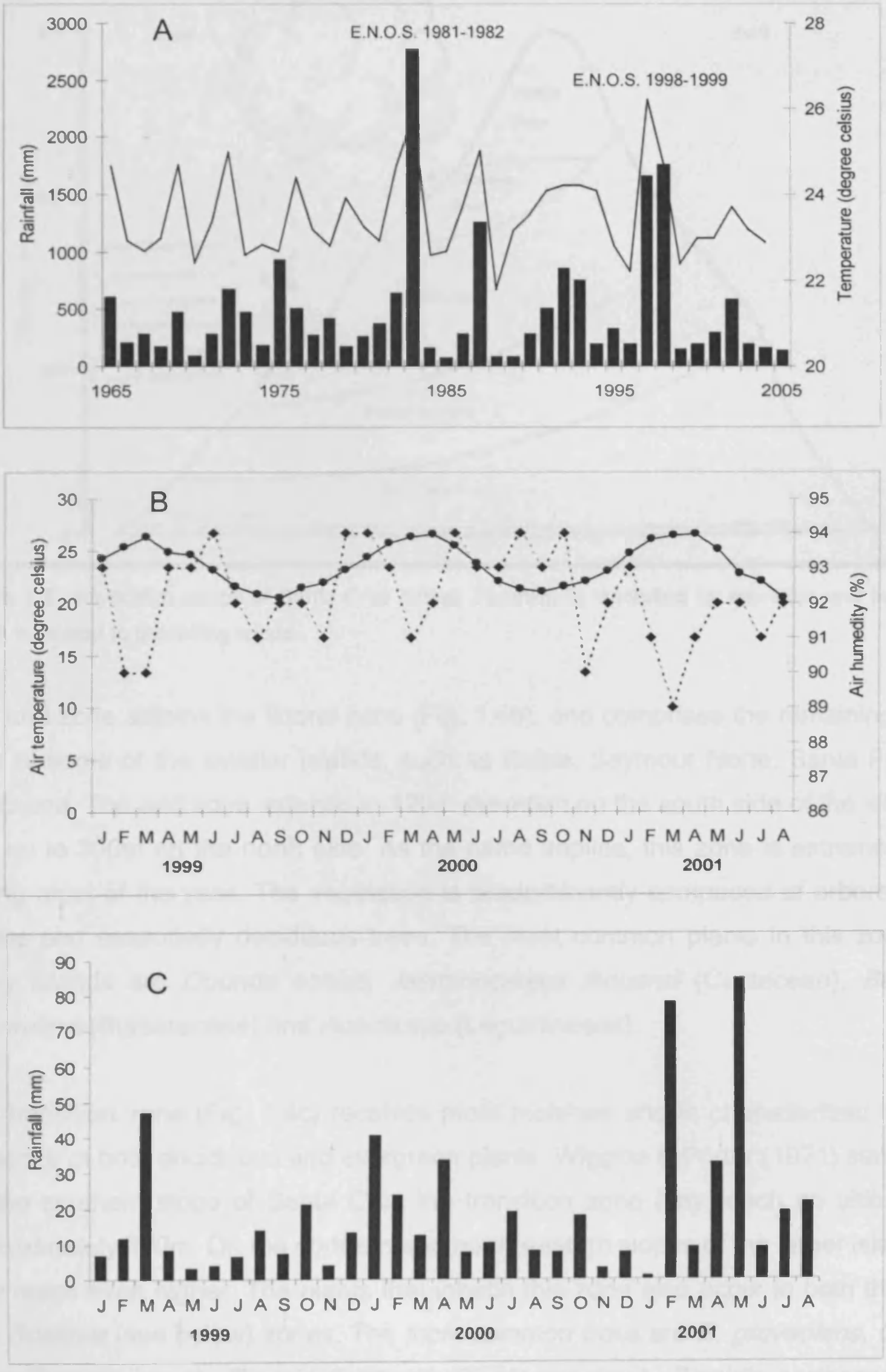


Figure 1.2. Climatic data of Santa Cruz Island based on data from CDRS meteorological station placed in the Arid Zone. A: Annual historical precipitation and temperature from 1966 to 2005; note the increasing of rainfall during "El Niño" Oscillation South (E.N.O.S.). B: Monthly temperature (dashed lines) and air humedity (solid lines) (1999- 2001). C: Cumulative monthly precipitation (1999- 2001).

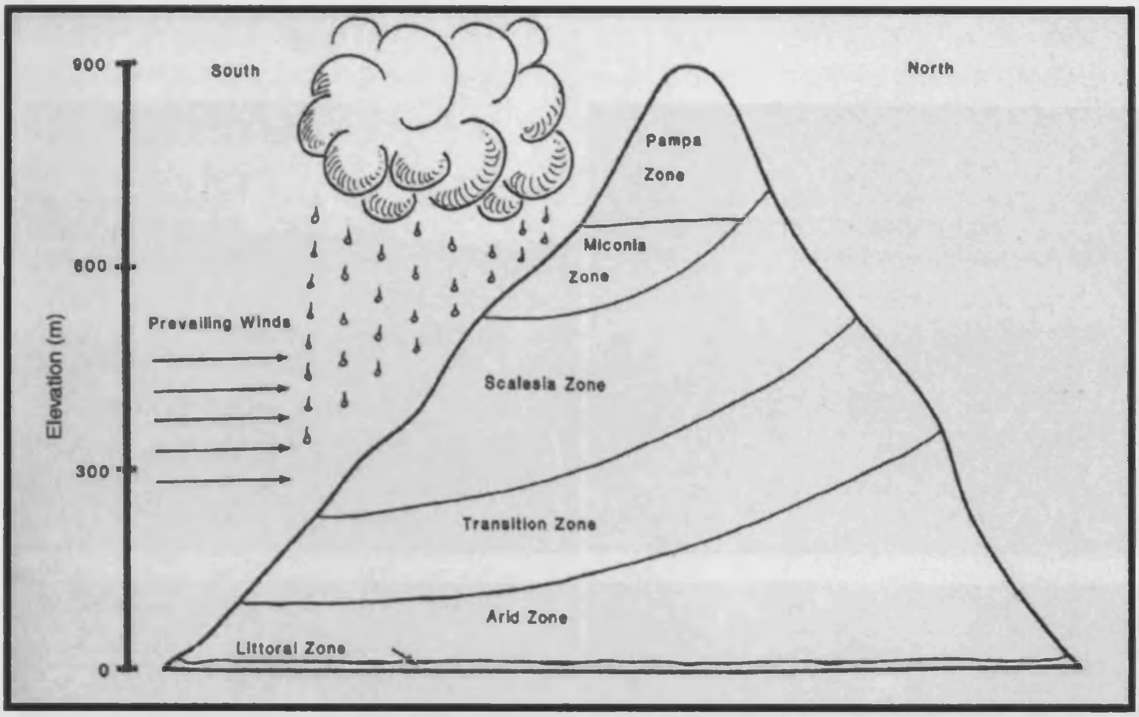


Figure 1.3. Vegetation zones of Santa Cruz Island. Zonation is controlled by elevation and humidity which is related to prevailing winds.

The arid zone adjoins the littoral zone (Fig. 1.4b), and comprises the remaining land area of some of the smaller islands, such as Baltra, Seymour Norte, Santa Fé and Marchena. The arid zone extends to 120m elevation on the south side of the islands, and up to 300m on the north side. As the name implies, this zone is extremely dry during most of the year. The vegetation is predominantly composed of arborescent cactus and seasonally deciduous trees. The most common plants in this zone on many islands are *Opuntia echios, Jasminocereus thouarsii* (Cactaceae), *Bursera graveolens* (Burseraceae) and *Acacia* spp (Leguminosae).

The transition zone (Fig. 1.4c) receives more moisture and is characterized by the presence of both deciduous and evergreen plants. Wiggins & Porter (1971) state that on the southern slope of Santa Cruz the transition zone may reach an altitude of approximately 200m. On the northern and north-eastern slopes of the larger islands it may reach even higher. The plants that inhabit this zone also occur in both the arid and *Scalesia* (see below) zones. The most common trees are *B. graveolens, Cordia lutea* (Boraginaceae), *Pisonia floribunda* (Nyctaginaceae), *Piscidia carthagenensis* (Leguminosae) and *Psidium galapageum* (Myrtaceae).

Figure 1.4. Vegetation zones on Galapagos Islands. A, Littoral zone at Tortuga bay, Santa Cruz; B, Arid zone, Santa Fe; C, Transition forest, Santa Cruz; D, Scalesia forest, Los Gemelos Santa Cruz; E, Miconia zone, Media Luna Santa Cruz; F, Pampas zone, Cerro Crocker Santa Cruz.

The *Scalesia* zone (Fig. 1.4d), also known as the humid forest zone, extends to an elevation of 400 - 500m on the southern slope of Santa Cruz and is dominated by the evergreen tree *Scalesia pedunculata* (Asteraceae) (Wiggins & Porter 1971). This same species forms the *Scalesia* zone on Floreana, San Cristobal and Santiago, but is represented by *Scalesia microcephala* on Fernandina and northern Isabela (Volcanoes Alcedo, Darwin, Wolf, Ecuador), and *Scalesia cordata* on the southern part of Isabela (Volcanoes Cerro Azul and Sierra Negra). Other common plants are *P. floribunda, Zanthoxylum fagara* (Rutaceae), *Tournefortia rufo-sericeae* (Boraginaceae) and *Chiococa alba* (Rubiaceae).

A *Miconia* or evergreen shrub zone adjoins the *Scalesia* zone (Fig. 1.4e), but is only found on Santa Cruz and San Cristobal. At one time the *Miconia* zone consisted almost entirely of the endemic shrub *Miconia robinsoniana* (Melastomataceae), but competition from introduced plants has greatly reduced its population density. On the other islands the pampas, or fern sedge zone (Fig. 1.4f), at around 525 - 550m in elevation follows the *Scalesia* zone. This is the highest zone and rises to the top of the mountains. The summits are mostly covered with sedges, bracken fern, club mosses and grasses.

1.2 CONSERVATION OF THE GALAPAGOS ISLANDS

Oceanic islands such as the Galapagos Islands are important for evolutionary studies, and as biological reserves where fauna and flora remain in a largely natural state (Larson 2001). The isolation that has led to the formation of a unique island biota is, however, endangered by four main threats provoked by human action: direct predation, the introduction of alien species, the spread of disease and habitat degradation or loss (Whittaker 1998).

The Galapagos Archipelago is characterized by a high level of endemism. This biodiversity, however, is fragile as human activities can, in a short period, profoundly modify habitats in some areas (Powell & Gibbs 1995). The scientific interest in the Archipelago as a natural laboratory of evolution prompted the government of Ecuador to designate the area a National Park in 1959, protecting 97% of the total land area. UNESCO placed the Islands on the World Heritage List in 1978 as one of its first "natural" sites. Even at that time the integrity of the area was threatened by accelerated human settlement accompanied by the importation of foreign animals and plants (Peck *et al.* 1998), uncontrolled fishing and tourism.

Given the young age of the Archipelago, the Galapagos are not a "hotspot" of biological diversity, but they are a vital area of endemism and a highly significant reservoir of unique and threatened evolutionary history. These features highlight the significance of the Galapagos to global biological diversity. Recognition of this fact on its own is, however, not sufficient and for the last 40 years two institutions have been leading the conservation effort on Galapagos ecosystems: The Charles Darwin Foundation (from 1959) and the Galapagos National Park Service (from 1968). Both institutions have been collaborating to develop conservation programs that include the prevention and control of introduced species′ impacts, and the protection of the endemic biota.

In spite of numerous environmental and social concerns, the Galapagos Islands still represent a magnificent showcase of biodiversity, mainly due to their late colonization by humans. Only discovered in 1535, and not colonised by humans until the early 1800s, the Islands have escaped many of the human pressures other island chains have experienced for thousands of years. The Islands are therefore still well preserved, and provide an opportunity to study the natural processes of organism diversification that gave birth to the biodiversity and endemism observed today.

The Galapagos are a rare remnant of a prehistoric pattern of global biological diversity where sizeable proportions of the world's distinctive and often bizarre species occurred on islands. Humans have altered much of that pattern. The biological diversity of the Galapagos provides one of the best examples of that pattern; few, if any, other opportunities remain for preserving intact biotas of archipelagos. This is why the Galapagos Archipelago warrants special attention - this is one of our last chances to preserve the Islands.

1.3. THE ORIGIN OF THE BIOLOGICAL DIVERSITY IN THE CONTEXT OF THE ISLANDS' BIOGEOGRAPHY

The Galapagos Islands are a large and complex archipelago. Their relatively recent (3 - 4 myr) origin, the oceanic isolation and the climate have promoted speciation in both plant and animal groups. Darwin's finches provide the best-known illustration of this. From a single ancestral colonization, under the influence of selection and isolation, the finch populations have diverged into 13 different species through the process of adaptive radiation (Lack 1947; Grant 1986). Evolution in invertebrates has been less spectacular although several species swarms have been recorded. The bulimulid land snails (Coppois 1984), the beetle *Stomion* (Finston & Peck 1997), and the moth genus *Galagete* (Landry 2002) are three examples.

Two main theories have been proposed to explain the origin and the biogeographical affinities of the Galapagos flora and fauna; the continental and oceanic theories (Vinton 1951).

Continental theory: Rosen (1978) suggested a vicariance model to explain the origin of the Galapagos. This model suggests that the components of major biota evolve together and are subject to parallel effects of geographical and climatic fluctuations. Modern biogeographical distributions result from the division of ancestral biotas by the formation of natural barriers. Rosen (1978) further suggested that either the Cocos and Carnegie submarine ridges to the east and northeast of the Archipelago may have provided a continuous dry land corridor for the colonization of the Galapagos, or that the Galapagos are a fragment of South America that has drifted to the west. There is, however, no convincing geological evidence to suggest that the Galapagos ever had direct land-bridge connections with Central or South America (Cox 1983).

An alternative model proposed by panbiogeography focuses on the geographic relationship between distribution and tectonics; rather than hypothetical geological history. The three tracks of the Galapagos biotas (Pacific, Eastern Pacific and Caribbean) imply the former presence of three different ancestral distribution ranges in the East Pacific that overlapped within the region now occupied by the Galapagos. These supposedly corroborate a direct contact between the Galapagos hotspot and American mainland mediated by dispersal over island arcs (Grehan 2001).

Oceanic theory: The Galapagos are young oceanic islands. Like the Hawaii Archipelago and Canary Islands, the current Galapagos Islands are the most recent products of a long-existing hotspot (Christie *et al.* 1992; White *et al.* 1993). Oceanic islands receive their original biotas solely through dispersal and later through speciation. Two models of dispersal have been considered for the colonization from the South and Central American mainland for Galapagos organisms. The first model consists of a single, long-distance dispersal event surpassing the oceanic barrier (Carlquist 1965; Thornton 1971). The second model, or stepping-stone dispersal theory, involves a series of comparatively short dispersal event that allows species to reach a distant area with intermediate populations establishing along the way (Croizat *et al.* 1974; Hogue & Miller 1981). Recent discoveries on the Carnegie Ridge shows that earlier volcanic islands, now submerged, were available for terrestrial colonization at least 5 to 11 myr ago (Christie *et al.* 1992). Those islands may have served as stepping-stones for colonization by ancestors of some of the current terrestrial fauna.

Phylogenetic studies based on various data for a few endemic taxa indicate variable times of divergence. Investigations of enzyme electrophoresis and immunological data of the Galapagos iguanas of the genera *Amblyrrhynchus* Bell and *Conolophus* Fitzinger suggest a divergence time of 15 - 20 myr from mainland iguana relatives (Wyles & Sarich 1983). This range of time was recently confirmed by DNA sequence-based estimates (Rassmann 1997). Favouring a range of ages older than the extant islands are the molecular clock calibrations for the gecko and lizard genera *Phyllodactylus* Gray and *Tropidurus* Wied; they yield ages of 8.9 and 10.2 myr, respectively (Wright 1983; Lopez *et al.* 1992). Although the ancestors of these lizards are likely to have originally colonised a now-submerged island, other elements of the fauna may be more recent in origin. For example, enzyme electrophoresis analyses of the Darwin finch species (Fringillidae: Emberizinae) suggest divergences within 5 myr or less (Grant 1994), within the age-range of the present islands (White *et al.* 1993). This is consistent with a recent study on beetles (Finston & Peck 1997), which showed little allozyme differentiation among marked morphological groups endemic to the various islands. All of these theories can be simultaneously true since arrival times may have differed between taxa. It does, however, suggest the likely beginning of evolutionary changes in the ancestors of endemic species that existed on islands now submerged prior to the emergence of islands currently present in the Archipelago.

1.4 THE DIVERSITY OF THE INSECT FAUNA WITH PARTICULAR REFERENCE TO LEPIDOPTERA

In term of the number of species, insects dominate the Galapagos ecosystem (Peck 1997) (Table 1.1). As in all terrestrial systems insects comprise a highly important component of biotic communities and play a major role in determining structural relationships within an ecosystem (Janzen 1987). Insects are also the most important primary consumers and act as both prey and host for numerous predators and parasitoids. Endemic terrestrial vertebrates such as Darwin's finches and lava lizards include insects as an important food resource in their diet.

The insect fauna of the Galapagos Islands presents a relatively high level of endemism (about 40%) (Peck 2001). Some orders show even higher levels. For example, about 67% of the Coleoptera that are found in the Galapagos are not encountered anywhere else (Peck & Kukalova-Peck 1990). Only a few ecological studies have been carried out on insect communities in the Galapagos Archipelago. Taxonomic works dominate the extensive entomological literature of the Islands. The few ecological studies that exist concentrate on invasive species (Causton *et al.* 2004), secondary succession (Abedrabbo 1989; Desender *et al.* 1999) and insect communities (Abedrabbo 1996).

The Lepidoptera are the second most diverse taxonomic group of insect in the Galapagos (Peck 2001). They are generally among the most species rich of phytophagous insects (Scoble 1992), emulated only by the coleopteran group, Phytophaga (Crowson 1981). Nearly all species are herbivorous but there are some exceptions (Powell *et al.* 1998). Moths and butterflies are an important element of the Islands' ecosystems because many species are potential and successful colonizers.

The Galapagos Islands were discovered by the Bishop of Panama, Fray Tomas de Berlanga, in 1535. No Galapagos Lepidoptera were collected on this expedition, and only one species was described over the next 300 years. The first lepidopteran collected and described on Galapagos appears to be the endemic *Psaphara interclusa* (Walker) (Noctuidae). This species was collected by one of the crew members of the *H. M. S. Herald* or *H. M. S. Pandora* in January 1846 (Hayes 1975).

Blattodea	17	11	2	5
Isoptera	4	0	3	1
Dermaptera	7	4	1	2
Embioptera	2	1	0	1
Zoraptera	1	0	1	0
Psocoptera	39	13	6	20
Thysanoptera	50	8	42	0
Phthiraptera	80	1	66	13
Hemiptera	129	16	35	78
Homoptera	141	56	13	72
Neuroptera	8	0	3	5
Strepsiptera	1	0	1	0
Coleoptera	420+	61	101	258
Lepidoptera	346+	46	200+	100+
Siphonaptera	4	3	0	1
Diptera	240+	39	93	108
Hymenoptera	280+	31	220	29
Total	1853+	295+	818+	736+

Table 1.1. Insect fauna diversity known from the Galapagos Islands. Species numbers wi the faunal study continues (After Peck 2001). Endemic (occurring only in the Galapag Natives (occurring in the Galapagos by natural dispersal), Introduced (through human age

Wallengren (1860) made the second mention of Lepidoptera from the A when he described three endemic species: *Utetheisa galapagensis* (*Leptotes parrhasioides* (Lycaenidae) and *Atteva hyrsginiella* (Yponoı collected in May 1856 during a trip by the Swedish frigate *Eugenie*.

Subsequently, Butler (1877), Holland (1889), Rothschild & Jordan (1903) a (1904, 1905) all added new data based on material collected fro expeditions. In 1911, Francis X. Williams published the first monographic work about the taxonomy and ecology of any Lepidoptera family on the Galapagos Islands (Williams 1911). He reported the occurrence of 14 species of Sphingidae and butterflies collected during the scientific trip of the California Academy of Sciences in 1905-06. Expeditions which visited the Islands in following years included the: Harrison Williams Galapagos Expeditions (1923), St. George Expedition (1924), Hancock Galapagos Expedition (1931), Templeton Crocker Expedition of the California Academy of Sciences (1932), Juan Föster Expedition (1959), Deutschen Galapagos Expedition (1962-1963), Galapagos International Scientific Project (1964) and Mission Zoologique Belge (1964-1965). The more significant papers from these expeditions were published by Schaus (1923), Beebe (1923), Meyrick (1926), Richards (1941) and Kernbach (1962).

From 1966 to 1975 two members of the staff of the Charles Darwin Research Station (CDRS) carried out collections of Lepidoptera on the Islands. Roger Perry and Tjitte DeVries's efforts were focused on collecting moths from different islands and studying the host plant relationships of these species. They sent part of their collections to England for further study. Stimulated by Perry and DeVries's collections, Alan Hayes (Natural History Museum, London), Frederick Rindge (American Museum Natural History, New York) and Claude Herbulot (Paris, France) published four extensive papers on the macro-moth fauna (Sphingidae, Uraniidae, Arctiidae, Noctuidae and Geometridae) of the Islands. The Lepidoptera species known up to 1977 were summarized by Linsley & Usinger (1966) and Linsley (1977).

From 1975 to 1989 no further Lepidoptera collections were carried out in the Archipelago and very few papers were published. During the last 15 years, however, important scientific studies have been re-initiated. Bernard Landry is conducting a taxonomic study of the moths (expeditions 1989, 1992, 2001 and 2004) focusing mainly on the Microlepidoptera. His valuable research had been published in 14 scientific papers. Finally, as a resident entomologist working for the Charles Darwin Foundation since 1996, the author has carried out collections in different islands and published 10 scientific papers describing some of the Lepidoptera taxa (see Appendix 3).

There is little additional information available on the ecology of the Galapagos Lepidoptera. McMullen (1986, 1990, 1993) and Linsley (1966) summarized the known flower-insect relationships in the Galapagos, and included some moths and butterflies. Kernbach (1964) and Curio (1965a, b) studied the development and behaviour of certain caterpillars, and Roque *et al.* (2002) have discussed the uses of alkaloids by arctiids.

1.5. OBJECTIVES AND AIMS OF THE STUDY

Profound changes are occurring in the Galapagos insect fauna. Increasing contact with the outside world has broken the isolation that allowed the survival and evolution of native species. The changing composition of the Galapagos insect fauna is readily apparent from the contrast between historical collections and reports (e.g., Linsley & Usinger 1966; Hayes 1975), and more recent records and surveys (Peck 2001). This change is particularly obvious in highland areas where land conversion and the establishment of alien species have eliminated or at least drastically reduced the abundance and diversity of native arthropods.

In the context of the conservation of Galapagos insects, the study of key or indicator groups such as Lepidoptera has been identified as one of the most important research areas in need of attention (Peck 1991). Understanding the bionomics of the species: for example, their seasonality, food and habitat preference, is essential for their protection. Lepidoptera are one of the most suitable groups for such comparative studies. For example, their abundance, species richness, response to vegetation and climate, their ease of sampling using traps and their advanced taxonomy, all make them useful signposts for conservation programmes. They are susceptible to change, or are being changed by habitat alteration, the introduction of mainland species, and the movement of introduced and endemic species between islands through ship and air transport (Peck *et al.* 1998; Roque-Albelo & Causton 1999). In addition, because Lepidoptera are important components of ecosystems, Lepidoptera surveys can be used to assess the health of native ecosystems; furthermore, reserve managers often need to be able to determine the status of species to manage properly other natural resources.

personal museum and fieldwork. The main aim was to establish a scientific r the Archipelago species, giving biogeographic data, where available, of whe species occur and their origin. A special effort was made throughout to docur occurrence of human-introduced pest species so that this knowledge may a the planning and monitoring of both natural and agricultural areas.

Chapter 3 describes the host plant relationships of the Galapagos Lepidopte to this study, practically nothing comprehensive had been published on th This chapter is intended to provide a relatively comprehensive coverag Lepidoptera families present in the Archipelago based on extensive fieldwor populations are characterized by typical patterns of seasonal app (phenology). This topic is covered in Chapter 4. While it is difficult to de seasonal patterns for the entire fauna, 15 species of the family Sphingidae o in Santa Cruz Island were chosen as a proxy group to study the seasonal abu of the Lepidoptera fauna. This long term-study provided the first data of ph carried out on any insect group in the Archipelago.

In summary, as far as the author is aware, the diversity and ecology of Lep assemblages in the Galapagos Islands have been investigated for the fi Using this key group of insects, the diversity, host plant relationships, sea and the relationship between Lepidoptera, and their abiotic and biotic envi have been explored. This work will assist agencies such as the Galapagos Park Service and Ministry of Agriculture to help preserve critical habitats esse survival of Galapagos's fauna and flora, of which the Lepidoptera comprise portion.

Chapter 2
Diversity of the Lepidoptera fauna of the Galapagos Islands

2.1 INTRODUCTION

Naturalists have long been fascinated by the biotas of remote oceanic islands (Darwin 1845; Wallace 1880; Carlquist 1973). The main interest has been to consider differences in species composition between these islands and the better-known biotas of continental areas (Whittaker 1998). This interest stems, at least partly, from a fascination with the variety of biological organisms, their evolution, their patterns of distribution (both spatially and temporally), and the search for an explanation of the observed patterns (i.e. the study of their biogeography). Oceanic islands are also interesting in the evolutionary trends displayed by their biota; for example, the reduction of dispersal capabilities, the changes in body size (Carlquist 1973) and the tendency towards developing drab colours (Zimmerman 1948). These lend insight into patterns of community structure, the processes of colonization of new habitats and the dynamics of speciation (Mueller-Dombois 1981).

In the Galapagos Islands, the study of biogeography remains as important for modern evolutionary theory as it was for Charles Darwin. Insects, including groups such as the Lepidoptera, offer great potential for the study of biogeography and evolutionary processes on islands. As well as being abundant and diverse, insects are also well suited as indicators of change across gradients at many scales (spatial across and among islands, temporal between seasons and years), and across trophic groups and ecological associations (Miller 1996).

Their inherent mobility enabled the Lepidoptera to be one of the first and most successful groups of insects to colonize oceanic islands. The Galapagos Lepidoptera fauna is rich and diverse, but impoverished in comparison with that of adjacent South America where there are estimated to be more than 90,000 species (Heppner 1991). The most comprehensive lists of Galapagos's Lepidoptera were published by Linsley & Usinger (1966) and Linsley (1977). The Lepidoptera fauna is now known to consist of nearly 310 species but many remain to be described and identified.

Studies of species, their taxonomy and distribution provide the foundation for conservation planning and management. Insufficient knowledge of these areas of the Lepidoptera fauna in the Galapagos Islands, along with lack of information on the evolutionary processes, have, to date, inhibited the development of appropriate conservation programmes. In this chapter the Lepidoptera fauna of the Galapagos Islands is described using both published and unpublished information. The chapter aims to provide an overview of the Lepidoptera species present, their ecological and taxonomic relationships, and their distribution in the Archipelago.

2.2 METHODS

2.2.1 Field and museum methods

Data describing species occurrence and distribution were drawn from three sources:

1) Literature review of all known papers concerning Galapagos Lepidoptera (see Table 2.1);
2) Study of specimens deposited in the following museum collections: Invertebrate Collection of the Charles Darwin Research Station (IC CDRS), Santa Cruz Island, Galapagos Islands; Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador; Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador; California Academy of Sciences (CAS), San Francisco, USA; Canadian National Collection (CNC), Ottawa, Canada; The Natural History Museum (NHM), London, U.K. and the Royal Institute of Natural Sciences (KBINRS), Brussels, Belgium; and.
3) Field collections made by the author in the Galapagos from 1995 to 2004.

For the latter, the sampling methods utilized to collect specimens in the field (Fig. 2.1) included net collecting of day-active species, lights (mercury vapour, ultraviolet and fluorescent) either suspended in front of a white sheet or inside a gauze cylinder (diameter 1m, height 2m, light tower, see Fig. 2.1b), universal ultraviolet light trap (Bioquip, Gardena, Ca. ®) (Fig. 2.1a) and Malaise traps (Fig. 2.1c). All major and most minor islands were sampled at least once, including the remote islands of Darwin and Wolf in the north of the Archipelago. Specimens were collected in glass tubes or cyanide jars and, subsequently, either mounted in the field (see Fig. 2.1f) or in the laboratory, or frozen until they were spread. Each specimen was labelled with information on the locality, geographical coordinates and altitude data (Garmin GPS III), collection date and collector. The majority of the specimens collected are deposited at the IC CDRS.

Following Kristensen (1999), data for each family are presented in the following sequence: *(i)* a summary of the diversity and distribution of the family in Galapagos and elsewhere; *(ii)* a summary of the literature records for Galapagos; *(iii)* new records for new or poorly known species; *(iv)* appropriate additional notes on the ecology of the taxa, and very general notes on morphology or colouring; *(v)* a checklist of known occurring species; and *(vi)* an illustration of a representative species for each family.

For each species status is given as endemic (E) (occurring only in the Galapagos Islands), native (N) (occurring on the Galapagos Islands by natural dispersal), or introduced (I) (through human agency).

The following island name abbreviations are used:
Ba: Baltra; Bam: Bambridge; Bt: Bartolomé, Dw: Darwin; Ed: Eden; Fe: Fernadina; Fl: Floreana; Gdr (Fl): Gardner near to Floreana; Gdr (Es): Gardner near to Española; Ge: Genovesa; Es: Española; Is: Isabela; Ma: Marchena; Pt: Pinta; Pz: Pinzon; Ra: Rabida; SCl: San Cristobal; SCz: Santa Cruz; SF: Santa Fé; Stg: Santiago; SN: Seymour Norte and Wo: Wolf. An asterisk (*) after scientific name or island name denotes a new record for Galapagos or a specific island respectively.

2.2.2 Analysis of data

Distribution data of all Galapagos Lepidoptera species were compiled into a matrix database. Because the species-area relationships is a consistent phenomenon (Williams 1943), the best way to consider other sources of variation in species number is through the analysis of residuals (deviations) from species area regressions (Wilcox 1978; Rosenzweig 1995). Area influences several processes that determine species richness, including extinction rate (MacArthur & Wilson 1967), immigration rate (Lomolino 1990) and speciation rate (Losos & Schluter 1999). In this study simple linear regressions were used to characterize the relationships between species richness of indigenous and introduced species and two potential geographical predictors: island area, and ecological complexity (as a measured by the number of major life zones). Additionally, simple linear regressions were performed in order to analyse the relationship between species richness and one historical factor, the age of the islands. Some of the data analysed were transformed to Log_{10} in order to find the best line of fit predicted between the variables. The values of the geographical predictors were taken from Peck (2001) as some previously published values are inaccurate. All statistical analyses were performed using the software package Minitab 13.31.

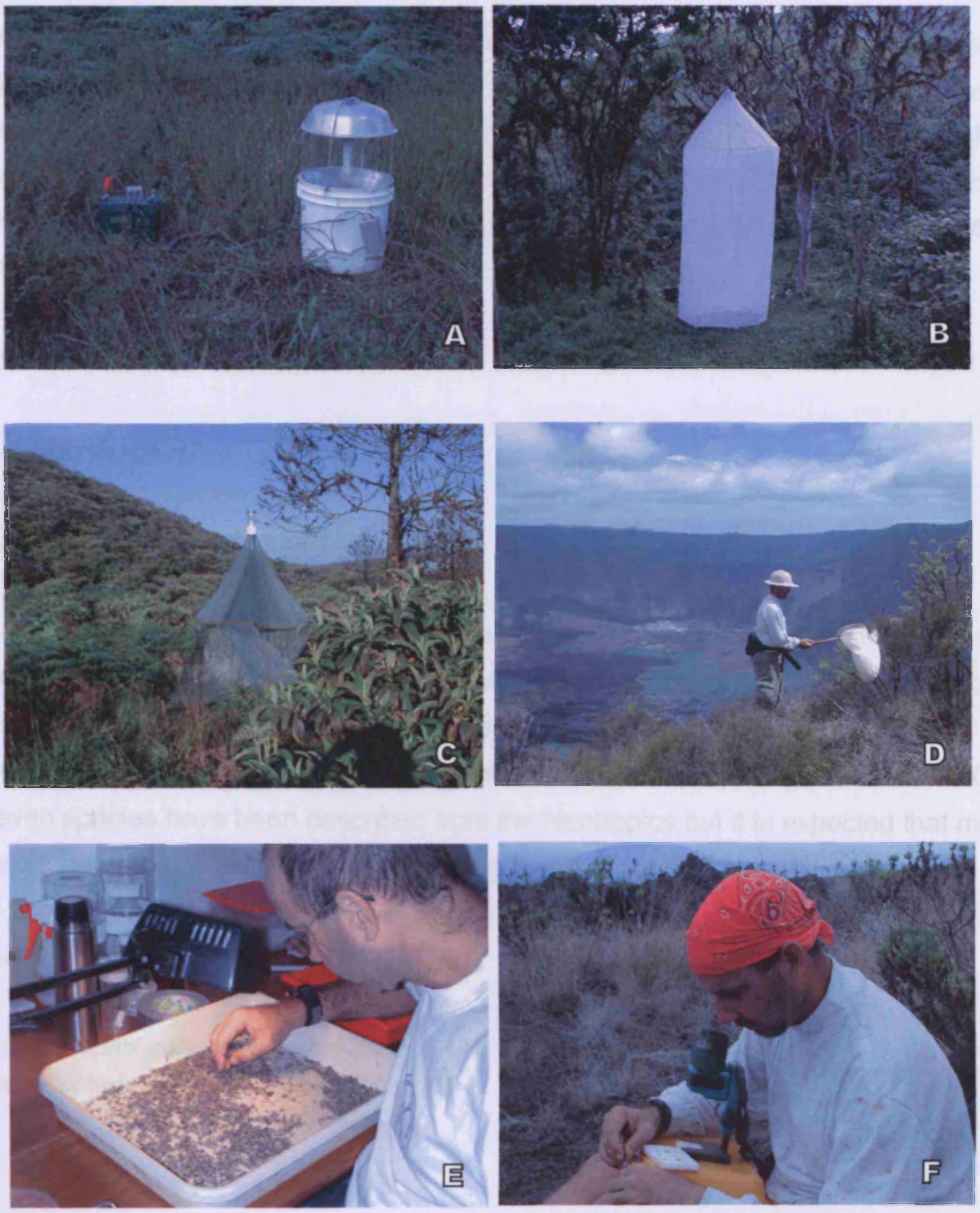


Figure 2.1. Sampling and mounting techniques. A, Universal light trap; B, Tower light; C, Malaise trap; D, Sweeping net; E, Sorting adults; F, Field mounting.

2.3 RESULTS

2.3.1. Opostegidae (Fig 2.2a)

One previously undescribed species was collected at light traps in all vegetation zones of several islands. The adults of this family are among the smallest known Lepidoptera in the Islands with a wingspan of about 5 mm. This small cosmopolitan family contains six genera and 106 described species (Davis 1989) although there are probably many species still remaining to be described worldwide (Scoble 1992). The Neotropical fauna consists of 16 species (Davis 1984).

Species checklist:

1. Pseudopostega sp.*; (E); Fe, Is, SCz.

2.3.2. Tischeriidae (Fig 2.2b)

A small group of primitive moths, the Galapagos Tischeriidae fauna consist of two endemic species belonging to the genus *Astrotischeria* (Landry & Roque-Albelo 2003). Some 101 species are described, mostly from the Holarctic region, but species are known also from the Neotropical region (Puplesis & Diskus 2003). Eleven species have been described from the Neotropics but it is expected that more species remain unrecorded; the leaf-mining fauna is poorly known.

Species checklist:

1. Astrotischeria scalesiaella Landry 2003*; (E); Fl, SCz, Wo.
2. Astrotischeria alcedoensis Landry 2003*; (E); Is.

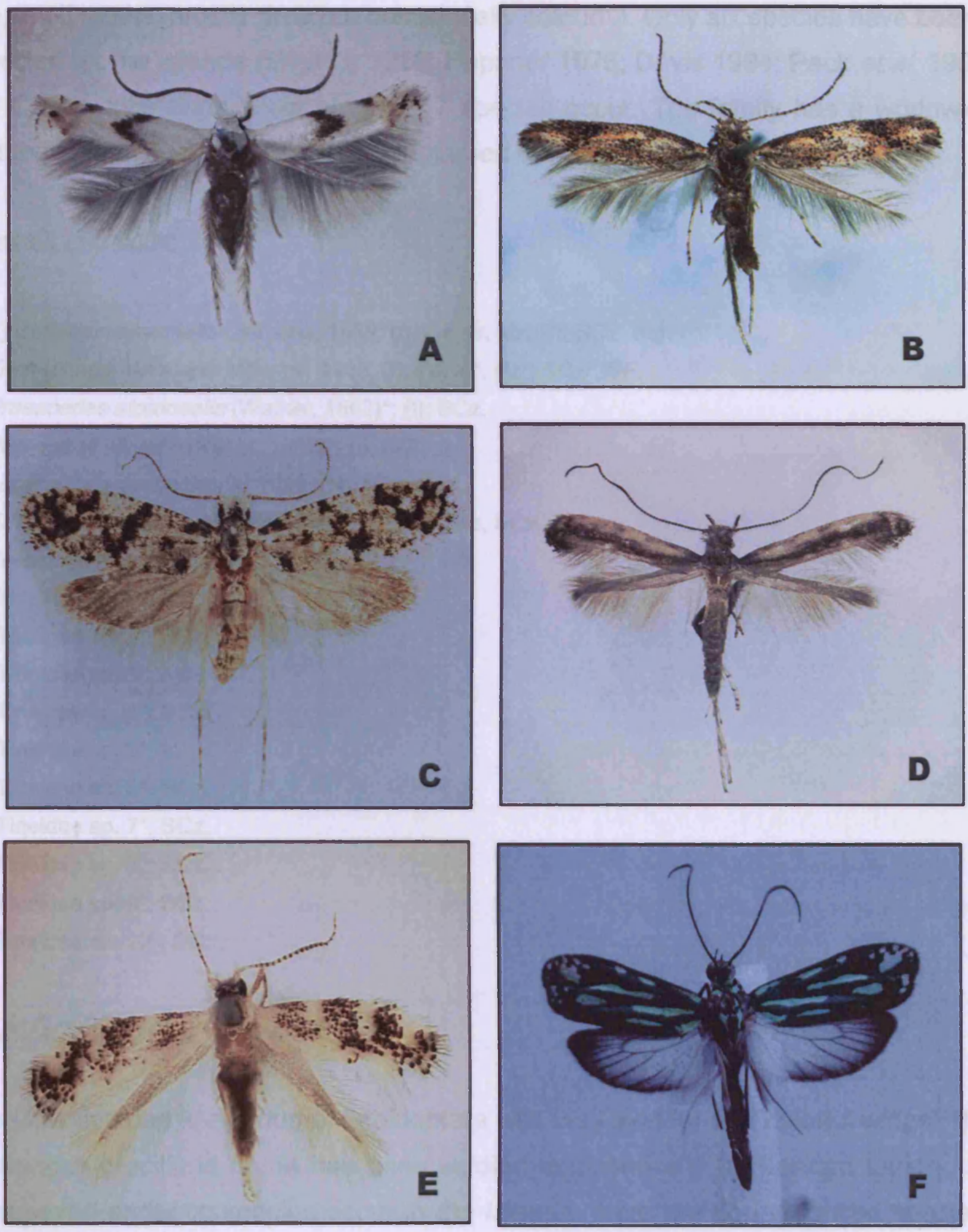


Figure 2.2. A, *Pseudopostega* sp. (Opostegidae); B, *Astrotischeria scalesiaella* (Tischeriidae); C, *Lepyrotica acantha* (Tineidae); D, *Caloptilia* sp. (Gracillariidae); E, *Bucculatrix cordiella* (Bucculatricidae); F, *Atteva hyrsginiella* (Yponomeutidae).

2.3.3. Tineidae (Fig 2.2c)

Tineid moths are rarely mentioned in studies of Lepidoptera in the Galapagos. They are small moths, mostly drab but occasionally colourful. Only six species have been reported for the Islands (Meyrick 1926; Heppner 1975; Davis 1994; Peck *et al.* 1998) but CDRS collections show at least 17 species occur. The family has a worldwide distribution and there are about 3,000 named species (Davis 1987c).

Species checklist:

1. *Xylesthia pruniramiella* Clemens, 1859; (I); Ge, Is, Ma, Pt, SCz, Stg.
2. *Trichophaga mormopis* Meyrick, 1935; (I); Fe, Is*, Pz*, SCz*, SF.
3. *Praeacedes atomosella* (Walker, 1863)*; (I); SCz.
4. *Phereoeca allutella* (Rebel, 1892)*; (I); SCl.
5. *Lepyrotica acantha* Davis, 1994; (N); SCz, SCl.
6. *Erechtias minuscula* (Walsingham, 1897); (I); Ma, SCz.
7. *Setomorpha rutella* Zeller, 1852* (I); SCz.
8. Tineidae sp. 1*; SCz.
9. Tineidae sp. 2*; SCz.
10. Tineidae sp. 3*; Fe.
11. Tineidae sp. 4*; SCz.
12. Tineidae sp. 5*; Is.
13. Tineidae sp. 6*; SCz.
14. Tineidae sp. 7*; SCz.
15. Tineidae sp. 8*; SCz.
16. Tineidae sp. 9*; SCz.
17. Tineidae sp. 10*; SCz.

2.3.4. Gracillariidae (Fig 2.2d)

The Gracillariidae is a group of Lepidoptera with very slender and colorful wings. The Galapagos gracillarid fauna has been studied taxonomically by Bernard Landry. At least seven endemic species occur in the Islands, there are no introduced species. Specimens were collected at light traps at all altitudes from the littoral to the pampas zone. The family is known to contain approximately 147 species in the Neotropics (Davis & Miller 1984).

Species checklist:

1. *Acrocercops* sp.*; (E); Fe, Ge, Is, Ma, Pt, Pz, SCI, SCz, Stg.
2. *Caloptilia* sp. 1*; (E); Es, Fe, Ge, Is, Ma, Pt, Ra, SCz, SF, Stg.
3. *Caloptilia* sp. 2*; (E); Is, SCI, SCz, Stg.
4. *Cryptolectica* sp.*; (E); SCz.
5. *Dialectica* sp. 1*; (E); Fl, Is, SCI, SCz, Stg.
6. *Dialectica* sp. 2*; (E); Is, Ma, SCz, SF, Stg.
7. Gracillaridae sp.*; (E); Scz.

2.3.5. Bucculatricidae (Fig 2.2e)

Only one species of this family has been reported from the Archipelago (Davis *et al.* 2002) and it is endemic. This family currently includes about 250 species worldwide (Davis & Robinson 1999). In the Americas the family is represented by 104 species but only six have been described from the Neotropical region (Davis *et al.* 2002).

Species checklist:

1. *Bucculatrix cordiella* Davis & Landry 2002*; (E); Fl, Ge, Is, SCz, Stg, SN.

2.3.6. Yponomeutidae (Fig. 2.2f)

In the Galapagos, two endemic species are known (Landry & Landry 1998). *Atteva hysginiella* is a very abundant species in all the ecological zones, although it is more abundant in the arid zone. The other species, *Prays galapagosella* (Landry & Landry 1998), is smaller and drab coloured. The family is cosmopolitan but best represented in the Tropics. The Neotropical fauna consists of around 122 described species (Heppner 1991).

Species checklist:

1. *Atteva hysginiella* (Wallengren, 1861); (E); Ba, Fe, Fl, Is, Ma, Pt, Pz, Ra, SCI, SCz, SF, SN, Stg.
2. *Prays galapagosella* Landry & Landry, 1998; (E); Fe*, Fl, Is, Pt, SCI, SCz, Stg.

2.3.7. Plutellidae (Fig. 2.3a)

The Plutellidae family is closely related to the Yponomeutidae and some authors include the former as a subfamily of the latter (Heppner 1987a). One species belonging to this family was collected in the Galapagos: the cosmopolitan *Plutella xylostella.*

Species checklist:

1. Plutella xylostella Linnaeus (1758)*; (I); SCz.

2.3.8. Heliodinidae (Fig. 2.3b)

This family was reported for the first time from the Galapagos by Heppner & Landry (1994b). Only one species is found on Galapagos, *Heliodines galapagoensis* and this is very common in the littoral and arid zones. The adult is commonly seen on the leaves of *C. pyriformis*, with its colourful hind legs drawn back over its head. The family is worldwide in distribution with about 48 species described (Heppner & Landry 1994b).

Species checklist:

1. Heliodines galapagoensis Heppner & Landry, 1994; (E); Ba, Es, Fl*, Ge, Is, Ma*, Pt, Ra*, SCz, SCl Stg, SN.

2.3.9. Coleophoridae (Fig. 2.3c)

Only two species have been described for the Galapagos with one, *Calosima darwini*, being endemic (Adamski & Landry 1997). A third previously undescribed or indeterminate species of *Coleophora* was collected at lights by the author. The group is rather small in the Neotropical region with 112 recorded species (Becker 1984b).

Species checklist:

1. Coleophora sp.*; (E); Es, Pz.
2. Calosima darwini Adamski & Landry, 1997; (E); SCl, Fl, Ra, SCz, Stg.
3. Blastobasis normalis (Meyrick, 1918); (N); Es, Fe, Fl, Ge, Is, Ma, Pt, Pz*, SCl, SCz, SF*, Stg, Wo*.

2.3.10. Cosmopterigidae (Fig 2.3d)

The Cosmopterigidae include some small, beautifully coloured moths, particularly in the genus *Cosmopterix.* This family was reported for the first time from the Galapagos by Landry (2001); eight species were recorded with six of them endemic. The Galapagos species are probably more closely to Neotropical genera than other Pacific island and Asian genera. In the Neotropical region the family contains about 130 described species (Landry 2001a). The family is well represented on many Pacific islands. In Hawaii, for example, the endemic genus *Hyposmocoma* has more than 250 species (Zimmerman 1978).

Species checklist:

1. Cosmopterix attenuatella (Walker, 1864); (N); Fe, Is, SCz, SCl, Stg.
2. Cosmopterix yvani Landry, 2001 (E); Fl, Is, Ma*, Pt.
3. Cosmopterix madeleinae Landry, 2001*; (E); Fl*, Is, Pt, SCl, SCz.
4. Cosmopterix galapagosensis Landry, 2001; (E); Is, SCl, SCz.
5. Pyroderces rileyi (Walsingham, 1882)*; (I); Is*, SCz.
6. Ithome volcanica Landry, 2001*; (E); Es, Fe*, Fl, Is, Ma, Pt, Pz*, SCl, SCz, SN.
7. Periploca darwini Landry, 2001; (E); Is.
8. Periploca longipenis Landry, 2001; (E); Is, Ma*, Pz*, SCz.

2.3.11. Xylorictidae (Fig. 2.3e)

This family of the Gelechioidea is very poorly studied on the Islands. Five previously undescribed species belonging to the subfamily Scythridinae were collected during this study, mostly at night in the littoral and arid zones. The Neotropical fauna is very poorly known with only 12 species reported (Heppner 1991), whereas the world fauna contains more than 370 described species (Scoble 1992). The Scythridinae are mostly restricted to arid or alpine habitats, and many species are diurnal.

Species checklist:

1. Scythridinae sp. 1*; (E); Fe, Is, SCz.
2. Scythridinae sp. 2*; (E); Ba, Bam, Is, SCz.
3. Scythridinae sp. 3*; (E); Fe, Is, SCz, Stg.
4. Scythridinae sp. 4*; (E); Is, SCz.
5. Scythridinae sp. 5*; (E); SCz.

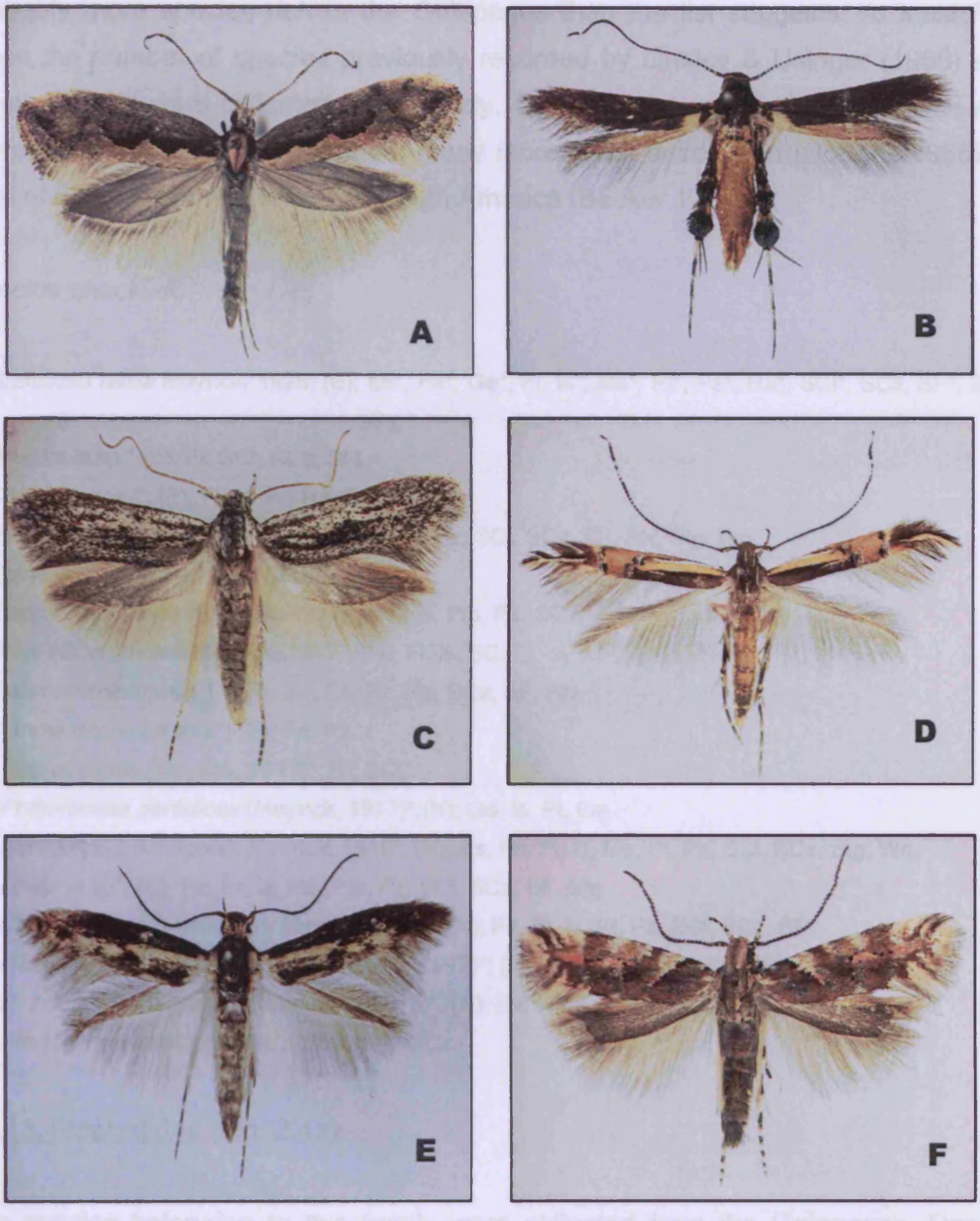


Figure 2.3. A, *Plutella xylostella* (Plutellidae);B, *Heliodines galapagoensis* (Heliodinidae); C, *Calosima darwini* (Coleophoridae);D, *Cosmopterix madeleinae* (Cosmopterigidae); E, Scythridinae sp. (Xylorictidae); F, *Aristotelia* sp. (Gelechiidae).

2.3.12. Gelechiidae (Fig. 2.3f)

The Gelechiidae is a family of very small to medium-sized moths. This family is probably more species rich in the Galapagos than the list suggests. At least four times the number of species previously recorded by Linsley & Usinger (1966) and Linsley (1977) were collected in this study. The group is represented worldwide and there are 4,000 species described; many more await description (Hodges 1986). A total of 830 species are known in South America (Becker 1984c).

Species checklist:

1. Aristotelia naxia Meyrick, 1926; (E); Es*, Fe*, Ge*, Fl, Is*, Ma*, Pt*, Pz*, Ra*, SCl*, SCz, SF*, SN*, Stg*.
2. Aristotelia sp.* (E); Fl, SCl, SCz, SN.
3. Chionodes sp.*; (E); Fl, Is, Pt, Ra, SCl, SCz.
4. Ephysteris sp. 1*; (E); Es, Fl, Ge, I, Ma, Pt, Pz, SCl, SCz, SF, SN, Stg, Wo.
5. Ephysteris sp. 2*; (E); Ma, SCz.
6. Evippe omphalopa (Meyrick, 1917)*; (N); Is, Pta, Pz, SCz.
7. Stegasta zygotoma Meyrick, 1917*; (N); Fl, Is, SCz.
8. Symmetrischema sp 1*; (E); Ba, Es, Pz, Ra, SCz, SF, SN.
9. Symmetrischema sp 2*; (E); Fe, Pz.
10. Tuta absoluta (Meyrick, 1917)*; (I); SCl.
11. Phthorimaea perfidiosa (Meyrick, 1917)*;(N); Ge, Is, Pt, Ge.
12. Anacampsis primigenia Meyrick, 1918*; (N); Es, Fe, Fl, Is, Ma, Pt, Pz, SCl, SCz, Stg, Wo.
13. Untomia sp*; (E); Fe, Fl, Is, Ma, Pta, Pz, SCl, SCz, SF, Stg.
14. Compsolechia? salebrosa Meyrick, 1918*; (N); Fe, Fl, Is, Pt, Pz, SCl, SCz, SF.
15. Mesophleps adustipennis (Walsingham, 1897)*; (N);. Es, Fl, Is, SCl, SCz, Ma, Stg.
16. Dichomeris acuminata (Staudinger, 1816)*; (N); Es, Is, Ma, Pta, Ra, SCz.
17. Sitotroga cerealella (Olivier, 1789)*; (I); SCz.

2.3.13. Elachistidae (Fig. 2.4a)

Two species belonging to this family were collected from the Galapagos. One is endemic and the other apparently introduced accidentally by humans (Landry & Roque-Albelo 2003). The endemic species *Haplochrois galapagosalis* (Agonoxeninae) is a common species living from sea level to the highest altitude on most of the islands. The Agonoxeninae moths of the Neotropics are poorly known (Hodges 1997). The other species is the avocado seed moth, *Stenoma catenifer*

(Stenomatidae). This species seems to have been introduced on avocado fruit imported to the Islands (Landry & Roque-Albelo 2003). The Stenomatinae in the Neotropical region are very rich, some 1,100 species, including 352 members of the genus *Stenoma*, are known (Becker 1984a).

Species checklist:

1. Haplochrois galapagosalis Landry, 2002; (E); Fl, Ge, Is, Ma, Pt, Pz*, SCl, SCz, Stg, Wo*.
2. Stenoma catenifer Walsingham, 1912*; (I); SCz, SCl.

2.3.14. Autostichidae (Fig. 2.4b)

Two genera of this family are present on the Islands: *Taygete* and *Galagete.* The endemic genus *Galagete* (Landry 2002) is formed of a group of small moths of 7 - 16mm in wingspan. They were placed by Landry (2002) in the family Autostichidae as defined by Hodges (1999) on the basis of morphological characters. This genus, with 11 described species, represents the most extensive radiation of species of Lepidoptera in the Galapagos Islands. *Galagete* appears most closely related to the genus *Taygete*, which has one species in the Galapagos Archipelago.

Species checklist:

1. Taygete sphecophila (Meyrick, 1936)*; (I); Fl, SCl, SCz.
2. Galagete gnathodoxa Meyrick, 1926; (E); Fe, Fl, Is, Pz, Stg.
3. Galagete protozona Meyrick, 1926; (E); Fe, Fl, Is, SF, SN.
4. Galagete seymourensis Landry 2002; (E); SN.
5. Galagete turritella Landry 2002*; (E); Fl, Is, SCz, Stg, SN.
6. Galagete espanolaensis Landry 2002; (E); Es.
7. Galagete consimilis Landry 2002*; (E); Ge, Fe, Fl, Is, SCl, SCz, Stg.
8. Galagete darwini Landry 2002*; (E); Es, Fl, Ge, Is, Ma, Pz, Ra, SCl, SCz, SN, Wo.
9. Galagete levequei Landry 2002*; (E); Is, SCz.
10. Galagete cristobalensis Landry 2002; (E); SCl.
11. Galagete pecki Landry 2002; (E); Is.
12. Galagete cinerea Landry 2002*; (E); Is.

2.3.15. Tortricidae (Fig. 2.4c)

Only six species of tortricid moths have been reported from the Galapagos. Of these, only *Platynota colobota* is reported to be endemic. Schaus (1923), however, mentioned the presence of three more species, which he did not describe. The diversity of Tortricidae in the Islands is probably much higher than that listed here. The adults are common at lights in all ecological zones but especially in the transition forests. The family Tortricidae occur worldwide and are most diverse in temperate and tropical regions. There are over 1,452 described species in the Neotropical region (Powell *et al.* 1995), many of economic importance.

Species checklist:

1. *Strepsicrates smithiana* Walsingham, 1892; (I); Ba.
2. *Crocidosema plebejana* Zeller, 1847; (I); B*, Is*, SCz, Stg.
3. *Bactra philocherda* Diakonoff, 1964; (I); SCz, Stg.
4. *Episimus transferranus* (Walker, 1863); (I); Is.
5. *Episimus utilis* Zimmerman, 1978; (N); SCz.
6. *Platynota colobota* Meyrick, 1926; (E); Is, SCz, Stg.

2.3.16. Pterophoridae (Fig. 2.4d)

The Pterophoridae is a group with distinctive well-developed clefts in both the fore- and hindwings. They are also called plume moths. The pterophorid fauna of the Archipelago was revised by Landry & Gielis (1992), Landry (1993) and Landry *et al.* (2004). A total of 15 species occurs in the Islands. All were collected at lights traps with most of the species being collected in the arid zone. There are about 206 species recorded for the Neotropic region (Miller & Gielis 1995). The plume moth fauna of South and Central America has not, however, been adequately described (Landry & Gielis 1992) and more species are expected to be recorded.

Species checklist:

1. *Megalorhipida leucodactyla* (Fabricius, 1794); (I); Ba, Es, Fe*, Fl, Ge, Is, Ma, Pt, Pz*, Ra, SCz, SCl*, Stg.
2. *Lantanophaga pusillidactyla* (Walker, 1864); (I); Ge, Is, Ma, SCz.
3. *Platyptilia vilema* Landry, 1993; (E); Fe*, Is, Pt.

4. *Bipunctiphorus nigroapicalis* (Landry & Gielis 1992); (E); Fl*, Is, Pt*, SCl, SCz.
5. *Postplatyptilia huigraica* Landry & Gielis 1992; (N); Is, SCz*.
6. *Postplatyptilia minima* Landry & Gielis 1992; (E); Is, Pt, SCz*.
7. *Stenoptilodes brevipennis* (Zeller, 1874); (I); Fl*, Is, Ma*, SCz.
8. *Stenoptilodes juanfernandicus* Gielis, 1991; (N); Is.
9. *Stenoptilodes gielisi* Landry 1993; (E); Is.
10. *Exelastis montischristi* (Walsingham, 1897); (I); Ba, Es, Fl, Ge, Is, Ma Pt, SCl, SCz, SF, Stg.
11. *Exelastis pumilio* (Zeller, 1873); (I); Is, Ra, SCl.
12. *Adaina scalesiae* Landry, Roque-Albelo & Mattew 2004; (E); Gdn (Fl)*, Fl*, Fe*, Is, Pt, SCz.
13. *Hellinsia nephogenes* (Meyrick. 1926); (N); Fe*, Fl, Is, SCz.
14. *Hellinsia cristobalis* (Landry & Gielis, 1992); (E); Fe*, Is, Pt, Stg, SCl.
15. *Hellinsia devriesi* (Landry & Gielis, 1992); (E); Fe*, Is, SCz*.

2.3.17. Choreutidae (Fig 2.4e)

Along with the Heliodinidae the Choreutidae are day-flying moths. The Choreutidae are reported for the first time from the Galapagos by Heppner & Landry (1994a). Only one species occurs in the Islands and although the species is active as an adult during the daytime, specimens were also collected at light traps in smaller numbers. The family, which includes around 350 described species, is found in all zoogeographical areas but is best represented in the Orient and Australasia (Heppner & Duckworth 1981). In South and Central America the choreutid fauna comprises 104 species (Heppner 1995).

Species checklist:

1. *Tebenna galapagoensis* Heppner & Landry 1994; (E); Fe*, Is, Pt, SCz, Stg.

2.3.18. Pyralidae (Fig. 2.4f)

The Pyralidae are divided into two main lineages that have been named variously Pyralinae and Crambinae, Pyraliformes and Crambiformes, and Pyralidae and Crambidae. Both groups are well represented in the Galapagos Archipelago. The current list of Galapagos Pyraliformes (Pyralinae, Phycitinae, Epipaschiinae, Galleriinae) includes 17 species, six of which are endemic. The Phycitinae belong to five different genera (Landry & Neunzig 1997). The Crambiformes of the Islands (Crambinae, Nymphulinae, Musotiminae, Glaphyriinae and Pyraustinae) is the most diverse group of Pyralidae. Few studies have, however, explored this lineage in detail. Species reported in the literature include the endemic *Euchromius galapagosalis*; but it is known that at least eight more species have been collected. Only one Nymphulinae species was collected in the Archipelago; as the immature stages of most Nymphulinae are aquatic, the littoral or the pampas zones of a few islands where suitable aquatic habitats are found need to be carefully sampled. Musotiminae and Glaphyriinae are represented by one species each. The Pyraustinae seems to be the most diverse group of pyralids from the Galapagos; 26 species are currently listed (Linsley & Usinger 1966; Linsley 1977; Peck *et al.* 1998), five of them endemic. At least 46 species have been collected in recent years (see checklist below) some of these being previously undescribed species and probably endemics. The pyraustine fauna also includes the genus *Beebea* Schaus 1923 which is endemic and monotypic. As a larva this very large species bores into *Opuntia* cacti (Williams 1930). As a result of this study the Pyralidae fauna of the Galapagos is probably richer by about 75 species. This family is probably the most speciose in the Lepidoptera with approximately 25,000 named species and many more as yet unnamed (Scoble 1992). The Neotropical fauna is also rich with 4,562 species (Munroe *et al.* 1995).

Species checklist:

1. Pyralis manihotalis Guenée, 1854*; (I); SCz.
2. Ocrasa nostralis (Guenée, 1854) *(I); SCz.
3. Phidotricha erigens Ragonot, 1888*; (N); Fl, Is, SCz.
4. Ancylostomia stercorea (Zeller, 1848); (I); Fl*, Ge, Is, Pt, SCz, Stg.
5. Coptarthria dasypyga (Zeller, 1881); (N); Is, Pt, SCz, Stg.
6. Etiella zinckenella (Treitschke, 1832); (I); Fe*, Ge, Is, Pt, Ra, SCl, SCz, SF, SN, Stg.
7. Fulrada carpasella (Schaus, 1923); (E); Es, Fl, Is, Pz, Ra, SCl, SCz, SF, SN, Stg.
8. Fundella argentina Dyar, 1919; (I); Fl*, Is, Ma*, SCz, SCl, Stg.
9. Hypsipyla grandella (Zeller, 1848); (I); SCl, SCz.
10. Macrorrhinia pinta Landry & Neunzig, 1997; (E); Es, Fe, Ge, Is, Pt, SF, SCl, SN, Stg, Wo*.
11. Nicetiodes apianellus Schaus, 1923; (E); Ba, Es, Fe, Fl, Ge, Is, Ma, Pt, Pz, Ra, SF, SCl, SCz, SN, Stg, Wo*.
12. Oryctometopia fossulatella Ragonot, 1888; (N); Ba, Es, Fl, Is, Ra, SCl, SCz, SN, Stg.
13. Shafferiessa galapagoensis Landry & Neunzig, 1997; (E); Ed*, Fe*, Fl, Is, Pt, SCl, SCz, Stg, Wo*.
14. Shafferiessa pumila Landry & Neunzig, 1997; (E); Es, Fe, Fl, Ge, Gd (Es)*, Is, Ma, Pt, Pz*, SF, SCl, SCz, Stg.

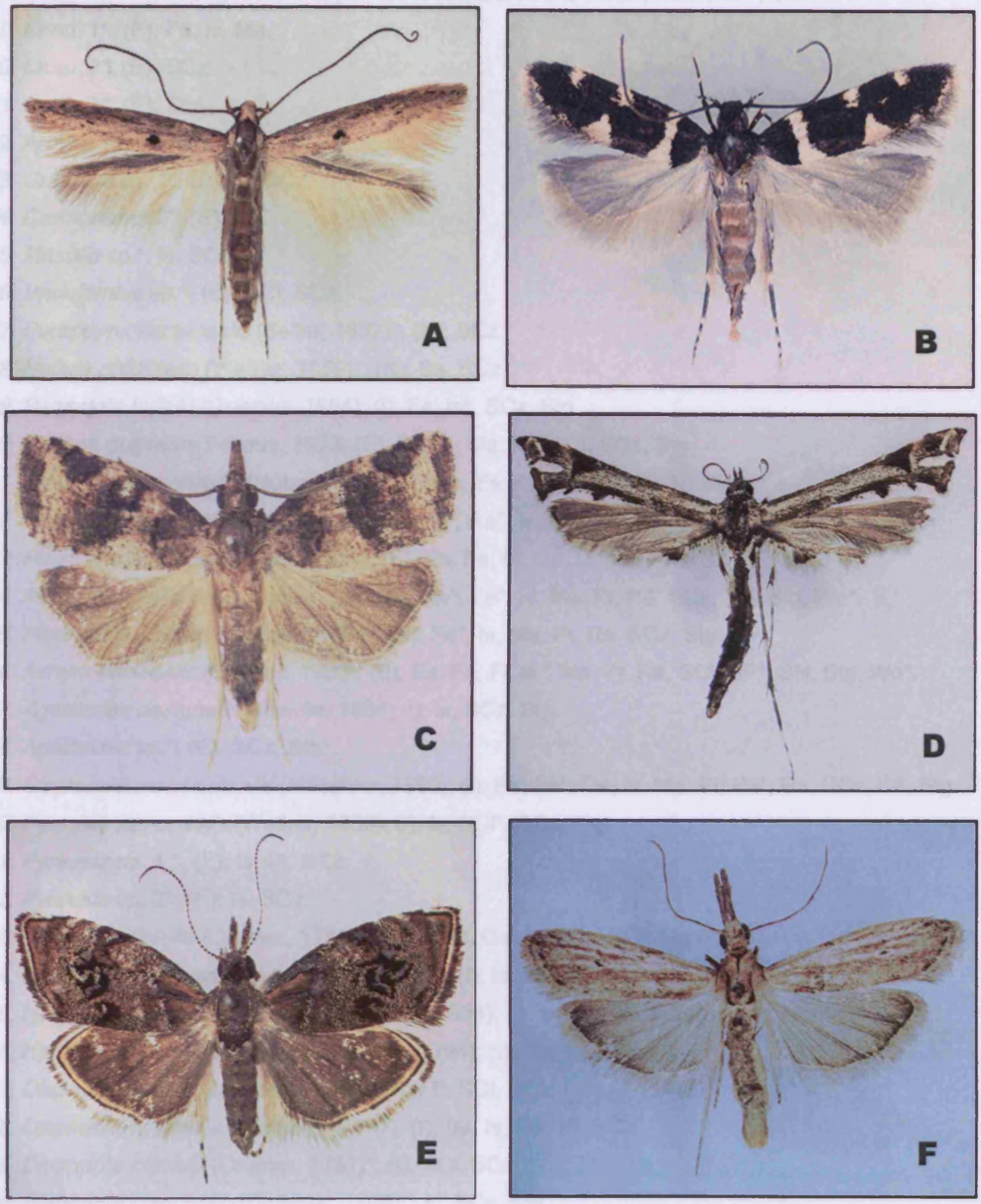


Figure 2.4. A, *Haplochrois galapagosalis* (Elachistidae); B, *Galagete protozona* (Autostichidae); C, *Platynota colobota* (Tortricidae); D, *Platyptilia vilema* (Pterophoridae); E, *Tebenna galapagoensis* (Choreutidae); F, *Macrorrhinia pinta* (Pyralidae).

15. Tota galdinella Schaus, 1923; (E); Ba, Es, Fe, Fl, Ge, Is, Ma, Pt, Ra, SCl, SCz, SF, SN, Stg.
16. Cadra cautella (Walker, 1863)*; (I); SCz.
17. Corcyra cephalonica (Stainton, 1886)*; (I); SCz.
18. Euchromius galapagosalis Capps, 1966; (E); Ba, Fl*, Is*, SCl*, SCz*, SF*, SN*.
19. La sp. 1*. (E); Fe, Is, Ma.
20. La sp. 2*; (E); SCz.
21. La sp. 3*; (E); Scz.
22. Argyria sp.*; (E); Is, SCz.
23. Crambus sp. 1*; (E); Is, SCz.
24. Crambus sp. 2*; (E); Is.
25. Mesolia sp.*; Is, SCz.
26. Undulambia sp.*; (E); SCl, SCz.
27. Parapoynx fluctuosalis (Zeller, 1852)*; (N); SCz.
28. Hellula phidilealis (Walker, 1859)*; (N); Ba, SCz.
29. Penestola bufalis (Guenée, 1854); (I); Fe, Is*, SCz, Stg.
30. Beebea guglielmi Schaus, 1923; (E); Ba, Is, Ma, Pz, SCl, SCz, Stg.
31. Hymenia perspectalis (Hübner, 1796); (I); Is, Es, Fe*, Pt, SCl, SCz, Stg.
32. Pilocrocis ramentalis Lederer, 1863; (I); Pt*, Ra*, Is, Ge*, Fl*, Ma*, SCz, Stg, SCl.
33. Psara chathamalis (Schaus, 1923); (E); Es, Fe, Fl, Ge, Is, Ma, Pt, SCz, SF, SN.
34. Asciodes gordialis (Guenée, 1854); (I); Dw*, Fe*, Is, Ma, Pt, Ra, SCz, SN, Stg, Wo*.
35. Pleuroptya silicalis (Guenée, 1854); (N); Fe*, Is, Ma, Pt, Ra, SCz, Stg.
36. Achyra eneanalis (Schaus, 1923); (E), Es, Fe, Fl, Is*, Ma, Pt, Ra, SCl, SF*, SN, Stg, Wo*.
37. Agathodes designalis Guenée, 1854; (I); Is, SCz, Stg.
38. Agathodes sp.*; (E); SCz, Stg.
39. Sisyracera inabsconsalis (Möschler, 1890); (I); Es, Fe*, Ge, Is, Ma, Pt, Pz*, Ra, SCz, SF, Stg.
40. Pyrausta panopealis (Walker, 1859); (I); Is, SCl*, SCz, Stg.
41. Pyrausta sp. 1 *; (E); Is, Pt, SCz.
42. Pyrausta sp. 2*; (E); Is, SCz.
43. Syngamia florella (Cramer, 1781); (I); Fe*, Fl, Ge, Is, SCz, SCl, Stg.
44. Rhectocraspeda periusalis (Walker, 1859); (I); Is, Pt, Stg.
45. Herpetogramma phaeopteralis (Guenée, 1854); (I); Is, SCl, SCz, Stg.
46. Herpetogramma bipunctalis (Fabricius, 1794); (I); Ge, Is, SCz, Stg.
47. Diaphania indica (Saunders, 1851); (I); Fl*, SCl, SCz.
48. Diaphania hyalinata (Linnaeus, 1767); (I); Ba, Is, Ma, Pt, SCz.
49. Diaphania nitidalis (Cramer, 1781)*; (I); SCl, SCz.
50. Diaphania glauculalis (Guenée, 1854)*; Is, SCz, Stg.
51. Omiodes indicata (Fabricius, 1775); (I); Fe*, Is, Pt, SCz, Stg.
52. Desmia sp.*; (E); Is, SCz, Stg.
53. Lineodes integra (Zeller, 1873)*; (N); Is, Pt, Stg.
54. Lineodes fontella Walsingham, 1913*; (N); Is, Stg.
55. Lineodes sp.*; (E); Is, SCz, Stg.
56. Marasmia trapezalis (Guenée, 1854); (I); Is, SCz, Stg.

57. Samea ecclesialis Guenée, 1854; (I); Is, SCl, SCz, Stg.

58. Samea sp. 1*; (E); Fe, Is, Pt, SCl, SCz, Stg.

59. Samea sp. 2*; (E); SCz.

60. Terastia meticulosalis Guenée, 1854; (I); Is*, Pt, SCz, Wo*.

61. Spoladea recurvalis (Fabricius, 1775); (I); Es, Fl, Is, SCl, SCz, Stg.

62. Microthyris anormalis (Guenée, 1854)*; (N); Fl*, Is, SCl, SCz.

63. Ercta vittata (Fabricius, 1794)*, (N); Ge, Ma, Pta, SCz.

64. Synclera jarbusalis (Walker, 1859)*; (N); SCz.

65. Palpita flegia (Cramer, 1777)*; (N); SCz.

66. Loxomorpha cambogialis (Guenée, 1854)*; (N); SCl, SCz.

67. Neohelvibotys sp.*; (E); Es, Fl, Is, Pt, Pz*, SCl, SCz.

68. Neoleucinodes elegantalis (Guenée, 1854)*; (I); SCz.

69. Neoleucinodes sp.*; (E); Fl*, Is, Pt, Stg.

70. Udea sp. 1*; (E); Is, SCl, SCz, Stg.

71. Udea sp. 2*; (E); Is, SCz, Stg.

72. Maruca vitrata (Fabricius, 1787)*; (N); Is.

73. Diatraea saccharalis (Fabricius, 1794)*, (I); SCl.

74. Pyraustinae sp. 1* (E); Is, Pt, Stg.

75. Pyraustinae sp. 2*; (E); Is, SCz, Stg.

2.3.19. Hesperiidae (Fig. 2.5a)

The Hesperiidae fauna of the Islands is species-poor with only two known species: the endemic *Urbanus dorantes galapagensis* and the recently introduced *Calpodes ethlius* (Roque-Albelo 2004). In contrast, the Neotropical fauna of Hesperiidae is large and diverse with as many as 2,365 species recorded (Mielke 2004).

Species checklist:

1. Urbanus dorantes galapagensis (Williams, 1911); (E); Ba, Ed, Es, Fe*, Fl, Ge, Is, Pt*, Pz, Ra*, SCl, SCz, Stg.

2. Calpodes ethlius (Stoll, 1782); (I); Is, SCz*.

2.3.20. Pieridae (Fig. 2.5b)

This family contains approximately 339 described species from the Neotropical region (Lamas 2004) but only one species occurs in the Galapagos.

Species checklist:

1. *Phoebis sennae marcellina* (Cramer, 1779); (N); Ba, Dp, Ed, Fe, Fl, Is, Ma*, Pt, Stg, SCl, SCz.

2.3.21. Lycaenidae (Fig. 2.5c)

Only two species, belonging the subfamily Lycaeniinae, have been reported in the Galapagos: the endemic *Leptotes parrhasioides* and the accidently introduced *Hemiargus ramon*. This is the largest and biologically most diverse of all butterfly families with more than 6,000 species described (Robbins 1982). The family is well represented in the Neotropics with 1,182 species described (Robbins & Lamas 2004).

Species checklist:

1. *Leptotes parrhasioides* (Wallengren, 1860)*; (E); Ba, Ed, Es, Fe, Fl, Is, Ma*, Pt*, Pz, Ra*, SCl, SCz, Stg.
2. *Hemiargus ramon* (Dognin, 1887); (I); Ba, Es, Fe, Fl, Is, Pz, Ra, SCl, SCz, SF, SN, Stg.

2.3.22. Nymphalidae (Fig. 2.5d, e)

This family is well represented in the Galapagos with some species abundant in the higher altitudes zones of the Islands, for example the endemic Heliconiinae *Agraulis vanillae galapagensis*. More localized but still common are the two danaines and *Vanessa virginiensis*. The other reported species of butterfly, the nymphaline *Vanessa carye* is rare. The Nymphalidae contains about 6,000 species, one-third of the entire butterfly fauna (Robbins 1982). The Neotropical fauna is comprised of 2,433 species (Lamas *et al.* 2004).

Species checklist:

1. *Agraulis vanillae galapagensis* Holland, 1889; (E); Ba, Ed, Fe, Fl, Is, Pt, SCl, SCz, Stg.
2. *Vanessa virginiensis* (Drury, [1773]); (N); Is, SCz*, Stg*.
3. *Vanessa carye* (Hübner, [1812]); (N); Fe, Fl*, SCl, SCz*.
4. *Danaus gilippus thersippus* (Bates, 1863); (N); Ba*, Fl*, Is*, SCl, SCz*, Stg*, SN*, Ra*.
5. *Danaus plexippus megalippe* (Hübner, [1819-1826]); (N); Fl, SCl, SCz.

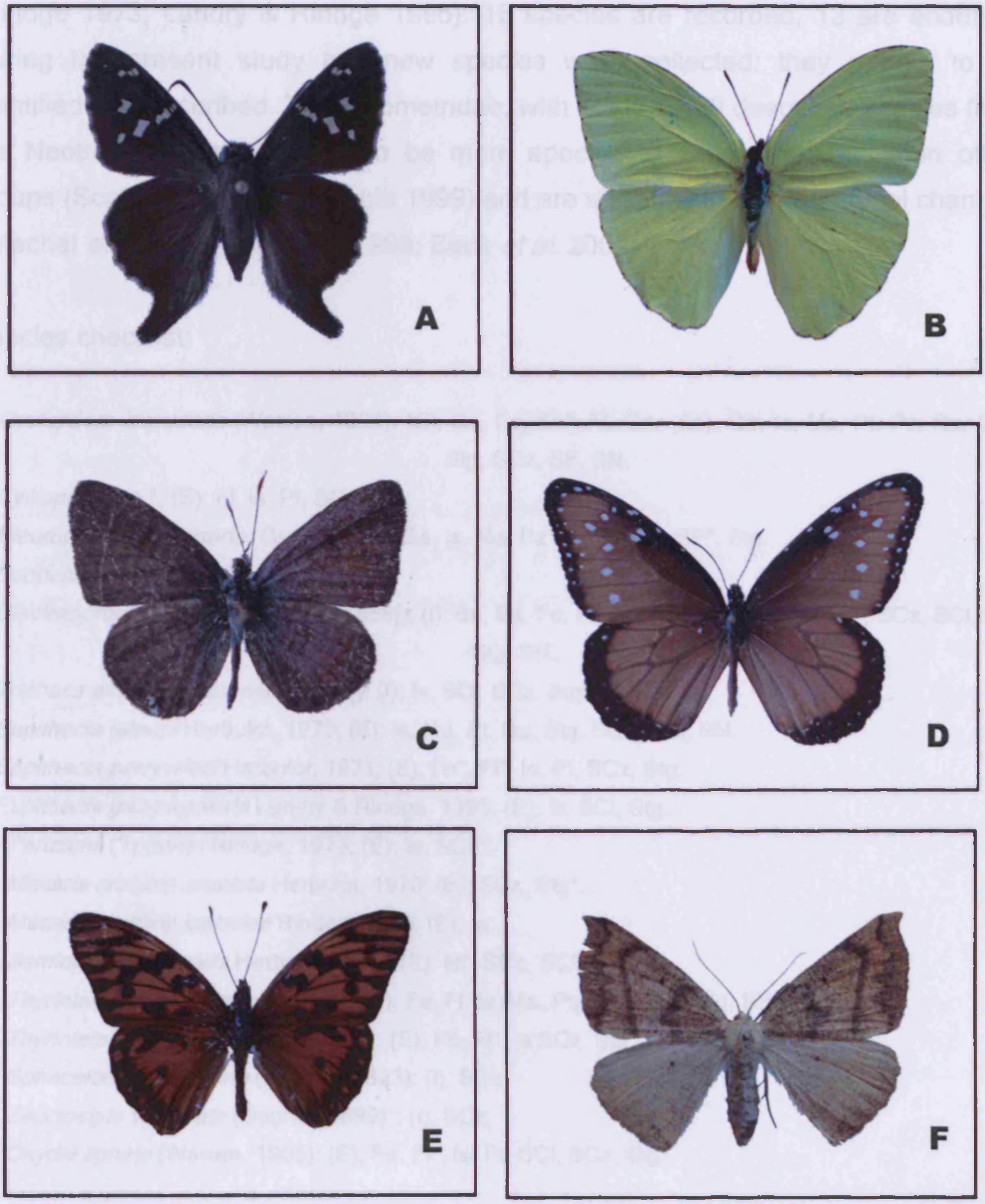


Figure 2.5. A *Urbanus dorantes galapagensis* (Hesperiidae); B, *Phoebis sennae marcellina* (Pieridae); C, *Leptotes parrhasioides* (Lycaenidae);D, *Danaus gilippus thersippus* (Nymphalidae); E, *Agraulis vanillae galapagensis* (Nymphalidae); F, *Oxydia lignata* (Geometridae).

2.3.23. Geometridae (Fig. 2.5f)

The Geometridae is one of the most-studied families of moths from the Archipelago (Rindge 1973; Landry & Rindge 1995). 18 species are recorded, 13 are endemic. During the present study two new species were collected; they remain to be identified and described. The Geometridae, with some 6,450 described species from the Neotropical region, tends to be more specific to certain habitats than other groups (Scoble *et al.* 1995; Scoble 1999) and are sensitive to environmental changes (Intachat *et al.* 1997; Holloway 1998; Beck *et al.* 2002).

Species checklist:

1. Cyclophora impudens (Warren, 1904); (E); Ba, Es, Fe*, Fl, Gdr (Es), Ge, Is, Ma, Pt, Pz, Ra, SCl, Stg, SCz, SF, SN.
2. Cyclophora sp.*; (E); Fl, Is, Pt, SCz, Stg.
3. Pleuroprucha insulsaria (Guenée) (N); Ge, Is, Ma, Pz*, SCl, SCz, SF*, Stg.
4. Scopula sp.* (N); Is, SCz.
5. Disclisioprocta stellata (Guenée, [1858]); (I); Ba, Es, Fe, Fl, Gen, Is, Ma, Pt, Pz*, Ra*, SCz, SCl, SF, Stg, SN.
6. Triphosa affirmata (Guenée, [1858]); (I); Is, SCl, SCz, Stg.
7. Eupithecia leleupi Herbulot, 1970; (E); Is, Ma, Pt, Ra, Stg, SCz, SCl, SN.
8. Eupithecia perryvriesi Herbulot, 1971; (E); Fe*, Fl*, Is, Pt, SCz, Stg.
9. Eupithecia galapagosata Landry & Rindge, 1995; (E); Is, SCl, Stg.
10. Perizoma (?) *perryi* Rindge, 1973; (E); Is, SCz*.
11. Macaria cruciata cruciata Herbulot, 1970; (E); SCz, Stg*.
12. Macaria cruciata isabelae Rindge, 1973; (E); Is.
13. Semiothisa cerussata Herbulot, 1970; (E); Is*, SCz, SCl.
14. Thyrinteina infans Herbulot, 1970; (E); Fe, Fl, Is, Ma, Pt, SCz, SCl, Stg, SF.
15. Thyrinteina umbrosa Herbulot, 1971; (E); Fe, Fl*, Is SCz, Stg.
16. Sphacelodes vulneraria (Hübner, 1823); (I); SCz.
17. Zeuctostyla vidrierata (Dognin, 1893)*; (I); SCz.
18. Oxydia lignata (Warren, 1905); (E); Fe, Fl*, Is, Pt, SCl, SCz, Stg.

2.3.24. Uraniidae (Fig. 2.6a)

Two species of Uraniidae (Epipleminae) are known from the Galapagos (Hayes 1975; Roque-Albelo & Mieles 2005). One is endemic while the other is widespread in South America. Epiplemines were collected from light traps in the transition and humid forests on Fernandina, San Cristobal, Isabela and Santa Cruz, but they are not common. A fauna of 230 species of epiplemines has been reported for the Neotropics (Heppner 1991).

Species checklist:

1. Epiplema becki Hayes, 1975; (E); Is, Fe.
2. Powondrella cingillaria Geyer, 1837; (N); Fe*, Fl*, Is, SCl*, SCz*.

2.3.25. Sphingidae (Fig. 2.6b, c)

Sphingidae, because they are large and conspicuous, have been well-studied in the Galapagos (Williams 1911; Schaus 1923; Beebe 1923; Kernbach 1962, 1964; Hayes 1975; Roque-Albelo & Landry 2001). 15 species are known to be established in the Islands. Only one species, *Xylophanes norfolki,* is endemic at the species level. Eight species have been recognized formally as distinct subspecies in Galapagos (Kernbach 1962). All the non-endemic species have a wide Neotropical or even cosmopolitan distribution. Sphingids are very common in the Archipelago and can be seen at dusk taking nectar from the flowers of both native and introduced trees in inhabited areas. Sphingidae are distributed worldwide, but are better represented in tropical areas. The family contains approximately 1,200 species (Kitching & Cadiou 2000) with 403 species recorded for the Neotropics (Carcasson & Heppner 1996).

Species checklist:

1. Manduca sexta leucoptera (Rothschild and Jordan, 1903); (E); Es*, Fl, Is, SCz, Stg*, SCl, Ra*.
2. Manduca rustica calapagensis (Holland, 1889); (E); Ba, Es, Fe*, Fl, Ge*, Is, Ma*, Pt*, SCz, Stg*, SCl, Ra*.
3. Cocytius antaeus (Drury, 1773)*; (N); SCz, SCl.
4. Agrius cingulata (Fabricius, 1775); (N); Ba, Es, Fe*, Fl, Is, Ma*, SCz, Stg*, SCl, Ra*, Wo.
5. Enyo lugubris delanoi Kernbach, 1962; (E); Fl, Is, SN*, SCz, SF*, Stg*, Ra*.
6. Perigonia lusca (Fabricius, 1777)*; (N); Is, Pz, SCz.
7. Erinnyis alope dispersa Kernbach, 1962; (E); Fl*, Is*, SCz, SCl.
8. Erinnyis ello encantada Kernbach, 1962; (E); Fl, Is, SCz, SF*, Stg*, SCl, Ra*.
9. Erinnyis obscura conformis Kernbach, 1962; (E); Ba, Bt*, Fe*, Fl, Ge*, Is, Ma*, Pt*, Pz, SCz, Stg*, SN*.
10. Eumorpha fasciatus tupaci (Kernbach, 1962); (E); Fl*, SCz.

11. Eumorpha labruscae yupanqui (Kernbach, 1962); (E); Fl, Is*, SCz.
12. Xylophanes norfolki Kernbach, 1962; (E); Fe*, Is*, SCz.
13. Xylophanes tersa (Linnaeus, 1771); (N); Fl*, Is, SCz*; Stg.
14. Xylophanes pluto (Fabricius, 1777)*; (N); SCz.
15. Hyles lineata (Fabricius, 1775); (N); Ba, Es, Fl, Is, Pt*, Ra*, SN*, SCz, SF, Stg, SCl.

2.3.26. Arctiidae (Fig. 2.6d)

The Arctiidae of the Galapagos are represented by four species in the genus *Utetheisa.* One, *Utetheisa ornatrix,* is widely distributed in the New World; while the other three are endemic. *Utetheisa galapagensis* is a very conspicuous moth of the arid zones throughout the Archipelago. The other two endemic species are more restricted in distribution and numbers. The small number of Galapagos arctiids does not compare well with the 6,000 species recorded from the Neotropics (Watson & Goodger 1986), but arctiids are not known for their migratory power.

Species checklist:

1. Utetheisa devriesi Hayes, 1975; (E); Pt, Is*, Fe*, Stg*.
2. Utetheisa galapagensis (Wallengren, 1860); (E); Ba, Fe, Fl, Ge*, Is, Ma*, Pt, SCl, SCz, SF*, Stg*.
3. Utetheisa ornatrix (Linnaeus, 1758); (N); Fe*, Fl*, Gd (Es), Is, Ma*, Pt*, Pz*, SCl, SCz, SF*, Stg.
4. Utetheisa perryi Hayes, 1975; (E); Is, SCz, Stg.

2.3.27. Noctuidae (Fig. 2.6e)

This family is the most diverse group of Lepidoptera in the Archipelago with 86 species, a third of which are endemics. A further eight more endemics are recognized at the subspecies level (see Hayes 1975). The Noctuidae contain an estimated 21,000 described species (Holloway *et al.* 2001) and constitute the most speciose and cosmopolitan lineage of Lepidoptera, with adults and larvae exhibiting a bewildering diversity of size, colouration, behaviour and ecological habits (Kitching & Rawlins 1997). Many species have been recorded as major agricultural pests (CAB International 2003).

Species checklist:

1. *Hypena microfuliginea* Hayes, 1975; (E); Fe*, Fl, Is, Ma*, Pt*, Ra*, SCl*, SF*, Stg.
2. *Hypena vetustalis* Guenée, 1854; (N); Fe*, Fl, Is, SCl*, SCz.
3. *Hypena fuliginea* (Hayes, 1975); (E); Fe*, Fl, Is, Pt*, SCz*, SCl*, Stg.
4. *Hypena lividalis* (Hübner, 1796); (N); Fl, Is*, SCl*, SCz*.
5. *Hypena minualis constans* Hayes, 1975; (E); Es*, Fe*, Fl, Is, Ma*, Pt, SCl*, SCz, Stg*.
6. *Rivula asteria* (Druce, 1898); (N); Fe*, Is*, SCz.
7. *Ommatochila mundula* (Zeller, 1872)*; (N); Es, Ma, SCl, SCz, Stg.
8. *Sorygaza variata* Hayes, 1975; (E); Is, SCz, Pt*, Stg*.
9. *Schrankia* sp.* (E); Is, SCl, SCz.
10. *Hypocala andremona* (Stoll, 1781)*; (N); SCz.
11. *Mocis incurvalis* Schaus, 1923; (E); Ba, Fe, Fl, Is, Pt, SCl, SCz, SF*, Stg*.
12. *Mocis latipes* (Guenée, 1852); (N); Ba, Es*, Fl, SCl, SCz, Stg*.
13. *Celiptera remigioides* (Guenée, 1852); (N); Ge, Is*, SCz.
14. *Zale obsita* (Guenée, 1852); (N); Fe*, Fl*, Is*, SCl*, SCz, SF*, Stg.
15. *Ascalapha odorata* (Linnaeus, 1758); (N); Fl, Is*, Ma*, SCl, SCz, SF*.
16. *Thysania zenobia* (Cramer, 1777)*; (N); Fl, SCz.
17. *Melipotis acontioides producta* Hayes, 1975; (E); Ba*, Es, Fl, Is, Ma*, Pz*, SCl*, SCz, SN*.
18. *Melipotis harrisoni* Schaus, 1923; (E); Ba, Fl, Is, Pz, Ra, SCl, SCz, SF*, Stg.
19. *Melipotis indomita* (Walker, [1858] 1857); (N); Ba, Cha*, Es, Fe*, Fl, Ge, Is, Ma*, Pt, Pz, Ra*, SCl, SCz, SF*, SN*, Stg, Wo*.
20. *Metalectra praecisalis* Hübner, 1823; (N); Fe*, Fl*, Is*, SCl*, SCz*, SF*, Stg*.
21. *Letis mycerina* (Cramer, 1777); (N); SCz.
22. *Hemeroplanis toddi* (Hayes, 1975); (E); Es*, Fl, Is, Ma*, Pt, Pz*, SCl*, SCz, SF*.
23. *Metallata absumens contiguata* Hayes, 1975; (E); Fl, Is, Ma, SCl, SCz, Stg*.
24. *Lesmone formularis* (Geyer, 1837); (N); Es*, Fe*, Fl, Pt*, SCz, SCl*, SF*, Stg*.
25. *Anticarsia gemmatalis* Hübner, 1818; (N); Ba, Fe, Fl, Ge, Is, Ma*, Pt, Pz* SCl, SCz, SF*.
26. *Epitausa prona* (Möschler, 1880); (N); Is, SCz.
27. *Psorya hadesia* Schaus, 1923; (E); Ba, Es, Fl, Is, Pz, SCl, SCz, SF*, Stg*.
28. *Epidromia zephyritis* Schaus, 1923; (E); Ba, Fe*, Fl, Is, Ma*, Pz, Ra*, SCl, SCz, Stg, SN*.
29. *Epidromia zetophora* Guenée, 1852; (N); Is, SCl*, SCz*.
30. *Anomis editrix* (Guenée, 1852); (N); Fl, Is*, SCz, SCl*.
31. *Anomis erosa* Hübner, [1821] 1816; (N); Es*, Fl, Is*, Ma*, SCz, Stg*.
32. *Anomis illita* Guenée, 1852; (N); Is*, Ma*, SCl*, SCz, SF*.
33. *Anomis luridula professorum* Schaus, 1923; (E); Ba, Fl, Ge, Is, Pt*, Ra, Ma*, SCl, SCz, SF*, SN*, Stg.
34. *Gonodonta biarmata evadens* Walker, [1858]; (E); Fe, Fl, Is, Pt, Pz*, SCl, SCz.
35. *Gonodonta fulvangula* Geyer, 1832; (N); Fl*, SCz.
36. *Gonodonta sicheas* (Cramer, 1777)*; (N); SCz.
37. *Gonodonta pyrgo* (Cramer, 1777)*; (N); SCz.
38. *Plusiodonta clavifera* (Walker, 1869); (N); Is*, Pt*, SCz, Stg*.

47. Leucania humidicola Guenée, 1852; (N); Ge*, Is*, SCl, SCz.

48. Leucania cooperi (Schaus, 1923); (E); Fe*, Is, Pt, SCl, SCz, Stg.

49. Pseudaletia sequax Franclemont, 1951; (N); Fl*, Is, SCl, SCz, Stg.

50. Magusa erema Hayes, 1975; (E); Fe*, Fl*, Ge*, Is, Ma*, SCz, SCl*, SF, Stg*.

51. Magusa orbifera (Walker, 1857)*; (E); Fe, Is.

52. Trachea cavagnaroi Hayes, 1975; (E); Is*, SCz.

53. Cropia infusa (Walker, [1858] 1857); (N); Es, Fe, Fl*, Gdr (Esp), Gen, Is, Ma*, SCl*, SCz, SN*.

54. Callopistria floridensis (Guenée, 1852); (N); Fe*, Fl*, Is, Pt, SCl, SCz, Stg*.

55. Catabenoides seorsa (Todd, 1972); (E); Es, Fl, Ge, Ma, Is, Ma*, Pt, Ra*, SCl, SCz, SF*, S

56. Neogalea sunia longfieldae Hayes, 1975; (E); Is, Fl*, SCz*.

57. Spodoptera dolichos (F., 1794); (N); Es*, Fe*, Fl, Is*, Ma*, Pt*, SCl*, SCz, Stg*.

58. Spodoptera eridania (Stoll, 1782); (N); Is, SCl, SCz, Stg.

59. Spodoptera frugiperda (Smith, 1797); (N); Es*, Fl, Is*, Pz*, SCl, SCz.

60. Spodoptera cosmioides Walker; (N); Fe*, Fl, Is, SCl, SCz.

61. Spodoptera roseae (Schaus, 1923); (E); Ba, Fl, Is, Ma*, Pt, SCl, SCz, Stg.

62. Elaphria encantada Hayes, 1975; (E); Es, Fe, Fl, Is, Ma*, Pt*, Pz, Ra*, SCz, Stg, SN*, SF*

63. Agrotisia williamsi (Schaus, 1923); (E); Ba, Es, Fl, Gdr (Es), Is, Pt, Ra*, SCz, SF* Stg, SN

64. Condica mobilis (Walker, [1857] 1856); (N); Fe*, Fl*, Is, Ma*, SCl*, SCz, SF*, Stg, SN*.

65. Condica ruthae (Schaus, 1923); (E); Ba, Fe*, Fl, Is, Pt, Pz, SCl*, SCz, Stg.

66. Condica sutor (Guenée, 1852); (N); Fe*, Fl*, Ba, Is, Ma*, Pz, SCl, SCz, Stg, SF*.

67. Condica concisa (Walker, 1856)*; (N); Es, Fl, Is, SF.

68. Paectes arcigera (Guenée, 1852); (I); Es*, Ba, Fe*, Fl, Ge*, Gdr (Es), Ge, Is, Ma* Pt, Pz, I SCz, SF, SN*, Stg.

69. Spragueia margana (Fabricius, 1794); (I); Ba, Es, Fe, Fl, Ge*, Gdr (Es), Ge, Is, Pt*, SCl, S SN*, SF*, Wo*.

70. Spragueia creton Schaus, 1923; (E); Ba, Es, Dp*, Fl, Gdr (Es), Ge, Is, Ma*, Pz*, Ra*, S Stg*.

71. Ponometia exigua (Fabricius, 1793); (I); Fe*, Fl*, Gdr (Es), Ge, Is, SCl, SCz, SF*, Stg*.

72. Bagisara repanda (Fabricius, 1793); (I); Fe*, Fl*, Is, SCz*.

73. Eublemma recta (Guenée, 1852); (I); Is*, Ge, Ma*, Pt*, SCz, Stg*.

74. Amyna insularum Schaus, 1923; (E); Ba, Es, Fe, Fl, Gdr (Es), Ge, Is, Ma*, Pt*, Pz, Ra, S Stg, SF, SN*, Wo*.

75. Ozarba consternans Hayes, 1975; (E); Es, Fe*, Fl, Ge*, Is*, Ma*, Pt, Pz*, SCz, SCl*, Stg, S

76. Cobubatha numa (Druce, 1889); (N); Fe*, Is*, Stg*.

77. Heliocheilus cystiphora (Wallengren, 1860); (I); Ba, Dp*, Es, Fe, Fl, Gdr (Es), Ge, Is, Ma*, Pt*, Pz*, Ra*, SCl, SCz, SF*, Stg.

78. Heliothis virescens (Fabricius, 1777); (N); Es*, Fl, Ge, Is, Ma*, Pt, SCl, SCz, SF*, Stg.

79. Agrotis consternans Hayes, 1975; (E); Is, Pt, SCl, SCz, Stg.

80. Agrotis ipsilon (Hufnagel, 1766); (N); Fe*, Is, Pz*, Ra*, SCl, SCz, Stg*.

81. Agrotis subterranea williamsi Schaus, 1923; (E); Es*, Ba, Fe, Fl*, Is, Ma*, Pt, Ra*, SCl*, SCz, SF*, SN*, Stg.

82. Psaphara conwayi (Richards, 1941); (E); Fl, Is, Pt, SCz, Stg*.

83. Psaphara interclusa Walker, 1857; (E); Is*, SCl.

84. Anicla infecta (Ochsenheimer, 1816); (N); Ba*, Is*, SCl*, SCz*, SN*.

85. Anicla oceanica (Schaus, 1923); (E); Ba Es*, Fe*, Fl*, Ge*, Is, Ma*, Pt, Pz, Ra*, SCz, SCl*, SF*, Stg, SN*.

86. Peridroma saucia (Hübner, [1808]); (N); Fl.

87. Noctuidae sp.*; (E?); SCz.

2.3.28. Nolidae (Fig. 2.6f)

A small family related to the Noctuidae with about 200 species described for the Neotropics (Heppner 1991); only one species reported on the Galapagos.
Species checklist:

1. Charocoma nilotica (Rogenhofer, 1881); (N); Fe, Is*, SCl, SCz, Stg.

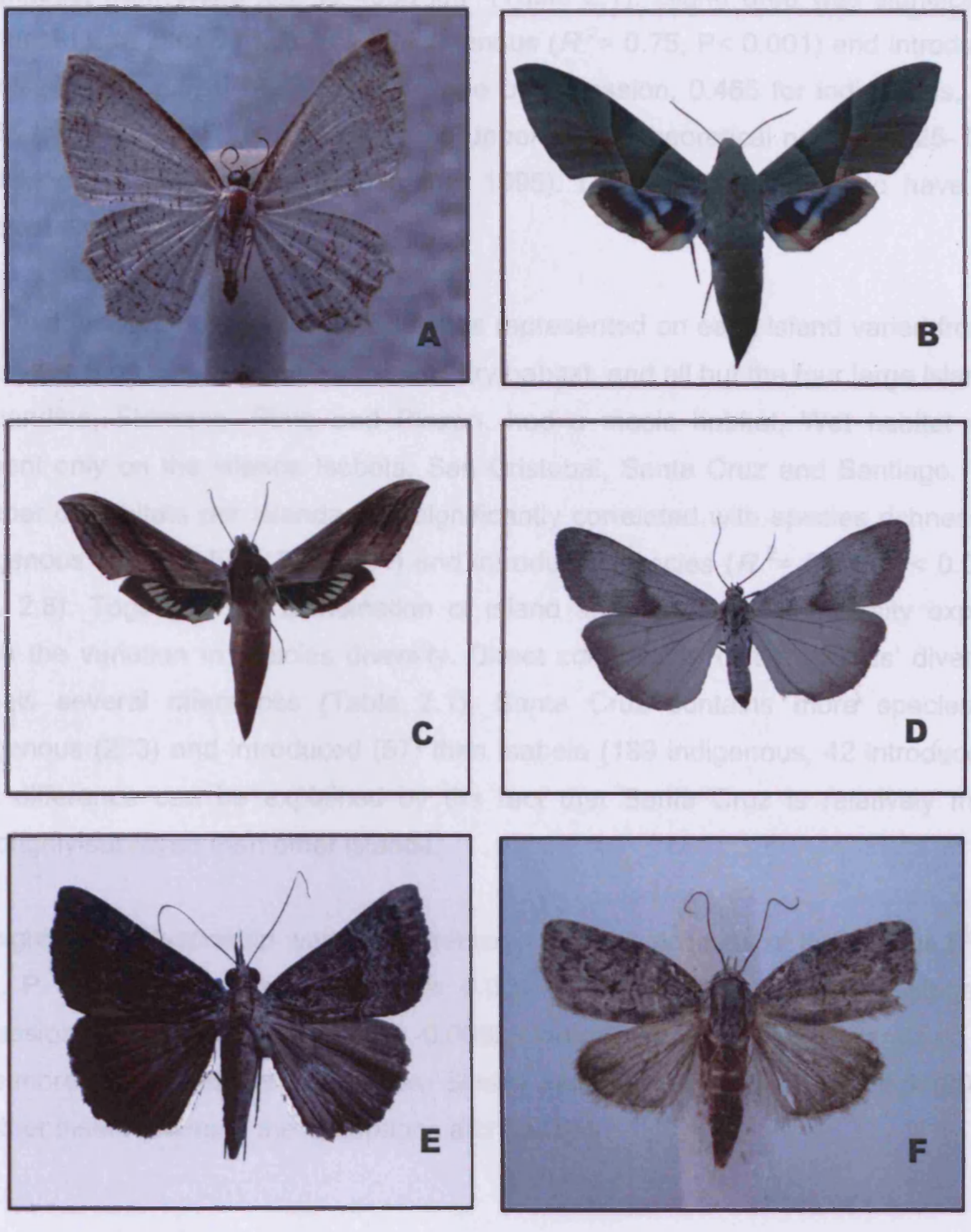


Figure 2.6. A, *Epiplema becki* (Uraniidae); B, *Eumorpha labruscae yupanquii* (Sphingidae); C, *Xylophanes norfolki* (Sphingidae); D, *Utetheisa devriesi* (Arctiidae); E, *Hypena microfuliginea* (Noctuidae); F, *Characoma nilotica* (Nolidae).

2.3.29. Determinants of species diversity

The areas of the 23 islands included in this study varied over two orders of magnitude, from 0.023 km^2 to 4588 km^2 (Table 2.1). Island area was significantly correlated with species richness of indigenous ($R^2 = 0.75$, $P < 0.001$) and introduced species ($R^2 = 0.80$, $P < 0.001$). The slope of regression, 0.465 for indigenous, and 0.358 for introduced species, are at the upper end of theoretical norm of 0.25- 0.47 for island groups species (Rosenzweig 1995). Largest islands tend to have the greatest diversity (Fig. 2.27 a, b).

The number of habitat or ecological zones represented on each island varied from 1 to 6. All islands had substantial areas of dry habitat, and all but the four large islands, Fernandina, Floreana, Pinta and Pinzon, had a mesic habitat. Wet habitat was present only on the islands Isabela, San Cristobal, Santa Cruz and Santiago. The number of habitats per islands was significantly correlated with species richness of indigenous ($R^2 = 0.575$, $P < 0.001$) and introduced species ($R^2 = 0.67$, $P < 0.001$) (Fig. 2.8). Together, the combination of island area and habitat diversity explain much the variation in species diversity. Direct comparison of the islands' diversity reveals several diferences (Table 2.1). Santa Cruz contains more species of indigenous (203) and introduced (57) than Isabela (189 indigenous, 42 introduced). This difference can be explained by the fact that Santa Cruz is relatively more thoroughly surveyed than other islands.

No significant relationship was found between species richness of indigenous ($R^2 = 0.02$, $P > 0.05$) and introduced ($R^2 = 0.001$, $P > 0.05$) (Fig. 2.9). The slope of regression for indigenous species, is -0.00632 indicating that the older islands do not have more, but actually fewer species. Similar results were obtained by Peck (2001) for other insect orders in the Galapagos archipelago.

Island	Size (Km^2)	Ecological complexity	Approximate age (myr)	Total number of indigenous species	Total number of introduced species
Baltra	26.19	2	3.6	41	10
Bartolome	1.24	2	2.4	1	0
Champion	0.095	1	3.3	1	0
Daphne Major	0.33	1	3.6	2	1
Darwin	1.063	1	<0.7	0	1
Eden	0.023	1	3.6	5	0
Española	60.48	2	5.6	52	11
Fernandina	642.48	4	0.3	86	16
Floreana	172.53	4	3.3	121	19
Gadner near to Floreana	0.812	1	3.3	1	0
Gadner near to Española	0.58	1	5.6	6	4
Genovesa	14.1	2	<0.7	36	16
Isabela	4588	6	0.7	189	42
Marchena	129.96	2	<0.7	66	14
Pinta	59.4	4	<0.7	83	18
Pinzon	18.15	4	2.7	47	7
Rabida	4.993	3	2.5	39	10
San Cristobal	528.09	6	6.3	120	29
Santa Cruz	985.55	6	3.6	203	57
Santa Fe	24.13	2	4.6	54	11
Santiago	584.65	6	2.4	118	33
Seymour North	1.838	2	3.6	37	7
Wolf	1.344	1	<0.7	13	3

Table 2.1 Geographical and historical characteristics of the principal islands of the Galapagos archipelago (ranged in alphabetical order). Ages are from Geist (1996), Ecological complexity is measured as number of the major vegetation zones. Lepidoptera species numbers are for the indigenous species (native plus endemic) and for introduced species.

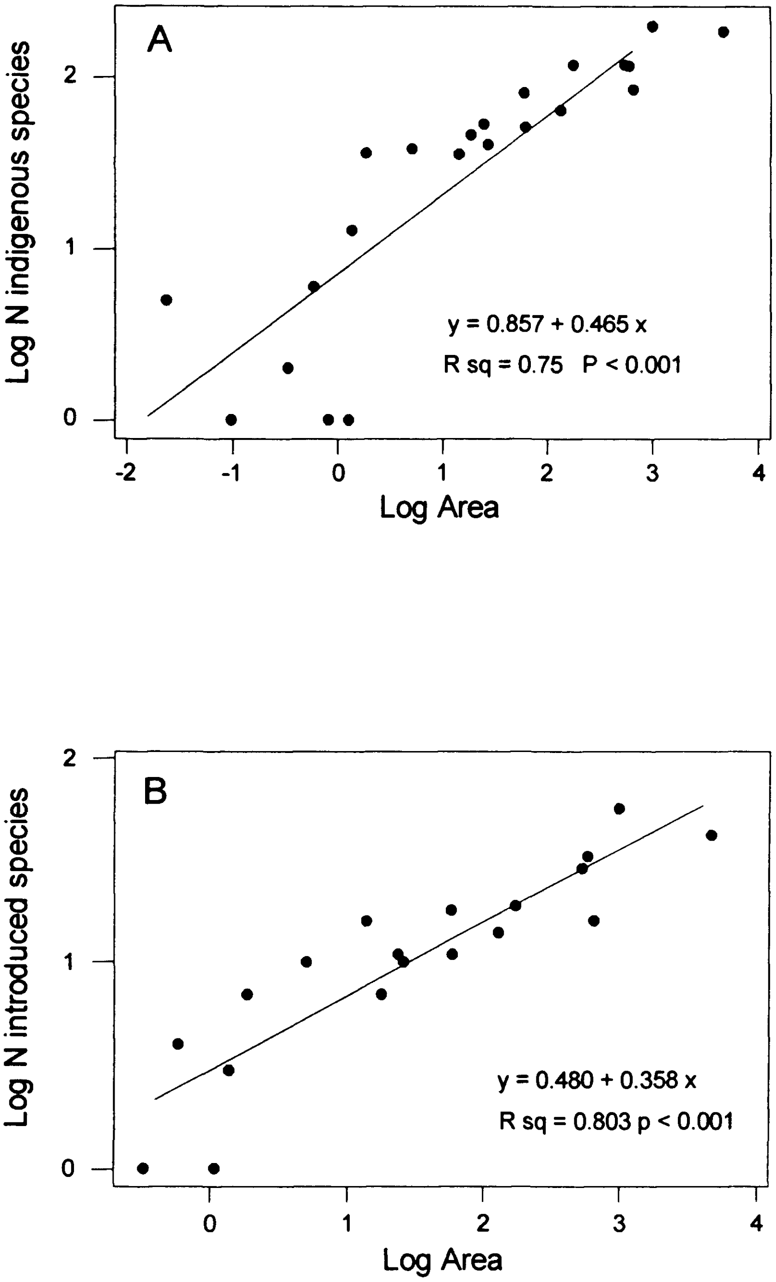
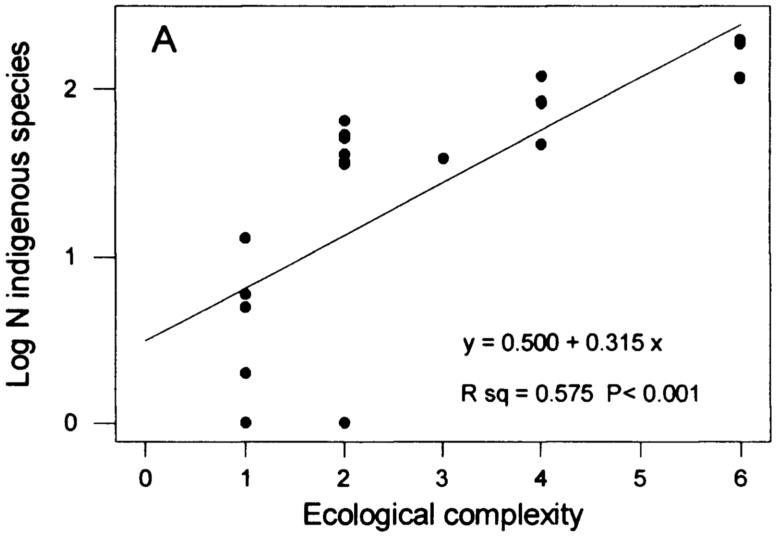


Figure 2.7. Relationships between species richness (A indigenous species, B introduced species) to island area (Km^2). for the Lepidoptera fauna of the Galapagos Islands. Log N indigenous species: Log_{10} of the number of indigenous species. Log N introduced species: Log_{10} of the number of introduced species. R sq: R^2.



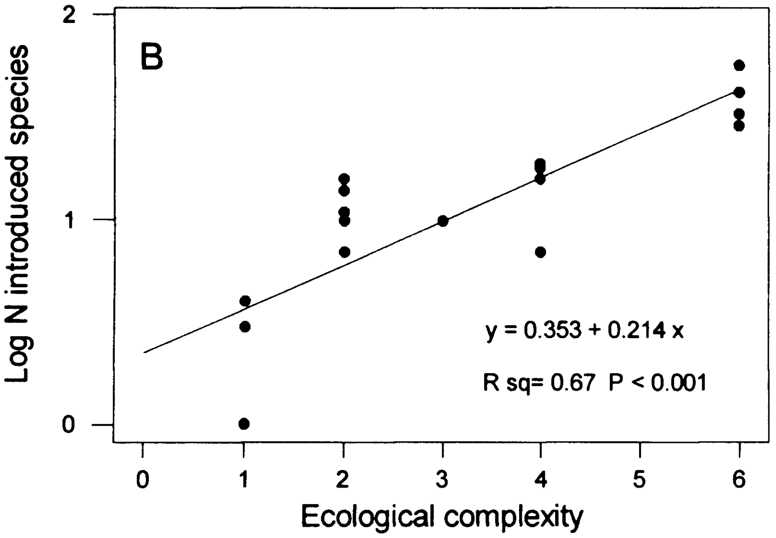
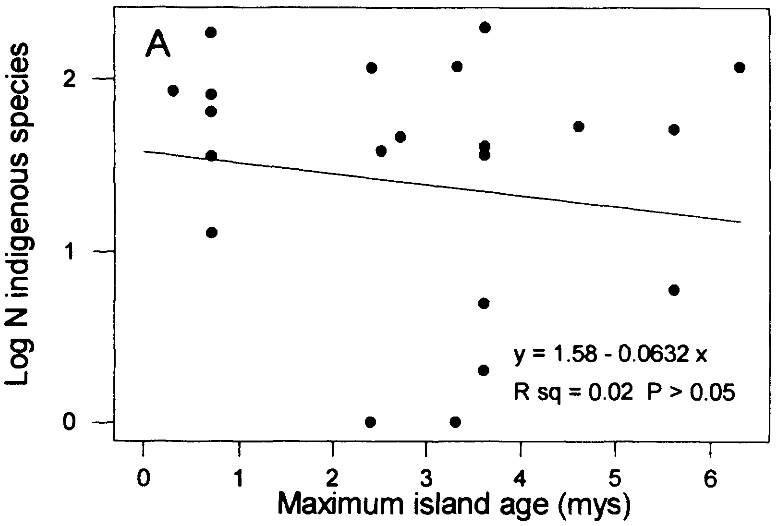


Figure 2.8. Relationships between species richness (A indigenous species, B introduced species) to Ecological complexity for the Lepidoptera fauna of the Galapagos Islands. Log N indigenous species: Log_{10} of the number of indigenous species. Log N introduced species: Log_{10} of the number of introduced species. R sq: R^2.



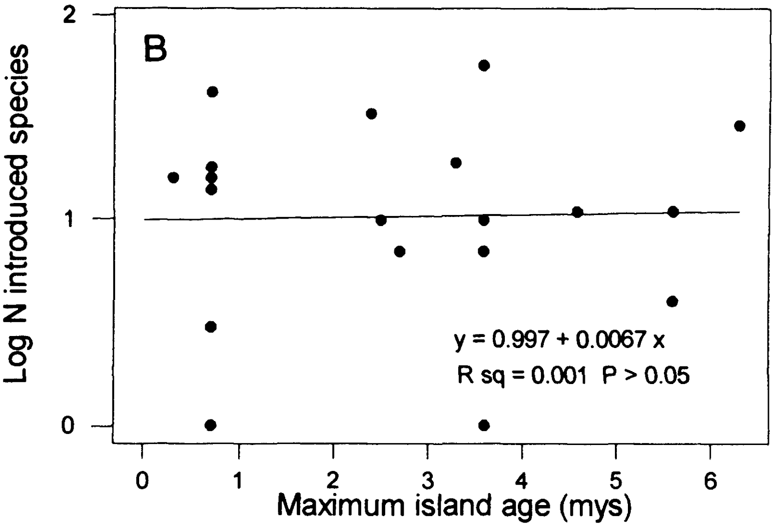


Figure 2.9. Relationships between species richness (A indigenous species, B introduced species) to Maximum island age (millions of years) for the Lepidoptera fauna of the Galapagos Islands. Log N indigenous species: Log_{10} of the number of indigenous species. Log N introduced species: Log_{10} of the number of introduced species. R sq: R^2.

2.4 DISCUSSION

2.4.1 Diversity

The recorded Galapagos Lepidoptera fauna currently consists of 313 species in 222 genera and 28 families; 64% of the indigenous component of this fauna is endemic although a further 58 species have an uncertain status and are probably also endemic. A total of 62 species have been introduced accidentally to the islands by humans (see Appendix 1). Following the Coleoptera, the Lepidoptera is the second most diverse terrestrial invertebrate taxonomic unit on the Galapagos (Peck 2001).

There has been a marked increased in the addition of new taxa in the past 15 years (Fig. 2.10, Table 2.2) and there is no indication that the discovery rate is reaching a plateau. The increase of species detections over the past 15 years is due to a number of factors: the use of more effective and intensive sampling techniques such as ultraviolet light; the fact that a number of specialists are available to study many taxonomically difficult groups of Microlepidoptera; as well as the establishment of the Charles Darwin Research Station in the Galapagos with its ever-growing interest in invertebrate ecology. Important groups such as the Pyralidae and some families of Microlepidoptera such as Tineidae, Gelechidae and Tortricidae, however, remain to be studied in detail.

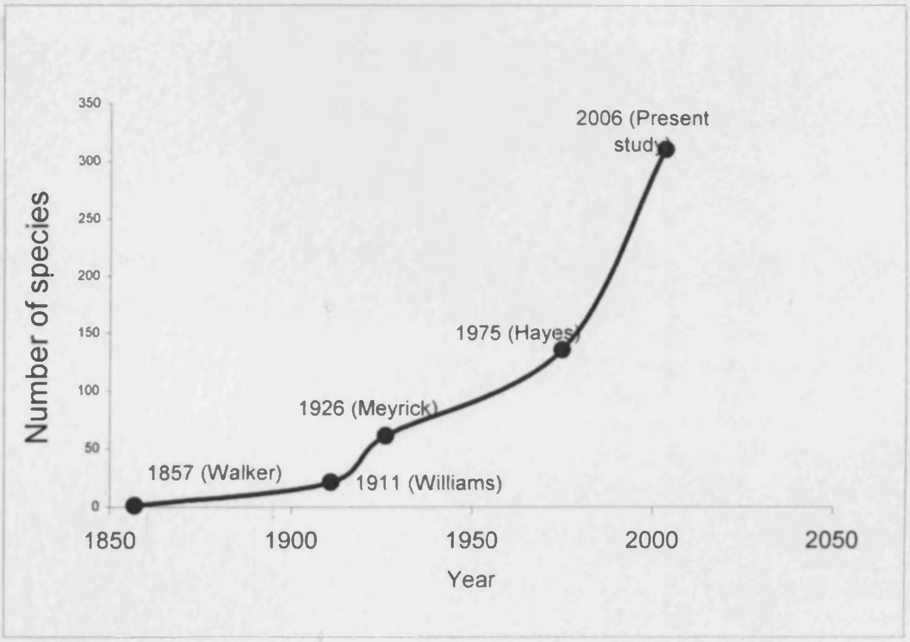


Figure 2.10. The increase in the number of Lepidoptera species recorded in the Galapagos Islands, with major reference points.

Of the 313 species of Lepidoptera occurring in the Galapagos Islands many are known to be migratory, or at least highly dispersive. Examples include *Agrius, Spodoptera, Mocis, Agrotis* and *Anticarcia* species. Practically all of the migrants are also agricultural pests and it is impossible to determine whether their presence in the Galapagos is the result of human introduction or of colonisation by migration. The Noctuidae (87 species) is the most diverse family followed by the Pyralidae (75 species). These are families that are also diverse in other remote islands such as Ascension, Bermuda and Cocos-Keeling (Holloway & Nielsen 1999).

Table 2.2. Summary of the diversity of the Lepidoptera fauna from the Galapagos Archipelago, and principal or most recent bibliographical references.

Family	Published		Unpublished		References
	Species Number	Genera Number	Species Number	Genera number	
Opostegidae	0	0	1	1	No articles published, data based on present study.
Tischeriidae	2	1	0	0	Landry & Roque-Albelo (2004).
Tineidae	4	4	17?	17?	Davis (1994); Heppner (1975); Linsley (1977); Linsley & Usinger (1966); Meyrick (1926); Peck *et al.* (1998); Perry & DeVries (2003); Silberglied (1978).
Gracillariidae	0	0	7?	5?	No articles published, data based on present study.
Bucculatricidae	1	1	0	0	Davis *et al.* (2002)
Yponomeutidae	2	2	0	0	Butler (1877); Landry & Landry (1998); Linsley & Usinger (1966); Meyrick (1926); Perry & DeVries (2003); Schaus (1923); Wallengren (1861).
Plutellidae	0	0	1	1	No articles published, data based on present study.
Heliodinidae	1	1	0	0	Heppner & Landry (1994b).
Coleophoridae	3	3	1	1	Adamski & Landry (1997); Linsley (1977); Linsley & Usinger (1966); Meyrick (1926); Perry & DeVries (2003).
Cosmopterigidae	8	4	0	0	Landry (2001a).
Xyloridctidae	0	0	5?	5?	No articles published, data based on present study.
Gelechiidae	1	1	16	14	Linsley (1977); Linsley & Usinger (1966); Meyrick (1926); Peck (1994a); Schaus (1923); Silberglied (1978).
Elachistidae	2	2	0	0	Landry (2001b); Landry & Roque-Albelo (2003).
Autostichidae	11	1	1	1	Landry (2002); Linsley & Usinger (1966); Meyrick (1926).
Tortricidae	6	5	0	0	Linsley (1977); Linsley & Usinger (1966); Meyrick (1926); Peck *et al* (1998); Perry & DeVries (2003); Schaus (1923).
Choreutidae	1	1	0	0	Hepner & Landry (1994a); Roque-Albelo (2003).
Pterophoridae	15	8	0	0	Landry(1993); Landry & Gielis (1992); Linsley & Usinger (1966); Meyrick (1926); Peck *et al.* (1998); Perry & DeVries (2003); Roque-Albelo (2003); Schaus (1923); Silberglied (1978).

Family	Published		Unpublished		References
	Species Number	Genera Number	Species Number	Genera number	
Pyralidae	35	32	40	28	Capps (1966); Gara & Onore (1989); Holland (1889); Landry & Neunzig (1997); Linsley (1977); Linsley & Usinger (1966); Munroe *et al.* (1995); Parkin *et al.* (1972); Peck (1994a); Peck *et al.* (1998); Perry & DeVries (2003); Schaus (1923); Silberglied (1978); Williams (1930).
Hesperiidae	2	2	0	0	Beebe (1923); Evans (1952); Linsley & Usinger (1966); Onore & Mielke (1988); Parkin *et al* (1972); Peck *et al.* (1998); Roque-Albelo (2004); Van Duzee (1933); Williams (1911); Williams & Hayward (1944).
Pieridae	1	1	0	0	Beebe (1923); Holland (1889); Linsley & Usinger (1966); Moreno *et al.* (1997); Parkin *et al.* (1972); Roque-Albelo (2004); Van Duzee (1933); Williams (1911).
Lycaenidae	2	2	0	0	Balint & Jonhson (1995); Beebe (1923); Bridges (1988); Linsley & Usinger (1966); Moreno *et al.* (1997); Peck *et al.* (1998); Roque-Albelo *et al.* (1997); Roque-Albelo (2004); Van Duzee (1933); Wallengren (1860; 1861); Williams (1911).
Nymphalidae	5	3	0	0	Ackery & Vane-Wright (1984); Beebe (1923); Holland (1889); Linsley (1977); Linsley & Usinger (1966); Michener (1942); Parkin *et al.* (1972); Roque-Albelo (1998 a; b; 2004); Stichel (1938); Van Duzee (1933); Williams (1911).
Geometridae	18	13	3	3	Herbulot (1970; 1971); Holland (1889); Landry & Rindge (1995); Linsley (1977); Linsley & Usinger (1966); Peck (1994a); Peck *et al.* (1998); Perry & DeVries (2003); Rindge (1973); Roque-Albelo (2003); Schaus (1923); Silberglied (1978); Warren (1904).
Uraniidae	2	2	0	0	Hayes (1975); Linsley (1977)

Table 2.2 (Continued)

Family	Published		Unpublished		References
	Species Number	Genera Number	Species Number	Genera number	
Sphingidae	15	9	0	0	Butler (1877); Clark (1926); Curio (1965a; b); Haxaire (1993); Hickin (1979); Holland (1889); Kernbach (1962; 1964); Kitching & Cadiou (2000); Linsley (1966; 1977); Linsley & Usinger (1966); McMullen (1986; 1990; 1993); Parkin *et al.* (1972); Perry & de Vries (2003); Roque-Albelo (1999); Roque-Albelo & Landry (2001); Rothschild & Jordan (1903); Schreiber (1978); Silberglied (1978); Williams (1911).
Arctiidae	4	1	0	0	Butler (1877); Forbes (1941); Hayes (1975); Holland (1889); Linsley (1977); Perry & DeVries (2003); Roque-Albelo *et al.* (2002); Schaus (1923); Silberglied (1978); Wallengren (1860).
Noctuidae	77	50	10	6	Butler (1877); Hayes (1975); Holland (1889); Kohler (1961); Linsley (1977); Linsley & Usinger (1966); Parkin *et al.* (1972); Perry & DeVries (2003); Richards (1941); Roque-Albelo (1999); Schaus (1923); Todd (1959); Tood (1972); Todd (1973); Silberglied (1978); Silvain & Lalane-Cassou (1997); Walker (1857), Wallengren (1860).
Nolidae	1	1	0	0	Hayes (1975)

Table 2.2 (Continued).

2.4.2 Is the Galapagos Lepidoptera fauna unbalanced?

The absence of some Lepidoptera families is characteristic of an oceanic biota. Dispersal capacity, survival mechanisms, trophic and morphological specialization (and resulting speciation rates) have a marked influence on the taxa present on islands (Peck 1996). Amongst the macrolepidoptera, the superfamilies Drepanoidea and Uraniidae of the geometroid group, all bombycoid families except Sphingidae, and Lymantriidae and Notodontidae of Noctuoidea are virtually excluded from oceanic islands (Barnett *et al.* 1999). The Galapagos fauna is consistent with this.

When comparing the Galapagos lepidopteran fauna with that of mainland Neotropical regions, some characteristic features become evident. One of these is the unbalanced composition of the fauna. Comparing the available list of taxa from the Neotropical region (Heppner 1991) and that of Galapagos Lepidoptera, the following observations can be made. Firstly, 56 families of Lepidoptera in the Neotropics are missing from the Galapagos. Among those absent are the most primitive Lepidoptera (13 families). The Opostegidae are the only non-Ditrysian Lepidoptera from the Islands. In the most primitive Ditrysians, the Tineoidea, four families are missing, although the Tineidae are present. Among the "higher" Ditrysia, Neotropical groups absent from the Galapagos include: the Oecophoridae (with 1,733 known species in the Neotropics), the Sesiidae (193 species), the Copromorphoidea (5 families, 121 species), the Zygaenoidea (2 families, 382 species), the Cossoidea (4 families, 610 species), the Castniidae (160 species), the Bombycoidea (7 families, 2,104 species), the Notodontidae (1,650 species), the Dioptidae (500 species) and the Lymantriidae (180 species) (See Heppner 1991).

Compared to the large Neotropical butterfly fauna (7,784 species), that of the Galapagos is very limited (10 species). Characteristic South American groups of butterflies such as the Papilionidae and the subfamilies of the Nymphalidae (i.e. Libytheinae, Morphinae and Satyrinae) are missing. The location of the centres of diversity of the South American butterflies (see Brown 1982), the ecological restrictions of the species imposed by habitat structure, the host plant, and the ecological and distributional characteristics of the species appear to be important explanatory determinants of these missing families. Few Neotropical butterfly species are likely to disperse to the Galapagos and even fewer would be able to survive upon arrival. This statement may also be generalized to be relevant to all other groups of Lepidoptera. It would, for example, be interesting to correlate the Lepidoptera fauna of comparable habitats in the Galapagos and the source area to obtain a more realistic figure of the total number of Galapagos migrant species compared to the number of potential migrants from Central and South America.

Some of these 'missing' groups (e.g. Hepialidae) are widely dispersed but not present on remote oceanic islands (Scoble 1992). Hepialids may have dispersed on rafts as their larvae are often root or stem borers, but they would have had major difficulties surviving the arid coastal habitats upon arrival on the Islands. These xeric environments are likely to be the greatest limitation upon establishment in Galapagos of groups of Neotropical Lepidoptera that have diversified in the wet equatorial forests. Not known for their dispersal potential, and unlikely to withstand the conditions traveling on a raft in the ocean, they also appear to be restricted to flying in the equatorial forest where they are not likely to be picked up by strong winds. Finally, if any equatorial forest inhabitants ever reached the Galapagos, it is highly unlikely that they could find suitable host plants.

To emphasize the unbalanced nature of the Galapagos lepidopteran fauna, comparison with another oceanic archipelago, Hawaii is appropiate. The islands of Hawaii possess both a much more species-rich fauna of Lepidoptera with over 1,000 species recorded and also a higher number of families (41 versus 28) (based on Zimmerman 1948; 1958a; b; 1978; Eldredge & Miller 1996). The proportion of endemic species is also much higher in Hawaii (82% versus 45%). The Hawaiian Islands are, however, much older (ca, 70 myr versus 3-4 myr) and larger (16,615 km^2 versus about 7,856 km^2) than the Galapagos. They are also further in distance from any mainland source of colonists than the Galapagos (ca, 3,850 km versus 900 km). Hawaii also shows a more varied source fauna with ancestors originating from the west (Asia), the south (Pacific Islands), as well as the east (Americas). Their more complex geological history presents a higher diversity of habitats and their plant diversity is also much higher.

2.4.3 Origin and evolution of the fauna

2.4.3.1 Arrival of the colonist

The unbalanced nature of the Galapagos fauna arises mainly from the differences in the abilities of each taxa to complete the proceses of dispersal and colonization (Peck 1996). Dispersal capability is determined by the ecology, behaviour and physiology of each taxon, and of the mode and frequency of transport opportunity. Colonization is also only successful if the life history strategies of the colonizing taxon and the characteristics of the new environment are well-matched (Peck *op.cit.*).

Natural colonization events from the continental mainland are infrequent; for insects, these events have been estimated to occur once every 2000 years (Peck 1996). The probability of colonization is influenced by an island's geographical and environmental setting, as well as by the attributes of the colonizing organism (MacArthur & Wilson 1967). Colonization of the Galapagos Archipelago by insects must have occurred in one of four ways: (i) by active flight or wind transport (anemochore dispersal), either voluntarily or involuntarily (blown by strong winds); (ii) with other animal assistance (biochore dispersal); (iii) passively on the sea surface on rafts of vegetation or debris (hydrochore dispersal) from coastal, estuarine or riverine habitats, and then brought to the Islands by the west-flowing equatorial Humboldt current in the dry season, or by waters from the Gulf of Panama in the rainy season (especially in strong "El Niño" years); or (iv) introduction by humans (anthropochore dispersal). The importance of these modes differs for different taxa. Only the anemochore and anthropocore dispersal modes are considered important for the Lepidoptera in the Archipelago (Peck 2001).

Flight or wind transport is probably the most important mechanism for insects to reach the Islands. Based on known distributional records and dispersal potential of the genera involved, it is possible to assume that all butterflies, all sphingids, the arctiids, some pyralids (mostly Pyraustinae), and most noctuids (altogether about 45% of the species) originally arrived by flight. Holloway & Nielsen (1999) reviewed the distribution of Lepidoptera on oceanic islands around the world and noted a surprising homogeneity in the faunal composition. For Macrolepidoptera, they noted the recurrence of 12 genera in the families Arctiidae, Sphingidae and Noctuidae, namely *Utetheisa, Agrius, Agrotis, Anomis, Anticarsia, Pseudoplusia, Condica, Helicoverpa, Hypena, Mocis, Mythimna* and *Spodoptera.* These genera contain many migrant long-distance, high-altitude fliers that travel widely. These are all represented in the Galapagos fauna. In some of these genera, endemic species or subspecies occur in the Galapagos but the ancestral types are known to travel long distances. The non-endemic Galapagos species in these genera probably disperse to the Islands rather frequently from the mainland Neotropics. A significant number of smaller Lepidoptera may have been brought by strong winds as aerial plankton.

Transport by humans. Humans have intentionally brought many domestic animals and horticultural plants to the Islands. Unintentional introductions have also occurred; and include rats, mice and weedy plants. The only example of an intentional introduction of an arthropod species to the Islands is the Australian coccinelid beetle

Rodolia cardinalis Mulsant in an attempt to control the cottony cushion scale *Icerya purchasi* Makell (Causton *et al.* 2004). A large number of terrestrial invertebrates have, however, been unintentionally introduced to the Archipelago and these include several Lepidoptera. Peck *et al.* (1998) reported 46 introduced Lepidoptera in the Islands (about 15% of the total number of Lepidoptera species known). The present study includes an additional 16 new records, which may be recent introductions, or long established and not previously detected. Many species in the Pyralidae, Tortricidae and some Tineidae are typically associated with humans and their plants, foodstuffs, wood, and personal goods such as clothes or carpets. The rate of accumulation of alien species is currently increasing in tandem with the increasing number of permanent human inhabitants on the Islands. Even with strict quarantine, and control of goods and people, it is expected that adventive species will continue to arrive.

The likely origin of the Galapagos Lepidoptera fauna is illustrated by grouping the species into biogeographical categories (Appendix 1). The endemic Lepidoptera are, without exception, closely related to Neotropical taxa (see also Hayes 1975; Rindge 1973). This is substantiated by evidence that shows that the origin of other terrestrial fauna and flora endemic to the Galapagos Islands is coastal South America (Wright 1983; Grant 1986; Lanteri 1992; Lopez *et al.* 1992; Peck 1994b, 1996; Cook *et al.* 1995; Finston & Peck 1997; Caccone *et al.* 1999; Sato *et al.* 2001). The native and introduced Lepidoptera are composed of widespread cosmopolitan and pantropical species. The remaining fauna have affinities with the Nearctic regions.

In theory, the number of colonist species on an island will fall somewhere between the total number of species and this number minus the total number of endemic species. Each endemic species present on the island must be descended from either one of the native species or from one species that has now vanished from the Islands. Based on published data alone, if it is assumed that all genera with more than one endemic species had one original colonist species, then a minimum of 184 colonization events were necessary for the establishment of the extant species of Lepidoptera. To establish accurate estimates of the percentages of naturally arriving species it is, however, necessary to understand the phylogenetic relationships between the Islands' species and their relatives on the mainland.

2.4.3.2 Endemicity

An oceanic island's biota is the product of colonization from overseas and local speciation. In the Galapagos, more than one third of the species (90) are native; that is, they are also known to occur in continental localities. It is assumed that colonization by these species has been recent (or is still continuing), and that morphological and genetic change has not occurred despite the isolated position of the Islands. On the other hand, 159 species are endemic to the Galapagos Archipelago. This suggests that they were colonized sufficiently long ago for genetic isolation to have led to differentiation. This 159 species represents 51% of the total fauna; including the introduced species.

The calculated proportion of endemic species in this study is within the expected range of endemism; plants show 29% endemism (McMullen 1999), Diptera 41% (B. Sinclair pers. comm.) and Coleoptera 67% (Peck & Kukalova-Peck 1990). Percentage endemism will, however, vary as knowledge of more families (especially in the Microlepidoptera) becomes available for the Neotropics. Families of smaller-sized moths such as the Tortricidae, Gelechiidae, Pyralidae and Tineidae have not been studied in South America and it is possible that some Galapagos "endemics" are also found in the Neotropical region.

Within the Galapagos Lepidoptera, endemicity at the generic level occurs in four genera; two genera in the Pyralidae (*Beebea* and *Schafferiessa*), one in the Autostichidae (*Galagete*), and one in the Noctuidae (*Psaphara*). Of the 202 or so genera found on the Islands, only five have three or more endemic species: *Cosmopterix* (Cosmopterigidae) with three species (Landry 2001a), *Galagete* (Autostichidae) with 11 (Landry 2002), *Stenoptilodes* and *Oidaematophorus* (Pterophoridae) with three species each (Landry 1993; Landry & Gielis 1992), *Eupithecia* (Geometridae) with three (Rindge 1973; Landry & Rindge 1995), and *Utetheisa* (Arctiidae) with three (Hayes 1975).

Endemism at the subspecific level has been reported for 20 species (nine Sphingidae, one geometrid, two butterflies, and eight noctuids). Inter-island subspecific endemism has been described in only one moth; the geometrid *Macaria* *cruciata* (Rindge 1973). There is however little doubts that further analysis is necessary for clarification.

Two cases of multiple-island speciation forming a "species swarm" are represented by the arctiid genus *Utetheisa* and the Autostichidae genus *Galagete*. This latter genus contains 11 species (Landry 2002) and seems to form a monophyletic group; the necessary data are not available to confirm this. Five of the endemic species have been collected from the same location during the same season (Landry 2002) but until their life history, morphological and genetic characteristics are better known, the possibility of adaptive radiation cannot be proven. The Arctiidae, on the other hand, provide an interesting phyletic radiation. Three different *Utetheisa* species have been collected from the Galapagos, two of which occur parapatrically on different islands. One species is found along the coast and in the other lower elevation vegetation zones on all islands. The other two species inhabit the *Scalesia* and pampas zones (highland areas) of Santa Cruz, Santiago and Volcan Sierra Negra (Isabela), however, only one of these inhabits Volcan Alcedo and Volcan Darwin (Isabela), Fernandina and Pinta. These species show a clear differentiation in the morphology of the male genitalia. This provides evidence of the Wallace effect for accomplishing complete speciation in parapatrically occurring species. It is important to investigate whether there is a relationship between these three species, however at present, the limited samples from different islands available for DNA studies are insufficient for conducting such a comparative study. Investigating the fauna of Cerro Azul and Volcan Wolf (Isabela), San Cristobal, Floreana, Española and Santa Fé in more detail would enable substantiation of the degree of speciation that has occurred in this family.

2.4.4 Determinant of species richness.

It is generally found that larger islands have more species and genera. This is not because of their larger area *per se*, but that greater area increases the chances for occurrence of more available habitats and microhabitats (Peck 2001). This is certainly the case for the Lepidoptera of the archipelago. The largest islands such as Isabela, Santa Cruz and San Cristobal have the greatest species diversity. Both the number of indigenous and introduced species are clearly positively correlated with island area and habitat diversity as is predicted by theory.

Is it to be expected that older islands have had more time to assemble and evolve species. All else being equal, older islands would be expected to have higher species diversity (Borges & Brown 1999). However, no significant relationship is found between species richness and island age for Lepidoptera. Peck (2001) suggested for other orders of insects in the Galapagos a loss of species on old islands caused by the loss of area and habitats and extinction of species as the island subsides and erodes in its old age. This explanation can be applicable also to the Lepidoptera fauna.

Island biogeographic theory postulates that the species richness of an island is primarily a function of physical variables such as insular area and distance to a source population (MacArthur & Wilson 1967). This is an ecological model and does not consider the influence of historical factors. Yet a historical rather than an ecological perspective may better explain the distributional patterns of many organisms (Rassmann 1997; Sequeira *et al.* 2000). Both historical and ecological factors have no doubt played important roles in determining the species richness and composition of Galapagos Lepidoptera fauna. Considerating the mechanisms by which Lepidoptera colonize oceanic islands may further elucidate the relative importance of these factors. Lepidoptera have dispersed to Galapagos Islands by two mechanisms (flight or wind transport, transported by humans), which have operated to different degrees (and interact) over time and have been differentially important in dispersal to and within archipelago.

Although collections have been made on twenty-three islands over a period 160 years, knowledge of Galapagos Lepidoptera distribution is still incomplete. The Galapagos are composing by 127 islands (Snell *et al.* 1995) and many remain unstudied. Future collecting efforts on the less thoroughly surveyed islands will most likely widen the distribution of known species, and species, which represent new records for the Galapagos probably await discovery. All major collecting trips to date have discovered some percentage of new species. Thus, a cautious approach in interpreting the available data for Galapagos Lepidoptera is indicated until additional surveys are conducted.

2.4.5 The influence of humans

Human activities on the Islands can be divided into agricultural, tourism and inter-island transportation, and introduction of exotic species. The impact of agriculture on the Lepidoptera fauna can be related to the destruction of native habitats to make space for agricultural plantations and pasture, the competition of introduced pest Lepidoptera species for native food plants, the possible broadening of the host-plant range of endemic species and the possible detrimental effect of the use of pesticides. Although relatively little is known about the detailed life history of Galapagos species, no lepidopteran pest species appear, to date, to have successfully colonized and exterminated the food plant of endemic species (although introduced vertebrates and plants may have done so), and no endemic species have switched hosts to feed on imported plants.

Tourism is having an increased impact on Lepidoptera conservation in the Galapagos Islands. A comparison of Linsley & Usinger (1966) and Linsley (1977), with the field data available on the Pyraloidea (see Table 2.2), a group with many widespread pest species, highlights the high number of recent Lepidoptera imports. Silberglied (1978) mentioned the attraction of several Lepidoptera species to shipboard lights, and the survival of many species aboard these ships during inter-island trips; and even after returning to the continent. It is more than likely that a number of Lepidoptera species (estimated at about 25% of the estimated total) could have been introduced into the Galapagos accidentally, and that endemic and non-endemic species have been transported from island to island. Undoubtedly this has led to important changes in Lepidoptera population composition in the various islands. In addition, the appearance of electric street and house lights, which attract Lepidoptera at night, and the planting of many non-native flowering plants, which attract various butterflies and moths, must be having an impact on the Lepidoptera fauna.

Humans are also responsible for accidentally introducing exotic Lepidoptera species to the Islands and directly affecting the composition and abundance of indigenous Lepidoptera populations as a result of resource extraction, farming and other activities. The influence of people on the Galapagos Islands is quite recent. The Islands were uninhabited prior to their discovery by Europeans in 1535. The first insect introductions could have been made at the time of discovery but are more likely to have occurred in the 1700s when the Islands were used as provision bases by pirates and privateers (Steadman 1986). The first human colonists in the 1800s might have introduced further species. Although no official records of any intentional introduction of Lepidoptera into the Islands exist, several unconfirmed reports suggest otherwise. For example, Rindge (1973) mentions the possible introduction of one or two unspecified geometrid species by humans while Meyrick (1926) mentions the introduction of the tineid *X. pruniramiella* by humans, and Heppner (1975) noted the introduction of the human commensal tineid *T. mormopis* (the case-bearing clothes moth). The phycitine pyralid *H. grandella* is reported to have been introduced in 1960 when seedlings of its host plant (*Cedrela odorata*) were brought to the Islands (Gara & Onore 1989). Although Linsley (1976) does not mention species by names, he comments on the fact that Linsley & Usinger (1966) reported 20 non-endemic noctuid species from the Archipelago while Hayes (1975) reported 39. Linsley further states that much of this increase must be due to the increase in transport and commerce with the mainland. In recent years, Peck *et al.* (1998) summarized the introduced insect fauna and reported 46 introduced Lepidoptera. Since then the list of introduced species has been increasing and in April 2004 the number of alien Lepidoptera species was reported to be approaching 60 (see Appendix 1).

Introduced species threaten the biodiversity of islands both through habitat alteration and directly through interactions with native species (Paulay 1994). In the Galapagos the absence of an effective quarantine system for imported goods has been detrimental to the Islands' native and endemic biota. The introduction of plants such as guava, mora, rose apple and *Lantana camara* (Verbenaceae), for example, have contributed to the alteration of vast areas of original habitat and transformed it into a large monospecific stand. Other serious threats are the fire-ant (*Wasmannia auropunctata*), goats and pigs that interact directly (competition and predation) with native species (Roque-Albelo 2003). These species disturb the natural equilibrium of the Islands and affect the unique fauna of the Galapagos Archipelago.

Chapter 3

Larvae host plant relationships of Galapagos Lepidoptera

3.1 INTRODUCTION

Interactions between insects and their host plant play an important role in biological diversification. Insect-host plants interactions tend to be governed by nutrient content (Slansky 1993), plant chemistry and architecture (Lawton 1983), phenology (Basset 1991a, b) and geographical distribution (Leather 1990).

Phytophagous insect species are generally characterized by specialized diets, with fewer than 10% having host ranges of more than three plant families (Bernays 1988, 1989). Ehrlich & Raven (1964) have argued that current patterns of insect-host plant associations are the result of stepwise coevolutionary processes in which plants evolve defenses against natural enemies, and these enemies, in turn, evolve new physiological or morphological capabilities to deal with these defenses. In the absence of enemies, plants that escape herbivores diversify. When insects colonize a novel host plant the herbivore enters a new adaptive zone. Eventually, and after establishment, the chemical similarity between closely related species allows these insects to diversify onto the relatives of the original plant species. Ehrlich & Raven argue that it is these processes that have led to the observed pattern where related butterflies tend to feed on related groups of plants. Phytophagous insects affect the growth and reproduction of plants by reducing photosynthetic area, consuming reproductive structures, and/or altering floral characteristics thus reducing attractiveness to pollinators. Janzen (1977) pointed out the dearth of knowledge on interactions between tropical herbivorous insects and their host plants and, more recently, a number of studies have been carried out on the natural history of Neotropical herbivores and their host plants. These have concentrated on Costa Rica (Janzen 1988, Marquis & Braker 1994) and Brazil (Diniz & Morais 1997, 2002); few, if any, studies have concentrated on the host plant-insect interactions of tropical oceanic islands such as the Galapagos Archipelago.

Lepidoptera are holometabolous insects, with larval (or caterpillar) stages devoted entirely to feeding, mostly on plant tissue such as leaves, but also on flowers, fruits, seeds and stems. Some species also feed on fungi, spores, and animal or plant detritus. As most Lepidoptera consume plants, comparatively little research has focused on the ecology of non-phytophagous species (Pierce 1995) although this group comprises both predatory, with larvae that feed on scale insects and eggs of other insects or ant broods, and parasitic species.

In the context of the Galapagos Lepidoptera it was Francis X. Williams who made the first reporting of Lepidoptera-host plant interactions (Williams 1911). He reported the host plant records for butterflies and Sphingidae collected during the expedition of the California Academy of Sciences in 1905-06, and later published notes on the life history of the endemic pyralid moth *B. guglielmi*. No other larval collections were carried out on the Islands until 1965 when, over the next 10 years, Roger Perry and Tjitte DeVries conducted the first intensive collection of Lepidoptera larvae. The records derived from this study were published by Herbulot (1971), Rindge (1973), Hayes (1975) and Perry & DeVries (2003). Since 1990, several taxonomic papers with host plant records have been published (e.g. Landry 1993, Landry & Landry 1998, Landry & Gielis 1992, Landry & Neunzig 1997, Heppner & Landry 1994b) enhancing our knowledge and understanding considerably.

25 years have elapsed since any comparable concentrated effort to study the host plant relationships of Lepidoptera. Since 2000 an insect-rearing programme has been developed by the Charles Darwin Research Station accumulating data on the host relationships of Lepidoptera. Personnel have processed more than 2300 larvae and some of the results have already been published (Davis *et al.* 2002, Landry 2001a, 2002, Landry & Roque-Albelo 2003, Landry *et al.* 2004, Roque-Albelo 1998a, 1998b, 1999, 2003, 2004, Roque-Albelo & Landry 2001, Roque-Albelo *et al.* 1997, 2002).

This chapter reviews and summarizes what is currently known about the host plant-insect relationships of Lepidoptera in the Galapagos Archipelago. It aims to review and interpret known host records of Galapagos Lepidoptera from scattered sources, compile the first comprehensive information source for future studies, and, from field observations, to contribute new host-plant information concerning species with previously unknown life cycles from the Galapagos Islands.

3.2 METHODS

Data were obtained and collected by literature review, and from field and museum collections.

Literature review

Published records of host affiliations for Galapagos Lepidoptera were collected from several sources: Landry & Roque-Albelo (2003) (Tischeriidae); Heppner (1975) (Tineidae); Landry (unpublished.) (Gracillariidae); Davis *et al.* (2002) and Landry & Landry (1998) (Yponomeutidae); Heppner & Landry (1994b) (Heliodinidae) and Landry (2001a) (Cosmopterigidae); Landry & Roque Albelo (2003) (Elachistidae), Landry (2002); (Autostichidae); Landry & Gielis (1992), Landry (1993), Roque-Albelo (2003) and Landry *et al.* 2004 (Pterophoridae); Roque-Albelo (2003) (Choreutidae); Williams (1930) and Landry & Neunzig (1997) (Pyralidae); Hayes (1975) (Noctuidae); Landry & Rindge (1995) (Geometridae); Roque-Albelo (2004) (Papilionoidea, Hesperioidea); and Roque-Albelo & Landry (2001) (Sphingidae).

For Lepidoptera species not restricted to the Islands more general host plant information is often available. Two easily accessible databases are those of Janzen & Hallwachs (2001) and Robinson *et al.* (2001). Lepidoptera host plant records for the Galapagos were also compared with host plant records compiled from other locations; this enabled determination of the potential range of host plants in the Galapagos even if records did not exist. The database provided by Janzen & Hallwachs is comprised of data from Costa Rica while that Robinson *et al.* (2001) provides information on a global scale, although biased towards the Nearctic Region. Information on species that occur in the Galapagos is also available at CAB International (2003) where host plant records of agricultural pests are presented.

Collating host plant data from published records is often fraught with difficulties mainly as a result of inaccuracies and inconsistencies in the literature (Weintraub 1995). Nevertheless, large databases tend to show emergent patterns that are typically robust against a small proportion of unreliable records (Leather 1990, Fielding & Coulson 1995).

Field and museum collections

For a 7-year period (1996-2003) information on Lepidoptera-host plant interactions was collected in the field by the author; entomological specimens were deposited in several museums. The majority of the material was deposited in the Invertebrate Collection of the Charles Darwin Research Station (IC-CDRS). Some specimens were recorded from the following collections: Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador and The Natural History Museum (NHM), London, U.K. Additional host records were obtained from the unpublished data of Bernard Landry, whose material is deposited in the Canadian National Collection (CNC), Ottawa, Canada and Muséum d'Histoire Naturelle (MHNG), Geneva, Switzerland, and from data labels of specimens deposited in the California Academy of Sciences (CAS), San Francisco, USA and The Natural History Museum (NHM), London, UK.

Foliage-feeding caterpillars were collected by hand and reared in the laboratory. Eggs and larvae were reared in plastic bags at room temperature under a natural day-night photoperiod. Fresh leaves were provided at least every other day. For those larvae which feed internally on reproductive structures, plant organs (e.g. flowers and fruits) were collected and kept in plastic pots covered with light fabric. Pupae were kept moist until adults hatched. The classification adopted throughout this study follows that of Kristensen (1999). Plant nomenclature follows that of Jorgensen & Leon-Yanez (1999).

Diet breadth of Lepidoptera species was defined as the number of recorded host plant families. On the basis of this information all Lepidoptera species were then grouped into three host range categories: (1) monophagous (at family level); (2) oligophagous (two or three host plant families); or (3) polyphagous (four or more host plant families).

3.3 RESULTS

3.3.1 Records from Galapagos Islands

Except where indicated the following list of 28 Lepidoptera families is annotated with biological and host plant range information arising from the present study.

Opostegidae

The plant hosts of the only species of this family that occur in the Galapagos are unknown. Larvae are known to mine leaves, petioles and the cambial layer under bark, or the stalks of flowers (Davis 1989). Host plants for other species of the family include Rutaceae, Saxifragaceae, Ranunculaceae and Fagaceae (Scoble 1992).

Tischeriidae (Fig. 3.1a)

Landry & Roque-Albelo (2004) recorded three host-plants for the two species of Tischeriidae in the Galapagos. The larvae of *Astrotischeria scalesiaella* and *A. alcedoensis* are leaf miners on *Scalesia* species, a group of endemic Asteraceae (Table 3.1). The larvae bore directly into the leaf eventually forming an upper surface or full depth blotch mine lined with silk. Frass is normally expelled from the mine through a single hole. Tischeriids are predominantly leaf miners throughout the larval stage and pupate within the mine (Davis 1987a). The genus *Astrotischeria* is associated with Asteraceae and Malvaceae in the Neotropical region (Puplesis & Diskus 2003).

Tineidae (Fig. 3.1b)

The larvae of tineid moths feed on a variety of substrates, but they are typically detritivorous, fungivorous, lichenivorous or keratinophagous (Scoble 1992). At least three species of this family were accidentally introduced to the Galapagos by humans (Peck *et al.* 1998). *Trichophaga mormopis* feeds on keratin and has been reported in owl pellets, tapestries, furs, wools, feathers and a variety of other substrates containing keratin. The other two introduced species, *E. minuscula* and *X. pruniramiella*, feed on dead plant material and stored products (Peck *et al.* 1998). Meyrick (1926) reported two other tineid species feeding in the wood of various tree species. During the present study larvae were found feeding on a number of substrates other than those associated with humans, for example walls, bird nests, bird pellets, a wasp nest, mammal burrows and weathered faeces (see Tables 3.1 and 3.2). Larval cases were abundant on house walls, these larvae probably feed on microscopic lichens.

Gracillariidae

The Gracillariidae constitute the principal family of plant-mining Lepidoptera (Davis 1987b). During the early instars the larva is a sap-feeder but later becomes a tissue feeder; corresponding changes in body anatomy occur simultaneously (hypermetamorphosis). Host-plant information on Galapagos gracillarids is only available for two species: *Acrocercops* sp. and *Cryptolectica* sp. Larvae of *Acrocercops* sp. were observed mining leaves of *Waltheria ovata* (Sterculiaceae) while those of *Cryptolectica* sp. feed on *Synedrella nodiflora* (Asteraceae). The host associations are not known for the other five species.

Bucculatricidae (Fig. 3.1c)

This family is also composed predominantly of leaf-mining species. During the present study *Bucculatrix cordiella,* the only Bucculatricidae present in the Archipelago, was observed mining *C. lutea*. This species undergoes a hypermetamorphic development similar to the Gracillariidae (Davis *et al.* 2002).

Yponomeutidae (Fig. 3.1d)

Yponomeutid moths have mostly external leaf-feeding larvae. Caterpillars spin webs over leaves or flowers, and typically skeletonize leaves by their feeding. The host-plants of the family are diverse and include Aceraceae, Betulaceae, Celastraceae, Corylaceae, Ericaceae, Fagaceae, Lauraceae, Rhamnaceae, Rosaceae and Simaroubaceae (Heppner 1987b). The two species in the Galapagos are monophagous. *Atteva hysginiella* caterpillars are very common and cryptical. They spin webs among the leaves of an endemic bush: *Castela galapageia* (Simaroubaceae) (Landry & Landry 1998). Several other members of genus *Atteva* also feed on Simaroubaceae (Powell *et al.* 1973). The caterpillars of *Prays galapagosella,* damage *Z. fagara.*

Plutellidae

Plutellid larvae are usually leaf feeders, often tying host-plant leaves together with loose silk webbings. They also skeletonize the leaves (Heppner 1987a). The

Galapagos species is the cosmopolitan *Plutella xylostella* whose larva is a serious pest on *Brassica* and other vegetables (see Appendix 2). Host plant records have not been reported in the Galapagos.

Heliodinidae (Fig. 3.1e)

This family contains species that are leaf miners, and skeletonizers, and fruit raceme borers (Heppner 1987c). The Galapagos species, *Heliodines galapagoensis*, is a leaf-miner reared from *C. pyriformis* (Heppner & Landry 1994b). This host plant is known to occur on the mainland, along the coast of Ecuador and Peru (Wiggins & Porter 1971).

Coleophoridae

The host range of this family is wide and includes species that are scavengers, predators of scale-insects, or borers in fruits and nuts. In the Galapagos, the natural history of the species is poorly known.

Coleophorinae: The host-plant of the only species of this subfamily occurring on the Islands is *Amaranthus* sp. (Amaranthaceae). This coleophorid species has caterpillars that construct a portable case from leaf fragments and remain on the leaf surface to feed.

Blastobasinae: In the Galapagos, the host plant relationship is only known for the endemic lepidoptera *Calosima darwini*. Larvae were found feeding on a wide variety of plants: fallen flowers of a *Jasminocereus* cactus, leaves of various plants, seeds and detritus. They were also observed as predators of scale insects (Table 3.2).

Cosmopterigidae

Larval feeding habits vary among the Cosmopterigidae. Some species are leaf-miners while others are seed feeders, stem-miners, scavengers and insect predators. The family is represented in the Galapagos by eight species in two subfamilies (Landry 2001a).

Cosmopteriginae: The biology of the Galapagos species are poorly studied; Landry (2001a) provides host plant information for two species. *Cosmopterix galapagosensis* larvae were found mining leaves of *Eleocharis mutata* (Cyperaceae) while caterpillars of *Pyroderces rileyi* have been reported not only as scavengers in dead plant material but also as leaf-miners and predators of scale insects (Zimmerman 1978, Pierce 1995). In the Galapagos, *P. rileyi* larvae were found in stems of *Laguncularia racemosa* (Combretaceae) infested by the cottony cushion scale *Icerya purchasi* (Homoptera). The larvae feed on the scale insect eggs and immatures. *Crysopeleiinae:* The feeding habits of species belonging to this subfamily are quite diverse. They include stem-mining, gall-making, leaf-binding, leaf and flower feeding, and fruit-boring (Stehr 1987a). The host relationship is recorded for one species, *Periploca darwini.* Larvae were found binding leaves of *Dodonaea viscosa.* A Hawaiian congener of *Ithome*, the other genus of the subfamily present in Galapagos is associated with the Leguminosae genus *Acacia* (Zimmerman 1978). Several species of this plant genus are recorded in the Galapagos Archipelago.

Xylorictidae

Poorly studied in the Islands, Xylorictidae larvae are known to be leaf miners and skeletonizers. Scythridinae is the only subfamily recorded in the Galapagos. They have larvae usually living in slight webs, feeding externally on buds or leaves (Powell 1976). One species was collected feeding on flower heads of *Darwiniothamnus tenuifolius* (Asteraceae). Another was reared from leaves of *Portulaca oleracea* (Portulacaceae), and a third was reared from leaves of *Alternanthera halimifolia* (Amaranthaceae).

Gelechiidae

This cosmopolitan family is represented in the Galapagos by 17 species belonging to four subfamilies. The larvae of gelechiid moths vary greatly in their bionomics; for example they can be leaf tiers or rollers, seed feeders, leaf-miners, and stem, fruit or tuber borers (Scoble 1992). Several species are major pests of vegetables and stored grain (CAB International 2003). In the Galapagos the host plant relationship is only known for a few species and little information exists in the literature.

Gelechiinae: Ten species from this subfamily occur in the Islands. Data of host relationships are only available for two species. During the present study *Evippe omphalopa* larvae were found boring the fruits of *Parkinsonia aculeata*

(Leguminosae) and caterpillars of an unidentified species of the genus *Ephysteris* were observed feeding on the fruits of *Sporobolus virginicus* (Poaceae).

Anacampsinae: Host plant information is available for two species, both of which are monophagous. The caterpillar of *Anacampsis primigenia* bores into the terminal ends of branches of *Croton scouleri* (Euphorbiaceae). *Compsolechia salebrosa* larvae feed on immatures flowers of *Desmodium incanum* (Leguminosae).

Dichomeridinae: Only two species occur in the Islands and no host plant records are available. In Hawaii, however, *Dichomeris acuminata* was recorded as feeding on several Leguminosae species, some of which are also present in the Galapagos (see Appendix 2).

Pexicopiinae: This subfamily has two species on the Archipelago, both of which are economically important. *Sitotroga cerealella* attacks stored grains of rice, corn and other dried goods. Eggs are deposited on the grain surface and emerging larvae bore into the grain. The other species, *Tuta absoluta*, is a leaf-miner on tomato and other Solanaceae (see Appendix 2). The larvae can attack and penetrate tomato fruits.

Elachistidae

Elachistidae are predominantly leaf-miners, although a few are known to bore into stems.

Agonoxeninae: Only one species from this subfamily occurs in the Islands and a host plant record is not available. According to Bottimer (1926), in Texas, larvae of another species of *Haplochrois* feed on leaf petioles and seeds of *Croton* (Euphorbiaceae). The Galapagos species probably feeds on *C. scouleri*.

Stenomatinae: The only species of this subfamily in the Islands, *Stenoma catenifer*, attacks and causes serious damage to avocado fruits at various stages of maturation (Landry & Roque-Albelo 2003).

Autostichidae

The caterpillars of the family mostly feed on dead or decaying plant, or animal tissue (Hodges 1999). The subfamily Symmocinae has two genera in the Galapagos. *Galagete* is the largest genus with 11 described species (Landry 2002). *Galagete* spp. uses a wide range of food types; one species (*G. protozona*) was reared from Galapagos tortoise (*Geochelone elephantopus*) scats, while caterpillars of two other species (*G. levequei* and *G. darwini*) were found among dead leaves along stems of three species of the endemic genus *Scalesia* (Asteraceae). *Taygete sphecophila* caterpillars are predators of *Polistes* wasp larvae in the Galapagos.

Tortricidae (Fig. 3.1f)

Tortricidae are commonly called "leaf-rollers", but the larvae of many species are stem, twig or shoot borers, others are seed-eaters and some are flower-head eaters. Only species whose larvae feed on flower heads or are leaf binders were recorded in Galapagos.

Tortricinae: The only species of this subfamily in the Galapagos, the endemic *Platynota colobota*, is a leaf binder of *C. alba*. The green larvae feed individually between leaves they have spun together.

Olethreutinae: Larvae of this subfamily, represented by at least five species in the Islands, feed on leaves and flowers buds. *Crocidosema plebejana* was found feeding on flower-heads of *Sida rhombifolia* (Malvaceae) and larvae of *Episimus transferranus* were collected from leaves of *Spondias purpurea* (Anacardiaceae). The host plant relationships of the other species are unknown; however, species of *Bactra* are reported to feed on grasses in Hawaii (Zimmerman 1978).

Pterophoridae (Fig. 3.2a)

Larvae of this family are usually leaf-rollers or borers, but some species feed openly. Feeding habit frequently depends on cryptic coloration and/or presence of protective cryptic setal and spinule covering. Plume-moth larvae feed on a variety of plant families; in the Galapagos they are recorded from Asteraceae, Leguminosae and Lamiaceae. Host plant associations in the Galapagos were already known for seven species (Landry & Gielis 1992; Landry 1993; Roque-Albelo 2003). During the present study new host records were collected for these species as well as for two other plume-moth species: *Stenoptilodes brevipennis* and *Platyptilia vilema*. Host plant relationships involve several species of the endemic genera *Scalesia* and *Darwiniothamnus* (Asteraceae) (see Table 3.1).

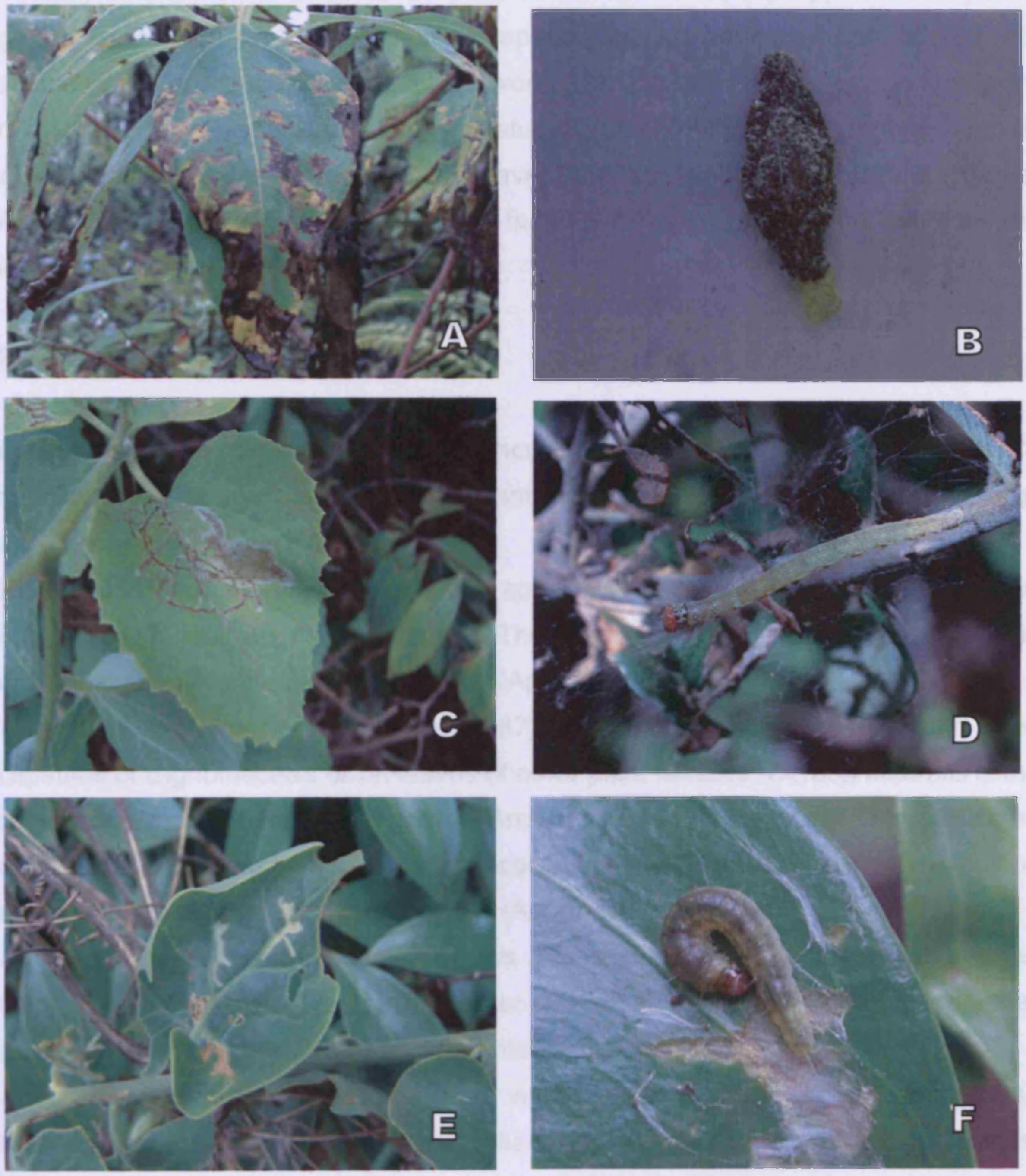


Figure 3.1 Lepidoptera larvae and plant damage caused by Lepidoptera collected, and successfully reared to adults, from the Galapagos Islands.
A: *Astrotischeria scalesiaella* (Tischeriidae). B: *Phereoeca allutella* (Tineidae).
C: *Bucculatrix cordiella* (Bucculatricidae). D: *Atteva hysginiella* (Yponomeutidae).
E: *Heliodines galapagoensis* (Heliodinidae). F: *Platynota colobota* (Tortricidae-Tortricinae).

Choreutidae

Virtually all known choreutid larvae are external leaf feeders (Heppner 1987c). The genus *Tebenna*, to which the single Galapagos species belongs, is associated with species of Asteraceae (Heppner & Duckworth 1981). In the Galapagos two host plant relationship were recorded during our study (Table 3.1). On the endemic genus, *Darwiniothamnus,* the larvae curl the leaves and "skeletonize" the surface (Roque-Albelo 2003). Pupation is on the leaf in a fluted webbing. Adults can be very common in the area surrounding the host-plant.

Pyralidae (Fig. 3.2b to f)

Pyralid larvae are generally terrestrial although a few are aquatic. The caterpillars are mainly phytophagous, consuming live plants, or dried plant material, but coprophagy and carnivory also occur (Scoble 1992).

Pyralinae: This subfamily has only one species in the Islands, *Pyralis manihotalis,* and its larvae have detritivorous habits. The larvae feed in stored food products and may cause important economic damage (Appendix 2).

Chrysauginae: According to Neunzig (1987), larvae of this subfamily feed within seed capsules of Bignoniaceae or on leaves of other plant families. *Ocrasa nostralis* is the only species of this subfamily in the Archipelago and caterpillars were collected defoliating *Mangifera indica* (Anacardiaceae) leaves. Records from other regions suggest that this species is polyphagous (Appendix 2).

Epipaschiinae: Only one species occurs in the Archipelago, *Phidotricha erigens*; unfortunately, host plant records are not available. According to Robinson *et al.* (2001) and Janzen & Hallwachs (2001) this species is also polyphagous.

Phycitinae: Phycitinae larvae feed on or within stored products (seeds, dried fruits); the majority, however, are webbers, rollers of leaves or borers of shoots, trunks, stems, petioles, flowers and fruits (Neunzig 1986). Host plant relationships in the Galapagos were determined for seven species (Table 3.1). The genera *Ancylostomia, Etiella, Fundella* and *Oryctometopia* are associated with Leguminosae. The endemic genus *Schafferiessa* is monophagous on Asteraceae and *Macrorrhinia* on Amaranthaceae. There is a single record of *Hypsipila grandella* on a Meliaceae host in the Islands (Gara & Onore 1989). *Cadra cautella* was collected feeding on dried and stored vegetable products. The latter species is cosmopolitan and is transported throughout the world by commerce (Clarke 1986). *Fulrada carpasella* larvae were collected feeding on fruits and leaves of *Maytenus octogona* (Celastraceae). The host plant of *Coptarthria dasypyga* is unknown in the Archipelago but *Annona cherimola* (Annonaceae), a plant that also occurs in the Galapagos, was recorded as a host plant in East Africa (Robinson *et al.* 2001). The host plants of the endemic *Nicetiodes apianellus* and *Tota goldinella* are unknown.

Galleriinae: The only known Galleriinae in the islands is the "rice meal moth" *Corcyra cephalonica.* According to CAB International (2003) this species attacks many stored foods, for example, cereals, cereal products, oilseeds, pulses, dried fruits, nuts and spices. It is, however, especially common as a pest of rice and rice products. It is also a major pest in flour mills in the tropics, and common on sorghum and millet in West Africa. It may also be found infesting copra.

Crambinae: This is a diverse group of moths represented by nine species in the Archipelago. Larvae of Crambinae bore or feed externally in stems, roots and leaves of grasses (Poaceae). Several species form silk tubes in the soil among grass roots and stems. Host plant relationships are unknown for all Galapagos species. Records from other regions suggest that the genera *Euchromius* and *Crambus* are associated with Poaceae including corn (Capps 1966, Robinson *et al.* 2001). *Argyria* is associated with the Leguminosae genera *Glycine* and *Phaseolus.* No data on host plants were found in the literature for the other genera recorded from the Galapagos.

Musotiminae: Only one species of this subfamily occurs in the Archipelago. The larvae of this previously undescribed species of *Undulambia* was found boring the stems of a native fern, *Pteridium arachnoideum* (Dennstaedtiaceae).

Nymphulinae: The larvae of Nymphulinae are associated with aquatic or semi-aquatic vascular plants in lentic environments (Neunzig 1987). The host plant relationship of the Galapagos species *Parapoynx fluctuosalis* is unknown, but the species has been found feeding on *Oryza sativa* (rice) (Poaceae) in several countries (see Appendix 2).

Glaphyriinae: One plant species has been recorded as a host of the only Glaphyriinae occurring in the Galapagos. Larvae of *Hellula phidilealis* were observed boring fruits of *Cleome viscosa* (Capparidaceae). In other countries this species also feeds on the Brassicaceae (see Appendix 2).

Pyraustinae: With 47 species this subfamily is the largest of the Pyralidae in the Galapagos. Larvae are generally leaf-folders, or stem- or fruit-borers. This group contains many serious pests of trees, crops and ornamental plants (Munroe 1976a).

During the present study host plant relationships were determined for 17 species (Table 3.1). The species range from monophagous to polyphagous. The monophagous species group is represented by several endemic and native taxa; for example, *Beebea guglielmi* larvae are specialists on *Opuntia* cacti, solitarily boring the leaves of the hosts (Williams 1930). Another endemic species, *Achyra eneanalis*, was found webbing leaves of *Amaranthus anderssonii* (Amaranthaceae) and eating under cover of the webs. Records of other species are sparse: *Penestola bufalis* larvae bore the fallen fruits of *A. germinans*. Species of the genus *Lineodes* show specialisation toward various Solanaceae (Appendix 2). Host plant records are only known for two species. *Palpita flegia* is monophagous on Apocynaceae. Larvae were collected in the Islands in folded leaves of the introduced *Cascabela thevetia*. *Marasmia trapezalis* was only recorded in Poaceae. Two Galapagos records are noted for *Pilocrocis ramentalis* on two species of Acanthaceae (Table 3.1). *Microthyris anormalis* is specialized on eating leaves of Convolvulaceae (Robinson *et al.* 2002), but was only collected defoliating *Stictocardia tilifolia*. No host records for *Syngamia florella* are reported for the Islands, but from literature reports (Robinson *et al.* 2001; Ferguson *et al.* 1991) it appears that this species is monophagous on the Rubiaceae. The genus *Diaphania*, with four species in the Galapagos, is closely associated with Cucurbitaceae and caterpillars were found in the Islands on this family. Three species of *Pyrausta* occur in the Archipelago, including one new species, but host plant data are only available for *P. panopealis*, which was reared on two Lamiaceae species. According to Munroe (1976b), *Pyrausta* species are associated with Lamiaceae. *Hymenia, Asciodes, Agathodes, Rhectocraspeda, Herpetogramma, Omiodes, Terastia, Spoladea, Loxomorpha* and *Maruca* species feed on a wide range of plants. The small tomato fruit borer, *Neoleucinodes elegantalis*, is a serious pest on tomato crops in many countries of Central and South America, and the Caribbean Islands. In the Galapagos, larvae have been collected from fruits of *Solanum betaceum* (Solanaceae). No information is available for *Sisyracera inabsconsalis, Ercta vittata, Samea* spp., *Udea* spp., *Neoleucinodes* sp., *Neohelvibotys* sp. and *Synclera jarbusalis*.

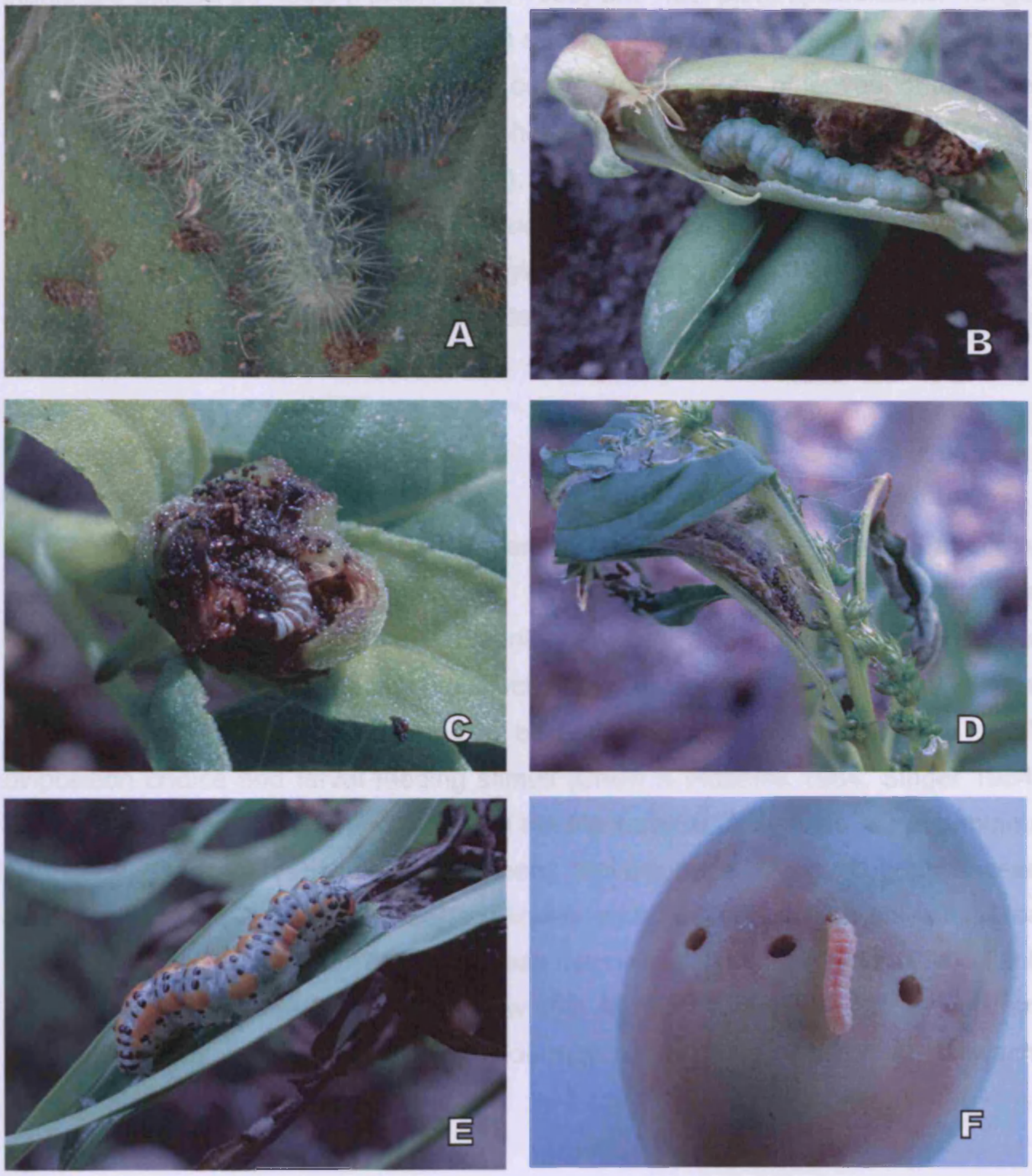


Figure 3.2 Larvae of Lepidoptera collected and successfully reared to adults from the Galapagos Islands.
A: *Hellinsia nephogenes* (Pterophoridae). B: *Etiella zinckinella* (Pyralidae-Phycitinae).
C: *Schafferiessa galapagoensis* (Pyralidae-Phycitinae). D: *Achyra eneanalis* (Pyralidae-Pyraustinae).
E: *Palpita flegia* (Pyralidae-Pyraustinae). F: *Neoleucinodes elegantalis* (Pyralidae-Pyraustinae).

Hesperiidae (Fig. 3.3a, b)

The family Hesperiidae has a worldwide distribution. About 70 families of flowering plants are utilized as hosts (Ackery *et al.* 1999) and host plant specialization ranges from monophagous to polyphagous. Both species recorded from the Archipelago are leaf-feeders. The larvae of most species cut and fold portions of leaves, or tie leaves together to form a shelter in which they hide. Host plant data are available for both species (Roque-Albelo 2004) (Table 3.1). *Urbanus dorantes galapagensis* feeds on five species of Leguminosae while *Calpodes ethlius* is associated with Cannaceae. Several records from the Neotropical Region indicate that the latter species can feed on a wide range of plants but this needs to be confirmed for the Galapagos (see Appendix 2).

Pieridae

The host plants of this species-rich family are principally legumes (Fabaceae, Caesalpinaceae and Mimosaceae), but Simaroubaceae, Capparidaceae, Brassicaceae, Tropaeolaceae and Loranthaceae are also utilized. Many of these plant families are known to contain distinct groups of chemical toxins which, in some instances, have been demonstrated to be both important determinants of female oviposition choice and larval feeding stimuli (Chew & Robbins 1984, Singer 1984). The host plant families of importance for the Neotropical Coliadinae are leguminous Fabaceae, Caesalpiniaceae, Mimosaceae, Simaroubaceae and Zygophyllaceae. Four *Senna* spp. (Caesalpiniaceae) are known as host plants for the only pierid that occurs in the Archipelago, *Phoebis sennae marcellina* (Roque-Albelo 2004) (Table 3.1). Records from the Neotropics show that at least four more *Senna* spp. are potential host plants on the islands (Robinson *et al.* 2001, Janzen & Hallwachs 2001).

Lycaenidae

The use of reproductive parts or young foliage is common in this family as is an obligate or facultative relationship with ants (Fiedler 1991). The range of flowering plant families used as host is extensive (Ehrlich & Raven 1964, Vane-Wright 1978), but most belong to the subclass Rosidae. Little is known about the immature stages of Neotropical Lycaenidae. Only two species, belonging to subfamily Lycaeniinae, have been reported for the Islands: the endemic *Leptotes parrhasioides* and the accidentally introduced *Hemiargus ramon*. The host plant list for Galapagos Lycaenidae covers four plant families and 12 species (Roque-Albelo 2004). Legumes (Fabaceae and Mimosaceae) are the preferred hosts. *Hemiargus ramon* is highly polyphagous but *L. parrhasioides* has only been found feeding on three plant families. Both species feed on flowers and young leaves.

Nymphalidae (Fig. 3.3c)

Host plant associations of nymphalid butterflies are very diverse (Ackery 1988). Of the six Nymphalidae species occurring on the Islands, host plants associations are confirmed for four species.

Heliconiinae: Agraulis vanillae galapagensis larvae were found feeding on two species of *Passiflora* (Roque-Albelo 2004) but four more species of passion fruits are potential hosts. *Agraulis vanillae* was also reported on Tiliaceae and Caprifoliaceae from the Neotropical region (Robinson *et al.* 2001).

Nymphalinae: Two species of the genus *Vanessa* represent this large subfamily in the Archipelago. Only one record for this subfamily has been collected on the Islands (Roque-Albelo 2004). DeVries (1987), however, reported that the larvae of *Vanessa* in the Neotropics feed predominantly on Asteraceae, Urticaceae, Scrophulariaceae and Malvaceae.

Danainae: The two species of *Danaus* reported from the Islands are monophagous (Roque-Albelo 2004). The host plants are two species of Asclepiadaceae: *Asclepias curassavica* and *Sarcostemma angustissimum*.

Geometridae (Fig. 3.3d to f)

The geometrid moths, with 18 species recorded, is the second largest Macrolepidoptera family occurring in the Archipelago. Little is known about the immature stages of Neotropical Geometridae except that larvae are external feeders and can utilize a wide spectrum of resources such as leaves and flowers. Under appropriate conditions several species may reach pest status through larval defoliating activities (Minet & Scoble 1999). In the Galapagos Islands, 18 host plants (eight of these new records) have been found for nine geometrid species. The species' feeding strategies range from monophagy to oligophagy. The most important hostplant families in the Galapagos appear to be Asteraceae, Mimosaceae, Boraginaceae and Rhamnaceae. More observations are needed to confirm host ranges.

Sterrhinae: No clear pattern can be revealed from the available Galapagos records. *Cyclophora impudens* appears to be associated with trees and shrubs of the genera *Acacia, Croton* and *Cordia*. *Cyclophora* species in Europe tend to be specialized on deciduous trees (Ebert 2001, Robinson et al. 2001). *Pleuroprucha insulsaria* was recorded on an introduced Asteraceae: *Adenostemma platyphyllum*; however, data from North America reveal a wide variety of both herbaceous and woody-stemmed plants. No data of host-plants are available for an unidentified species of the genus *Scopula* recently collected on the Islands, and no Neotropical host record is known for this species-rich genus. *Scopula* species are often polyphagous (Robinson *et al.* 2001), but a degree of specialization is observed towards certain herbaceous plants and shrubs (Ebert 2001).

Larentiinae: This subfamily is represented by four genera in the Archipelago. The genus *Eupithecia* is the largest among all geometrids with more than 1000 described species (Scoble 1999). A wide spectrum of food resources is used with a few Hawaiian species even feeding on small insects (Montgomery 1982). Among the three endemic species described from Galapagos, there are host records for only one (Table 3.1). *Diclisioprocta stellata* is a monophage specializing on Nyctaginaceae. On the Galapagos *D. stellata* feeds on three species, but another three Nyctaginaceae could also be used utilized. Only one host plant record is known in the Islands for *Triphosa affirmata,* the leguminous plant *Senna obtusifolia* (Caesalpinaceae). Records from North America show a wider range of plants being utilized as potential hosts (Robinson *et al.* 2001). Records for Neotropical *Perizoma* species suggest that they specialize on reproductive organs of herbaceous plants of Caryophyllaceae and Lamiaceae (Skou 1996), but no data of host plants are available for the endemic *Perizoma perryi*.

Ennominae: Galapagos ennomine moths mainly consume leaves of trees and shrubs. Host plant data on the Islands are available for three species. *Macaria cruciata* has two endemic subspecies but only one host plant, *Scutia spicata* (Rhamnaceae), has been recorded. The two *Thyrinteina* species occurring on the Islands feed on a wide variety of plant families. Three out of five records available for Galapagos species are new. This corresponds with Rindge's (1983) statement that species of this genus are polyphagous. One other record of the subfamily is

Sphacelodes vulneraria which feeds on *Gouania polygama* (Rhamnaceae) (Janzen & Hallwachs 2001), a plant that is also native to Galapagos. The host plants of *Semiothisa cerussata* and *Zeuctostyla vidrierata* are the endemic bush, *D. tenuifolius,* and the introduced tree, *Phyllanthus acidus* (Euphorbiaceae), respectively.Two plant species are hosts for the endemic *Oxydia lignata*(Table 3.1). Plant distribution extends from the arid lowland to moist upland zones.

Uraniidae

This family has a worldwide distribution with around 700 described species, but very little is known about the life history of the species. In the Galapagos Islands the family is represented by only two species of Epipleminae. No host record is known for the Galapagos representative of the genus *Powondrella.* Minet & Scoble (1999) reported various plant families including Bignoniaceae, Caprifoliaceae, Rosaceae, Verbenaceae and Rubiaceae as hosts of several epiplemid species. The other Epipleminae moth occurring in the Galapagos, *Epiplema becki,* feeds on leaves of *Duranta dombeyana* (Verbenaceae) (Roque-Albelo & Mieles 2005).

Sphingidae (Fig. 3.4a, b)

The Galapagos fauna of Sphingidae consist of 15 species (Roque-Albelo & Landry 2001). Given the quantity of foliage they can consume, the large caterpillars have the potential to inflict considerable damage on their host plants, and several species are considered agricultural pests (CAB International 2003). All Galapagos sphingid caterpillars are herbivores and external plant feeders. Of about 500 genera of angiosperms occurring on the Archipelago about 26 have been reported as host plants of Galapagos Sphingidae. During the present study 14 new host plant records were recorded (Table 3.1). The species range from being monophagous (*Xylophanes norfolki*) to polyphagous (*Manduca sexta leucoptera*).

Sphinginae: Galapagos Sphinginae consists of a small group of four species. *Agrius cingulata*, a near cosmopolitan species, is host specific on Convolvulaceae and Solanaceae. Six species have been recorded as host plants in the Galapagos. In the Neotropics the larvae have also been recorded from *Merremia, Datura* and *Nicotiana*, three genera with species occurring also on the Islands.

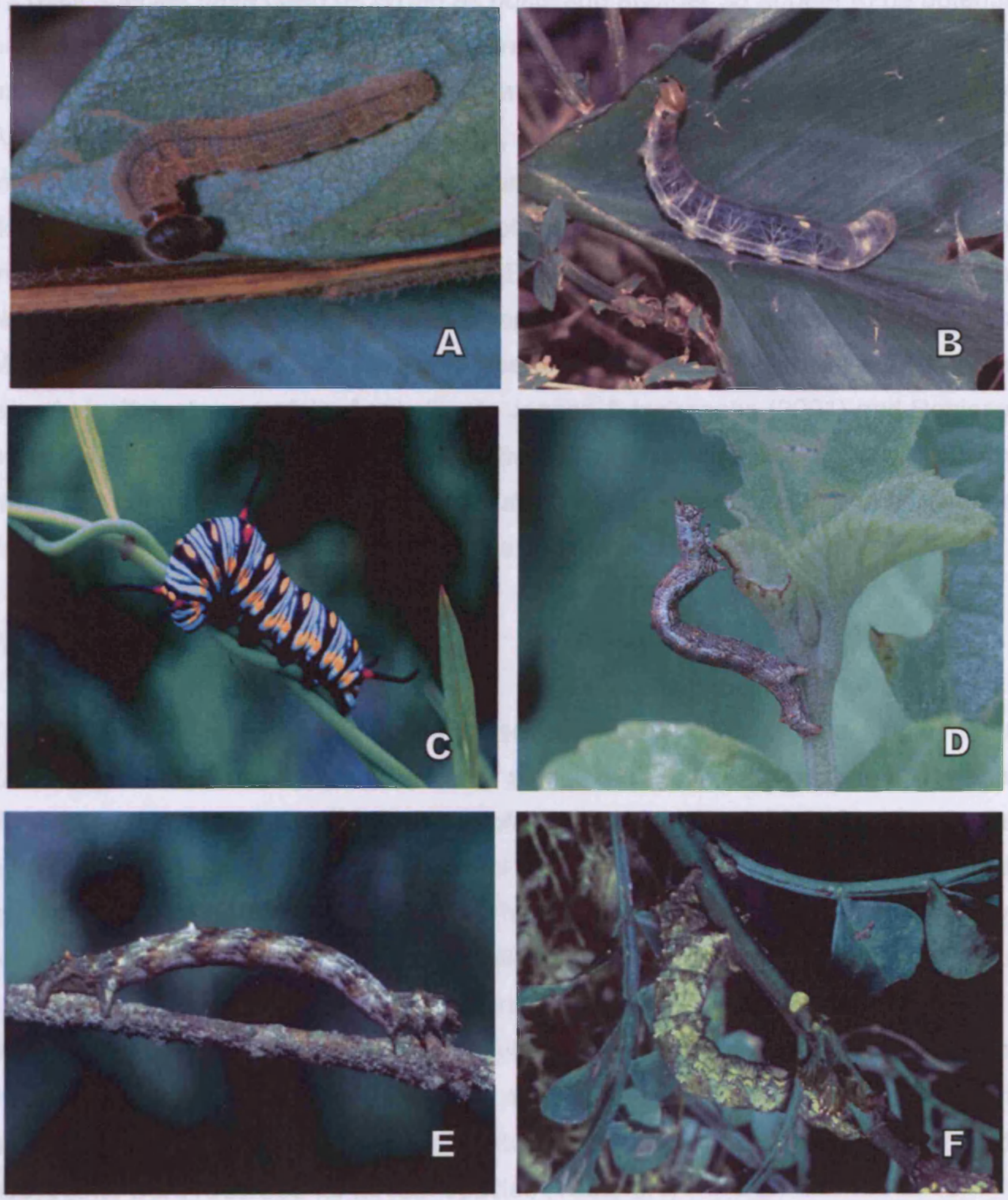


Figure 3.3 Larvae of Lepidoptera collected and successfully reared to adults from the Galapagos Islands.
A: *Urbanus dorantes galapagensis* (Hesperiidae-Hesperiinae).
B: *Calpodes ethlius* (Hesperiidae-Hesperiinae). C: *Danaus gilippus megalippe* (Nymphalidae-Danainae).
D: *Cyclophora impudens* (Geometridae-Sterrhinae). E: *Thyrinteina umbrosa* (Geometridae-Ennominae).
F: *Oxydia lignata* (Geometridae-Oenochrominae).

The two species of the genus *Manduca* have been recorded feeding on a wide variety of plants including some aggressive non-native species such as *L. camara.* 12 plant species have been recorded as hosts and another 30 appear to be potential host plants (Robinson *et al.* 2001, Janzen & Hallwachs 2001). *Cocytius antaeus* is monophagous and associated with plants of the genus *Annona.* No native Annonaceae occur on the Archipelago, but two cultivated species have been introduced and *C. antaeus* larvae were found on both.

Macroglossinae: Host plant associations of this large subfamily are very diverse and include, for example, the Apocynaceae, Euphorbiaceae, Rubiaceae, Vitaceae and Nyctaginaceae. To date, 15 host plant species are known for the 10 Galapagos Macroglossinae (Table 3.1). The only species for which no host is known on the Islands is *Xylophanes pluto.* According to Janzen & Hallwachs (2001) and Robinson *et al.* (2001) the genera *Hamelia, Psychotria, Spermacoce* and *Chiococca* in the Neotropic contain potential hosts of *X. pluto.* Several native species of these genera can potentially serve as hosts to the species on the Islands.

Arctiidae (Fig. 3.4c)

The Galapagos arctiid fauna is composed of four species in the single genus *Utetheisa.* Larvae are typically densely setose with setae arising from verrucae ringing each segment of the body (Scoble 1992). The adult moths can sequester pyrrolizidine alkaloids from their larval host-plant and store the compounds systemically (Roque-Albelo *et al.* 2002). The alkaloids sequestered by Arctiidae have been implicated both in defense (Rothschild *et al.* 1979) and in the synthesis of adult pheromones (Conner *et al.* 1981). Three endemic species appear to form a monophyletic group associated with plants of the genera *Tournefortia* and *Heliotropium* (Boraginaceae) while the remaining species, *Utetheisa ornatrix,* is associated with the legume genus *Crotalaria* (Fabaceae). During the present study host plants were recorded for all four species (Table 3.1)

Noctuidae (Fig. 3.4d, f)

This family is the most diverse group of Lepidoptera in the Archipelago with 87 species, of which approximately one third is endemic. Feeding habits of noctuid larvae are quite diverse. Most known larvae are phytophagous, but a few are carnivorous or scavengers. In addition, many species have been recorded as major agricultural pests (CAB International 2003).

Hypeninae: The subfamily is dominated by the large genus *Hypena*. According to Kitching & Rawlins (1999), species of the subfamily have host preferences restricted to a few plant families. Four new host records were noted during this study (Table 3.1). Species appear to show preferences for Sterculiaceae, Acanthaceae and Malvaceae, but more data are clearly needed to confirm this pattern. No host plant records for species belonging to the genera *Schrankia, Ommatochila* and *Rivula* are available from the Galapagos. The various representatives of *Rivula* in the Palaeartic feed on grasses and sedges (Forster & Wohlfahrt 1971).

Herminiinae: Only one species from this subfamily occurs in the Archipelago and no host plant records are available. According to Scoble (1992) the larvae of the Herminiinae feed on dead leaves of dicotyledonous angiosperms or conifers, but occasionally consume live plant tissue.

Catocalinae: This is the most diverse group of noctuid moths in the Archipelago. Host plant records are available for nine species on the Galapagos, and for six of them these records are new. Neotropical food plant records for species present on the Islands are available for nine species in Robinson *et al.* (2001) and Janzen & Hallwachs (2001) (see Appendix 2). Food plants are diverse, but there is a special relationship of several groups with legumes. The genera *Zale, Ascalapha, Thysania, Anticarsia, Lesmone, Melipotis* and *Letis* are associated with the legume families Fabaceae, Mimosaceae and Caesalpinaceae. *Hypocala, Epidromia, Psoria* and *Epitausa* feed on a small number of plant families such as Juglandaceae, Rosaceae, Nyctaginaceae, Convolvulaceae, Anacardiaceae, Rhamnaceae, Combretaceae and Celastraceae.

Calpinae: A total of six plant species are recorded as hosts for five of the nine species occurring on the Archipelago. The subfamily is dominated by *Anomis* (four species) and *Gonodonta* (four species). Species show specialization toward different plant families. In the Galapagos, the *Gonodonta* show a strong association with Annonaceae whereas *Anomis* species are associated with Malvaceae. The only available host record from the Neotropics for *Plusiodonta clavifera* is the Sterculiaceae *Guazuma ulmifolia* (Janzen & Hallwachs 2001). This plant species was introduced to the Islands (Lawesson *et al.* 1987).

Plusiinae: A wide variety of plant families serve as plusiine hosts in the Neotropics (Appendix 2). The larvae of *Argyrogramma, Autoplusia, Pseudoplusia* and

Ctenoplusia species are pests (defoliators) of crops, vegetables and ornamentals (Robinson *et al.* 2001, Janzen & Hallwachs 2001). In the Galapagos, host plant records have been found for five species.

Hadeninae: This is the second largest noctuid subfamily in the Galapagos. Hadeninae include numerous economically important pests. The worst economic losses are attributable to *Spodoptera* species (Kitching & Rawlins 1999). Documentation on host plants in the Archipelago is available for nine species. The genus *Spodoptera* is known to be highly polyphagous and almost all records for the four species are from different plant families. This is in accordance with patterns known from the Neotropical region (Robinson *et al.* 2001). *Leucania* species appear to be related to Poaceae. There is only one record of *Cropia infusa* on a Boraginaceae host in the Archipelago. *Catabenoides seorsa* was reported by Hayes (1975) feeding on *Lantana peduncularis* (Verbenaceae). The Galapagos species of the genera *Magusa*, *Callopistria* and *Neogalea* feed on a wide range of host-plants, whereas hosts of the related taxa, *Agrotisia, Elaphria, Pseudaletia* and *Trachea,* are unknown.

Condicinae: The plant family Asteraceae, in particular species containing pyrrolizidine alkaloids, appear to play an important role as larval host plants for this subfamily (Kitching & Rawlins 1999). The only record available in the Galapagos for this group is for the endemic *Condica ruthae*. Other Neotropical host records in the subfamily are avaiable for *C. sutor* and *C. concisa* (Robinson *et al.* 2001), which also occur on Galapagos.

Euteliinae: In the Galapagos this subfamily is composed of a single species, *Paectes arcigera*. The host plant is *B. graveolens*.

Acontiinae: Species of the genus *Spragueia* appear to be monophagous. Most records from Galapagos are from Malvaceae and Convolvulaceae. This corresponds to a report of Kitching & Rawlins (1999), who stated that Acontiinae are frequently obligate feeders on Malvales and Asterales. *Ponometia exigua,* which is widely distributed in the Neotropical region, feeds on an endemic Sterculiaceae (Hayes 1975).

Bagisarinae: No Galapagos record is available for the only species occurring on the Archipelago. *Bagisara repanda* feeds on a Mimosaceae in Puerto Rico (Robinson *et al.* 2001). In Costa Rica several species of the genus have been reared on Euphorbiaceae, Sterculiaceae, Malvaceae and Tiliaceae (Janzen & Hallwachs 2001).

Eustrotiinae: No clear host plant pattern can be revealed from the available Galapagos records. Host plant records have been found for only two species. *Eublemma recta* has been recorded feeding on *Ipomoea triloba* (Convolvulaceae), but some species of this genus diverge from the usual herbivorous pattern and feed on coccids (Holloway *et al.* 1987). *Amyna insularum* seems to be associated with the plant genus *Alternanthera* (Amaranthaceae) (Hayes 1975). The life cycles of *Ozarba* and *Cobubatha* are poorly known, only one record has been found reporting a *Cobubatha* species feeding on Acanthaceae (Janzen & Hallwachs 2001).

Heliothinae: Larvae of this subfamily tend to feed on flowers and fruits rather than leaves (Kitching & Rawlins 1999). *Heliothis cystiphora* seems to be a monophagous species associated with Poaceae in the Archipelago, but data from Janzen & Hallwachs (2001) show that this species can feed on unrelated taxa such as Malvaceae. *Heliothis virescens* is a well-known polyphagous species (see Appendix 2) attacking not only indigenous plants, but also crops and ornamentals.

Noctuinae: Little is known about immature stages of Galapagos Noctuinae. The host records discussed here come from the mainland Neotropics and their finding need to be corroborated on the Islands. Some members of the group are known to be highly polyphagous on herbaceous angiosperms (Holloway 1989) and sometimes play a role as pests (CAB International 2003). Host plants for the pest species of the genera *Anicla*, *Agrotis* and *Peridroma* are exceedingly varied and include several crops (see Appendix 2). No host-plant information is available for the endemic species of *Agrotis, Psaphara* and *Anicla.*

Nolidae

Nolidae are a noctuid-related family with larvae usually living in a weak shelter formed from a folded leaf or webbed terminals (Stehr 1987b). Only one species occurs in the Archipelago. Two genera of the plant family Combretaceae are reported in Galapagos as host plants of *Characoma nilotica* (Table 3.1).

Figure 3.4 Larvae of Lepidoptera collected and successfully reared to adults from the Galapagos Islands.
A: *Manduca rustica calapagensis* (Sphingidae-Sphinginae).
B: *Eumorpha labruscae yupanqui* (Sphingidae-Macroglossinae).
C: *Utetheisa devriesi* (Arctiidae). D: *Gonodonta fulvangula* (Noctuidae-Calpinae).
E: *Melipotis indomita* (Noctuidae-Catocalinae). F: *Spodoptera rosae* (Noctuidae-Hadeninae)

3.3.2 Diversity of Lepidoptera-hosts relationships

In total, 310 host plant records have been found and/or determined for the Galapagos Lepidoptera (Tables 3.1 and 3.2). Of the 191 records collected during the present study 156 are new. The total number of species with available host data reviewed in this chapter is 155, including new records for 113 species. This corresponds to 49.5% of the 313 - recorded species in the Galapagos. The level of understanding of host relationships is high compared with other remote islands (e.g. Rapa (Clarke 1971), Marquesas (Clarke 1986), Norfolk (Holloway 1977), Hawaii (Zimmerman 1978) and Bermuda (Ferguson *et al.* 1991). There remains, however, a dearth of information regarding the biology of Galapagos Lepidoptera.

In the largest taxa, Noctuoidea and Pyralidae, host associations are very diverse. This is shown by the larger number of host plant families used by the species. Compared with other taxa knowledge of their feeding habits is limited. Papilionoidea and Sphingoidea larvae, for example, have been sampled more often because they are very visible and easy to find. Surprisingly, knowledge of host relationships for the Geometroidea is also limited, but the high number of endemic taxa with very restricted habitat and host plants could explain this. Plants of the families Leguminosae and Asteraceae play an important role as hosts for Lepidoptera in the Galapagos (Fig. 3.5). Both families are amongst the largest worldwide as well as Galapagos.

Table 3.1 Summary of the known host plant records for Galapagos Lepidoptera. Asterisk after reference indicates published record derived from present study. Leguminosae are divided into three subgroups Fabaceae (Fab.), Caesalpiniaceae (Caes.), Mimosaceae (Mim.).

Taxa	Plant family	Plant species	References
Tischeriidae			
Astrotischeria scalesiaella	Asteraceae	*Scalesia pedunculata*	Landry & Roque-Albelo 2004*
	Asteraceae	*Scalesia baurii*	Landry & Roque-Albelo 2004*
Astrotischeria alcedoensis	Asteraceae	*Scalesia affinis*	Landry & Roque-Albelo 2004*
Bucculatricidae			
Bucculatrix cordiella	Boraginaceae	*Cordia lutea*	Davis *et al.* 2002*
Gracillaridae			
Acrocercops sp.	Sterculiaceae	*Waltheria ovata*	Present study
Cryptolectica sp.	Asteraceae	*Synedrella nodiflora*	Present study
Yponomeutidae			
Atteva hysginiella	Simaroubaceae	*Castela galapageia*	Landry & Landry 1998; Perry & DeVries 2003
Prays galapagosella	Rutaceae	*Zanthoxylum fagara*	Present study
Heliodinidae			
Heliodines galapagoensis	Nyctaginaceae	*Cryptocarpus pyriformis*	Heppner & Landry 1994 b
Coleophoridae			
Coleophora sp.	Amaranthaceae	*Amaranthus* sp.	Present study
Calosima darwini	Asteraceae	*Scalesia gordilloi*	Present study
	Boraginaceae	*Cordia lutea*	Present study
	Cactaceae	*Jasminocereus thouarsii*	Present study
	Leguminosae (Caes.)	*Parkinsonia aculeata*	Present study
	Leguminosae (Mim.)	*Acacia macracantha*	Present study
	Scrophularariaceae	*Capraria peruviana*	Present study
Cosmopterigidae			
Cosmopterix galapagosensis	Cyperaceae	*Eleocharis mutata*	Landry 2001 a

Taxa	Plant family	Plant species	References
Periploca darwini	Sapindaceae	*Dodonaea viscosa*	Present study
Xylorictidae			
Scythridinae sp.1	Asteraceae	*Darwiniothamnus tenuifolius*	Present study
Scythridinae sp. 2	Portulacaceae	*Portulaca oleraceae*	Present study
Scythridinae sp. 3	Amaranthaceae	*Althernanthera halimifolia*	Present study
Gelechiidae			
Ephysteris sp.	Poaceae	*Sporobolus virginicus*	Present study
Evippe omphalopa	Leguminosae (Mim.)	*Prosopis juliflora*	Present study
Anacampsis primigenia	Euphorbiaceae	*Croton scouleri*	Present study
Compsolechia salebrosa	Leguminosae (Fab.)	*Desmodium incanum*	Present study
Tuta absoluta	Solanaceae	*Lycopersicon esculentum*	Present study
Elachistidae			
Stenoma catenifer	Lauraceae	*Persea americana*	Landry & Roque-Albelo 2003*
Tortricidae			
Platynota colobota	Rubiaceae	*Chiococca alba*	Present study
Episimus transferratus	Anacardiaceae	*Spondias purpurea*	Present study
Crocidosema plebejana	Leguminosae (Mim.)	*Acacia* sp.	Perry & DeVries 2003
Pterophoridae			
Megalorhipida leucodactyla	Nyctaginaceae	*Boerhavia caribaea*	Landry 1993
	Nyctaginaceae	*Commicarpus tuberosus*	Landry 1993
Stenoptilodes brevipennis	Scrophulariaceae	*Capraria peruviana*	Present study
Platyptilia vilema	Asteraceae	*Darwiniothamnus tenuifolius*	Roque-Albelo 2003*
Postplatyptilia huigraica	Lamiaceae	*Hyptis spicigera*	Landry 1993
	Lamiaceae	*Hyptis mutabilis*	Present study
Exelastis montischristi	Leguminosae (Fab.)	*Rhynchosia minima*	Landry 1993
Exelastis pumilio	Leguminosae (Fab.)	*Desmodium glabrum*	Landry 1993

Taxa	Plant family	Plant species	References
Adaina scalesiae	Asteraceae	*Scalesia microcephala*	Landry 1993
	Asteraceae	*Scalesia incisa*	Landry 1993
	Asteraceae	*Scalesia pedunculata*	Landry *et al.* 2004*
	Asteraceae	*Scalesia retroflexa*	Landry *et al.* 2004*
	Asteraceae	*Scalesia gordilloi*	Landry *et al.* 2004*
	Asteraceae	*Scalesia villosa*	Landry *et al.* 2004*
	Asteraceae	*Lecocarpus lecocarpioides*	Landry *et al.* 2004*
Hellinsia nephogenes	Asteraceae	*Scalesia affinis*	Landry 1993; Perry & DeVries 2003
	Leguminosae (Fab.)	*Rhynchosia minima*	Perry & DeVries 2003
Choreutidae			
Tebenna galapagoensis	Asteraceae	*Darwiniothamnus tenuifolius*	Roque-Albelo 2003*
	Asteraceae	*Darwiniothamnus lancifolius*	Present study
Pyralidae			
Ocrasa nostralis	Anacardiaceae	*Mangifera indica*	Present study.
Etiella zinckenella	Leguminosae (Fab.)	*Crotalaria incana*	Present study.
Fulrada carpasella	Celastraceae	*Maytenus octogona*	Landry & Neunzig 1997
Fundella argentina	Leguminosae (Fab.)	*Rhynchosia minima*	Present study.
Hypsipyla grandella	Meliaceae	*Cedrela odorata*	Gara & Onore 1989
Macrorrhinia pinta	Amaranthaceae	*Alternanthera halimifolia*	Present study
	Amaranthaceae	*Alternanthera echinocephala*	Present study
Oryctometopia fossulatella	Leguminosae (Caes.)	*Senna picta*	Present study
	Leguminosae (Caes.)	*Parkinsonia aculeata*	Landry & Neunzig 1997
Shafferiessa galapagoensis	Asteraceae	*Scalesia affinis*	Present study
	Asteraceae	*Scalesia helleri*	Present study
	Asteraceae	*Scalesia gordilloi*	Present study
	Asteraceae	*Scalesia pedunculata*	Present study
	Asteraceae	*Scalesia retroflexa*	Present study

Taxa	Plant family	Plant species	References
	Asteraceae	*Scalesia stewartii*	Present study
Shafferiessa pumila	Asteraceae	*Scalesia affinis*	Present study
	Asteraceae	*Scalesia aspera*	Present study
	Asteraceae	*Lecocarpus lecocarpoides*	Present study
	Asteraceae	*Lecocarpus darwinii*	Present study
Undulambia sp.	Dennstaedtiaceae	*Pteridium arachnoideum*	Present study
Hellula phidilealis	Capparaceae	*Cleome viscosa*	Present study
Penestola bufalis	Avicenniaceae	*Avicennia germinans*	Present study
Beebea guglielmi	Cactaceae	*Opuntia echios*	Present study
	Cactaceae	*Opuntia insularis*	Perry & DeVries 2003
	Cactaceae	*Opuntia helleri*	Present study
Asciodes quietalis	Nyctaginaceae	*Cryptocarpus piriformis*	Perry & DeVries 2003
	Nyctaginaceae	*Pisonea floribunda*	Perry & DeVries 2003
	Nyctaginaceae	*Commicarpus tuberosus*	Perry & DeVries 2003
Pilocrocis ramentalis	Acanthaceae	*Justicia galapagana*	Present study
Pleuroptya silicalis	Urticaceae	*Pilea baurii*	Present study
Pyrausta panopealis	Lamiaceae	*Salvia occidentalis*	Present study
	Lamiaceae	*Hyptis mutabilis*	Present study
Rhectocraspeda periusalis	Solanaceae	*Lycopersicon esculentum*	Present study
	Solanaceae	*Solanum americanum*	Present study
Diaphania indica	Cucurbitaceae	*Cucumis dipsaceus*	Present study
	Cucurbitaceae	*Momordica charantia*	Present study
Diaphania nitidalis	Cucurbitaceae	*Cucurbita ficifolia*	Present study
Omiodes indicata	Convolvulaceae	*Merremia aegyptia*	Present study
Desmia sp.	Rubiaceae	*Psychotria rufipes*	Present study
Lineodes sp.	Solanaceae	*Acnistus ellipticus*	Present study
Microthyris anormalis	Convolvulaceae	*Stictocardia tilifolia*	Present study

Taxa	Plant family	Plant species	References
Palpita flegia	Apocynaceae	*Cascabela thevetia*	Present study
Neoleucinodes elegantalis	Solanaceae	*Solanum quitoense*	Present study
Loxomorpha cambogialis	Asteraceae	*Lecocarpus darwinii*	Present study
Pyraustinae sp. 1	Boraginaceae	*Tournefortia pubecens*	Present study
Uraniidae			
Epiplema becki	Verbenaceae	*Duranta dombeyana*	Roque-Albelo & Mieles 2005*
Arctiidae			
Utetheisa ornatrix	Leguminosae (Fab.)	*Crotalaria incana*	Present study
	Leguminosae (Fab.)	*Crotalaria pumila*	Perry & DeVries 2003
	Leguminosae (Fab.)	*Crotalaria retusa*	Present study
Utetheisa galapagenis	Boraginaceae	*Tournefortia pubecens*	Hayes 1975; Perry & DeVries 2003
	Boraginaceae	*Tournefortia psylostachia*	Hayes 1975; Perry & DeVries 2003
	Boraginaceae	*Tournefortia rufo-sericea*	Perry & DeVries 2003
	Boraginaceae	*Heliotropium curassavicum*	Perry & DeVries 2003
Utetheisa perryi	Boraginaceae	*Tournefortia pubecens*	Present study
	Boraginaceae	*Tournefortia rufo-sericea*	Present study
Utetheisa devriesi	Boraginaceae	*Tournefortia pubecens*	Present study
	Boraginaceae	*Tournefortia rufo-sericea*	Present study
Noctuidae			
Hypena microfuliginea	Sterculiaceae	*Waltheria ovata*	Perry & DeVries 2003
Hypena fuliginea	Sterculiaceae	*Waltheria ovata*	Present study
Hypena vetustalis	Acanthaceae	*Blechum pyramidatum*	Present study
Hypena minualis constans	Malvaceae	*Sida rombifolia*	Present study
Hypocala andremona	Juglandaceae	*Juglans neotropica*	Present study
Zale obsita	Musaceae	*Musa paradisea*	Present study
Epidromia zephyritis	Rhamnaceae	*Scutia spicata*	Hayes 1975; Perry & DeVries 2003
	Combretaceae	*Laguncularia racemosa*	Hayes 1975; Perry & DeVries 2003

Taxa	Plant family	Plant species	References
Psara hadesia	Celastraceae	*Maytenus octagona*	Hayes 1975; Perry & DeVries 2003
Epitausa prona	Amaranthaceae	*Amaranthus lividus*	Present study
	Amaranthaceae	*Alternanthera echinocephala*	Present study
	Convolvulaceae	*Ipomoea pes-caprae*	Present study
	Nyctaginaceae	*Commicarpus tuberosus*	Present study
	Portulacaceae	*Portulaca oleraceae*	Present study
Anticarsia gemmatalis	Leguminosae (Fab.)	*Piscidia carthagenensis*	Hayes 1975; Perry & DeVries 2003
	Leguminosae (Fab.)	*Rhynchosia minima*	Hayes 1975; Perry & DeVries 2003
	Nyctaginaceae	*Cryptocarpus pyriformis*	Hayes 1975; Perry & DeVries 2003
Lesmone formularis	Leguminosae (Caes.)	*Senna pistaciifolia*	Present study
Melipotis acontioides producta	Leguminosae (Caes.)	*Parkinsonia acualeata*	Hayes 1975; Perry & DeVries 2003
Melipotis indomita	Leguminosae (Mim.)	*Prosopis juliflora*	Hayes 1975; Perry & DeVries 2003
Melipotis harrisoni	Leguminosae (Mim.)	*Acacia macracantha*	Hayes 1975; Perry & DeVries 2003
	Leguminosae (Mim.)	*Acacia rorundiana*	Hayes 1975; Perry & DeVries 2003
Gonodonta fulvangula	Annonaceae	*Annona cherimola*	Present study
Gonodonta pyrgo	Annonaceae	*Annona cherimola*	Present study
Gonodonta biarmata evadens	Annonaceae	*Annona cherimola*	Present study
	Annonaceae	*Annona muricata*	Present study
Anomis erosa	Malvaceae	*Abutilon depauperatum*	Present study
Anomis illita	Malvaceae	*Hibiscus tiliaceus*	Hayes 1975; Perry & DeVries 2003
Mouralia tinctoides	Commelinaceae	*Commelina diffusa*	Present study
Argyrogramma verruca	Boraginaceae	*Tournefortia rufo-sericea*	Present study
Autoplusia egena galapagensis	Labiatae	*Mentha piperita*	Present study
Notioplusia illustrata	Verbenaceae	*Lantana camara*	Present study
Pseudoplusia includens	Asteraceae	*Lactuca sativa*	Present study
	Boraginaceae	*Cordia leucophlyctis*	Hayes 1975; Perry & DeVries 2003
	Boraginaceae	*Tournefortia psilostachya*	Hayes 1975; Perry & DeVries 2003

Taxa	Plant family	Plant species	References
	Boraginaceae	*Heliotropium angiospermun*	Hayes 1975; Perry & DeVries 2003
	Cruciferae	*Brassica olareacea*	Present study
	Euphorbiaceae	*Manihot esculenta*	Present study
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Present study
	Leguminosae (Fab.)	*Pisum sativum*	Present study
	Loasaceae	*Mentzelia aspera*	Hayes 1975; Perry & DeVries 2003
	Solanaceae	*Solanum tuberosum*	Present study
	Verbenaceae	*Lantana peduncularis*	Hayes 1975; Perry & DeVries 2003
Spodoptera cosmioides	Euphorbiaceae	*Manihot esculenta*	Present study
	Malvaceae	*Gossypium darwinii*	Present study
	Nyctagenaceae	*Cryptocarpus pyriformis*	Present study
Spodoptera frugiperda	Euphorbiaceae	*Manihot esculenta*	Present study
	Liliaceae	*Allium cepa*	Present study
	Poaceae	*Zea mays*	Present study
	Umbelliferae	*Daucus carota*	Present study
Spodoptera eridania	Amaranthaceae	*Amaranthus lividus*	Hayes 1975; Perry & DeVries 2003
	Asteraceae	*Lactuca sativa*	Present study
	Convolvulaceae	*Ipomoea pes-caprae*	Hayes 1975; Perry & DeVries 2003
	Convolvulaceae	*Ipomoea batatas*	Present study
	Cruciferae	*Brassica olaracea*	Present study
	Cruciferae	*Brassica napus*	Present study
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Present study
	Menispermaceae	*Cissampelos pereira*	Hayes 1975; Perry & DeVries 2003
	Nyctagenaceae	*Cryptocarpus pyriformis*	Hayes 1975; Perry & DeVries 2003
	Portulacaceae	*Portulaca oleracea*	Hayes 1975; Perry & DeVries 2003
	Solanaceae	*Capsicum annum*	Present study
	Solanaceae	*Lycopersicum esculentum*	Present study

Taxa	Plant family	Plant species	References
Spodoptera dolichos	Nyctaginaceae	*Cryptocarpus pyriformis*	Hayes1975; Perry & DeVries 2003
	Malvaceae	*Gossypium darwinii*	Present study
Leucania humidicola	Poaceae	*Sporobolus virginicus*	Hayes 1975; Perry & DeVries 2003
Magusa erema	Rhamnaceae	*Scutia spicata*	Hayes 1975; Perry & DeVries 2003
Magusa orbifera	Rhamnaceae	*Scutia spicata*	Present study
Cropia infusa	Boraginaceae	*Cordia lutea*	Perry & DeVries 2003
Catabenoides seorsa	Verbenaceae	*Lantana peduncularis*	Hayes 1975; Perry & DeVries 2003
Condica ruthae	Asteraceae	*Lecocarpus darwinii*	Present study
	Asteraceae	*Darwiniothamnus tenuifolius*	Present study
Paectes arcigera	Burseraceae	*Bursera graveolens*	Hayes 1975; Perry & DeVries 2003
Spragueia margana	Malvaceae	*Sida* sp	Hayes 1975; Perry & DeVries 2003
	Malvaceae	*Sida rhombifolia*	Perry & DeVries 2003
	Malvaceae	*Abutilon depauperatum*	Hayes 1975; Perry & DeVries 2003
Spragueia creton	Convolvulaceae	*Ipomoea habeliana*	Perry & DeVries 2003
Ponometia exigua	Sterculiaceae	*Waltheria ovata*	Hayes1975; Perry & DeVries 2003
Eublemma recta	Convolvulaceae	*Ipomoea triloba*	Hayes 1975; Perry & DeVries 2003
Amyna insularum	Amaranthaceae	*Alternanthera echinocephala*	Hayes 1975; Perry & DeVries 2003
	Amaranthaceae	*Alternanthera filifolia*	Hayes 1975; Perry & DeVries 2003
Heliocheilus cystiphora	Poaceae	*Sporobolus virginicus*	Hayes 1975; Perry & DeVries 2003
	Poaceae	*Cenchrus platyacanthus*	Perry & DeVries 2003
Heliothis virescens	Asteraceae	*Scalesia affinis*	Hayes 1975; Perry & DeVries 2003
	Passifloraceae	*Passiflora foetida*	Hayes 1975; Perry & DeVries 2003
Nolidae			
Characoma nilotica	Combretaceae	*Laguncularia racemosa*	Hayes 1975; Perry & DeVries 2003
	Combretaceae	*Conocarpus erectus*	Perry & DeVries 2003
Geometridae			
Cyclophora impudens	Amaranthaceae	*Amaranthus andersonii*	Present study

Taxa	Plant family	Plant species	References
	Boraginaceae	*Cordia lutea*	Rindge 1973; Perry & DeVries 2003
	Euphorbiaceae	*Croton scouleri*	Rindge 1973; Perry & DeVries 2003
	Leguminosae (Mim.)	*Acacia macracantha*	Rindge 1973; Perry & DeVries 2003
	Leguminosae (Mim.)	*Acacia insulae-iacobi*	Present study
Pleuroprucha insulsaria	Asteraceae	*Adenostemma platyphyllum*	Present study
Disclisioprocta stellata	Nyctaginaceae	*Cryptocarpus pyriformis*	Rindge 1973
	Nyctaginaceae	*Pisonia floribunda*	Rindge 1973
	Nyctaginaceae	*Commicarpus tuberosus*	Rindge 1973
Triphosa affirmata	Leguminosae (Caes.)	*Senna obtusifolia*	Present study
	Leguminosae (Caes.)	*Senna occidentalis*	Perry & DeVries 2003
Eupithecia perryvriesi	Asteraceae	*Darwiniothamnus tenuifolius*	Present study
	Asteraceae	*Scalesia microcephala*	Present study
	Asteraceae	*Scalesia pedunculata*	Present study
	Verbenaceae	*Duranta repens*	Present study
Macaria cruciata cruciata	Rhamnaceae	*Scutia spicata*	Rindge 1973; Perry & DeVries 2003
Semiothisa cerussata	Asteraceae	*Darwiniothamnus tenuifolius*	Roque-Albelo 2003*
Thyrinteina infans	Boraginaceae	*Cordia lutea*	Rindge 1973; Perry & DeVries 2003
	Celastraceae	*Maytenus octagona*	Rindge 1973; Perry & DeVries 2003
	Sapindaceae	*Dodonea viscosa*	Present study
Thyrinteina umbrosa	Asteraceae	*Scalesia pedunculata*	Present study
	Sterculiaceae	*Waltheria ovata*	Present study
Zeuctostyla vidrierata	Euphorbiaceae	*Phyllanthus acidus*	Present study
Oxydia lignata	Verbenaceae	*Clerodendron molle*	Rindge 1973; Perry & DeVries 2003
	Rutaceae	*Zanthoxylum fagara*	Present study
Sphingidae			
Agrius cingulata	Convolvulaceae	*Ipomoea pes-caprae*	Williams 1911; Roque-Albelo & Landry 2001
	Convolvulaceae	*Ipomoea habeliana*	Roque-Albelo & Landry 2001*

Taxa	Plant family	Plant species	References
	Convolvulaceae	*Ipomoea nil*	Roque-Albelo & Landry 2001*
	Convolvulaceae	*Ipomoea triloba*	Williams 1911; Roque-Albelo & Landry 2001
	Convolvulaceae	*Stictocardia tilifolia*	Williams 1911; Roque-Albelo & Landry 2001
Manduca sexta leucoptera	Solanaceae	*Physalis pubescens*	Hayes 1975
	Solanaceae	*Nicotiana tabacum*	Hayes 1975; Perry & DeVries 2003
	Solanaceae	*Acnistus ellipticus*	Roque-Albelo & Landry 2001*
Manduca rustica calapagensis	Asteraceae	*Darwiniothamnus lancifolius*	Roque-Albelo & Landry 2001*
	Boraginaceae	*Cordia lutea*	Williams 1911; Roque-Albelo & Landry 2001
	Boraginaceae	*Cordia leucophlyctis*	Williams 1911; Hayes 1975; Roque-Albelo & Landry 2001; Perry & DeVries 2003
	Boraginaceae	*Tournefortia rufo-sericea*	Hayes 1975; Roque-Albelo & Landry 2001; Perry & DeVries 2003
	Euphorbiaceae	*Croton scouleri*	Williams 1911; Roque-Albelo & Landry 2001
	Malvaceae	*Bastardia viscosa*	Williams 1911; Roque-Albelo & Landry 2001
	Nyctagenaceae	*Commicarpus tuberosus*	Williams 1911; Roque-Albelo & Landry 2001
	Verbenaceae	*Clerodendrum molle*	Williams 1911; Hayes 1975; Roque-Albelo & Landry 2001, Perry & DeVries 2003
	Verbenaceae	*Lantana camara*	Roque-Albelo & Landry 2001*
Cocytius antaeus	Annonaceae	*Annona cherimola*	Roque-Albelo 1999*; Roque-Albelo & Landry 2001
	Annonaceae	*Annona muricata*	Present study
Erinnyis alope dispersa	Caricaceae	*Carica papaya*	Roque-Albelo & Landry 2001*
	Euphorbiaceae	*Manihot esculenta*	Roque-Albelo & Landry 2001*
Erinnyis ello encantada	Euphorbiaceae	*Hippomane mancinella*	Williams 1911; Curio 1965 a; Hayes 1975; Perry & DeVries 2003
	Euphorbiaceae	*Psidium guajava*	Williams 1911; Roque-Albelo & Landry 2001
	Euphorbiaceae	*Chamaesyce viminea*	Roque-Albelo & Landry 2001*
Erinnyis obscura conformis	Asclepiadaceae	*Sarcostemma angustissimum*	Williams 1911; Hayes 1975; Roque-Albelo & Landry 2001, Perry & DeVries 2003
Enyo lugubris delanoi	Vitaceae	*Cissus verticillata*	Williams 1911; Perry & DeVries 2003

Taxa	Plant family	Plant species	References
Perigonia lusca lusca	Rubiaceae	*Cinchona pubecens*	Roque-Albelo & Landry 2001*
Eumorpha labruscae yupanqui	Vitaceae	*Cissus verticillata*	Roque-Albelo & Landry 2001*
Xylophanes tersa tersa	Rubiaceae	*Dioidia radula*	Roque-Albelo & Landry 2001*
	Verbenaceae	*Clerodendrum molle*	Williams 1911; Roque-Albelo & Landry 2001
Xylophanes norfolki	Rubiaceae	*Psychotria rufipes*	Roque-Albelo & Landry 2001*
Hyles lineata	Portulacaceae	*Portulaca oleracea*	Hayes 1975; Roque-Albelo & Landry 2001; Perry & DeVries 2003
	Nyctaginaceae	*Commicarpus tuberosus*	Hayes 1975; Roque-Albelo & Landry 2001; Perry & DeVries 2003
	Nyctaginaceae	*Boerhavia caribaea*	Roque-Albelo & Landry 2001*; Perry & DeVries 2003
Hesperiidae			
Urbanus dorantes galapagensis	Leguminosae (Fab)	*Phaseolus atropurpureus*	Roque-Albelo 2004*
	Leguminosae (Fab)	*Phaseolus mollis*	Roque-Albelo 2004*
	Leguminosae (Fab)	*Desmodium incanum*	Roque-Albelo 2004*
	Leguminosae (Fab)	*Galactia striata*	Roque-Albelo 2004*
Calpodes ethlius	Cannaceae	*Canna lambertii*	Roque-Albelo 2004*
	Cannaceae	*Canna indica*	Roque-Albelo 2004*
Pieridae			
Phoebis sennae marcellina	Leguminosae (Caes)	*Senna pistaciifolia*	Williams 1911
	Leguminosae (Caes)	*Senna obtusifolia*	Roque-Albelo 2004*
	Leguminosae (Caes)	*Senna bicapsularis*	Roque-Albelo 2004*
	Leguminosae (Caes)	*Senna occidentalis*	Roque-Albelo 2004*
Lycaenidae			
Leptotes parrhasioides	Leguminosae (Fab.)	*Crotalaria incana*	Roque-Albelo 2004*
	Leguminosae (Fab.)	*Rynchosia minima*	Roque-Albelo 2004*
	Plumbaginaceae	*Plumbago scandens*	Roque-Albelo 2004*
	Sapindaceae	*Cardiospermum halicacabum*	Williams 1911; Roque-Albelo 2004
	Sapindaceae	*Cardiospermum galapageium*	Williams 1911; Roque-Albelo 2004

Taxa	Plant family	Plant species	References
Hemiargus ramon	Cucurbitaceae	*Cucumis dipsaceus*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Mim.)	*Acacia macracantha*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Caes.)	*Senna obtusifolia*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Mim.)	*Neptunia plena*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Fab.)	*Phaseolus atropurpureus*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Mim.)	*Prosopis juliflora*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
	Leguminosae (Fab)	*Tephrosia decumbens*	Roque-Albelo *et al.* 1997*; Roque-Albelo 2004*
Nymphalidae			
Danaus gilippus thersippus	Asclepiadaceae	*Sarcostemma angustissimum*	Roque-Albelo 2004*
	Asclepiadaceae	*Asclepias curassavica*	Roque-Albelo 2004*
Danaus plexippus megalippe	Asclepiadaceae	*Sarcostemma angustissimum*	Roque-Albelo 1998a; Roque-Albelo 2004*
	Asclepiadaceae	*Asclepias curassavica*	Roque-Albelo 1998b; Roque-Albelo 2004*
Agraulis vanillae galapagensis	Passifloraceae	*Passiflora* spp	Williams 1911
	Passifloraceae	*Passiflora suberosa*	Roque-Albelo 2004*
	Passifloraceae	*Passiflora tridactylites*	Roque-Albelo 2004*
Vanessa virginiensis	Asteraceae	*Gamochaeta purpurea*	Roque-Albelo 2004*

Table 3.2. Summary of the known host records for non-phytophagous Lepidoptera species from the Galapagos. Asterisk after references indicates published record derived from present study.

Taxa	Feeding categories	Food item	References
Tineidae			
Trichophaga mormopis	Detritophagous	Skin of dead Galapagos flightless cormorant Regurgitated pellets of owl and hawk	Heppner 1975; Perry & DeVries 2003
Setomorpha rutella	Detritophagous	Stored vegetable	Present study
Praeacedes atomosella	Detritophagous	Dead plant material, micro-lichen	Present study
Phereoeca allutella	Detritophagous	Flannel, fur etc.	Present study
Erechtias minuscula	Detritophagous/ Carnivorous	Dead plant material, dead donkey skin	Present study
Tineidae sp.1	Detritophagous	Rotten wood of *Scalesia pedunculata*	Present study
Cosmopterigidae			
Pyroderces rileyi	Detritophagous/ Carnivorous	Dead plant material; predator of *Icerya purchasi* (Homoptera)	Landry 2001a*
Gelechiidae			
Sitotroga cerealella	Detritophagous	Stored grains	Present study
Autostichidae			
Taygete sphecophyla	Detritophagous/ Carnivorous	*Polistes versicolor* (Hymenoptera) larvae and nest material	Present study
Galagete gnathodoxa	Detritophagous	Tortoise scats	Landry 2002
Galagete darwini	Detritophagous	Dead plant material	Landry 2002*
Pyralidae			
Cadra cautella	Detritophagous	Stored foods	Present study
Corcyra cephalonica	Detritivorous	Stored foods	Present study

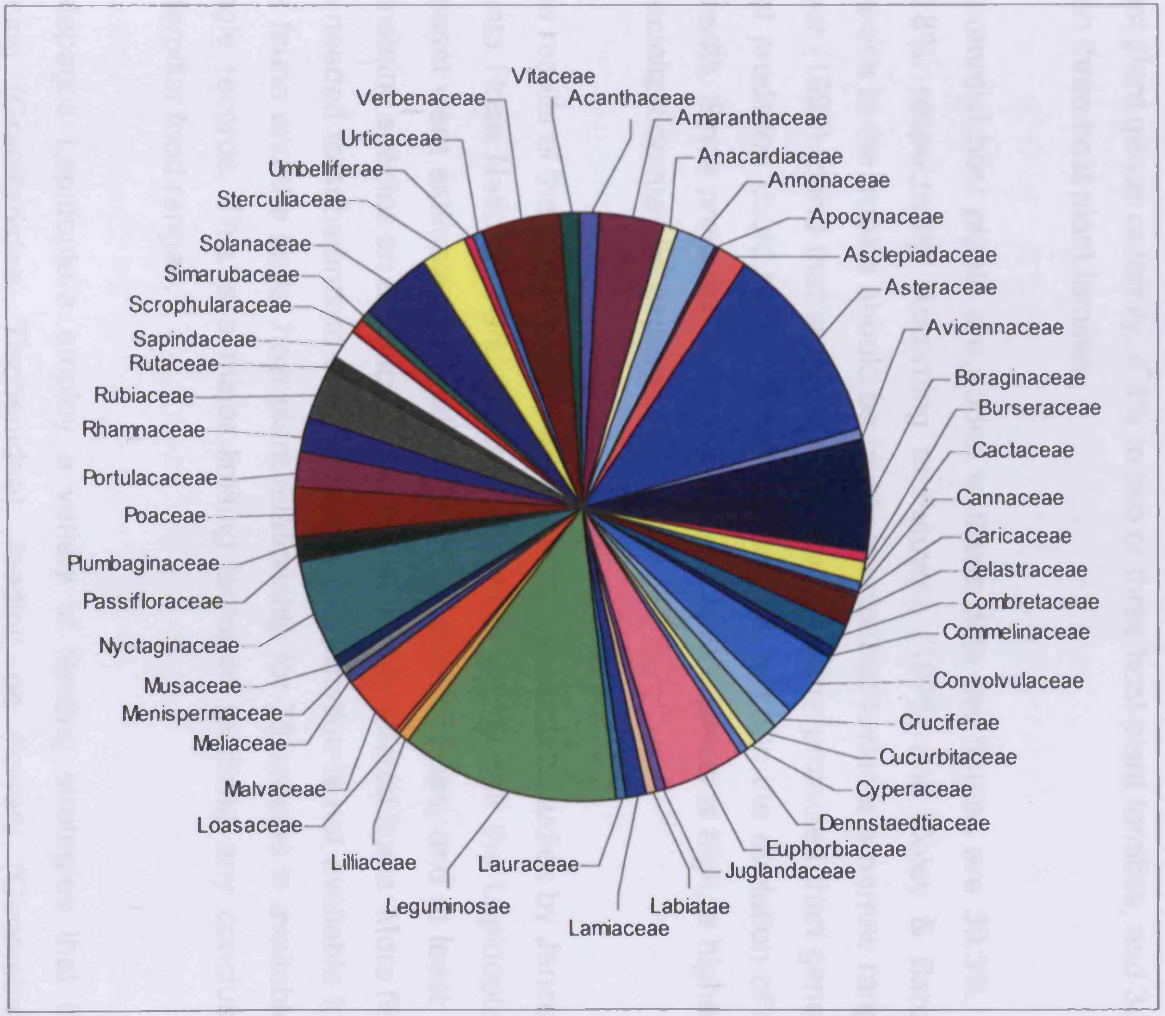


Figure 3.5 Host plant families used by Lepidoptera species in the Galapagos Islands.

3.3.3 Feeding habits

The Lepidoptera 'guild' in the Galapagos can be divided into three functional groups with 272 herbivores, 13 detritivores and three carnivores (see Tables 3.1, 3.2 and Appendix 2). Of the herbivores, host plant usage suggests a relatively high degree of specialization. The data presented in this chapter indicate that monophagy at the plant family level is high. A high proportion (43.7%) of species are restricted to one host plant genus or family, 4.4% to two or three host plant families, and 3.3% to more than three host plant families.

If potential host plants are added to these data the figures are 39.3%, 11.3% and 15.8%, respectively. According to Futuyma (1976) and Coley & Barone (1996), species in the tropics should be highly specialized towards a narrow range of hosts. Dyer (1995) found that specialist larvae were better protected than generalists, and that predation could be a substantial selective force in the evolution of narrow diet breadth. Since predation pressure on Lepidoptera larvae is high, a higher degree of specialization may be expected.

The results of the present study are similar to those from studies by Janzen (1988) at Santa Rosa National Park, Costa Rica where nearly half the Lepidoptera species present were estimated to feed on only one plant species, and at least 80% of the remaining species on chemically and taxonomically related hosts. More field data will be needed to substantiate this result since information is not available for 48.5% of the fauna and the larval host plant relationship for 78 species is available only from single records. This is a major limiting factor in reaching any conclusions about caterpillar food ranges.

Galapagos Lepidoptera employ a variety of feeding strategies that include leaf mining (Gracillariidae, Tischeriidae), feeding on flowers (Geometridae), fruits (Elachistidae) and dead bark (Pyralidae), scavenging on *Polistes* nests (Autostichidae), and feeding on live foliage. While fresh foliage is the most frequent host component consumed by herbivorous larvae, some caterpillars, such as *Ocrasa nostralis*, prefer older foliage.

3.3.4 Conservation

The future of the diverse and endemic specialist Lepidoptera fauna in the Galapagos Islands is intricately bound with the fate of their host plant. According to Nieminen (1996), moth species that feed exclusively on deciduous hosts are significantly more likely to suffer local extinction than those feeding on evergreen hosts. Nieminen also found that the risk of extinction of herbivorous moths is significantly affected by the host plant characteristics rather than by the characteristics of the moths themselves. Endemic hosts are distinctive in being displaced by introduced plants in disturbed habitats (Mauchamp 1997). Over the 100 years of intensive settlement of Galapagos, endemic hosts have suffered disproportionately where they occupied favoured sites for settlement and farming. Much of the highland zones of Santa Cruz, San Cristobal and Floreana Islands have been cleared for pasture, agriculture and habitation. 97% of the total land area of the Islands is, however, protected as National Park. In these areas the original vegetation has been conserved to some degree, although it has invariably been affected by the invasion of non-native plants. More than 62 endemic plant species are endangered in Galapagos and already three are extinct (CDRS Herbarium database).

Roque-Albelo (2003) highlighted the local extinction of three endemic moth species: *T. galapagoensis*, *P. vilema* and *S. cerussata,* from the southeast side of Volcano Alcedo, Isabela, due to a reduction in their host plant populations. The reduction of the populations of *D. dombeyana*, the host plant of *E. becki*, by the introduction of feral goats and habitat destruction on Isabela Island has increased the risk of extinction of the moth species (Roque-Albelo & Mieles 2005); it is currently present only as fragmented small populations. *Macaria cruciata cruciata* and *X. norfolki*, two specialist moths, are extinct from their type locality, despite the fact that their host plants are still common. If habitat fragmentation has resulted in local extinction there is little chance of recolonisation and efforts are needed to protect large enough areas of these habitats to maintain species with specialist needs.

3.4 CONCLUSIONS

Host plant lists for Galapagos Lepidoptera are still incomplete, but much progress has been made to unravel the basic larval food requirements of most species, including local endemics from remote islands. For the majority of the species where Rindge (1973) and Hayes (1975) had previously indicated that the larval host-relationships were unknown, associations have now been documented.

Monophagy at the family level appears to be widespread in Galapagos Lepidoptera. Most host plant additions in the future will either concern certain rare Microlepidoptera, noctuid and geometrid moths (many of which will almost certainly turn out to feed on grasses), or will further extend the known host plant list for species that are polyphagous.

Host plant information is now available for all Galapagos species in the Tischeriidae, Bucculatricidae, Yponomeutidae, Heliodinidae, Plutellidae, Choreutidae, Lycaenidae, Pieridae, Hesperiidae, Arctiidae and Nolidae. The databases for the Sphingidae, Geometridae, Nymphalidae, and Noctuidae have also been improved significantly.

Chapter 4
Flight periods of sphingid moths of the Galapagos Islands.

4.1 INTRODUCTION

Seasonality, the variation in abundance of species through climatic seasons, is a common phenomenon among insects (Wolda & Wong 1988). Insect abundance can change over time for various reasons, including macro and microclimatic changes, and variation in the availability of food resources (Wolda 1988). Wolda (1978a, b) proposed two general hypotheses to explain the variability in abundance of tropical insects: climatic predictability and seasonal variation of food resources. The first hypothesis suggests that populations should fluctuate less in areas where the climate is more predictable. The second hypothesis implies that insect numbers should be directly related to seasonal variations in abundance of food resources.

In the Galapagos, environmental conditions regulate periods of insect activity (Peck 2001). The difficult period for most Lepidoptera is the dry season, when leaves undergo a reduction in nutritional quality (Braby 1995). To understand how Galapagos Lepidoptera populations respond to seasonal variations, it is necessary to examine both their phenological patterns and life strategies. In this chapter I concentrate on the 15 sphingid moth species occurring on Santa Cruz Island. This is the first phenological study of any Galapagos Lepidoptera.

Hawk moths (Sphingidae) are medium to large-sized moths with elongate wings and a large body enabling powerful flight. They are often seen at dusk hovering and sucking nectar from flowers with their long proboscis. They are ubiquitous in the Neotropics with over 1100 described species (Heppner 1998). The caterpillars generally have a dorsal horn-shaped projection on their second to last abdominal segment. The Sphingidae are a suitable group for ecological studies in that their taxonomy is known, and there are limited data available on their geographic distribution and life history. This contrasts with many other insect groups in the tropics, where it is necessary to work with morphospecies only. In the Neotropics, Sphingidae tend to occur during all months of the year with some of the commonest species reaching peak numbers during a well-defined period of the year, generally at the onset of the rains. Studies of seasonal fluctuations in the abundance of tropical

Sphingidae are uncommon; those reported are restricted to Central America (Garcia 1978; Young 1972; Haber & Frankie 1989; Narvaez & Soriano 1996) and Africa (Owen 1969, 1972).

The specific aims of this study were (i) to obtain information about the seasonal changes in the species composition and behaviour of selected species of hawk moths, some of which are of very restricted distribution or only recently established in the Archipelago; and (ii) to provide data of Galapagos Lepidoptera communities, based on a complete list of species and statistics of their ecological determinants.

4.2 MATERIAL AND METHODS

4.2.1 Study area

The study was carried out in the arid zone of Santa Cruz Island in a locality known as "El Barranco" near the Charles Darwin Research Station" (CDRS; 2 km east of Puerto Ayora, S 00º 73769, N 090º 30106) reaching over 20m a.s.l (Fig. 4.1a, b). The locality is representative of the arid zone on Santa Cruz Island (*sensu* Wiggins & Porter 1971). "El Barranco" is an open dry deciduous forest dominated by *Opuntia echios*, *Jasminocereus thouarsii* var. *delicatus*, *Cordia lutea, Croton scouleri, Lantana peduncularis, Acacia macracantha* and *Prosopis juliflora* (Leguminosae), *Cryptocarpus pyriformis* and *Bursera graveolens.* The trees and shrubs support vines such as *Passiflora foetida* (Passifloraceae). In general, "El Barranco" dry forest conforms with the characteristics of a Galapagos dry forest as described by Wiggins & Porter (1971). Climatic data (rainfall, night air temperature and humidity) were available from the meteorological station of the CDRS (1 km from the study site in the same vegetation zone).

4.2.2 Field methods

Intensive regular night sampling was carried out for 29 months between April 1999 and August 2001 in "El Barranco". Each collection coincided with the new moon phase and averaged four days per month. A 175 Volt mercury vapour lamp and a vertically-set white sheet were placed each night, from 18.00 to 06.00 h, to attract moths.

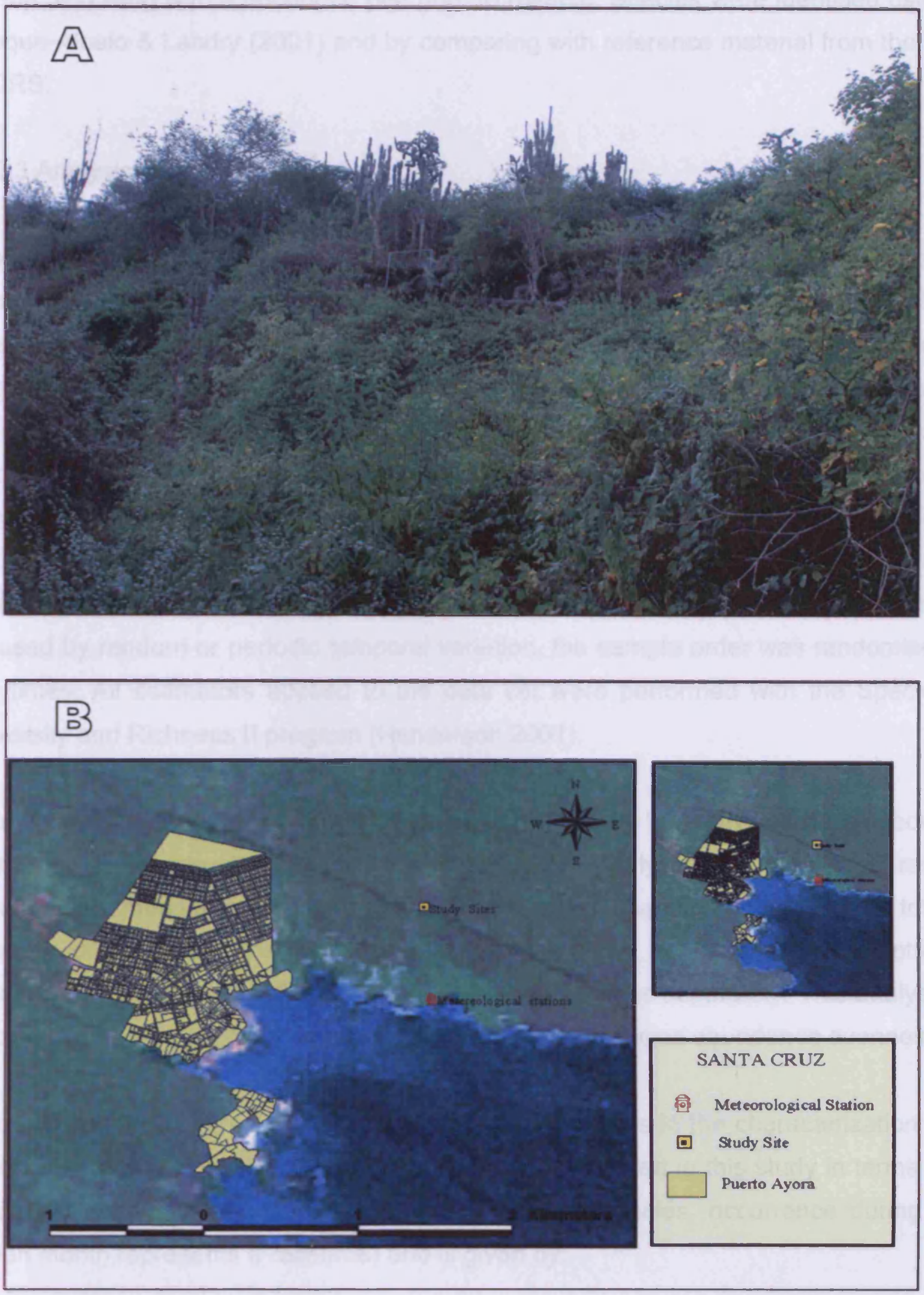


Figure 4.1. Study area: "El Barranco" located on the south side of Santa Cruz Island. A: Dry forest vegetation during the wet season, B: Geographical location of the study site and meteorological station.

At the time of capture, each specimen was numbered and marked on the underside of the hind wing with a felt-tipped pen prior to release. Species were identified using Roque-Albelo & Landry (2001) and by comparing with reference material from the IC CDRS.

4.2.3 Analysis of data

Data collected were analysed in two different ways to assess changes in both community diversity and structure. Species accumulation curves were used to plot the cumulative number of new species collected over unit effort (number of collection nights). To estimate the total number of species in each month four different non-parametric approaches were applied and compared: a) Chao 1, b) Chao 2, c) first-order Jack-knife, and d) bootstrap (Colwell & Coddington 1994). In addition, and since some rare and/or localized species may have been missed, a Michaelis-Menten enzyme kinetic curve (see Colwell & Coddington 1994) approach was also used to estimate the species richness in the community. To eliminate features caused by random or periodic temporal variation, the sample order was randomised 60 times. All estimators applied to the data set were performed with the Species Diversity and Richness II program (Henderson 2001).

The diversity of the species within the community or alpha diversity and the temporal variation in the structure of the community were analysed using species rank abundance, measures of niche breadth and alpha diversity indexes. The total number of individuals per each species marked ($\log_{10}$ transformed) was plotted against the rank in order of abundance for the two seasons separately. This analysis provided a means of giving detailed consideration into species abundance evenness.

Niche breadth measures were calculated for each species in the characterization of the community (Levins 1968). Niche breadth was measured in this study in terms of temporal pattern of abundance (where, for a given species, occurrence during a given month represents a resource) and is given by:

$$B = \frac{1}{\sum P_i^{2}}$$

where P_i is the number of individuals of each species i in the sample. B ranges from 1 to h, the number of resource units (months), and assumes that all resource units (months) are equally suitable.

Four measures of alpha diversity have been used; these were calculated using the full data set with the program Species Diversity Richness (Henderson 2001). They were: (i) species richness which is the total number of species recorded, (ii) Margaleff index which primarily measures species richness, and (iii) Berger Parker and (iv) Shannon indexes which measure both richness and relative abundance. All diversity indices were tested for correlation with relative humidity, air temperature and cumulative rainfall. Since relationships between data in this study are non-linear, the Spearman rank correlation coefficient was used. All standard statistical analyses were performed using the software package Minitab 13.31. In addition, Principal Component Analysis (PCA, Kent & Coker 1992; Legendre & Legendre 1983) based on covariance square matrix was performed to identify the general pattern of association between adult abundance with months of collections. This ordination analysis was carried out using the software Community Analysis Package 2.04 (Henderson, 2002).

A total of 5577 individuals belonging to 14 species were marked during th (Table 4.1) representing almost all the sphingid fauna known from the Ga Islands (Roque-Albelo & Landry 2001). The only species missing from "El B was *Cocytius antaeus.* This species was recorded from the Galapagos in 19 very rare and has a localized distribution in Santa Cruz Island (Roque-Albel During the study two new records for the Archipelago were collected: *Xyl pluto* and *Perigonia lusca lusca.*

The samples recorded were dominated by species of two genera, *Mand Erinnyis,* and represented 81.6% of the total individuals. Specimens of the t frequent species, *Manduca rustica calapagensis* and *Erinnyis ello en* represented 65.4% of the total. The minimum total number of individuals c was four in September 2000.

Estimator	Samples			
	5	20	40	60
Chao 1	11.02	11	13	14
Chao 2	11.02	11	13	14
First Order Jackknife	11.80	11	13	14.98
Bootstrap	11.66	11.04	13.03	14.36
Michaelis-Menten	13.34	11.68	12.76	13.10
Species observed	11	11	13	14

Table 4.2 Species diversity non-parametric estimators after 5, 20, 40 and 60 samples.

The species accumulation curve (Fig. 4.2) gives an indication of the confid the sampling effort. After 22 nights of collection 13 species were captured. A the curve rises fairly steeply and begins to level off relatively quickly, the curv

SPECIES	CUMULATIVE NUMBER OF ADULTS PER MONTHS (MALE/ FEMALE)																												
	1999									2000												2001							
	Wet season		Dry season							Wet season					Dry season							Wet season					Dry season		
	Apr (n=2)	May (n=9)	Jun (n=8)	Jul (n=8)	Aug (n=5)	Sep (n=4)	Oct (n=4)	Nov (n=4)	Dec (n=4)	Jun (n=4)	Feb (n=4)	Marc (n=4)	Apr (n=4)	May (n=4)	Jun (n=4)	Jul (n=4)	Aug (n=4)	Sep (n=4)	Oct (n=4)	Nov (n=4)	Dec (n=4)	Jan (n=4)	Feb (n=4)	Mar (n=4)	Apr (n=4)	May (n=4)	Jun (n=4)	Jul (n=4)	Aug (n=4)
A. cingulata	2 0/2	25 19/6	14 11/3	7 7/0	4 3/1	1 1/0	2 0/2	13 5/8	5 2/3	10 7/3	4 4/0	8 7/1	4 1/3	4 2/2	0	0	0	0	0	2 2/0	1 1/0	2 0/2	22 18/4	12 11/1	1 1/0	10 2/8	0	0	0
M. s. leucoptera	92 65/27	7 5/2	1 1/0	0	0	1 1/0	0	0	1 0/1	6 3/3	1 1/0	5 3/2	10 6/4	3 2/1	0	0	0	0	0	0	1 1/0	0	77 30/47	8 6/2	11 7/4	22 14/8	0	0	0
M. r. calapagensis	34 26/8	19 16/3	0	1 1/0	0	0	0	1 1/0	7 3/4	53 38/15	305 235/70	72 55/17	23 17/6	46 31/15	3 1/2	2 2/0	0	0	0	0	3 3/0	5 1/4	951 519/432	289 103/186	20 14/6	444 301/143	1 1/0	0	0
E. a. dispersa	1 1/0	12 10/2	19 18/1	15 13/2	0	0	0	0	1 1/0	1 1/0	0	2 2/0	1 0/1	3 2/1	0	3 3/0	0	0	1 1/0	1 1/0	1 1/0	0	4 4/0	7 7/0	0	4 3/1	4 4/0	3 1/2	0
E. e. encantada	2 0/2	178 119/59	241 157/84	87 50/37	12 11/1	8 2/6	8 1/7	9 8/1	5 4/1	3 1/2	5 5/0	103 69/34	119 84/35	38 14/24	2 0/2	9 6/3	6 2/4	2 1/1	8 7/1	4 4/0	9 9/0	2 1/1	11 8/3	99 61/38	82 53/29	40 18/22	103 43/60	64 33/31	111 50/61
E. o. conformis	59 27/32	154 80/74	3 2/1	3 2/1	1 0/1	1 1/0	0	4 3/1	3 0/3	10 8/2	6 2/4	89 35/54	19 11/8	8 5/3	7 3/4	4 1/3	8 6/2	0	1 1/0	5 2/3	18 10/8	5 2/3	18 4/14	88 24/64	27 6/21	31 12/19	7 3/4	2 1/1	0
E. l. delanoi	76 48/28	90 37/53	91 32/59	18 10/8	2 1/1	3 2/1	1 1/0	1 1/0	7 4/3	13 10/3	20 16/4	48 10/38	19 9/10	53 28/25	10 10/0	6 4/2	0	2 2/0	4 4/0	0	5 5/0	0	9 4/5	32 17/15	15 4/11	14 11/3	17 10/7	20 2/18	0
P. lusca	0	0	0	1 1/0	0	0	0	0	0	2 2/0	1 1/0	3 3/0	0	1 1/0	0	0	0	0	0	0	1 1/0	1 1/0	4 3/1	1 1/0	3 1/2	13 13/0	3 3/0	0	0
E. f. tupaci	0	0	0	0	0	0	0	0	0	0	1 1/0	0	0	0	0	0	0	0	0	0	0	0	0	1 1/0	0	0	0	0	0
E. l. yupanqui	1 0/1	26 22/4	31 31/0	13 8/5	4 4/0	0	0	2 1/1	0	1 1/0	3 1/2	3 0/3	4 1/3	0	1 0/1	0	3 1/2	0	1 0/1	0	1 0/1	0	2 0/2	0	4 2/2	20 13/7	17 9/8	11 8/3	4 2/2
X. pluto	0	0	0	7 7/0	0	1 1/0	0	0	0	0	0	1 1/0	0	1 0/1	0	0	0	0	0	0	0	0	0	0	1 1/0	17 14/3	1 0/1	0	0
X. t. tersa	4 3/1	22 21/1	9 9/0	4 4/0	1 1/0	1 0/1	0	4 2/2	5 0/5	15 15/0	9 8/1	2 1/1	2 1/1	16 12/4	2 2/0	0	0	0	0	0	7 5/2	2 1/1	28 21/7	19 16/3	5 3/2	54 40/14	14 11/3	1 0/1	0
X. norfolki	2 2/0	6 6/0	3 2/1	3 3/0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2 1/1	5 2/3	0	1 1/0	0	0	0
H. lineata	2 0/2	2 1/1	0	1 1/0	1 1/0	0	0	1 1/0	0	0	6 2/4	6 1/5	0	3 1/2	0	0	0	0	0	1 0/1	0	0	89 13/76	31 5/26	0	17 3/14	1 0/1	0	0

Table 4.1. Seasonal distribution of Sphingidae caught and marked in "El Barranco" (April 1999 to August 2001). For each month of study, the total number and the number of male/ female of each species marked is given. 'n' is the number of collection night per month. *A. cingulata: Agrius cingulata, M.s. leucoptera: Manduca sexta leucoptera, M. r. calapagensis: Manduca rustica calapagensis, E. a. dispersa: Erinnyis alope dispersa, E. e. encantada: Erinnyis ello encantada, E. o. conformis: Erinnyis obscura conformis, E. l. delanoi: Enyo lugubris delanoi, P. l. lusca: Perigonia lusca lusca, E. f. tupaci: Eumorpha fasciatus tupaci, E. l. yupanqui: Eumorpha labruscae yupanqui, X. pluto: Xylophanes pluto, X. t. tersa: Xylophanes tersa tersa, X. norfolki: Xylophanes norfolki, H. lineata: Hyles lineata.*

reaches a definite asymptote. This is because of the existence of rare and or localized species (such as *C. antaeus*) in the area, and the possibility of some small number of additional, yet undiscovered species. A comparison of the four non-parametric estimators (Table 4.2) suggests that Chao 1 and Chao 2 provide the most reliable estimates of the species richness observed. An evaluation of these methods suggests however, that all (or at least almost all) species present in the study area have been recorded.

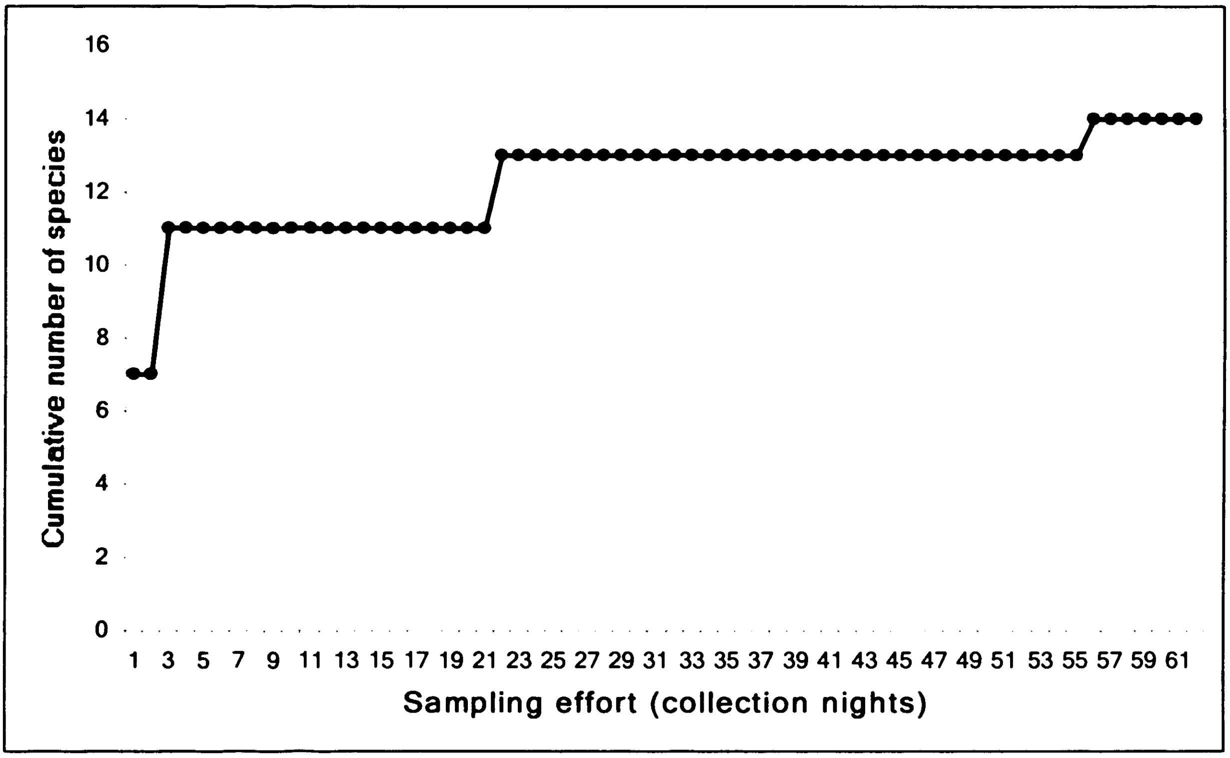


Figure 4.2 Sphingidae species accumulation curve of "El Barranco", Santa Cruz, Galapagos.

4.3.2 Seasonality of individual species

4.3.2.1 *Agrius cingulata*

Agrius cingulata (Fig. 4.3a) was active throughout the survey, showing peaks that possibly indicate the activity of different generations. The species had an annual cycle with peak abundance occurring during the wet season (November to June), corresponding to the beginning and end of the rainy season. In 1999 the major peaks were in May and November, in 2000 in January and March, and in 2001 February to May. Males were recorded more frequently than females in the light traps, females being found mainly at the beginning and end of the rainy season. In the Galapagos the larvae host plants reported for this species are members of the vine family Convolvulaceae, genera *Ipomea* and *Stictochardia* (Hayes 1975; Roque-Albelo & Landry 2001; Williams 1911). These plants are common in the arid zone of Santa Cruz Island.

4.3.2.2 *Manduca* spp.

The seasonal activity of the two dominant hawk moths is shown in Fig. 4.3b, c. *Manduca rustica calapagensis* is the most common sphingid of the Archipelago and was found to be the most dominant species during the survey (Fig 4.3b). This species shows the typical activity pattern of a "rain-breeder" with a peak of abundance during the rainy season. The data confirm that this species is strongly hygrophilous. In February 2001, 951 individuals were marked. Males were always more common than females in the light traps and the sex ratio was 1368 males to 911 females. *Manduca sexta leucoptera* also showed an annual cycle with a peak of abundance during the rainy season. In 1999 the major peak was in April (Fig. 4.3c). In 2000 activity was low but after the first rainfall in January 2001 a peak was observed in February. The sex ratio of individuals captured and marked was male-biased in all but one month (February 2001). In all, 145 males and 101 females were captured and marked. In the Galapagos larvae of these species have been reported feeding on a wide variety of plant species including some ecologically aggressive introduced species such as *L. camara* (Roque-Albelo & Landry 2001).

4.3.2.3 *Enyo lugubris delanoi*

Enyo lugubris delanoi was a common species during the study. It is a day-flying species that is also attracted to light at night. Of the 576 individuals marked 282 were males and 294 females. The species occurred in all months of the year except for August and November 2000, and January and August 2001. It was especially abundant in the wet season with several peaks of abundance observed between April and June 1999, March and May 2000 and March and July 2001 (Fig 4.4a). Larvae and eggs have been reported on the native Vitaceae, *Cissus verticillata* by Williams (1911) and Hayes (1975); the plant is a common vine in the transition and humid zones of the islands.

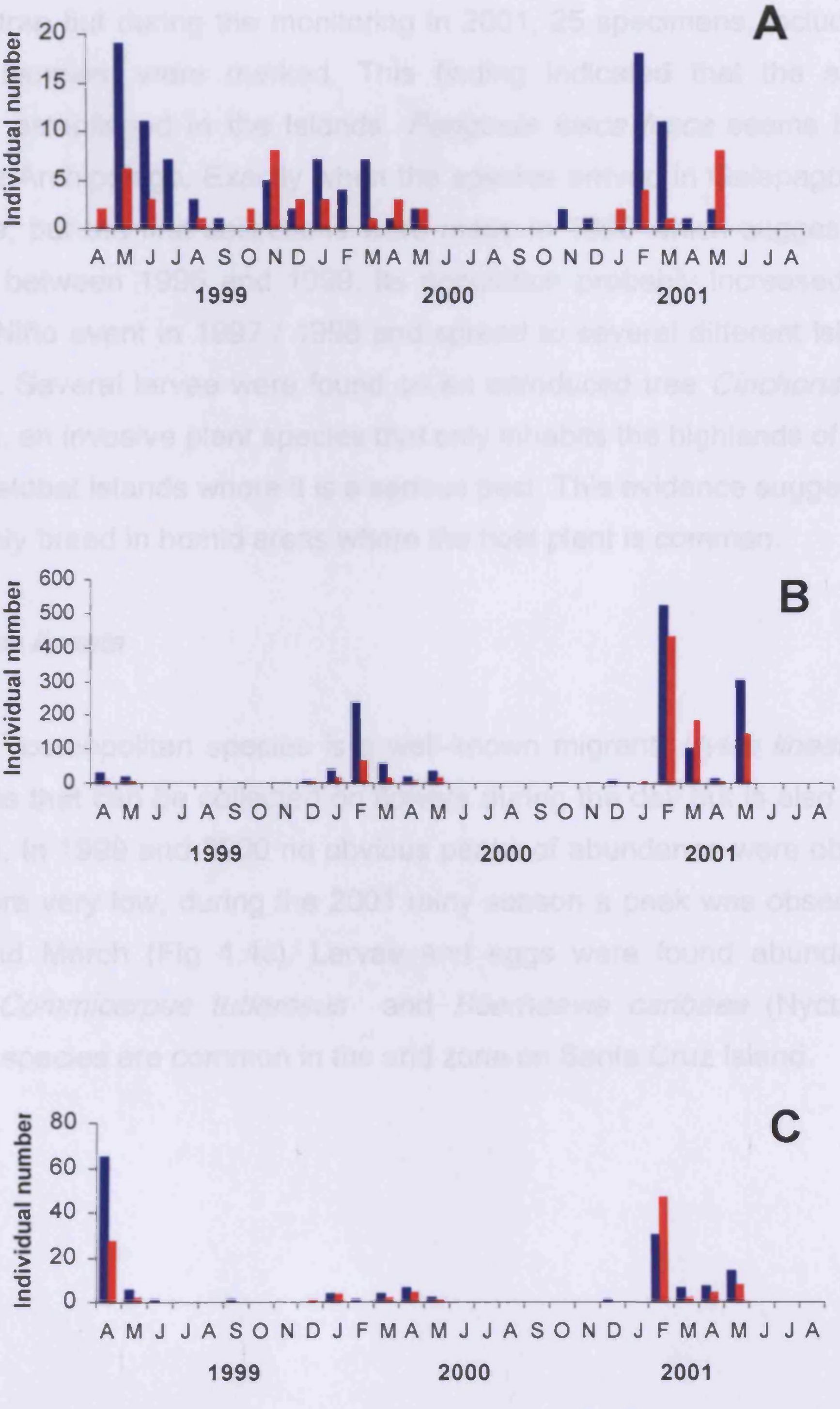


Figure 4.3 Seasonal abundance of individual species marked on "El Barranco" from 1999 to 2001. A: *Agrius cingulata*, B: *Manduca rustica calapagensis*, C: *Manduca sexta leucoptera*. Blue bar represent male abundance; red bar represent female abundance.

4.3.2.4. *Perigonia lusca lusca*

During the study 34 specimens were marked; all were observed during the rainy season (Fig. 4.4b). During 1999 and 2000, only nine male specimens were attracted by the light trap but during the monitoring in 2001, 25 specimens, including a small number of females, were marked. This finding indicated that the species had successfully established in the Islands. *Perigonia lusca lusca* seems be a recent arrival to the Archipelago. Exactly when the species arrived in Galapagos is difficult to determine, but the first collections were made in 1999 which suggests it arrived somewhere between 1996 and 1999. Its population probably increased during the extreme El Niño event in 1997 / 1998 and spread to several different islands of the Archipelago. Several larvae were found on an introduced tree *Cinchona pubescens* (Rubiaceae), an invasive plant species that only inhabits the highlands of Santa Cruz and San Cristobal Islands where it is a serious pest. This evidence suggests that *P. l. lusca* can only breed in humid areas where the host plant is common.

4.3.2.5. *Hyles lineata*

This almost cosmopolitan species is a well-known migrant. *Hyles lineata* is a day-flying species that can be collected on flowers during the day but is also attracted to light at night. In 1999 and 2000 no obvious peaks of abundance were observed and numbers were very low, during the 2001 rainy season a peak was observed in both February and March (Fig 4.4c). Larvae and eggs were found abundantly on *P. oleraceae*, *Commicarpus tuberosus* and *Boerhaavia caribaea* (Nyctaginaceae). These plant species are common in the arid zone on Santa Cruz Island.

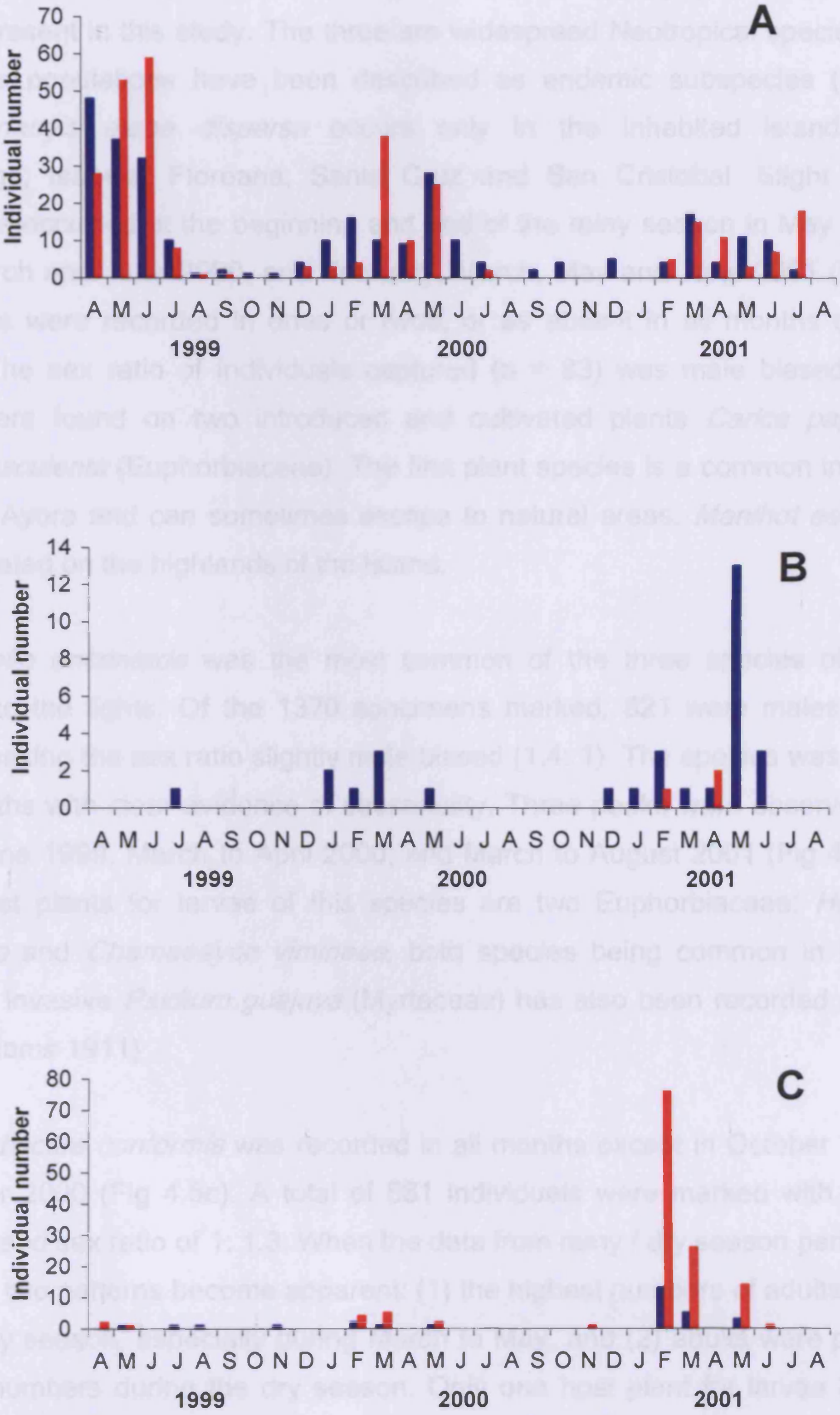


Figure. 4.4 Seasonal abundance of individual species marked on "El Barranco" from 1999 to 2001. A: *Enyo lugubris delanoi*, B: *Perigonia lusca lusca*, C: *Hyles lineata.* Blue bar represent male abundance; red bar represent female abundance.

4.3.2.6. *Erinnyis* spp.

Three species of *Erinnyis* have been reported from the Galapagos Archipelago and all were present in this study. The three are widespread Neotropical species but the Galapagos populations have been described as endemic subspecies (Kernbach 1962). *Erinnyis alope dispersa* occurs only in the inhabited islands of the Archipelago; Isabela, Floreana, Santa Cruz and San Cristobal. Slight peaks in abundance occurred at the beginning and end of the rainy season in May and June 1999, March and June 2000, and February, March, May and June 2001 (Fig 4.5a). Specimens were recorded in ones or twos, or as absent in all months of the dry season. The sex ratio of individuals captured (n = 83) was male biased (7.3: 1). Larvae were found on two introduced and cultivated plants *Carica papaya* and *Manihot esculenta* (Euphorbiaceae). The first plant species is a common in the town of Puerto Ayora and can sometimes escape to natural areas. *Manihot esculenta* is only cultivated on the highlands of the Island.

Erinnyis ello encantada was the most common of the three species of *Erinnyis* attracted to the lights. Of the 1370 specimens marked, 821 were males and 549 females making the sex ratio slightly male biased (1.4: 1). The species was recorded in all months with clear evidence of seasonality. Three peaks were observed during May to June 1999, March to April 2000, and March to August 2001 (Fig 4.5b). The known host plants for larvae of this species are two Euphorbiaceae: *Hippomane mancinella* and *Chamaesyce vimineae*, both species being common in the study area. The invasive *Psidium guajava* (Myrtaceae) has also been recorded as a host plant (Williams 1911)

Erinnyis obscura conformis was recorded in all months except in October 1999 and September 2000 (Fig 4.5c). A total of 581 individuals were marked with a slightly female biased sex ratio of 1: 1.3. When the data from rainy / dry season periods were compared two patterns become apparent: (1) the highest numbers of adults occurred in the rainy season, especially during March to May, and (2) adults were present in very low numbers during the dry season. Only one host plant for larvae has been recorded for this species in the Archipelago, the endemic vine *S. angustissimum*. This plant is common in the arid zone of many of the Galapagos Islands (Wiggins & Porter 1971).

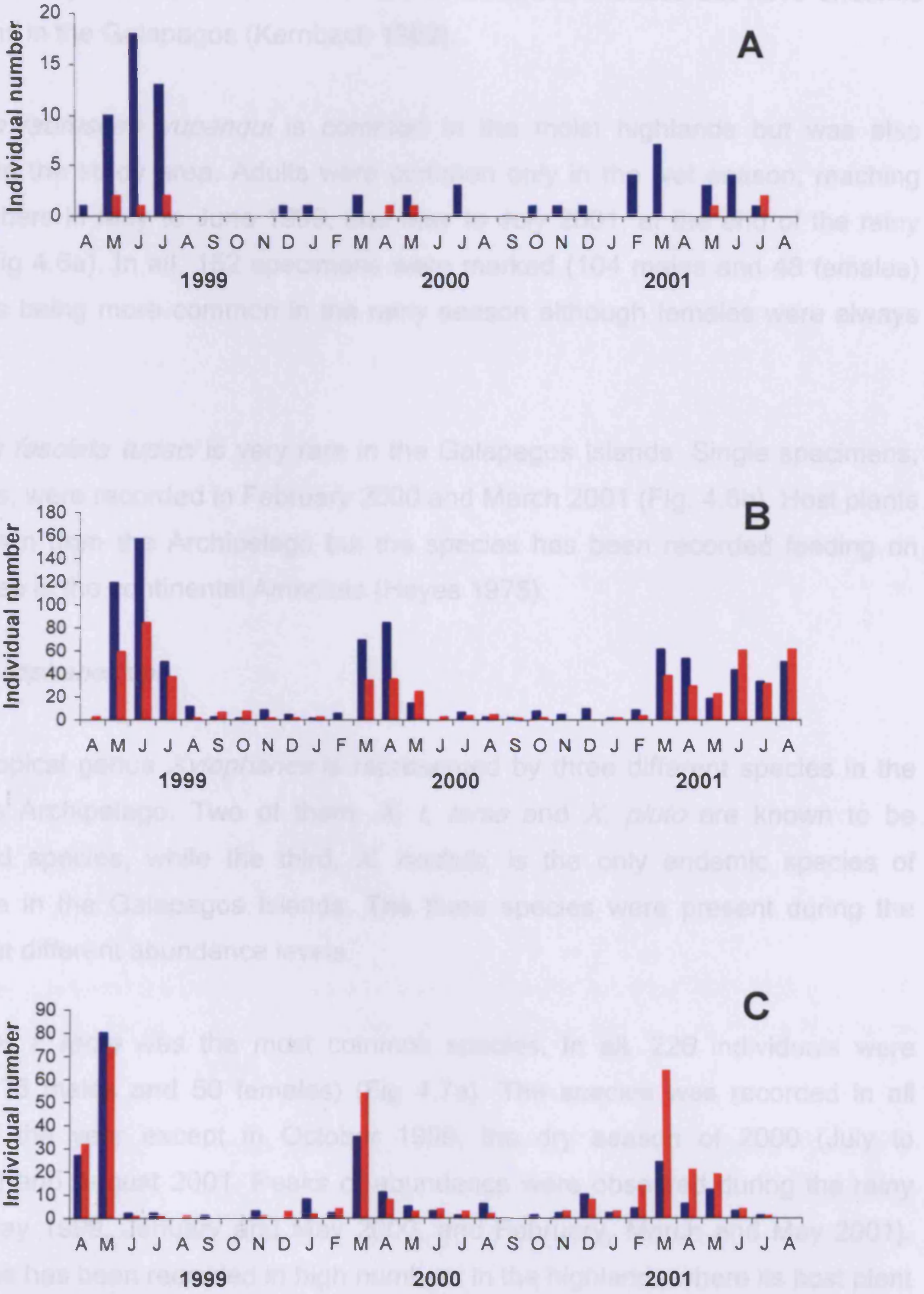


Figure. 4.5 Seasonal abundance of individual species marked on "El Barranco" from 1999 to 2001. A: *Erinnyis alope dispersa*, B: *Erinnyis ello encantada*, C: *Erinnyis obscura conformis*. Blue bar represent male abundance; red bar represent female abundance.

4.3.2.7. *Eumorpha* spp.

Two species of *Eumorpha* are present in the Archipelago and both were recorded during the study. The species occur in the continental Americas but have endemic populations in the Galapagos (Kernbach 1962).

Eumorpha labruscae yupanqui is common in the moist highlands but was also recorded in the study area. Adults were common only in the wet season; reaching peak numbers in May to June 1999, and May to July 2001, at the end of the rainy season (Fig 4.6a). In all, 152 specimens were marked (104 males and 48 females) with males being more common in the rainy season although females were always present.

Eumorpha fasciata tupaci is very rare in the Galapagos Islands. Single specimens, both males, were recorded in February 2000 and March 2001 (Fig. 4.6b). Host plants are unknown from the Archipelago but the species has been recorded feeding on Onagraceae in the continental Americas (Hayes 1975).

4.3.2.8. *Xylophanes* spp.

The neotropical genus *Xylophanes* is represented by three different species in the Galapagos Archipelago. Two of them: *X. t. tersa* and *X. pluto* are known to be widespread species, while the third, *X. norfolki,* is the only endemic species of Sphingidae in the Galapagos Islands. The three species were present during the study but at different abundance levels.

Xylophanes t. tersa was the most common species. In all, 226 individuals were marked (176 males and 50 females) (Fig 4.7a). The species was recorded in all months of the year except in October 1999, the dry season of 2000 (July to November) and August 2001. Peaks of abundance were observed during the rainy season (May 1999, January and May 2000, and February, March and May 2001). The species has been recorded in high numbers in the highlands where its host plant *Diodia radula* (Rubiaceae) is very abundant. An endemic Verbenaceae: *Clerodendrum molle* has been reported as a larvae host plant (Williams 1911). This plant species is very common in the study area.

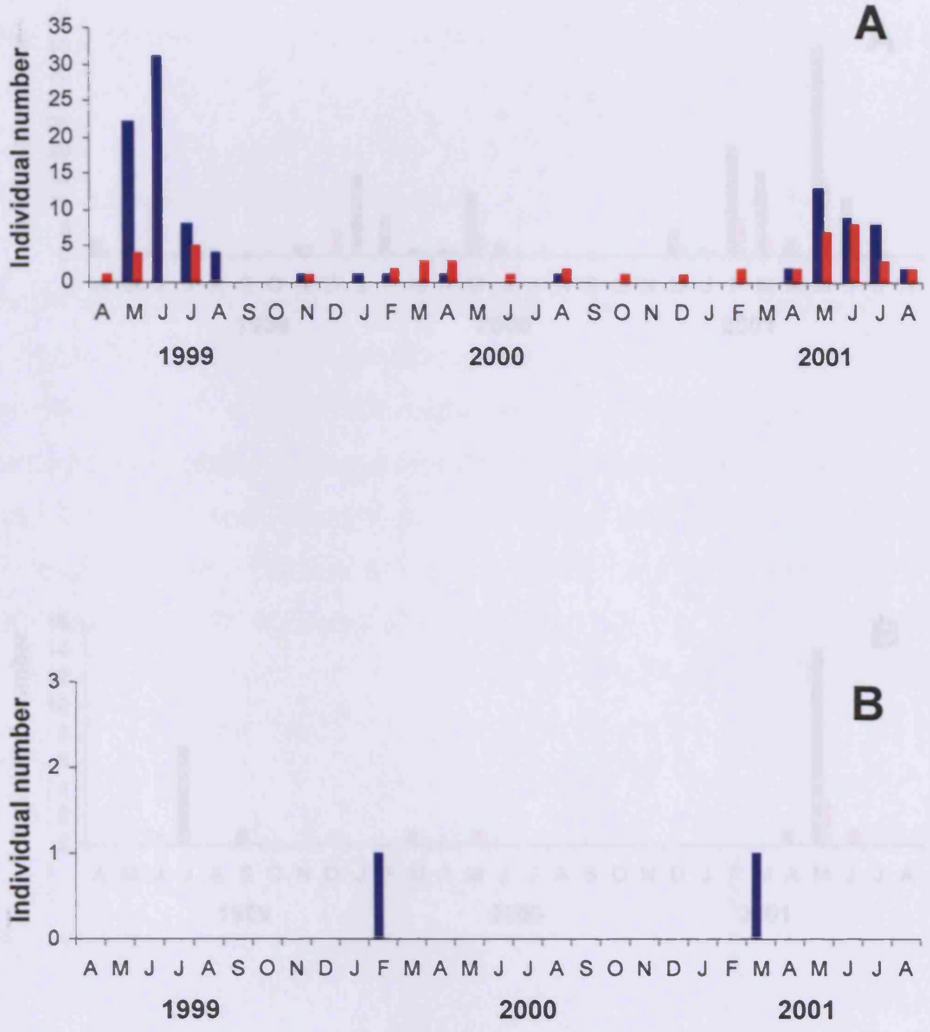


Figure 4.6 Seasonal abundance of individual species marked on "El Barranco" from 1999 to 2001. A: *Eumorpha labruscae yupanqui*, B: *Eumorpha fasciatus tupaci*. Blue bar represent male abundance; red bar represent female abundance.

Xylophanes pluto was recorded for first time from the Galapagos Islands by Roque-Albelo & Landry (2001). The species represents a recent arrival to the Archipelago and seems to follow similar patterns of abundance as those discussed for *P. l. lusca*. 29 specimens were marked, with 17 of these collected in May 2001 (Fig. 4.7b). A species of Rubiaceae, *C. alba,* has been reported by Hodges (1971) as host plant in North America. This plant is a common species in the Islands and is the most probable host plant of *X. pluto* in Galapagos.

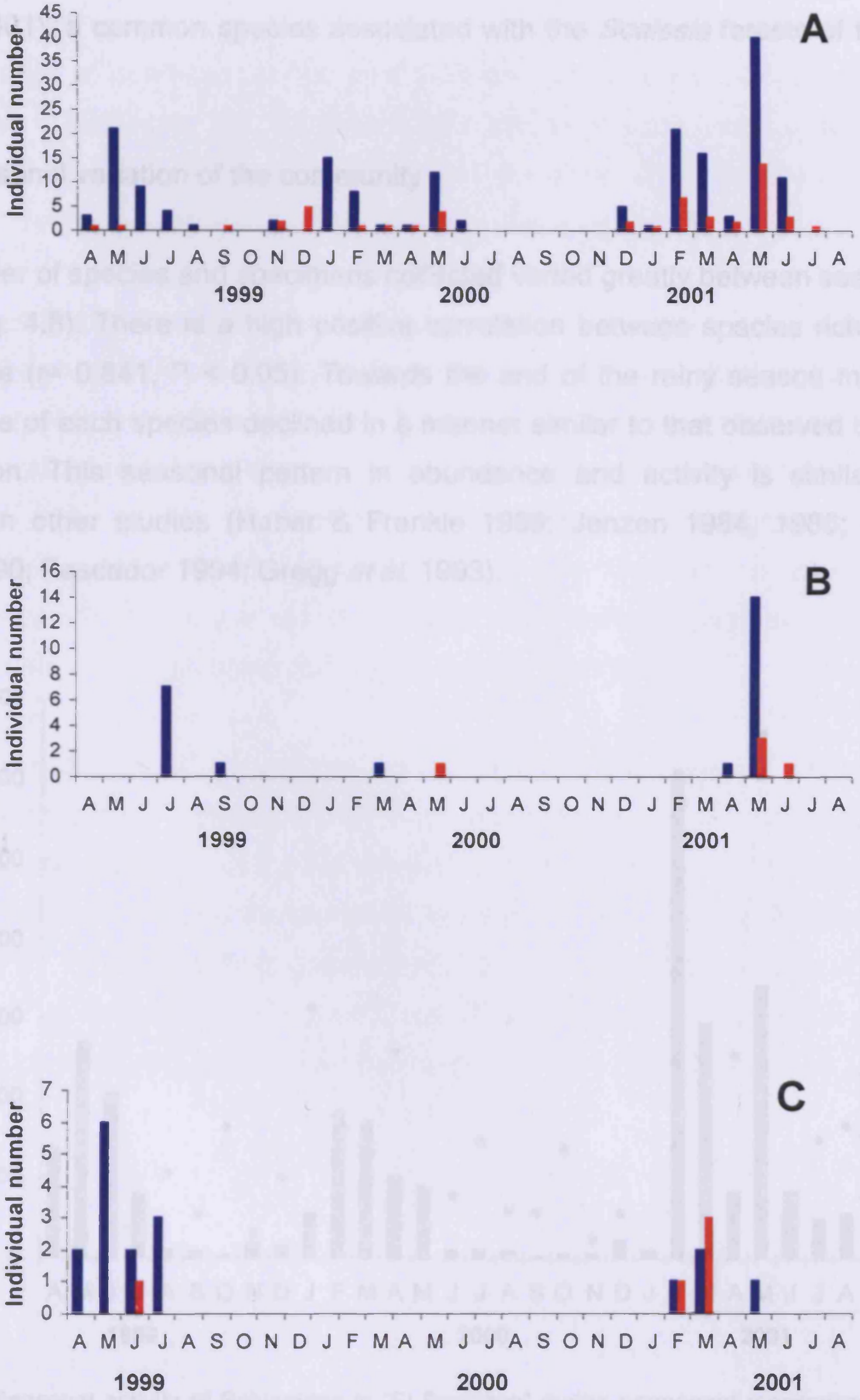


Figure. 4.7 Seasonal abundance of individual species marked on "El Barranco" from 1999 to 2001. A: *Xylophanes tersa*, B: *Xylophanes pluto*, C: *Xylophanes norfolki*. Blue bar represent male abundance; red bar represent female abundance.

Xylophanes norfolki breeds only in the moist highlands and appears to be rare in the lowland arid zone. It was occasionally recorded during the rainy season in the study area but these sightings were likely to be vagrant individuals (Fig. 4.7c). The host plant of this species is an endemic Rubiaceae: *Psychotria rufipes* (Roque-Albelo & Landry 2001), a common species associated with the *Scalesia* forests of the humid zone.

4.3.3 Seasonal variation of the community

The number of species and specimens collected varied greatly between seasons and years (Fig. 4.8). There is a high positive correlation between species richness and abundance (r= 0.841, P < 0.05). Towards the end of the rainy season months the abundance of each species declined in a manner similar to that observed during the dry season. This seasonal pattern in abundance and activity is similar to that reported in other studies (Haber & Frankie 1989; Janzen 1984, 1986; Powell & Brown 1990; Pescador 1994; Gregg *et al.* 1993).

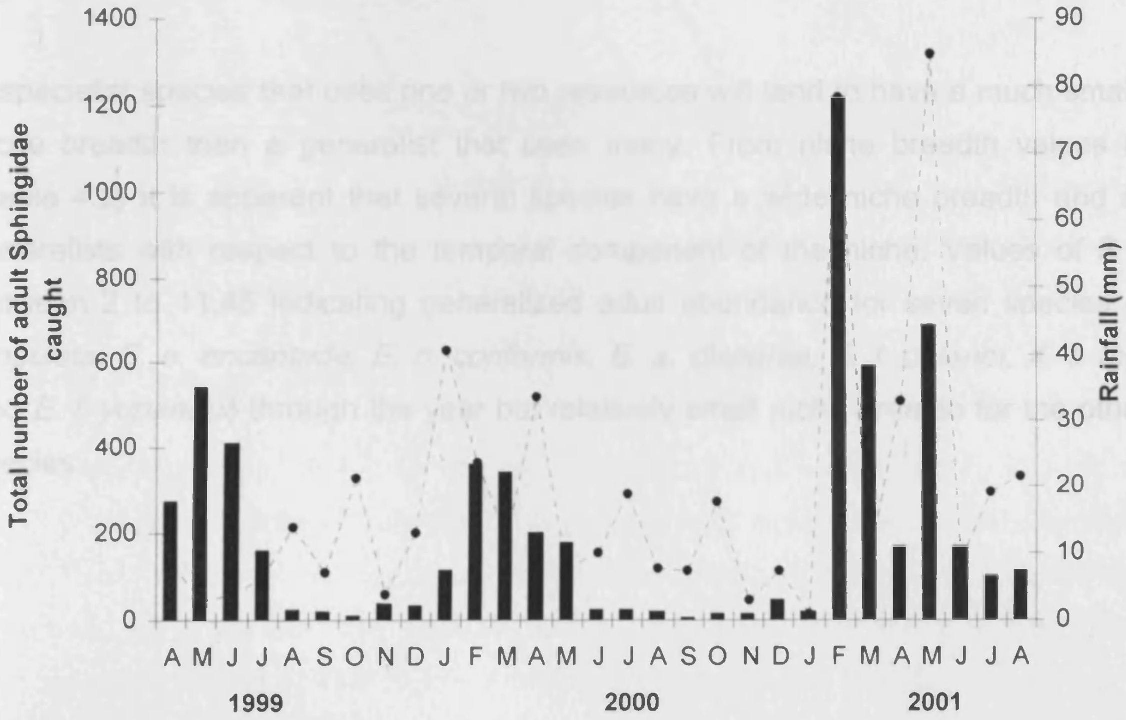


Figure. 4.8 Seasonal activity of Sphingidae in "El Barranco" during permanent monitoring from April 1999 to August 2001. Solid bars represent adult abundance, dotted lines cumulative number of rainfall per months.

The species differ mainly in their relative abundance during the year. Diversity did not, however, increase during the rainy periods of April, May and July 1999, February to May 2000, and February to May 2001, when the sphingids were much more abundant than at other time of the year. The overall increase in abundance of common species at the onset of the rains did not coincide with the occurrence of large numbers of species that had until then been absent. Haber & Frankie (1989) and Janzen (1984) state that the precipitation and vegetation production are closely linked to the life cycle of the sphingids. In the arid zone of the Islands rainfall is the most important event that determines seasonal changes.

Species distribution evenness was highest during the wet season (Fig 4.9a) and less so in the dry season (Fig. 4.9b). With the exception of January 2001 all months of the wet season recorded high values of equitability. Some months were highly influenced by the abundance of three species: *M. r. calapagensis*, *E. o. conformis* and *E. e. encantada*. This was to be expected as the number of species but not total Sphingidae abundance declined. A few infrequent collections were made of generally vagrant species throughout all months during the dry season. Only July 1999 showed high evenness value coinciding with the end of wet season.

A specialist species that uses one or two resources will tend to have a much smaller niche breadth than a generalist that uses many. From niche breadth values (B) (Table 4.2) it is apparent that several species have a wide niche breadth and are generalists with respect to the temporal component of the niche. Values of B lie between 2 to 11.48 indicating generalized adult abundance for seven species (*A. cingulata, E. e. encantada, E. o. conformis, E. a. dispersa, E. l. delanoi, X. t. tersa* and *E. l. yupanqui*) through the year but relatively small niche breadth for the others species.

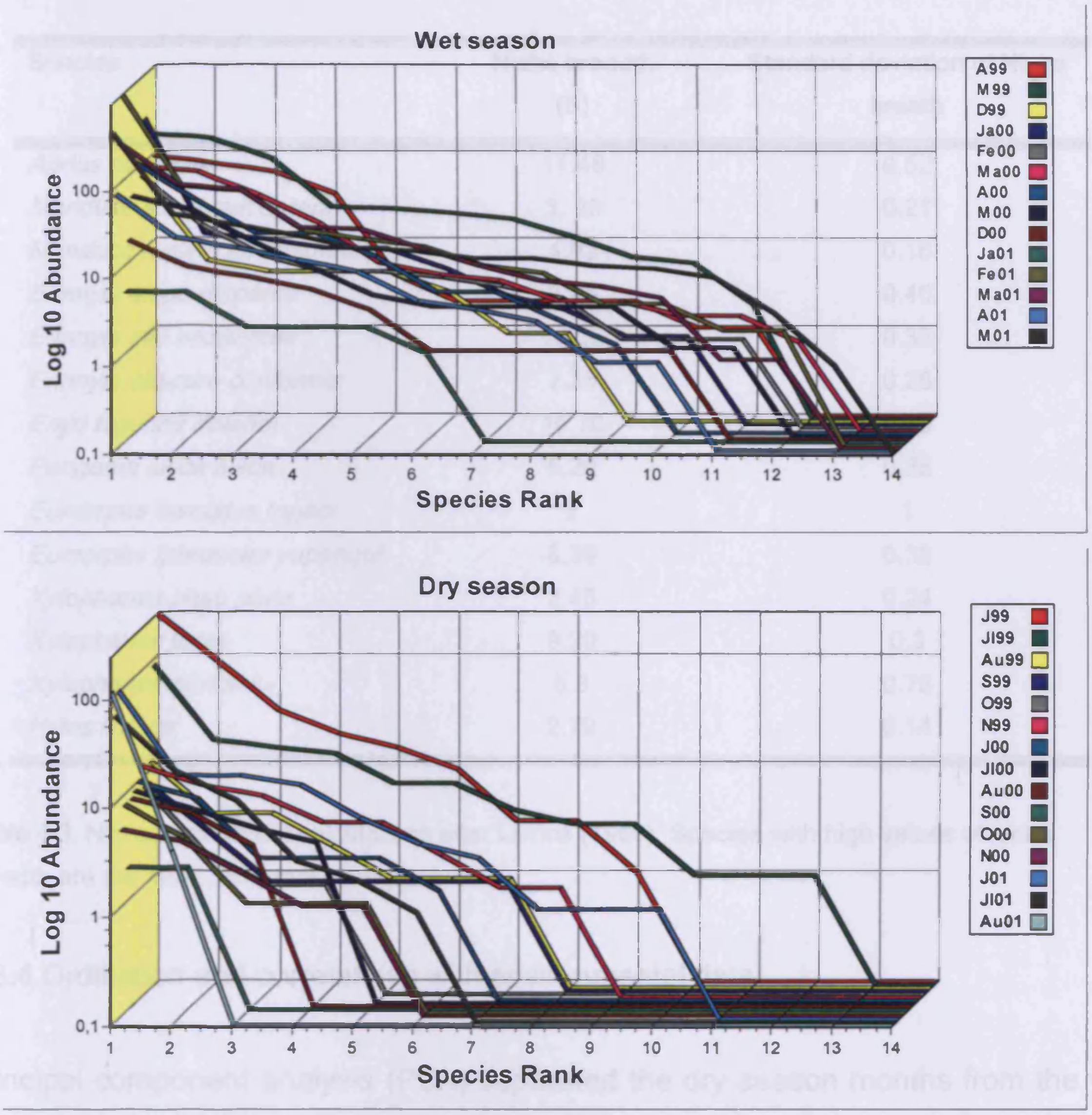


Figure 4.9 Log $_{10}$ abundance against the rank abundance for rain season (December to May) and dry season (June to November). Color bars represent different months and years. Ja: January, Fe: February, M: March, A: April, Ma: May, J: June, Jl: July, Au: August, S: September, O: October, N: November, D: December. Years of study 99: 1999, 00: 2000, 01: 2001.

Environmental factors that promote high speciation and high diversity include the stability or predictability of habitats in ecological and evolutionary time (Connell & Orias 1964; Slobodkin & Sanders 1969; Levins 1968). More stable environments composed of heterogeneous habitats will support more species than less stable homogeneous habitats. The Sphingidae of the arid zone of the Galapagos Islands would therefore be predicted to be characterized by low species diversity, high population densities in several species and wide niche breadths with respect to resource utilization. Few species maintain the same level of abundance over long periods of time.

Species	Niche breadth (B)	Standard deviation of Niche breath
Agrius cingulata	11.48	0.52
Manduca sexta leucoptera	3. 95	0.21
Manduca rustica calapagensis	4.02	0.16
Erinnyis alope dispersa	7.96	0.40
Erinnyis ello encantada	10.25	0.33
Erinnyis obscura conformis	7.33	0.25
Enyo lugubris delanoi	10.70	0.40
Perigonia lusca lusca	5.20	0.38
Eumorpha fasciatus tupaci	2	1
Eumorpha labruscae yupanqui	8.39	0.38
Xylophanes pluto pluto	2.45	0.24
Xylophanes tersa	9.20	0.3
Xylophanes norfolki	5.5	0.75
Hyles lineata	2.79	0.14

Table 4.3. Niche breadth (B) calculations after Levins (1968). Species with high values of niche breadth are the most commonly caught.

4.3.4 Ordination and correlations with environmental data

Principal component analysis (PCA) separated the dry season months from the wet season months (Fig. 4.10). Axis 1 seems to be a season gradient on which the dry season samples are clustered with similarity greater than between wet season months. The species vectors are spread to the left of the ordination space indicating a strong correlation with the wet season. That correlation seems to be confirmed because 84.13% of the specimens were marked in the wet season. Several patterns can be observed in the ordination plot. The common species were associated with the months of peak abundance; for instance, *E. e. encantada,* one of the two most abundant species, was associated with June 1999 when 241 specimens were marked. A group of species consisting of *E. l. delanoi, E. a. dispersa, E. l. yupanqui* and, to a lesser degree, *X. norfolki* and *E. o. conformis* were associated with May 1999, the month with the highest index of evenness of the wet season. *Manduca rustica calapagensis* was the most abundant species overall but was most numerous

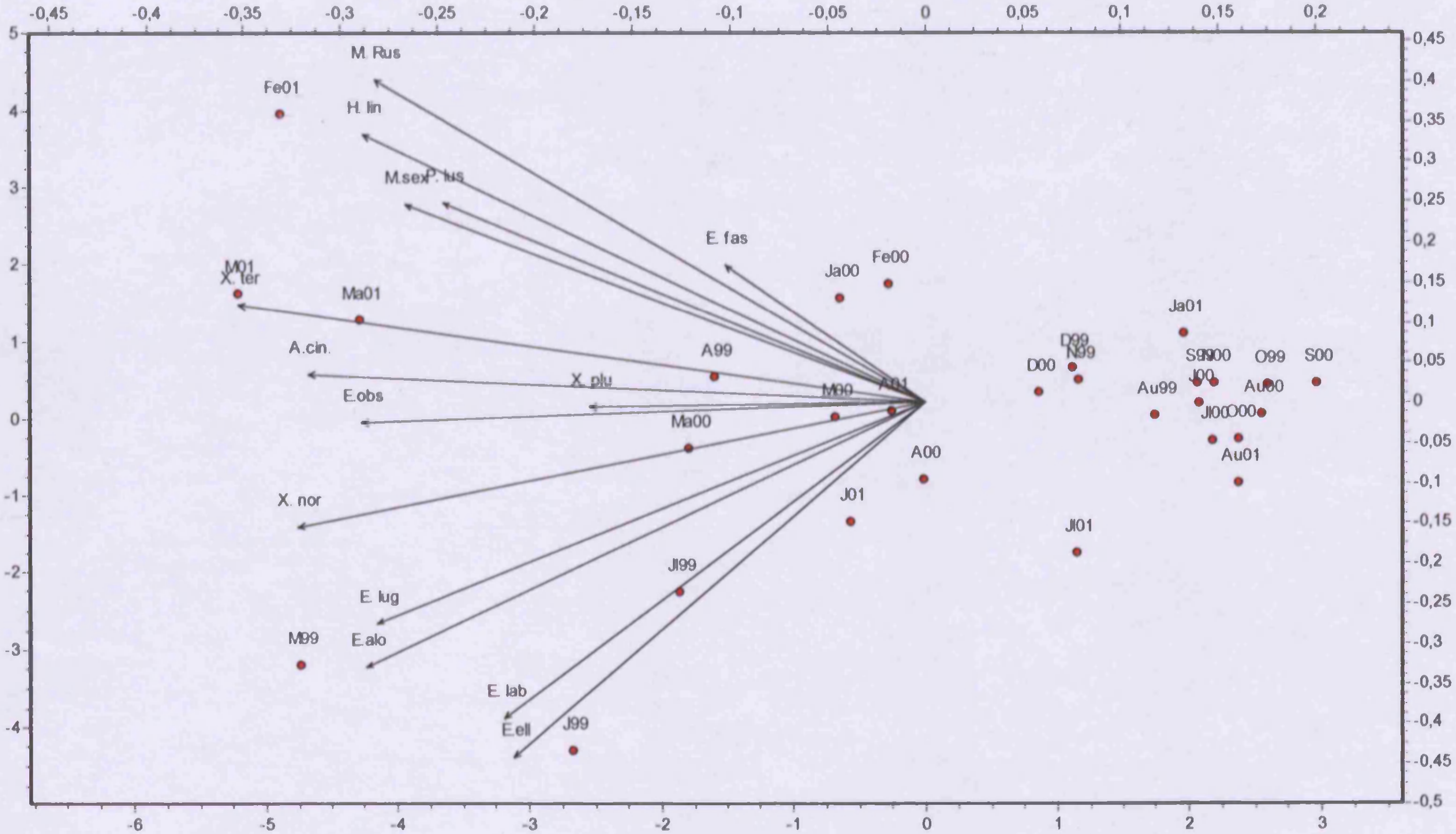


Figure 4.10 Principal component analysis (PCA) ordination plot. Position of species axes with respect to Axis 1 and Axis 2. Individual species are identified: M. Rust = *Manduca rustica,* M. sex = *Manduca sexta,* H. lin = *Hyles lineata,* P. lus = *Perigonia lusca,* X. plu = *Xylophanes pluto,* X. ter = *Xylophanes tersa,* X. nor = *Xylophanes norfolki,* A. cin = *Agrius cingulata,* E. obs = *Erinnyis obscura,* E. ell = *Erinnyis ello,* E. alo = *Erinnyis alope,* E. lab = *Eumorpha labruscae,* E fas = *Eumorpha fasciata,* E. lug = *Enyo lugubris.* Sampling month (•).

in February 2001 (951 specimens marked). This is reflected in their location close to February 2001 in the ordination space.

Spearman's correlations between diversity indices and environmental variables indicate that only a few correlations were statistically significant (Table 4.3). Air temperature was significantly correlated only with species richness and precipitation with Berger-Parker and Shannon indices. Diversity indices were highly influenced by the increase in abundance of two common species, *M. r. calapagensis* and *E. e. encantada*. This situation is in marked contrast to a temperate area where species tend to succeed one another as the season progresses and where most species are absent for most of the year (Owen 1972).

	Richness based index				Abundance based index			
Factors	**Margaleff**		**Species richness**		**Berger Parker**		**Shannon**	
	r	p	r	p	r	p	r	p
Air temperature	0.263	ns	0.701	**	-0.133	ns	0.369	*
Relative humidity	-0.218	ns	0.203	ns	0.064	ns	-0.234	ns
Rainfall	-0.258	ns	0.127	ns	0.651	**	-0.246	*

Table 4.4. Spearman rank correlations between four measures of alpha-diversity (Margaleff, Species richness, Berger Parker and Shannon) and the environmental factors air temperature, relative humidity and rainfall. ns not significant, * $p< 0.05$, ** $p< 0.001$.

4.4 CONCLUSIONS

Although the Galapagos climate has two distinct seasons these do not affect the tendency of some species to occur as adults in all months of the year. In almost every species, however, there is a seasonal peak of abundance that in one way or another is associated with the alternation of wet and dry seasons. For many species it is possible to complete the life cycle at any time of the year, but certain times are more optimal than others. Weather conditions vary from year to year in the

Archipelago, and a given species may experience marked fluctuations in both emergence times and abundance.

Local population dynamics can depend on factors such as predation and parasitism rates, migration and success in mating and oviposition, and weather (Krebs 1972). A complete evaluation of these factors in the Galapagos fauna is not possible until further data are available.

From the seasonal point of view the arid zones are particularly interesting as they include species without pronounced seasonality, species with seasonality induced by environmental variation, and species migrating from the humid highlands. Species abundances recorded at a given site can be influenced by weather conditions and dispersal abilities. Some of the species reported from "El Barranco" during the study, for example, *X. norfolki* and *P. l. lusca*, were probably vagrant individuals from the highland and seasonal patterns for these species are consequently difficult to determine in the locality. Similar results were report by Janzen (1986) from Santa Rosa National Park, a dry deciduous forest in Costa Rica.

Migration from low to high elevation, from one side of the island to another, and between islands has been reported in the Galapagos (Beebe 1923). Massive movements of sphingids were also observed by B. Landry at Media Luna, a locality in the highlands of Santa Cruz, in 1992. Landry observed between 200-300 sphingid moths being attracted to the Mercury vapour lamp and suggests that the species migrate to escape the drier conditions of lower elevations (B. Landry *pers. comm.*). Another possible migration was observed in 1996 by the author of this study at Volcano Sierra Negra in Isabela Island coinciding with the end of the rainy season. In one night 53 individuals of *X. t. tersa* were collected in a Malaise trap. Lacking from this study are data on adult food sources. In the Galapagos, there is virtually no information available on insect visitation to flowers (McMullen 1986, 1990, 1993; Linsley 1966). Such data are needed to demonstrate niche specialization in relation to food sources, and to correlate habitat heterogeneity and ecological specialization with local species diversity in order to demonstrate their role as determinants of diversity.

Chapter 5
General Conclusions

Oceanic islands are living laboratories of evolution. Each island has a unique geographic position and an individual evolutionary history. Their Lepidoptera faunas, however, share common attributes (Ferguson *et al.* 1991, Holloway & Nielsen 1999); they are poor in diversity but rich in endemism. In general, the Neotropical region has one of the greatest global diversities of Lepidoptera (Heppner 1991); the Galapagos Islands, however, support a relatively low number of species (313 species).

Three criteria are useful in using Lepidoptera in assessing the potential conservation value of the Islands: i) presence of endemic taxa; ii) presence of widespread species; and iii) species richness. The numerous endemic species present in the Galapagos indicates the presence of important native habitats supporting biological resources of regional significance. Although no species is yet listed as threatened or endangered, some species are restricted to very few islands or habitats (e. g. *Epiplema becki* on the wet forests of Isabela and Fernandina, and *Xylophanes norfolki* in the *Scalesia* forest of Santa Cruz, Isabela and Fernandina).

The abundance of several widespread pest species in the Islands, including *Spodoptera dolichos, Pseudoplusia includens, Eublemma recta* (all Noctuidae) and *Discliosiprocta stellata* (Geometridae), indicates the presence of disturbed or degraded habitat. While the occurrence of these species can be explained, at least in part, by the presence of human settlement, there are few doubts that resident populations of these polyphagous pests are also present in natural habitats (Hayes 1975). It is very likely that the native Lepidoptera fauna has suffered from the introduction of invasive weeds that serve as host plants to these widespread species. Monitoring strategies capable of detecting changes in the abundance of these species may provide insight into the effects of future environmental change and/or habitat perturbation.

Although the conservation of maximum species diversity may appear to be closely related with the preservation of habitats of highest species richness this is not always the case. Areas of highest species richness may represent habitats with the greatest overlap of ranges of common or widespread species. The number of widespread pest species in disturbed areas can sometimes exceed the number of native or endemic species in undisturbed natural areas. Hence the total number of species may give very limited information about the overall conservation value of a site or region. For the Lepidoptera of the Galapagos Islands species richness is highest on Santa Cruz; this island, however, also supports a great number of widespread species and is also a large, relatively aged island with considerable disturbance.

As expected for oceanic islands' ecosystems, the majority of Lepidoptera species in the Galapagos Archipelago are herbivores although other functional groups such as detritivores and carnivores do occur. Holloway (1977) found a high proportion of generalist herbivore species (polyphagous) in the fauna of Norfolk Island. Although more data are required, the present study has shown that specialization at plant family level is widespread in the Galapagos fauna.

Lepidoptera are unique among Galapagos insects in that sufficiently large samples can be collected during each individual light trapping session to provide a quantitative evaluation. Lepidoptera assemblages can therefore be used to provide insight into temporal aspects of diversity and community composition that cannot be achieved with other taxa. The mid- to long-term faunal survey (24 month) carried out in this study has the important feature of having sampled the Lepidoptera over at least one entire year. Shapiro (1975) and Hill (1988) have discussed the importance of temporal distribution and seasonality to the measurement of Lepidoptera species-richness. Studies of the Lepidoptera fauna of tropical forests in Panama (Emmel & Leck 1970) and Sierra Leone (Owen 1969) indicate that Lepidoptera seasonal abundance is a complex phenomenon linked to environmental factors such as precipitation, temperature, humidity etc..

In the present study, a group of 15 species belonging the family Sphingidae were chosen as a proxy of the seasonal abundance of the Lepidoptera fauna. This analysis provides a number of generalizations about the Lepidoptera community. A wide variation exists in community abundance and diversity that appears to be correlated with climatic conditions. Both abundance and diversity are maximal during the rain season and dominant species form more than 70% of the Sphingidae community. Essentially the results indicate that comparison of the diversity between sites requires sampling designs that can detect seasonal effects on spatial dimensions within and between years. Such conclusions affect the interpretation of communities and how best to conserve them.

The detailed inventories of the diversity, host associations and the analysis structures of the communities of Lepidoptera communities collected in this stu the groundwork for developing more experimental approaches and d investigations on their functional role in the Galapagos ecosystems. Future may follow a number of directions, all using Lepidoptera as a model grou example:

(i) investigate further the insect host-plant relationship and study the parasite relationships;
(ii) study intensively the bionomics of the endemic species;
(iii) continue to investigate which taxa are present, and analyse and synt the evolutionary relationships of the taxa between the Islands a continental sources; and
(iv) in genera with many endemic species (e.g. *Galagete, Ute Eupithecia*) conduct a search for morphological features, beha ecological, seasonal, etc., which may be indicators of niche parti and adaptive radiation using model groups such as Darwin finches.

Other further investigations can be carried out to collect information from little- habitats such as caves and lava tubes, monitor the introduction and establish alien species, study the factors affecting the conservation of the endemic and use selected Lepidoptera families as indicator of habitat disturbance.

Conservationists are unable to preserve all species under threat; conse planning places a premium on identifying priorities. A promising approac identify biodiversity hotspots, or areas featuring exceptional concentrati endemic species and experiencing exceptional loss of habitat (Myers *et al.*

The conservation priority perspective that focuses on species' communities suffers in that until relatively recently conservation planning has focused more on patterns than processes. Researchers from several fields of evolutionary biology now agree that the conservation of genetic diversity must be planned around two dimensions: (i) the protection of areas inhabited by historically isolated lineages that cannot be recovered after their demise, and 2) the protection of the processes of adaptation and diversification by maintaining the context for migration and selection in heterogeneous landscape habitats (e.g. Bowen 1999; Moritz 2002). These two dimensions for conservation planning need to be anchored on solid knowledge of phylogenies, systematic, species inventories, and the understanding of the evolutionary origin and processes which created and maintain endemic areas or biodiversity hotspots (Richardson *et al.* 2001). The studies presented in this thesis are important in conservation planning because of their various ground uses: they serve as an indicator of endemicity within an area and provide as well information on the number of introduced species. They can be used for comparisons between and among areas, and for formulating questions about centres of origin, colonisation pathways, evolutionary histories and conservation.

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Appendixes

LIST OF APPENDIXES

1. Geographical distribution of Galapagos Lepidoptera.
2. Host plant affiliation of Galapagos Lepidoptera.
3. Scientific papers published by author related to this thesis.

Appendix 1. Geographical distribution of Galapagos Lepidoptera. Asterisk after species name denote introduced species.

Pantropical	Neotropical & Nearctic	Neotropical region	Endemic	Undetermined (probably endemics)
Tineidae	**Tineidae**	**Tineidae**	**Tischeriidae**	**Opostegidae**
_Phereoeca allutella_*	_Xylesthia pruniramiella_*	_Lepyrotica acantha_	_Astrotischeria scalesiaella_	_Pseudopostega_ sp.
_Erechtias minuscula_*	**Gelechiidae**	**Coleophoridae**	_Astrotischeria alcedoensis_	**Tineidae**
_Praecedes atomosella_*	_Tuta absoluta_*	_Blastobasis normalis_	**Bucculatricidae**	Tineidae sp. 1
Cosmopterigidae	_Dichomeris acuminata_	**Gelechiidae**	_Bucculatrix cordiaella_	Tineidae sp. 2
Cosmopterix attenuatella	**Tortricidae**	_Evippe omphalopa_	**Yponomeutidae**	Tineidae sp. 3
_Pyroderces rileyi_*	_Strepsicrates smithiana_*	_Stegasta zygotoma_	_Atteva hysginiella_	Tineidae sp. 4
Pterophoridae	_Episimus utilis_	_Phthorimaea perfidiosa_	_Prays galapagosella_	Tineidae sp. 5
_Megalorhipida leucodactyla_*	_Episimus transferranus_*	_Anacampsis primigenia_	**Heliodinidae**	Tineidae sp. 6
_Lantanophaga pusillidactyla_*	_Bactra philocherda_*	_Compsolechia salebrosa_	_Heliodines galapagoensis_	Tineidae sp. 7
Pyralidae	**Pterophoridae**	_Mesophleps adustipennis_	**Coleophoridae**	Tineidae sp. 8
Pyralis manihotalis	_Exelastis montischristi_*	**Elachistidae**	_Calosima darwini_	Tineidae sp. 9
_Corcyra cephalonica_*	_Exelastis pumilio_*	_Stenoma catenifer_*	**Cosmopterigidae**	Tineidae sp. 10
_Marasmia trapezalis_*	**Pyralidae**	**Autostichidae**	_Cosmopterix yvani_	**Gracillariidae**
_Omiodes indicata_*	_Diaphania hyalinata_*	_Taygete sphecophila_	_Cosmopterix madeleinae_	_Acrocercops_ sp.
_Terastia meticulosalis_*	_Diaphania nitidalis_	**Pterophoridae**	_Cosmopterix galapagosensis_	_Caloptilia_ sp. 1
Maruca vitrata	_Herpetogramma bipunctalis_*	_Bipunctiphorus nigroapicalis_	_Ithome volcanica_	_Caloptilia_ sp. 2
Parapoynx fluctuosalis	_Agathodes designalis_*	_Postplatyptilia huigraica_	_Periploca darwini_	_Cryptolectica_ sp.
Noctuidae	_Phidotricha erigens_	_Stenoptilodes brevipennis_*	_Periploca longipenis_	_Dialectica_ sp. 1
Anomis erosa	_Penestola bufalis_*	_Stenoptilodes juanfernandicus_	**Elachistidae**	_Dialectica_ sp. 2
Nolidae	_Pilocrocis ramentalis_*	**Pyralidae**	_Haplochrois galapagosalis_	Gracillaridae sp. 1
Characoma nilotica	_Pleuroptya silicalis_	_Ancylostomia stercorea_*	**Autostichidae**	**Coleophoridae**
	_Pyrausta panopealis_*	_Coptarthria dasypyga_	_Galagete gnathodoxa_	_Coleophora_ sp.

Pantropical	Neotropical & Nearctic	Neotropical region	Endemic	Undetermined (probably endemics)
	_Syngamia florella_*	_Fundella argentina_*	_Galagete protozona_	**Xylorictidae**
	_Rhectocraspeda periusalis_*	_Hypsipyla grandella_*	_Galagete seymourensis_	Scythridinae sp.1
	Synclera jarbusalis	_Oryctometopia fossulatella_	_Galagete turritella_	Scythridinae sp. 2
	Palpita flegia	_Hymenia perspectalis_*	_Galagete espanolaensis_	Scythridinae sp. 3
	Lineodes fontella	_Micropthyris anormalis_	_Galagete darwini_	Scythridinae sp. 5
	_Lineodes integra_*	_Neoleucinodes elegantalis_*	_Galagete levequei_	**Gelechiidae**
	Ercta vittata	_Sisyracera inabsconsalis_*	_Galagete cristobalensis_	_Aristotelia_ sp.
	Loxomorpha cambogialis	_Diaphania glauculalis_*	_Galagete pecki_	_Chionodes_ sp.
	Ocrasa nostralis *	_Samea ecclesialis_*	_Galagete cinerea_	_Ephysteris_ sp. 1
	Geometridae	_Hellula phidilealis_	**Tortricidae**	_Ephysteris_ sp. 2
	Pleuroprucha insulsaria	**Pieridae**	_Platynota colobota_	_Symmetrischema_ sp. 1
	_Disclisioprocta stellata_*	_Phoebis sennae marcellina_	**Choreutidae**	_Symmetrischema_ sp. 2
	Hesperiidae	**Lycaenidae**	_Tebenna galapagoensis_	_Untomia_ sp.
	_Calpodes ethlius_*	_Hemiargus ramon_*	**Pterophoridae**	**Pyralidae**
	Sphingidae	**Nymphalidae**	_Adaina scalesiae_	_Agathodes_ sp.
	Agrius cingulata	_Danaus gilippus thersippus_	_Platyptilia vilema_	_Pyrausta_ sp. 1
	Xylophanes tersa tersa	_Danaus plexippus megalippe_	_Postplatyptilia minima_	_Pyrausta_ sp. 2
	Noctuidae	**Geometridae**	_Stenoptilodes gielesi_	_Desmia_ sp.
	Argyrogramma verruca	_Triphosa affirmata_*	_Hellinsia nephogenes_	_Lineodes_ sp.
	Pseudoplusia includens	_Zeuctostyla vidrierata_	_Hellinsia cristobalis_	_Samea_ sp. 1
	Ctenoplusia oxygramma	_Sphacelodes vulneraria_*	_Hellinsia devriesi_	_Samea sp2_
	Anticarsia gemmatalis	**Sphingidae**	**Pyralidae**	_Neohelvibotis_ sp.
	Callopistria floridensis	_Cocytius antaeus_	_Fulrada carpasella_	_Neoleucinodes_ sp.

Pantropical	Neotropical & Nearctic	Neotropical region	Endemic	Undetermined (probably endemics)
	Spodoptera eridania	*Perigonia lusca lusca*	*Macrorrhinia pinta*	*Udea* sp. 1
	Spodoptera frugiperda	*Xylophanes pluto*	*Nicetiodes apianellus*	*Udea* sp. 2
	Heliothis virescens	**Uraniidae**	*Schafferiessa pumila*	Pyraustinae sp. 1
	Hypocala andremona	*Powondrella cingillaria*	*Schafferiessa galapagoensis*	Pyraustinae sp. 2
	Ommatochila mundula	**Arctiidae**	*Tota galdinella*	*La* sp. 1
	Condica concisa	*Utetheisa ornatrix*	*Euchromius galapagosalis*	*La* sp. 2
	Anicla infecta	**Noctuidae**	*Beebea guglielmi*	*La* sp. 3
	Anomis editrix	*Hypena vetustalis*	*Psara chathamalis*	*Argyria* sp.
	Ascalapha odorata	*Celiptera remigioides*	**Hesperiidae**	*Crambus* sp. 2
	Lesmone formularis	*Zale obsita*	*Urbanus dorantes galapagensis*	*Mesolia* sp.
	Gonodonta sicheas	*Metalectra praecisalis*	**Lycaenidae**	*Undulambia* sp.
	Gonodonta pyrgo	*Letis mycerina*	*Leptotes parrhasioides*	**Geometridae**
	Condica mobilis	*Epidromia zetophora*	**Nymphalidae**	*Cyclophora* sp.
	Condica sutor	*Gonodonta fulvangula*	*Agraulis vanillae galapagensis*	*Scopula* sp.
	Bagisara repanda	*Plusiodonta clavifera*	**Geometridae**	**Noctuidae**
	Melipotis indomita	*Leucania humidicola*	*Cyclophora impudens*	*Schrankia* sp.
	Spodoptera dolichos	*Pseudaletia sequax*	*Eupithecia leleupi*	Noctuidae sp. 1
	Spodoptera cosmioides	*Cropia infusa*	*Eupithecia perryvriesi*	*Plusiodonta* sp.
	Melipotis latipes	*Eublemma recta**	*Eupithecia galapagosata*	
	Thysania zenobia	*Heliocheilus cystiphora**	*Perizoma perryi*	
	Melipotis tinctoides		*Macaria cruciata cruciata*	
	Notioplusia illustrata		*Macaria cruciata isabelae*	
	Magusa orbifera		*Semiothisa cerussata*	

Pantropical	Neotropical & Nearctic	Neotropical region	Endemic	Undetermined (probably endemics)
	*Paectes arcigera**		*Thyrinteina infans*	
	*Spragueia margana**		*Thyrinteina umbrosa*	
	*Ponometia exigua**		*Oxydia lignata*	
	Leucania subpuncta		**Uraniidae**	
	Epitausa prona		*Epiplema becki*	
	Cobubatha numa		**Sphingidae**	
			Manduca sexta leucoptera	
			Manduca rustica calapagensis	
			Enyo lugubris delanoi	
			Erinnyis alope dispersa	
			Erinnyis ello encantada	
			Erinnyis obscura conformis	
			Eumorpha labruscae yupanquii	
			Xylophanes norfolki	
			Arctiidae	
			Utetheisa devriesi	
			Utetheisa galapagenis	
			Utetheisa perryi	
			Noctuidae	
			Hypena microfuliginea	
			Hypena fuliginea	
			Hypena minualis constans	
			Sorygaza variata	

Pantropical	Neotropic & Nearctic	Neotropical region	Endemic	Undetermined (probably endemics)
			Mocis incurvalis	
			Melipotis acontioides producta	
			Melipotis harrisoni	
			Hemeroplanis toddi	
			Metallata absumens contiguata	
			Psorya hadesia	
			Epidromia zephyritis	
			Autoplusia egena galapagensis	
			Anomis luridula professorum	
			Gonodonta biarmata evadens	
			Leucania cooperi	
			Magusa erema	
			Trachea cavagnaroi	
			Catabenoides seorsa	
			Neogalea sunia longfieldae	
			Spodoptera roseae	
			Agrotisia williamsi	
			Condica ruthae	
			Spragueia creton	
			Amyna insularum	
			Ozarba consternans	
			Agrotis consternans	
			Agrotis subterranea williamsi	
			Psaphara conwayi	
			Psaphara interclusa	
			Anicla oceanica	

Appendix 2. Galapagos Lepidoptera and their host plant relationship derived from this study and other information sources. Abbreviations indicate regions and countries where the record was obtained **A&N**: Andaman & Nicobar Islands, **ATr**: Afrotropical, **Au**: Australia, **Bah**: Bahamas, **Bang**: Bangladesh, **Bar**: Barbados, **Bel**: Belize, **Bem**: Bermuda, **Br**: Brazil, **Bl**: British Isles, **Bm**: Burma, **Cam**: Cameroon, **Can**: Canada, **Ch**: Chile, **Co**: Colombia, **Cos**: Cosmopolitan, **Cu**: Cuba, **Cyp**: Cyprus, **EAf**: East Africa, **Eu**: Europe, **Fin**: Finland, **Fj**: Fiji, **G**: Galapagos, **Gu**: Guam, **Gy**: Guyana, **HK**: Hong Kong, **Hw**: Hawaii, **IAu**: Indo Australian, **In**: India, **Ind**: Indonesia, **Ir**: Iraq, **Ja**: Jamaica, **Mr**: Mauritius, **Mx**: Mexico, **Na**: Nearctic, **Ni**: Nigeria, **Nt**: Neotropical, **NW**: New World, **OW**: Old World, **OWT**: Old World Tropic, **Pa**: Paraguay, **Pe**: Peru, **Pk**: Pakistan, **PR**: Puerto Rico, **PNG**: Papua New Guinea, **Pt**: Pan tropical, **SAf**: Southern Africa, **SB**: Sabah, **SeAs**: South East Asia, **SI**: Solomon Island, **SL**: Sri Lanka, **Sp**: Spain, **Ta**: Tanzania, **Th**: Thailand, **TT**: Trinidad & Tobago, **WAf**: West Africa, **WI**: West Indies, **WM**: West Malaysia, **V**: Viet Nam, **Za**: Zaire.

Taxa	Family Plant	Plant Species	Region or Country	Reference
Tischeriidae				
Astrotischeria scalesiaella	Asteraceae	*Scalesia pedunculata*	G.	Landry & Roque-Albelo (2003)
	Asteraceae	*Scalesia baurii*	G.	Landry & Roque-Albelo (2003)
Astrotischeria alcedoensis	Asteraceae	*Scalesia affinis*	G.	Landry & Roque-Albelo (2003)
Tineidae				
Xylesthia pruniramiella	Rosaceae	*Prunus* sp.	Na.	Robinson *et al.* 2001
Bucculatricidae				
Bucculatrix cordiella	Boraginaceae	*Cordia lutea*	G.	Davis *et al.* (2002)*
Gracillaridae				
Acrocercops sp.	Sterculiaceae	*Waltheria ovata*	G.	Present study
Cryptolectica sp.	Asteraceae	*Synedrella nodiflora*	G.	Present study
Yponomeutidae				
Atteva hysginiella	Simaroubaceae	*Castela galapageia*	G.	Landry & Landry (1998)
Prays galapagosella	Rutaceae	*Zanthoxylum fagara*	G.	Present study
Plutellidae				
Plutella xylostella	Apiaceae	*Apium graveolens*	Br.	Robinson *et al.* 2001.
	Apiaceae	*Daucus carota*	Br.	Robinson *et al.* 2001
	Asteraceae	*Galinsoga* sp.	Cos.	Robinson *et al.* 2001
	Brassicaceae	*Brassica* sp.	Au, Cos, Fj, In, Mr, SL, Sp, WM.	Robinson *et al.* 2001
	Brassicaceae	*Brassica napus*	Cu.	Robinson *et al.* 2001
	Brassicaceae	*Brassica oleracea*	Br, Cos, Cu, Hw, HK, In, SL, Na, WM, PR, Cos, EAf, PR, EAf, Th, SAf.	Robinson *et al.* 2001
	Brassicaceae	*Brassica rapa*	Cos, EAf, Hw, In, PR.	Robinson *et al.* 2001
	Brassicaceae	*Lepidium* sp.	Au, Hw.	Robinson *et al.* 2001
	Brassicaceae	*Raphanus sativus*	Br, Cos, HK, In, Ind, SL,WM.	Robinson *et al.* 2001
	Brassicaceae	*Rorippa* sp.	Au.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Capparaceae	*Capparis* sp.	Cos, Hw.	Robinson *et al.* 2001
	Caprifoliaceae	*Lonicera* sp.	Cos.	Robinson *et al.* 2001
	Poaceae	*Saccharum officinarum*	Na.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Cos, Na.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	In.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vicia faba*	Cos.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogea*	Na.	Robinson *et al.* 2001
Heliodinidae				
Heliodines galapagoensis	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Heppner & Landry (1998 b)
Coleophoridae				
Coleophora sp.	Amaranthaceae	*Amaranthus* sp.	G.	Present study
Calosima darwini	Asteraceae	*Scalesia gordilloi*	G.	Present study
	Boraginaceae	*Cordia lutea*	G.	Present study
	Cactaceae	*Jasminocereus thouarsii*	G.	Present study
	Leguminosae (Caes.)	*Parkinsonia aculeata*	G.	Present study
	Leguminosae (Mim.)	*Acacia macracantha*	G.	Present study
	Scrophulariaceae	*Capraria peruviana*	G.	Present study
Cosmopterigidae				
Cosmopterix galapagosensis	Cyperaceae	*Eleocharis mutata*	G.	Landry 2001
Cosmopterix attenuatella	Cyperaceae	*Cyperus rotundus*	Na.	Fletcher (1920)
	Cyperaceae	*Cyperus* sp.	NA.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Cu.	Robinson *et al.* 2001
Periploca darwini	Sapindaceae	*Dodonaea viscosa*	G.	Present study
Xilorictidae				
Scythridinae sp. 1	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Present study
Scythridinae sp. 2	Amaranthaceae	*Alternanthera halimifolia*	G.	Present study
Scythridinae sp. 3	Portulacaceae	*Portulaca oleracea*	G.	Present study

Taxa	Family Plant	Plant Species	Region or Country	Reference
Gelechiidae				
Ephysteris sp. 1	Poaceae	*Sporobolus virginicus*	G.	Present study
Evippe omphalopa	Leguminosae (Mim.)	*Prosopis juliflora*	G.	Present study
Anacampsis primigenia	Euphorbiaceae	*Croton scouleri*	G.	Present study
Compsolechia ? *salebrosa*	Leguminosae (Fab.)	*Desmodium incanum*	G.	Present study
Tuta absoluta	Poaceae	*Saccharum officinarum*	Co.	Robinson *et al.* 2001
	Solanaceae	*Datura stramonium*	Nt.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Ch.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Nt.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	G.	Present study
			Nt.	Robinson *et al.* 2001
Dichomeris acuminata	Solanaceae	*Nicotiana* sp.	Nt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Desmodium* sp.	Hw.	Zimmerman (1978)
	Leguminosae (Fab.)	*Medicago* sp.	Hw.	Zimmerman (1978)
	Leguminosae (Fab.)	*Cajanus cajan*	Hw.	Zimmerman 1978
	Leguminosae (Fab.)	*Sesbania* sp.	Hw.	Zimmerman 1978
	Leguminosae (Fab.)	*Tephrosia* sp.	Hw.	Zimmerman 1978
Elachistidae				
Stenoma catenifer	Lauraceae	*Persea americana*	G.	Landry & Roque-Albelo 2003*
			B, Nt	Robinson *et al.* 2001
Tortricidae				
Strepsicrates smithiana	Leguminosae (Fab.)	*Vicia faba*	Br.	Robinson *et al.* 2001
	Myrtaceae	*Psidium guajava*	Cu, Hw, PR.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	Cu.	Robinson *et al.* 2001
	Myrtaceae	*Eugenia* sp.	Na, Nt.	Robinson *et al.* 2001
Crocidosema plebejana	Chenopodiaceae	*Atriplex* sp.	Au.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita* sp	Na.	Robinson *et al.* 2001
	Malvaceae	*Abutilon* sp.	Au, EAf, Na, Pk, SEAs.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Malvaceae	*Anoda cristata*	Cos.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Au, Cos, Na, SEAs.	Robinson *et al.* 2001
	Malvaceae	*Herissantia crispa*	Na.	Robinson *et al.* 2001
	Malvaceae	*Hibiscus* sp.	Au, Cos, EAf, Na, SEAs.	Robinson *et al.* 2001
	Malvaceae	*Hibiscus rosa-sinensis*	Na.	Robinson *et al.* 2001
	Malvaceae	*Malvastrum americanum*	Na.	Robinson *et al.* 2001
	Malvaceae	*Malvaviscus arboreus*	Cos.	Robinson *et al.* 2001
	Malvaceae	*Sida rhombifolia*	Br, Na.	Robinson *et al.* 2001
	Verbenaceae	*Lantana camara*	Fj.	Robinson *et al.* 2001
Episimus transferranus	Anacardiaceae	*Spondias purpurea*	G.	Present study
Platynota colobota	Rubiaceae	*Chiococca alba*	G.	Present study
Pterophoridae				
Megalorhipida leucodactyla	Amaranthaceae	*Amaranthus* sp.	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	In.	Robinson *et al.* 2001
	Nyctaginaceae	*Boerhavia caribaea*	G.	Landry (1993)
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Landry (1993)
	Portulacaceae	*Portulaca* sp.	Bar.	Robinson *et al.* 2001
	Zygophyllaceae	*Tribulus terrestris*	In.	Robinson *et al.* 2001
Lantanophaga pusillidactyla	Verbenaceae	*Phyla nodiflora*	NA.	Mattew *et al.* 1990
	Verbenaceae	*Lantana camara*	Hw.	Zimmerman 1958
			Au, HK, In, Na, Saf, Za.	Robinson *et al.* 2001
Stenoptilodes brevipennis	Scrophulariaceae	*Capraria peruviana*	G.	Landry *et al.* 2004*
Platyptilia vilema	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Roque-Albelo 2003*
Postplatyptilia huigraica	Lamiaceae	*Hyptis spicigera*	G.	Landry (1993)
	Lamiaceae	*Hyptis mutabilis*	G.	Landry *et al.* 2004*
Exelastis montischristi	Leguminosae (Fab.)	*Rhynchosia minima*	G.	Landry (1993)
Exelastis pumilio	Leguminosae (Fab.)	*Desmodium glabrum*	G.	Landry (1993)
	Leguminosae (Fab.)	*Desmodium incanum*	Na.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Leguminosae (Fab.)	*Desmodium* sp.	In, NA	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	In.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vicia* sp.	In.	Robinson *et al.* 2001
Adaina scalesiae	Asteraceae	*Scalesia microcephala*	G.	Landry (1993)
	Asteraceae	*Scalesia incisa*	G.	Landry (1993)
	Asteraceae	*Scalesia pedunculata*	G.	Landry *et al.* 2004*
	Asteraceae	*Scalesia retroflexa*	G.	Landry *et al.* 2004*
	Asteraceae	*Scalesia gordilloi*	G.	Landry *et al.* 2004*
	Asteraceae	*Scalesia villosa*	G.	Landry *et al.* 2004*
	Asteraceae	*Lecocarpus lecocarpioides*	G.	Landry *et al.* 2004*
Hellinsia nephogenes	Asteraceae	*Scalesia affinis*	G.	Landry (1993)
Choreutidae				
Tebenna galapagoensis	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Roque-Albelo (2003)*
	Asteraceae	*Darwiniothamnus lancifolius*	G.	Present study
Pyralidae				
Pyralis manihotalis	Apiaceae	*Coriandrum sativum*	Ind.	Robinson *et al.* 2001
	Dioscoreaceae	*Dioscorea* sp.	Ind.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Tamarindus* sp.	Ind.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Ind.	Robinson *et al.* 2001
	Rubiaceae	*Coffea arabica*	Ind.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Ind.	Robinson *et al.* 2001
	Sterculiaceae	*Theobroma cacao*	Ind.	Robinson *et al.* 2001
	Zingiberaceae	*Zingiber officinale*	In.	Robinson *et al.* 2001
Ocrasa nostralis	Anacardiaceae	*Mangifera indica*	G.	Present study
	Leguminosae (Fab.)	*Medicago sativa*	Cu, PR.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	EAf	Robinson *et al.* 2001
	Agavaceae	*Agave* sp.	CR.	Janzen & Hallwachs 2001
Phidotricha erigens	Anacardiaceae	*Mangifera indica*	Na.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Rosaceae	*Eriobotrya japonica*	Na.	Robinson *et al.* 2001
	Leguminosae (Caes)	*Tamarindus indica*	Na.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Na.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Na.	Robinson *et al.* 2001
	Zingiberaceae	*Zingiber* sp.	Na.	Robinson *et al.* 2001
Ancylostomia stercorea	Leguminosae (Fab.)	*Cajanus cajan*	Bel, Br, Nt, Na, Pan, PR, Wi.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	Na, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Crotalaria* sp.	Br.	Robinson *et al.* 2001
	Polygonaceae	*Rumex* sp.	Na.	Robinson *et al.* 2001
Etiella zinckenella	Arecaceae	*Elaeis guineensis*	WMa.	Robinson *et al.* 2001
	Cactaceae	*Opuntia* sp.	Na.	Robinson *et al.* 2001
	Capparaceae	*Cleome* sp.	Na.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita* sp.	Na.	Robinson *et al.* 2001
	Cucurbitaceae	*Citrullus* sp.	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	WMa.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	Br, Cos, EAf, In, Na, PR, SL, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Crotalaria incana*	Na, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Crotalaria retusa*	Cu.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Lablab purpureus*	A&N, Bm, Cos, EAf, In, Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Br, Cyp, In, Na, Pr, SL.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	Cos, In, Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Tephrosia* sp.	NA, WMa.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vicia* sp.	Ind, Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	Ind, Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Sesbania* sp.	Na	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Caesalpinia* sp.	In.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Cassia* sp.	Ind.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Canavalia* sp.	Br.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Leguminosae (Fab.)	*Mucuna* sp.	Br.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Na.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annuum*	NA.	Robinson *et al.* 2001
Fulrada carpasella	Celastraceae	*Maytenus octogona*	G.	Landry & Neunzig 1997
Fundella argentina	Leguminosae (Caes.)	*Cassia* sp.	Na, Nt.	Robinson. *et al.* 2001
	Leguminosae (Caes.)	*Senna alata*	Na.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna bicapsularis*	Cu, Na, Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Rhynchosia minima*	G.	Present study
Hypsipyla grandella	Araliaceae	*Schefflera* sp.	Br.	Robinson *et al.* 2001
	Meliaceae	*Cedrela odorata*	G.	Gara & Onore 1989
			CR.	Janzen & Hallwachs 2001
	Meliaceae	*Swietenia* sp.	Nt.	Robinson *et al.* 2001
	Meliaceae	*Swietenia macrophylla*	Na.	Robinson *et al.* 2001
Macrorrhinia pinta	Amaranthaceae	*Alternanthera halimifolia*	G.	Present study
	Amaranthaceae	*Alternanthera echinocephala*	G.	Pressent study
Oryctometopia fossulatella	Leguminosae (Caes.)	*Senna picta*	G.	Present study
	Leguminosae (Caes.)	*Parkinsonia aculeata*	G.	Landry & Neunzig 1997
	Leguminosae (Caes.)	*Bauhinia* sp.	NW.	Robinson *et al.* 2001
Schafferiessa galapagoensis	Asteraceae	*Scalesia affinis*	G.	Present study
	Asteraceae	*Scalesia helleri*	G.	Present study
	Asteraceae	*Scalesia gordilloi*	G.	Present study
	Asteraceae	*Scalesia pedunculata*	G.	Present study
	Asteraceae	*Scalesia retroflexa*	G.	Present study
	Asteraceae	*Scalesia stewartii*	G.	Present study
Schafferiessa pumila	Asteraceae	*Scalesia affinis*	G.	Present study
	Asteraceae	*Scalesia aspera*	G.	Present study
	Asteraceae	*Lecocarpus lecocarpoides*	G.	Present study
	Asteraceae	*Lecocarpus darwinii*	G.	Present study

Taxa	Family Plant	Plant Species	Region or Country	Reference
Undulambia sp.	Dennstaedtiaceae	*Pteridium arachnoideum*	G.	Present study
Parapoynx fluctuosalis	Poaceae	*Oryza sativa*	Bm, Br, Gu, Hw, In, Nt, OW, SB, SL,	Robinson *et al.* 2001
Hellula phidilealis	Brassicaceae	*Brassica napus*	Na.	Robinson *et al.* 2001
	Brassicaceae	*Brassica oleracea*	Br, Na, Pt, TT.	Robinson *et al.* 2001
	Brassicaceae	*Brassica rapa*	Br, Cu, Na.	Robinson *et al.* 2001
	Capparaceae	*Cleome viscosa*	Gy.	Robinson *et al.* 2001
Penestola bufalis	Avicenniaceae	*Avicennia germinans*	G.	Present study
Beebea guglielmi	Cactaceae	*Opuntia echios*	G.	Present study
	Cactaceae	*Opuntia insularis*	G.	Present study
	Cactaceae	*Opuntia helleri*	G.	Present study
Hymenia perspectalis	Asteraceae	*Synedrella nodiflora*	G.	Present study
	Amaranthaceae	*Amaranthus* sp.	PR.	Robinson *et al.* 2001
	Amaranthaceae	*Alternanthera* sp.	Na.	Robinson *et al.* 2001
	Asteraceae	*Eclipta prostrata*	Na, NW.	Robinson *et al.* 2001
	Balsaminaceae	*Impatiens balsamica*	PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	In.	Robinson *et al.* 2001
Pilocrocis ramentalis	Acanthaceae	*Odontonema* sp.	Na.	Robinson *et al.* 2001
	Acanthaceae	*Justicia galapagana*	Na.	Robinson *et al.* 2001
Asciodes quietalis	Euphorbiaceae	*Manihot esculenta*	G.	Present study
	Nyctaginaceae	*Bouganvillea* sp.	Co.	Robinson *et al.* 2001
	Nyctaginaceae	*Pisonia floribunda*	Bh, Br, Na, PR.	Robinson *et al.* 2001
	Nyctaginaceae	*Mirabilis jalapa*	G.	Perry & DeVries 2003.
	Nyctaginaceae	*Cryptocarpus piriformis*	PR.	Robinson *et al.* 2001
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Perry & DeVries (2003).
	Rutaceae	*Citrus* sp.	G.	Perry & DeVries (2003).
Pleuroptya silicalis	Araliaceae	*Schefflera* sp.	Ja.	Robinson *et al.* 2001
	Nyctaginaceae	*Bougainvillea spectabilis*	PR.	Robinson *et al.* 2001
	Urticaceae	*Urtica* sp.	Cu.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Urticaceae	*Pilea baurii*	Nt.	Robinson *et al.* 2001
Agathodes designalis	Asclepiadaceae	*Asclepias* sp.	G.	Present study
	Verbenaceae	*Citharexylum* sp.	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Erythrina* sp.	Na, PR.	Robinson *et al.* 2001
			Au, Br, Cu, EAf, Ind, Nt, PR, SAf.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Leguminosae (Mim.)	*Inga vera*	Na, PR.	Robinson *et al.* 2001
			Cu.	Alayo & Valdes 1982
	Myrtaceae	*Psidium guajava*	Br.	Robinson *et al.* 2001
Pyrausta panopealis	Lamiaceae	*Salvia occidentalis*	G.	Present study
	Lamiaceae	*Hyptis mutabilis*	G.	Present study
Syngamia florella	Rubiaceae	*Spermacoce* sp.	Na.	Robinson *et al.* 2001
	Rubiaceae	*Borreria* sp.	Bem.	Ferguson *et al.* 1991
Rhectocraspeda periusalis	Amaranthaceae	*Amaranthus* sp	Na	Robinson *et al.* 2001
	Cucurbitaceae	*Momordica charantia*	Na	Robinson *et al.* 2001
	Myrtaceae	*Eugenia* sp.	WI	Robinson *et al.* 2001
	Piperaceae	*Piper* sp.	Na.	Robinson *et al.* 2001
	Solanaceae	*Capsicum frutescens*	CR.	Janzen & Hallwachs 2001
	Solanaceae	*Lycopersicon* sp.	PR	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Na, NW.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Bem, Br, Cu, Pr, Na.	Robinson *et al.* 2001
			G.	Present study
	Solanaceae	*Solanum eriathum*	Cu, Na, PR	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Na	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Na, Nw, PR, WI	Robinson *et al.* 2001
	Solanaceae	*Solanum americanum*	Br, Na, PR, NW.	Robinson *et al.* 2001
			G.	Present study
Herpetogramma phaeopteralis	Amaranthaceae	*Celosia* sp.	Cos.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Amaranthaceae	*Gomphrena globosa*	PR.	Robinson *et al.* 2001
	Poaceae	*Cynodon* sp.	Cos.	Robinson *et al.* 2001
	Poaceae	*Stenotaphrum secundatum*	Cu, Na, PR.	Robinson *et al.* 2001
Herpetogramma bipunctalis	Amaranthaceae	*Achyranthes aspera*	Na, PR.	Robinson *et al.* 2001
	Amaranthaceae	*Alternanthera* sp.	Cos.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus* sp.	Cos, Na, PR.	Robinson *et al.* 2001
	Amaranthaceae	*Gomphrena globosa*	Cu, Na.	Robinson *et al.* 2001
	Araceae	*Xanthosoma* sp.	Na.	Robinson *et al.* 2001
	Brassicaceae	*Brassica* sp.	Na.	Robinson *et al.* 2001
	Euphorbiaceae	*Codiaeum* sp.	In.	Robinson *et al.* 2001
	Hydrangeaceae	*Hydrangea* sp.	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Cos, Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	Na.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Na.	Robinson *et al.* 2001
	Myrtaceae	*Eugenia* sp.	WM.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Na.	Robinson *et al.* 2001
	Rubiaceae	*Spermacoce* sp.	Cos, Th.	Robinson *et al.* 2001
	Solanaceae	*Capsicum frutescens*	PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum erianthum*	WM.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	A&N, In, Na, PR, SL, WM.	Robinson *et al.* 2001
	Tiliaceae	*Corchorus olitorius*	Na.	Robinson *et al.* 2001
Diaphania indica	Annonaceae	*Annona muricata*	SL.	Robinson *et al.* 2001
	Cucurbitaceae	*Citrillus lanatus*	Th, WM.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis melo*	Cos, Gu, Na, Th.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis sativus*	Cos, EAf, Gu, HK, Th, Na, WM.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis dipsaceus*	G.	Present study
	Cucurbitaceae	*Cucurbita moschata*	Cos, HK, Gu.	Robinson *et al.* 2001
	Cucurbitaceae	*Momordica charantia*	A & N, Na, SL, Th, WM.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
			G.	Present study
	Leguminosae (Fab.)	*Glycine max*	Cos.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Cos, EAf, SAf.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora* sp.	Th.	Robinson *et al.* 2001
	Solanaceae	*Solanum* sp.	SL.	Robinson *et al.* 2001
Diaphania hyalinata	Cucurbitaceae	*Citrullus lanatus*	Cu, Na, PR.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis melo*	Br, Na, PR.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis sativus*	Br, Cu, Na, NW, PR.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita* sp.	Br, Na, NW.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita moschata*	Cu, Pr.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita ficifolia*	CR.	Janzen & Hallwachs 2001
	Cucurbitaceae	*Momordica* sp.	Cu.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea* sp.	PR.	Robinson *et al.* 2001
	Euphorbiaceae	*Acalypha* sp.	Na.	Robinson *et al.* 2001
Diaphania nitidalis	Cucurbitaceae	*Citrullus lanatus*	Br, Cu.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis sativus*	Br, Cu, Na, NW, PR.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis melo*	Br, Na, NW.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucurbita ficifolia*	G.	Present study
	Cucurbitaceae	*Momordica charantia*	Na.	Robinson *et al.* 2001
Omiodes indicata	Acanthaceae	*Justicia* sp.	In.	Robinson *et al.* 2001
	Amaranthaceae	*Alternanthera* sp.	Th.	Robinson *et al.* 2001
	Annonaceae	*Annona muricata*	SL.	Robinson *et al.* 2001
	Convolvulaceae	*Merremia aegyptia*	G.	Present study
	Euphorbiaceae	*Manihot esculenta*	Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	EAf, In, Pt, SL, WAf, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Desmodium intortum*	Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Lablab purpureus*	Bm, Pt, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	Cu, In, Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Mucuna* sp.	Cu.	Robinson *et al.* 2001

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	Leguminosae (Fab.)	*Phaseolus vulgaris*	Pt, Ind, PR, SL, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pueraria phaseoloides*	PR.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Pt.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Pt.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon* sp.	Pt.	Robinson *et al.* 2001
	Verbenaceae	*Lantana camara*	PR.	Robinson *et al.* 2001
Desmia sp.	Rubiaceae	*Psychotria rufipes*	G.	Present study
Lineodes integra	Solanaceae	*Capsicum annuum*	Na.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Cu, Na.	Robinson *et al.* 2001
	Solanaceae	*Physalis peruviana*	Na.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Na.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Solanum quitoense*	CR.	Janzen & Hallwachs 2001
	Solanaceae	*Nicotiana* sp.	Na.	Robinson *et al.* 2001
Lineodes sp.	Solanaceae	*Acnistus ellipticus*	G.	Present study
Marasmia trapezalis	Poaceae	*Saccharum officinarum*	PR.	Robinson *et al.* 2001
Terastia meticulosalis	Leguminosae (Fab.)	*Erythrina* sp.	In, Ind, Na, Nt, Pt, SAf.	Robinson *et al.* 2001
	Meliaceae	*Cedrela* sp.	SL.	Robinson *et al.* 2001
	Rubiaceae	*Coffea* sp.	EAf, V.	Robinson *et al.* 2001
	Sterculiaceae	*Theobroma cacao*	Pt.	Robinson *et al.* 2001
Spoladea recurvalis	Aizoaceae	*Sesuvium portulacastrum*	Hw.	Robinson *et al.* 2001
	Aizoaceae	*Trianthema portulacastrum*	In.	Robinson *et al.* 2001
	Amaranthaceae	*Achyranthes aspera*	In.	Robinson *et al.* 2001
	Amaranthaceae	*Alternanthera sessilis*	Th.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus* sp.	Au, Br, Cos, EAf, Gu, Hw, In, Ind, Na, PR, SEAs, WM.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus dubius*	Cu.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Amaranthaceae	*Amaranthus hybridus*	Na.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus spinosus*	Th.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus viridis*	Th.	Robinson *et al.* 2001
	Amaranthaceae	*Gomphrena* sp.	In.	Robinson *et al.* 2001
	Amaranthaceae	*Celosia argentea*	Cu.	Robinson *et al.* 2001
	Amaranthaceae	*Gomphrena* sp.	PR.	Robinson *et al.* 2001
	Araceae	*Colocasia* sp.	Na.	Robinson *et al.* 2001
	Araceae	*Xanthosoma* sp.	Na.	Robinson *et al.* 2001
	Bataceae	*Batis maritima*	Hw.	Robinson *et al.* 2001
	Balsaminaceae	*Impatiens* sp.	Na.	Robinson *et al.* 2001
	Chenopodiaceae	*Chenopodium* sp.	Au, EAf.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Na.	Robinson *et al.* 2001
	Rutaceae	*Citrus* sp.	WM.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	PR.	Robinson *et al.* 2001
	Labiatae	*Mentha* sp.	Na.	Robinson *et al.* 2001
	Labiatae	*Solenostemon* sp.	WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	In.	Robinson *et al.* 2001
	Nyctaginaceae	*Boerhavia* sp.	Th.	Robinson *et al.* 2001
	Phytolaccaceae	*Phytolacca americana*	Na.	Robinson *et al.* 2001
	Polygonaceae	*Polygonum* sp.	Na.	Robinson *et al.* 2001
	Portulacaceae	*Portulaca oleraceae*	Na.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Na.	Robinson *et al.* 2001
Microthyris anormalis	Convolvulaceae	*Ipomoea batatas*	PR.	Robinson *et al.* 2001
	Convolvulaceae	*Stictocardia tilifolia*	G.	Present study
	Convolvulaceae	*Merremia umbellata*	CR.	Janzen & Hallwachs 2001
Palpita flegia	Apocynaceae	*Nerium oleander*	Na.	Robinson *et al.* 2001
	Apocynaceae	*Thevetia peruviana*	Br, Cu, Na, PR.	Robinson *et al.* 2001
	Apocynaceae	*Thevetia* sp.	CR.	Janzen & Hallwachs 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Apocynaceae	*Cascabela thevetia*	G.	Present study
Neoleucinodes elegantalis	Cactaceae	*Cereus* sp.	Na.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annuum*	Br, Na.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Br, Na, PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Br, Na, Nt, TT.	Robinson *et al.* 2001
	Solanaceae	*Solanum quitoense*	Na.	Robinson *et al.* 2001
	Solanaceae	*Solanum betaceum*	G.	Present study
Maruca vitrata	Euphorbiaceae	*Ricinus* sp.	Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	Pt, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	Na, Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Mucuna* sp.	WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Na, WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Sesbania* sp.	WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vicia* sp.	WM.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	Na, Pt, WM.	Robinson *et al.* 2001
	Malvaceae	*Hibiscus* sp.	Pt.	Robinson *et al.* 2001
	Poaceae	*Oryza sativa*	Pt.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana* sp.	Pt.	Robinson *et al.* 2001
Loxomorpha cambogialis	Amaranthaceae	*Amaranthus* sp.	Br.	Robinson *et al.* 2001
	Asteraceae	*Lecocarpus darwinii*	G.	Present study
	Cactaceae	*Opuntia* sp.	Cu.	Robinson *et al.* 2001
	Portulacaceae	*Talinum paniculatum*	Br.	Robinson *et al.* 2001
Pyraustinae sp.1	Boraginaceae	*Tournefortia pubecens*	G.	Present study
Uraniidae				
Epiplema becki	Verbenaceae	*Duranta dombeyana*	G.	Roque-Albelo & Mieles 2005*
Arctiidae				
Utetheisa ornatrix	Leguminosae (Fab.)	*Crotalaria incana*	G.	Present study

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	Leguminosae (Fab.)	*Crotalaria pumila*	G.	Present study
			CR.	Janzen & Hallwachs 2001.
	Leguminosae (Fab.)	*Crotalaria retusa*	G.	Present study
			Br, PR.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Malvaceae	*Gossypium* spp	Br.	Robinson *et al.* 2001
Utetheisa galapagenis	Boraginaceae	*Tournefortia pubecens*	G.	Hayes 1975
	Boraginaceae	*Tournefortia psylostachia*	G.	Hayes 1975
	Boraginaceae	*Tournefortia rufo-sericea*	G.	Perry & DeVries 2003
	Boraginaceae	*Heliotropium curassavicum*	G.	Perry & DeVries 2003
Utetheisa perryi	Boraginaceae	*Tournefortia pubecens*	G.	Present study
	Boraginaceae	*Tournefortia rufo-sericea*	G.	Present study
Utetheisa devriesi	Boraginaceae	*Tournefortia pubecens*	G.	Present study
	Boraginaceae	*Tournefortia rufo-sericea*	G.	Present study
Noctuidae				
Hypena microfuliginea	Sterculiaceae	*Waltheria ovata*	G.	Present study
Hypena fuliginea	Sterculiaceae	*Waltheria ovata*	G.	Present study
Hypena vetustalis	Acanthaceae	*Blechum pyramidatum*	G.	Present study
	Convolvulaceae	*Ipomoea batatas*	Bar.	Robinson *et al.* 2001
Hypena minualis constans	Malvaceae	*Sida rombifolia*	G.	Present study
Hypocala andremona	Juglandaceae	*Juglans neotropica*	G.	Present study
	Rosaceae	*Eriobotrya japonica*	Cu.	Robinson *et al.* 2001
Zale obsita	Leguminosae (Caes.)	*Senna* sp.	Cu.	Robinson *et al.* 2001
Ascalapha odorata	Anacardiaceae	*Mangifera indica*	NW.	Robinson *et al.* 2001
	Leguminosae (Mim.)	*Acacia* sp.	Br.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna* sp.	Br, Nt, PR.	Robinson *et al.* 2001
	Leguminosae (Mim.)	*Inga* sp.	Br.	Robinson *et al.* 2001
	Moraceae	*Ficus* sp.	CR.	Janzen & Hallwachs 2001

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			PR.	Robinson *et al.* 2001
Thysania zenobia	Leguminosae (Caes.)	*Senna* sp.	Br.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
Epidromia zephyritis	Rhamnaceae	*Scutia spicata*	G.	Hayes 1975
	Combretaceae	*Laguncularia racemosa*	G.	Hayes 1975
Psorya hadesia	Celastraceae	*Maytenus octagona*	G.	Hayes 1975
Epitausa prona	Amaranthaceae	*Amaranthus lividus*	G.	Present study
	Amaranthaceae	*Alternanthera echinocephala*	G.	Present study
	Convolvulaceae	*Ipomoea pes-caprae*	G.	Present study
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Present study
	Portulacaceae	*Portulaca oleracea*	G.	Present study
Anticarsia gemmatalis	Leguminosae (Fab.)	*Piscidia carthagenensis*	G.	Hayes 1975
	Leguminosae (Fab)	*Rhynchosia minima*	G.	Hayes 1975
	Leguminosae (Fab.)	*Dioclea* sp.	CR.	Janzen & Hallwachs 2001
	Leguminosae (Fab.)	*Galactia striata*	CR.	Janzen & Hallwachs 2001
	Leguminosae (Fab.)	*Tephrosia* sp.	CR.	Janzen & Hallwachs 2001
	Leguminosae (Fab.)	*Arachis hypogea*	Br, Cu, Nt, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	Bar.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Br, Cu, PR, WI.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	Br, Cu, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Mucuna* sp.	Br, Cu, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	Bar, PR, WI.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Sesbania* sp.	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cannavalia* sp.	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Mucuna* sp.	Br.	Robinson *et al.* 2001
	Poaceae	*Oryza sativa*	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	Br.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Leguminosae (Fab.)	*Pueraria phaseoloides*	Br.	Robinson *et al.* 2001
	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Hayes 1975
Lesmone formularis	Leguminosae (Caes.)	*Senna pistaciifolia*	G.	Present study
			PR.	Robinson *et al.* 2001
Melipotis acontioides producta	Leguminosae (Caes.)	*Parkinsonia acualeata*	G.	Hayes 1975
			PR.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Caesalpinia* sp.	NW.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Delonix regia*	Ja, PR.	Robinson *et al.* 2001
Melipotis indomita	Leguminosae (Mim.)	*Prosopis juliflora*	G.	Hayes 1975
	Leguminosae (Mim.)	*Prosopis* spp.	Br, NW.	Robinson *et al.* 2001
Melipotis harrisoni	Leguminosae (Mim.)	*Acacia macracantha*	G.	Hayes 1975
	Leguminosae (Mim.)	*Acacia rorundiana*	G.	Hayes 1975
Letis mycerina	Anacardiaceae	*Mangifera indica*	Bel.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Inga* spp.	CR.	Janzen & Hallwachs 2001
	Rubiaceae	*Coffea arabica*	PR.	Robinson *et al.* 2001
Gonodonta fulvangula	Annonaceae	*Annona cherimola*	G.	Present study
	Annonaceae	*Annona purpurea*	CR.	Janzen & Hallwachs 2001
	Annonaceae	*Annona reticulata*	CR.	Janzen & Hallwachs 2001
	Piperaceae	*Piper* sp.	CR.	Janzen & Hallwachs 2001
Gonodonta pyrgo	Annonaceae	*Annona cherimola*	G.	Present study
	Annonaceae	*Annona purpurea*	CR.	Janzen & Hallwachs 2001
	Annonaceae	*Annona reticulata*	CR.	Janzen & Hallwachs 2001
	Anacardiaceae	*Mangifera indica*	Bel, V.	Robinson *et al.* 2001
Gonodonta biarmata evadens	Annonaceae	*Annona cherimola*	G.	Present study
	Annonaceae	*Annona muricata*	G.	Present study
	Solanaceae	*Cestrum* sp.	Br	Robinson *et al.* 2001
Gonodonta sicheas	Menispermaceae	*Cissampelos pareira*	CR.	Janzen & Hallwachs 2001
Anomis editrix	Malvaceae	*Malvaviscus arboreus*	CR.	Janzen & Hallwachs 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Malvaceae	*Malachra alceifolia*	Cu	Robinson *et al.* 2001
	Tiliaceae	*Corchorus* spp.	Cu, Gy.	Robinson *et al.* 2001
	Tiliaceae	*Triumfetta* sp.	PR.	Robinson *et al.* 2001
Anomis erosa	Malvaceae	*Abutilon depauperatum*	G.	Present study
	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001
	Malvaceae	*Hibiscus* sp.	Cu.	Robinson *et al.* 2001
	Malvaceae	*Sida* sp.	Br, PR.	Robinson *et al.* 2001
Anomis illita	Malvaceae	*Hibiscus tiliaceus*	G.	Hayes 1975
	Malvaceae	*Gossypium* sp.	Cu.	Robinson *et al.* 2001
	Malvaceae	*Malachra capitata*	PR.	Robinson *et al.* 2001
	Malvaceae	*Urena* sp.	Cu.	Robinson *et al.* 2001
Anomis luridula	Malvaceae	*Gossypium barbadense*	Bar.	Robinson *et al.* 2001
Plusiodonta clavifera	Sterculiaceae	*Guazuma ulmifolia*	CR.	Janzen & Hallwachs 2001
Mouralia tinctoides	Commelinaceae	*Commelina difusa*	G.	Present study
	Commelinaceae	*Tradescantia* sp.	NW.	Robinson *et al.* 2001
Argyrogramma verruca	Boraginaceae	*Tournefortia rufo-sericea*	G.	Present study
	Boraginaceae	*Heliotropium indicum*	CR.	Janzen & Hallwachs 2001
	Cruciferae	*Brassica oleracea*	NW.	Robinson *et al.* 2001
	Labiatae	*Hyptis* sp.	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	NW.	Robinson *et al.* 2001
	Portulacaceae	*Portulaca oleracea*	PR.	Robinson *et al.* 2001
Autoplusia egena galapagensis	Labiatae	*Mentha piperita*	G.	Present study
	Labiatae	*Melissa officinalis*	Br	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus* sp.	NW, PR.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	CR.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	PR.	Robinson *et al.* 2001
Notioplusia illustrata	Verbenaceae	*Lantana camara*	G.	Present study
Pseudoplusia includens	Asteraceae	*Lactuca sativa*	G.	Present study

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Asteraceae	*Ageratum conyzoides*	Br.	Robinson *et al.* 2001
	Boraginaceae	*Cordia leucophlyctis*	G.	Hayes 1975
	Boraginaceae	*Tournefortia psilostachya*	G.	Hayes 1975
	Boraginaceae	*Heliotropium angiospermun*	G.	Hayes 1975
	Convolvulaceae	*Ipomoea batatas*	PR.	Robinson *et al.* 2001
	Cruciferae	*Brassica olareacea*	G.	Present study
	Euphorbiaceae	*Manihot sculenta*	G.	Present study
	Labiatae	*Salvia* sp.	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	G.	Present study
			Br, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Desmodium* sp.	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	G.	Present study
	Linaceae	*Linum* sp.	Br.	Robinson *et al.* 2001
	Loasaceae	*Mentzelia aspera*	G.	Hayes 1975
	Malvaceae	*Gossypium* sp.	Br.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	G.	Present study
			Br.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculenta*	Br, CR, PR.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Br.	Robinson *et al.* 2001
	Umbelliferae	*Petrosedlinum crispum*	Br.	Robinson *et al.* 2001
	Verbenaceae	*Lantana peduncularis*	G.	Hayes 1975
Ctenoplusia oxygramma	Asteraceae	*Helianthus annuus*	Cos.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Cos.	Robinson *et al.* 2001
Spodoptera cosmioides	Amaryllidaceae	*Crinum* sp.	CR.	Janzen & Hallwachs 2001
	Annonaceae	*Annona purpurea*	CR.	Janzen & Hallwachs 2001
	Asteraceae	*Lactuca sativa*	NW.	Robinson *et al.* 2001
	Asteraceae	*Helianthus annuus*	Cu.	Robinson *et al.* 2001
	Asparagaceae	*Asparagus officinalis*	Co.	Robinson *et al.* 2001
	Cucurbitaceae	*Luffa* sp.	Cu.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Dioscoreaceae	*Dioscorea* sp.	CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Manihot sculenta*	G.	Present study
	Euphorbiaceae	*Ricinus communis*	Cu.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Croton* sp.	CR.	Janzen & Hallwachs 2001
	Labiatae	*Solenostemon* sp.	Cu.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogea*	Cu, NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* spp.	Cu, NW.	Robinson *et al.* 2001
	Liliaceae	*Allium cepa*	Br, NW.	Robinson *et al.* 2001
	Malvaceae	*Gossypium darwinii*	G.	Present study
	Malvaceae	*Gossypium barbadense*	Bar.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* spp.	Br, Cu, NW.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	NW.	Robinson *et al.* 2001
	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Present study
	Poaceae	*Avena sativa*	NW.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annuum*	Br	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculenta*	Br, Cu, PR.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Solanaceae	*Lycopersicon* sp.	NW.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Cu, PR.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana* sp.	NW.	Robinson *et al.* 2001
	Vitaceae	*Vitis* sp.	NW.	Robinson *et al.* 2001
	Ulmaceae	*Trema micrantha*	CR.	Janzen & Hallwachs 2001
Spodoptera frugiperda	Amaranthaceae	*Amaranthus hybridus*	Cos.	Robinson *et al.* 2001
	Apocynaceae	*Plumeria* sp.	Cos.	Robinson *et al.* 2001
	Asparagaceae	*Asparagus officinalis*	Co.	Robinson *et al.* 2001
	Asteraceae	*Helianthus annuus*	Cos, Nt.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Caricaceae	*Carica papaya*	Cu.	Robinson *et al.* 2001
	Chenopodiaceae	*Chenopodium* sp.	Cos.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Cos.	Robinson *et al.* 2001
	Euphorbiaceae	*Manihot esculenta*	G.	Present study
	Iridaceae	*Gladiolus* sp.	Cu, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogea*	Cos, Cu.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	Cu.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Cos.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Macroptilium lathyroides*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	Cos, PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pueraria* sp.	Cu.	Robinson *et al.* 2001
	Liliaceae	*Allium cepa*	G.	Present study
			PR.	Robinson *et al.* 2001
	Linaceae	*Linum* sp.	Cos.	Robinson *et al.* 2001
	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001
	Musaceae	*Musa sapientum*	PR.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	Cu, PR.	Robinson *et al.* 2001
	Poaceae	*Urochloa decumbens*	Cos.	Robinson *et al.* 2001
	Poaceae	*Urochloa mutica*	C, PR.	Robinson *et al.* 2001
	Poaceae	*Cynodon* sp.	Cos.	Robinson *et al.* 2001
	Poaceae	*Echinochloa colonum*	Cos.	Robinson *et al.* 2001
	Poaceae	*Eleusine* sp.	NW.	Robinson *et al.* 2001
	Poaceae	*Oryza sativa*	Cu, Cos, Gu, PR.	Robinson *et al.* 2001
	Poaceae	*Panicum maximum*	Cu.	Robinson *et al.* 2001
	Poaceae	*Pennisetum* sp.	Cos.	Robinson *et al.* 2001
	Poaceae	*Saccharum officinarum*	Cu, Cos, PR, WI.	Robinson *et al.* 2001
	Poaceae	*Stenotaphrum secundatum*	PR.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Cu, Cos, PR, WI.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
			G.	Present study
	Poaceae	*Zoysia matrella*	PR.	Robinson *et al.* 2001
	Poaceae	*Eriochloa* sp.	PR.	Robinson *et al.* 2001
	Portulacaeae	*Portulaca oleracea*	Cu.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annuum*	Cu.	Robinson *et al.* 2001
	Solanaceae	*Capsicum frutescens*	PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	PR.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	PR.	Robinson *et al.* 2001
	Rutaceae	*Citrus* sp.	Ja.	Robinson *et al.* 2001
	Umbelliferae	*Daucus carota*	G.	Present study
	Umbelliferae	*Petroselinum crispum*	Cos.	Robinson *et al.* 2001
	Vitaceae	*Vitis* sp.	Cos.	Robinson *et al.* 2001
Spodoptera eridania	Amaranthaceae	*Amaranthus lividus*	G.	Hayes 1975
	Amaranthaceae	*Amaranthus dubius*	Cu.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus spinosus*	PR.	Robinson *et al.* 2001
	Asteraceae	*Lactuca sativa*	G.	Present study
	Convolvulaceae	*Ipomoea pes-caprae*	G.	Hayes 1975
	Convolvulaceae	*Ipomoea batatas*	G.	Present study
			Bar, Br, NW.	Robinson *et al.* 2001
	Caryophyllaceae	*Dianthus caryophyllus*	Br.	Robinson *et al.* 2001
	Cruciferae	*Brassica olaracea*	G.	Present study
			NW.	Robinson *et al.* 2001
	Cruciferae	*Brassica napus*	G.	Present study
	Cucurbitaceae	*Cucumis sativus*	Br.	Robinson *et al.* 2001
	Euphorbiaceae	*Manihot esculenta*	Br, NW.	Robinson *et al.* 2001
	Euphorbiaceae	*Ricinus communis*	Br, Cu.	Robinson *et al.* 2001
	Labiatae	*Mentha piperita*	Cu, NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	G.	Present study

Taxa	Family Plant	Plant Species	Region or Country	Reference
			Br, NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Cu, NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	Br, NW	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	NW.	Robinson *et al.* 2001
	Liliaceae	*Allium cepa*	Br.	Robinson *et al.* 2001
	Portulacaceae	*Portulaca oleraceae*	G.	Hayes 1975
			NW.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Br, Cu, NW.	Robinson *et al.* 2001
	Menispermaceae	*Cissampelos pereira*	G.	Hayes 1975
	Myrtaceae	*Eucalyptus* sp.	Br.	Robinson *et al.* 2001
	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Hayes 1975
	Phytolaccaceae	*Phytolacca* sp.	NW, PR.	Robinson *et al.* 2001
	Piperaceae	*Piper peltatum*	Cu.	Robinson *et al.* 2001
	Poaceae	*Melinis minutiflora*	Br.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	NW.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annum*	G.	Present study
	Solanaceae	*Capsicum frutescens*	PR.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicum sculentum*	G.	Present study
			B, PR.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Br, Cu, PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Br, PR.	Robinson *et al.* 2001
Spodoptera dolichos	Alliaceae	*Allium cepa*	Br.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Nt.	Robinson *et al.* 2001
	Cruciferae	*Brassica rapa*	Nt.	Robinson *et al.* 2001
	Euphorbiaceae	*Ricinus communis*	Cu.	Robinson *et al.* 2001
	Malvaceae	*Gossypium darwinii*	G.	Present study
	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Hayes 1975
	Rubiaceae	*Coffea* sp.	Br.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Cu.	Robinson *et al.* 2001
Leucania humidicola	Poaceae	*Sporobolus virginicus*	G.	Hayes 1975
	Poaceae	*Oryza sativa*	Br.	Robinson *et al.* 2001
	Poaceae	*Saccharum officinarum*	TT.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Nt.	Robinson *et al.* 2001
Magusa erema	Rhamnaceae	*Scutia spicata*	G.	Hayes 1975
Magusa orbifera	Bromeliaceae	*Ananas comosus*	Br.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna alata*	Br.	Robinson *et al.* 2001
	Rhamnaceae	*Scutia spicata*	Br.	Robinson *et al.* 2001
			G.	Hayes 1975
Callopistria floridensis	Adiantaceae	*Adiantum* sp.	Br.	Robinson *et al.* 2001
	Dryopteridaceae	*Tectaria* sp.	PR.	Robinson *et al.* 2001
	Dennstaedriaceae	*Pteridium* sp.	CR.	Janzen & Hallwachs 2001
	Leguminosae (Fab.)	*Phaseolus* sp.	Br.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Br.	Robinson *et al.* 2001
	Oleandraceae	*Nephrolepis* sp.	Br.	Robinson *et al.* 2001
	Polypodiaceae	*Thelypteris* sp.	CR.	Janzen & Hallwachs 2001
	Tectariaceae	*Megalastrum* sp.	CR.	Janzen & Hallwachs 2001
Cropia infusa	Boraginaceae	*Cordia lutea*	G.	Present study
Catabenoides seorsa	Verbenaceae	*Lantana peduncularis*	G.	Hayes 1975
Neogalea sunia	Asparagaceae	*Asparagus officinalis*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	PR.	Robinson *et al.* 2001
	Malvaceae	*Gossypium barbadense*	Bah, PR.	Robinson *et al.* 2001

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	Solanaceae	*Nicotiana tabacum*	Ja, PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	PR.	Robinson *et al.* 2001
	Umbelliferae	*Apium graveolens*	PR.	Robinson *et al.* 2001
	Verbenaceae	*Lantana camara*	CR.	Janzen & Hallwachs 2001
			Co.	Robinson *et al.* 2001
Condica sutor	Umbelliferae	*Apium* sp.	Br.	Robinson *et al.* 2001
Condica ruthae	Asteraceae	*Lecocarpus darwinii*	G.	Present study
	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Present study
Condica concisa	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001
Paectes arcigera	Burseraceae	*Bursera graveolens*	G.	Hayes 1975
Spragueia margana	Malvaceae	*Sida* sp.	G.	Hayes 1975
	Malvaceae	*Sida rhombifolia*	G.	Present study
	Malvaceae	*Abutilon depauperatum*	G.	Hayes 1975
	Malvaceae	*Malvastrum* sp.	Br.	Robinson *et al.* 2001
Spragueia creton	Convolvulaceae	*Ipomoea habeliana*	G.	Present study
Ponometia exigua	Sterculiaceae	*Waltheria ovata*	G.	Hayes 1975
Eublemma recta	Convolvulaceae	*Ipomoea triloba*	G.	Hayes 1975
Amyna insularum	Amaranthaceae	*Alternanthera echinocephala*	G.	Hayes 1975
	Amaranthaceae	*Alternanthera filifolia nudicaulis*	G.	Hayes 1975
Heliocheilus cystiphora	Poaceae	*Sporobolus virginicus*	G.	Hayes 1975
	Poaceae	*Cenchrus platyacanthus*	G.	Perry & DeVries 2003
Heliothis virescens	Asteraceae	*Scalesia affinis*	G.	Hayes 1975
	Asteraceae	*Helianthus annus*	Cu, NW.	Robinson *et al.* 2001
	Asteraceae	*Lactuca sativa*	NW.	Robinson *et al.* 2001
	Cruciferae	*Brassica rapa*	NW.	Robinson *et al.* 2001
	Geraniaceae	*Pelargonium* sp.	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Cajanus cajan*	Ba, Cu, Guy, NW, WI.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Desmodium* sp.	NW.	Robinson *et al.* 2001

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	Leguminosae (Fab.)	*Glycine max*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	PR, WI.	Robinson *et al.* 2001
	Malvaceae	*Abutilon* sp.	PR.	Robinson *et al.* 2001
	Malvaceae	*Bastardia viscosa*	NW.	Robinson *et al.* 2001
	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001
	Malvaceae	*Hibiscus rosa-sinensis*	PR.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	NW.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora foetida*	G.	Hayes 1975
	Poaceae	*Cynodon dactylon*	NW.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon* sp.	NW.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Cu, Pe, PR.	Robinson *et al.* 2001
	Solanaceae	*Physalis angulata*	Ba, NW.	Robinson *et al.* 2001
Anicla infecta	Apocynaceae	*Nerium* sp.	TT.	Robinson *et al.* 2001
	Poaceae	*Panicum miliaceum*	PR.	Robinson *et al.* 2001
	Poaceae	*Saccharum officinarum*	PR.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Br.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon* sp.	NW.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana* sp.	NW.	Robinson *et al.* 2001
Agrotis subterranea	Asteraceae	*Helianthus annuus*	Cu.	Robinson *et al.* 2001
	Asteraceae	*Lactuca sativa*	NW.	Robinson *et al.* 2001
	Asteraceae	*Lactuca* sp.	Br.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	NW.	Robinson *et al.* 2001
	Cruciferae	*Brassica oleracea*	Cu, NW.	Robinson *et al.* 2001
	Cucurbitaceae	*Citrullus lanatus*	Br.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis melo*	Br.	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis sativus*	PR.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	NW.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Medicago sativa*	NW, PR.	Robinson *et al.* 2001

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	Leguminosae (Fab.)	*Mucuna* sp.	Cu.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Phaseolus vulgaris*	Br.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	Cu.	Robinson *et al.* 2001
	Malvaceae	*Gossypium barbadense*	PR.	Robinson *et al.* 2001
	Poaceae	*Avena sativa*	Br.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Br, Cu.	Robinson *et al.* 2001
	Poaceae	*Oryza sativa*	Br.	Robinson *et al.* 2001
	Rutaceae	*Citrus* sp.	Br.	Robinson *et al.* 2001
	Rubiaceae	*Coffea* sp.	Br.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Br, Cu.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Br, Cu, PR.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Br.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Br.	Robinson *et al.* 2001
	Umbelliferae	*Daucus carota*	NW.	Robinson *et al.* 2001
Agrotis ipsilon	Alliaceae	*Allium cepa*	Pt.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus viridis*	Pt.	Robinson *et al.* 2001
	Asteraceae	*Lactuca sativa*	Pt.	Robinson *et al.* 2001
	Chenopodiaceae	*Chenopodium* sp.	Pt.	Robinson *et al.* 2001
	Cruciferae	*Brassica oleracea*	Pt.	Robinson *et al.* 2001
	Cruciferae	*Brassica rapa*	Pt.	Robinson *et al.* 2001
	Cruciferae	*Coronopus* sp.	PT.	Robinson *et al.* 2001
	Cruciferae	*Raphanus sativus*	Pt.	Robinson *et al.* 2001
	Convolvulaceae	*Evolvulus* sp.	Pt.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomea batatas*	Pt.	Robinson *et al.* 2001
	Labiatae	*Mentha piperita*	Pt.	Robinson *et al.* 2001
	Labiatae	*Stachys* sp.	Pt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Arachis hypogaea*	Nt.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Glycine max*	Pt.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Leguminosae (Fab.)	*Medicago sativa*	Pt.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Pt.	Robinson *et al.* 2001
	Poaceae	*Oryza sativa*	Pt.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Pt.	Robinson *et al.* 2001
	Portulacaceae	*Portulaca oleracea*	Pt.	Robinson *et al.* 2001
	Polygonaceae	*Rumex* sp.	Pt.	Robinson *et al.* 2001
	Solanaceae	*Capsicum* sp.	Pt.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Pt.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon* sp.	Nt	Robinson *et al.* 2001
Peridroma saucia	Asteraceae	*Lactuca* sp.	Br.	Robinson *et al.* 2001
	Cruciferae	*Brassica oleracea*	Br.	Robinson *et al.* 2001
	Linaceae	*Linum* sp.	Br.	Robinson *et al.* 2001
	Solanaceae	*Capsicum annuum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Br.	Robinson *et al.* 2001
	Solanaceae	*Solanum tuberosum*	Br.	Robinson *et al.* 2001
Nolidae				
Charocoma nilotica	Combretaceae	*Laguncularia racemosa*	G.	Hayes 1975, Perry & DeVries 2003
			Cu.	Robinson *et al.* 2001
	Combretaceae	*Conocarpus erectus*	G.	Present study
Geometridae				
Cyclophora impudens	Amaranthaceae	*Amaranthus andersonii*	G.	Present study
	Boraginaceae	*Cordia lutea*	G.	Rindge 1973, Perry & DeVries 2003
	Euphorbiaceae	*Croton scouleri*	G.	Rindge 1973, Perry & DeVries 2003
	Leguminosae (Mim)	*Acacia macracantha*	G.	Rindge 1973, Perry & DeVries 2003
	Leguminosae (Mim)	*Acacia insulae-iacobi*	G.	Present study

Taxa	Family Plant	Plant Species	Region or Country	Reference
Pleuroprucha insulsaria	Asteraceae	*Adenostemma platyphyllum*	G.	Present study
Discliosiprocta stellata	Nyctaginaceae	*Cryptocarpus pyriformis*	G.	Rindge 1973
	Nyctaginaceae	*Pisonia floribunda*	G.	Rindge 1973
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Rindge 1973
	Nyctaginaceae	*Bougainvillea spectabilis*	Cu.	Robinson *et al.* 2001
	Nyctaginaceae	*Mirabilis jalapa*	Cu.	Robinson *et al.* 2001
Triphosa affirmata	Leguminosae (Caes.)	*Senna obtusifolia*	G.	Present study
	Leguminosae (Caes.)	*Senna occidentalis*	G.	Perry & DeVries 2003
Eupithecia perryvriesi	Asteraceae	*Scalesia microcephala*	G.	Present study
	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Present study
	Verbenaceae	*Duranta repens*	G.	Present study
Macaria cruciata cruciata	Rhamnaceae	*Scutia spicata*	G.	Rindge 1973, Perry & DeVries 2003.
Semiothisa cerussata	Asteraceae	*Darwiniothamnus tenuifolius*	G.	Roque-Albelo 2003*
Thyrinteina infans	Boraginaceae	*Cordia lutea*	G.	Rindge 1973, Perry & DeVries 2003
	Celastraceae	*Maytenus octagona*	G.	Rindge 1973, Perry & DeVries 2003
	Sapindaceae	*Dodonea viscosa*	G.	Present study
Thyrintina umbrosa	Asteraceae	*Scalesia pedunculata*	G.	Present study
	Sterculiaceae	*Waltheria ovata*	G.	Present study
Sphacelodes vulneraria	Rhamnaceae	*Gouania polygama*	CR.	Janzen & Hallwachs 2001
Zeuctostyla vidrierata	Euphorbiaceae	*Phyllanthus acidus*	G.	Present study
Oxydia lignata	Rutaceae	*Zanthoxylum fagara*	G.	Present study
	Verbenaceae	*Clerodendrum molle*	G.	Rindge 1973, Perry & DeVries 2003
Sphingidae				
Agrius cingulata	Convolvulaceae	*Ipomoea pes-caprae*	G.	Williams 1911, Roque-Albelo & Landry 2001
			PR.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Convolvulaceae	*Ipomoea habeliana*	G.	Roque-Albelo & Landry 2001*
	Convolvulaceae	*Ipomoea nil*	G.	Roque-Albelo & Landry 2001*
	Convolvulaceae	*Ipomoea triloba*	G.	Williams 1911, Roque-Albelo & Landry 2001
	Convolvulaceae	*Ipomoea alba*	Br, Cu, Na, PR.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Br, Cu, Hw, Na, NW, Pt, PR.	Robinson *et al.* 2001
	Convolvulaceae	*Stictocardia tilifolia*	G.	Williams 1911, Roque-Albelo & Landry 2001
	Convolvulaceae	*Merremia umbellata*	CR.	Janzen & Hallwachs 2001
	Solanaceae	*Datura stramonium*	Na	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Br	Robinson *et al.* 2001
Manduca sexta leucoptera	Cannaceae	*Canna generalis*	Na, Nw.	Robinson *et al.* 2001
	Cruciferae	*Brassica rapa*	Na, Nw.	Robinson *et al.* 2001
	Cruciferae	*Raphanus sativus*	Na, NW.	Robinson *et al.* 2001
	Euphorbiaceae	*Manihot esculenta*	Br.	Robinson *et al.* 2001
	Geraniaceae	*Pelargonium hortorum*	Na, Nw.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Vigna* sp.	NW.	Robinson *et al.* 2001
	Moraceae	*Ficus* sp.	Br.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	Na, Nw.	Robinson *et al.* 2001
	Solanaceae	*Physalis pubescens*	G.	Hayes 1975, Perry & DeVries 2003
	Solanaceae	*Physalis* spp.	CR.	Janzen & Hallwachs 2001
	Solanaceae	*Nicotiana tabacum*	CR.	Janzen & Hallwachs 2001
			G.	Roque-Albelo & Landry 2001*
			Br, Cu, Mx, Na, Pa, PR, WI.	Robinson *et al.* 2001
	Solanaceae	*Acnistus ellipticus*	G.	Roque-Albelo & Landry 2001*
	Solanaceae	*Capsicum annuum*	CR.	Janzen & Hallwachs 2001
			Br, Na, NW.	Robinson *et al.* 2001
	Solanaceae	*Cestrum* sp.	CR.	Janzen & Hallwachs 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Solanaceae	*Lycopersicon esculentum*	CR.	Janzen & Hallwachs 2001
			Br, Cu, PR, Mx, Na, NW, WI.	Robinson *et al.* 2001
	Solanaceae	*Solanum americanum*	CR.	Janzen & Hallwachs 2001
	Solanaceae	*Solanum tuberosum*	Br, Cu, Mx, Na, NW.	Robinson *et al.* 2001
	Solanaceae	*Solanum melongena*	Br, Na.	Robinson *et al.* 2001
	Solanaceae	*Datura stramonium*	Ca, Na, NW.	Robinson *et al.* 2001
	Solanaceae	*Brugmansia* sp.	Br, Na.	Robinson *et al.* 2001
Manduca rustica calapagensis	Annonaceae	*Annona* sp.	Br.	Robinson *et al.* 2001
	Apocinaceae	*Plumeria* sp.	Br.	Robinson *et al.* 2001
	Asteraceae	*Darwiniothamnus lancifolius*	G.	Williams 1911, Roque-Albelo & Landry 2001.
	Bignoniaceae	*Crescentia* sp.	CR.	Janzen & Hallwachs 2001
	Boraginaceae	*Cordia alliodora*	CR.	Janzen & Hallwachs 2001
	Boraginaceae	*Cordia lutea*	G.	Williams 1911, Hayes 1975, Roque-Albelo & Landry 2001,
	Boraginaceae	*Cordia leucophlyctis*	G.	Hayes 1975, Roque-Albelo & Landry 2001, Perry & DeVries
	Boraginaceae	*Tournefortia rufo-sericea*	G.	Williams 1911, Roque-Albelo & Landry 2001.
	Convolvulaceae	*Merremia umbellata*	CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Croton scouleri*	G.	Williams 1911, Roque-Albelo & Landry 2001
	Lamiaceae	*Hyptis* sp.	CR.	Janzen & Hallwachs 2001
	Malvaceae	*Bastardia viscosa*	G.	Williams 1911, Roque-Albelo & Landry 2001
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Roque-Albelo & Landry 2001*
	Scrophulariaceae	*Russelia* sp.	CR.	Janzen & Hallwachs 2001
	Verbenaceae	*Lantana camara*	G.	Roque-Albelo & Landry 2001*
			CR.	Janzen & Hallwachs 2001
			Na.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Verbenaceae	*Lippia* sp.	CR.	Janzen & Hallwachs 2001
	Verbenaceae	*Stachytarpheta* sp.	CR.	Janzen & Hallwachs 2001
	Verbenaceae	*Clerodendrum molle*	G.	Williams 1911, Hayes 1975, Roque-Albelo & Landry 2001,
Cocytius antaeus	Annonaceae	*Annona cherimola*	G.	Roque-Albelo 1999*
	Annonaceae	*Annona muricata*	G.	Present study
			Br, PR.	Robinson *et al.* 2001
Erinnyis alope dispersa	Apocynaceae	*Allamanda* sp.	Na, NW.	Robinson *et al.* 2001
	Caricaceae	*Carica papaya*	G.	Roque-Albelo & Landry 2001*
			Br, Cu, Na, NW, PR.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Manihot esculenta*	G.	Roque-Albelo & Landry 2001*
			Br, Cu, PR.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Jatropha* sp.	Br, Na.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Nw.	Robinson *et al.* 2001
Erinnyis ello encantada	Apocynaceae	*Allamanda cathartica*	Br.	Robinson *et al.* 2001
	Caricaceae	*Carica papaya*	PR, NW.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Hippomane mancinella*	G.	Williams 1911, Curio 1965 a, Hayes 1975, Roque-Albelo & Landry 2001, Perry & DeVries 2003.
	Euphorbiaceae	*Euphorbia pulcherrima*	CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Euphorbia heterophylla*	Br, Na, NW.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Euphorbiaceae	*Manihot esculenta*	CR.	Janzen & Hallwachs 2001
			Br, Cu, NW, PR, WI.	Robinson *et al.* 2001
	Euphorbiaceae	*Ricinus communis*	Br, Na.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Euphorbiaceae	*Jatropha* sp.	Br, Na	Robinson *et al.* 2001
	Euphorbiaceae	*Chamaesyce viminea*	G	Roque-Albelo & Landry 2001*
	Leguminosae (Fab.)	*Arachis hypogea*	Br.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	NW.	Robinson *et al.* 2001
	Myrtaceae	*Psidium guajava*	G.	Williams 1911, Roque-Albelo & Landry 2001
	Myrtaceae	*Eucalyptus* sp.	Na.	Robinson *et al.* 2001
	Solanaceae	*Lycopersicon esculentum*	NW.	Robinson *et al.* 2001
	Sapotaceae	*Chrysophyllum* sp.	Br.	Robinson *et al.* 2001
			Na.	Robinson *et al.* 2001
Erinnyis obscura conformis	Asclepiadaceae	*Sarcostemma angustissimum*	G.	Williams 1911, Hayes 1975, Roque-Albelo & Landry 2001, Perry & DeVries 2003.
Enyo lugubris delanoi	Vitaceae	*Cissus verticillata*	G.	Williams 1911, Roque-Albelo & Landry 2001Perry & DeVries 2003.
			Br, Cu, PR.	Robinson *et al.* 2001
	Vitaceae	*Vitis vinifera*	Na, PR.	Robinson *et al.* 2001
Perigonia lusca lusca	Rubiaceae	*Cinchona pubescens*	G.	Roque-Albelo & Landry 2001*
	Rubiaceae	*Coffea arabica*	PR.	Robinson *et al.* 2001
Eumorpha labruscae yupanqui	Onagraceae	*Ludwigia* sp.	Br.	Robinson *et al.* 2001
	Vitaceae	*Cissus verticillata*	G.	Roque-Albelo & Landry 2001*
			Cu.	Robinson *et al.* 2001
	Vitaceae	*Vitis vinifera*	Cu, PR.	Robinson *et al.* 2001
Eumorpha fasciata tupaci	Onagraceae	*Ludwigia leptocarpa*	CR.	Janzen & Hallwachs 2001
			Na.	Robinson *et al.* 2001
	Vitaceae	*Cissus verticillata*	Br.	Robinson *et al.* 2001
	Vitaceae	*Vitis* sp.	Br, Na.	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
Xylophanes tersa tersa	Leguminosae (Fab.)	*Phaseolus* sp.	Na.	Robinson *et al.* 2001
	Malvaceae	*Sida* sp.	Br.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus* sp.	Na, NW.	Robinson *et al.* 2001
	Poaceae	*Zea mays*	Na.	Robinson *et al.* 2001
	Rubiaceae	*Dioidia radula*	G.	Roque-Albelo & Landry 2001*
	Rubiaceae	*Psychotria* sp.	CR.	Janzen & Hallwachs 2001
			Br.	Robinson *et al.* 2001
	Rubiaceae	*Spermacoce* sp.	Br, Cu, PR, Na, NW.	Robinson *et al.* 2001
			CR.	Janzen & Hallwachs 2001
	Verbenaceae	*Clerodendrum molle*	G.	Williams 1911, Roque-Albelo & Landry 2001
Xylophanes norfolki	Rubiaceae	*Psychotria rufipes*	G.	Roque-Albelo & Landry 2001*
Xylophanes pluto	Rubiaceae	*Hamelia patens*	CR.	Janzen & Hallwachs 2001
	Rubiaceae	*Psychotria* sp.	CR.	Janzen & Hallwachs 2001
	Rubiaceae	*Spermacoce* sp.	CR.	Janzen & Hallwachs 2001
	Rubiaceae	*Chiococca alba*	Na.	Robinson *et al.* 2001
	Rubiaceae	*Cinchona* sp.	Na, NW, PR.	Robinson *et al.* 2001
Hyles lineata	Aloaceae	*Aloe* sp.	EAf.	Robinson *et al.* 2001
	Amaranthaceae	*Amaranthus* sp.	Na.	Robinson *et al.* 2001
	Asteraceae	*Lactuca sativa*	Na.	Robinson *et al.* 2001
	Asteraceae	*Sonchus* sp.	EA.f	Robinson *et al.* 2001
	Caprifoliaceae	*Sambucus* sp.	Na	Robinson *et al.* 2001
	Caryophyllaceae	*Stellaria media*	Na.	Robinson *et al.* 2001
	Chenopodiaceae	*Chenopodium* sp.	Na.	Robinson *et al.* 2001
	Convolvulaceae	*Ipomoea batatas*	Na, NW.	Robinson *et al.* 2001
	Cruciferae	*Brassica oleraceae*	Na.	Robinson *et al.* 2001
	Cruciferae	*Brassica rapa*	Na.	Robinson *et al.* 2001
	Cucurbitaceae	*Citrullus lanatus*	Na	Robinson *et al.* 2001
	Cucurbitaceae	*Cucumis melo*	Na	Robinson *et al.* 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
	Euphorbiaceae	*Euphorbia* sp.	Fin.	Robinson *et al.* 2001
	Geraniaceae	*Pelargonium* sp.	Na.	Robinson *et al.* 2001
	Leguminosae (Fab.)	*Pisum sativum*	Na.	Robinson *et al.* 2001
	Linaceae	*Linum* sp.	Fin.	Robinson *et al.* 2001
	Malvaceae	*Gossypium* sp.	Na, NW.	Robinson *et al.* 2001
	Myrtaceae	*Eucalyptus camaldulensis*	Ir.	Robinson *et al.* 2001
	Nyctaginaceae	*Commicarpus tuberosus*	G.	Hayes 1975, Perry & DeVries 2003
	Nyctaginaceae	*Boerhavia caribaea*	G.	Roque-Albelo & Landry 2001, Perry & DeVries 2003
	Nyctaginaceae	*Mirabilis jalapa*	Na.	Robinson *et al.* 2001
	Onagraceae	*Ludwigia* sp.	PR.	Robinson *et al.* 2001
	Portulacaceae	*Portulaca oleracea*	Cu, Na.	Robinson *et al.* 2001
			G.	Hayes 1975, Roque-Albelo & Landry 2001, Perry & DeVries 2003.
	Plantaginaceae	*Plantago* sp.	Na.	Robinson *et al.* 2001
	Polygonaceae	*Rumex* sp.	Bl, EAf, Eu, Fin, Na.	Robinson *et al.* 2001
	Polygonaceae	*Polygonum* sp.	Na.	Robinson *et al.* 2001
	Solanaceae	*Nicotiana tabacum*	Ja, Wl.	Robinson *et al.* 2001
	Rosaceae	*Prunus* sp.	EAf, Na, NW.	Robinson *et al.* 2001
	Rosaceae	*Rosa* sp.	Na.	Robinson *et al.* 2001
	Rosaceae	*Rubus* sp.	Na.	Robinson *et al.* 2001
	Rubiaceae	*Galium* sp.	Bl, Ca, EAf, Eu, Fin.	Robinson *et al.* 2001
	Valeraniaceae	*Valeriana* sp.	EAf.	Robinson *et al.* 2001
	Vitaceae	*Vitis vinifera*	Bl, Na.	Robinson *et al.* 2001
	Zygophyllaceae	*Tribulus* sp.	Au.	Robinson *et al.* 2001

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Hesperiidae				
Urbanus dorantes galapagensis	Leguminosae (Fab.)	*Phaseolus atropurpureus*	G.	Roque-Albelo 2004*
	Leguminosae (Fab.)	*Phaseolus mollis*	G.	Roque-Albelo 2004*
	Leguminosae (Fab.)	*Desmodium incanum*	G.	Roque-Albelo 2004*
	Leguminosae (Fab.)	*Galactia striata*	G.	Roque-Albelo 2004*
Calpodes ethlius	Araceae	*Colocasia esculenta*	NW.	Robinson *et al.* 2001
	Cannaceae	*Canna lambertii*	G.	Roque-Albelo 2004*
	Cannaceae	*Canna indica*	G.	Roque-Albelo 2004*
			CR.	Janzen & Hallwachs 2001
			Br, Cu, NW, PR.	Robinson *et al.* 2001
	Cannaceae	*Canna generalis*	NW.	Robinson *et al.* 2001
	Euphorbiaceae	*Phyllanthus* sp.	NW.	Robinson *et al.* 2001
	Marantaceae	*Calathea* sp.	CR.	Janzen & Hallwachs 2001
	Umbelliferae	*Apium graveolens*	NW.	Robinson *et al.* 2001
	Zingiberaceae	*Hedychium coronarium*	Br.	Robinson *et al.* 2001
Pieridae				
Phoebis sennae marcellina	Leguminosae (Caes.)	*Senna pistaciifolia*	G.	Williams 1911, Roque-Albelo 2004
	Leguminosae (Caes.)	*Senna obtusifolia*	G.	Roque-Albelo 2004*
			CR.	Janzen & Hallwachs 2001
			NW.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna bicapsularis*	G.	Roque-Albelo 2004*
			Br, NW.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna occidentalis*	G.	Roque-Albelo 2004*
			Cu, NW, PR.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna alata*	Br, Cu, PR.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna hirsuta*	NW.	Robinson *et al.* 2001
	Leguminosae (Caes.)	*Senna uniflora*	Br.	Robinson *et al.* 2001

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Lycaenidae				
Leptotes parrhasioides	Leguminosae (Fab)	*Crotalaria incana*	G.	Roque-Albelo 2004*
	Leguminosae (Fab.)	*Rynchosia minima*	G.	Roque-Albelo 2004*
	Plumbaginaceae	*Plumbago scandens*	G.	Roque-Albelo 2004*
	Sapindaceae	*Cardiospermum halicacabum*	G.	Williams 1911, Roque-Albelo 2004
	Sapindaceae	*Cardiospermum galapageium*	G.	Williams 1911, Roque-Albelo 2004
Hemiargus ramon	Cucurbitaceae	*Cucumis dipsaceus*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Mim.)	*Acacia macracantha*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Caes.)	*Senna obtusifolia*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Mim.)	*Neptunia plena*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Fab.)	*Phaseolus atropurpureus*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Mim.)	*Prosopis juliflora*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
	Leguminosae (Fab.)	*Tephrosia decumbens*	G.	Roque-Albelo *et al* 1997, Roque-Albelo 2004
Nymphalidae				
Danaus gilippus thersippus	Asclepiadaceae	*Sarcostemma angustissimum*	G.	Roque-Albelo 2004*
	Asclepiadaceae	*Asclepias curassavica*	G.	Roque-Albelo 2004*
			CR.	Janzen & Hallwachs 2001
			Br, Cu, Na, NW.	Robinson *et al.* 2001
Danaus plexippus megalippe	Asclepiadaceae	*Sarcostemma angustissimum*	G.	Roque-Albelo 1998 a, Roque-Albelo 2004
	Asclepiadaceae	*Asclepias curassavica*	G.	Roque-Albelo 1998 b, Roque-Albelo 2004
			CR.	Janzen & Hallwachs 2001

Taxa	Family Plant	Plant Species	Region or Country	Reference
			Cos Cu, Fj, Hw, PR, Na.	Robinson *et al.* 2001
Agraulis vanillae galapagensis	Caprifoliaceae	*Lonicera* sp.	Br, Nt.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora suberosa*	G.	Roque-Albelo 2004*
			Na, Nt, NW.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora tridactylites*	CR.	Janzen & Hallwachs 2001
			G.	Roque-Albelo 2004*
	Passifloraceae	*Passiflora foetida*	CR.	Janzen & Hallwachs 2001
			Na, NW.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora edulis*	Br, Nt, NW.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora ligularis*	Nt.	Robinson *et al.* 2001
	Passifloraceae	*Passiflora quadrangularis*	Nt.	Robinson *et al.* 2001
	Tiliaceae	*Corchorus* sp.	Ja.	Robinson *et al.* 2001
Vanessa virginiensis	Asteraceae	*Gamochaeta purpurea*	G.	Roque-Albelo 2004*
			NW.	Robinson *et al.* 2001
	Asteraceae	*Helianthus* sp.	NW.	Robinson *et al.* 2001
	Balsaminaceae	*Impatiens* sp.	NW.	Robinson *et al.* 2001
Vanessa carye	Geraniaceae	*Pelargonium* sp.	Br, Nt.	Robinson *et al.* 2001

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BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE ENTOMOLOGIE, 73: 177-180, 2003
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN ENTOMOLOGIE, 73: 177-180, 2003

Population decline of Galapagos endemic Lepidoptera on Volcán Alcedo (Isabela Island, Galapagos Islands, Ecuador): An effect of the introduction of the cottony cushion scale?

by Lázaro ROQUE-ALBELO

Summary

By eliminating its food plant, *Darwiniothamnus tenuifolius* (HOOK. *f.*, Asteraceae), the cottony cushion scale, *Icerya purchasi* MASKELL (Insecta, Homoptera, Margarodidae), may have extirpated three Lepidoptera species from the east slope of Volcán Alcedo, Isabela Island, Galapagos Archipelago, Ecuador.

Key words: Lepidoptera, exotic species, competition, local extinction.

Résumé

En éliminant sa plante hôte, *Darwiniothamnus tenuifolius* (HOOK. *f.*, Asteraceae), la cochenille australienne, *Icerya purchasi* MASKELL (Insecta, Homoptera, Margarodidae), a causé la disparition de trois espèces de Lépidoptères de la pente ouest du volcan Alcedo, ile d'Isabela, archipel des Galapagos, Equateur.

Mots-clefs: Lepidoptera, espèces introduites, compétition interspécifique, extinction locale.

Introduction

Exotic species introduced into habitats with suitable resources and few native competitors often find conditions conducive to rapid population growth. A dramatic example of an exotic phytophagous insect which has invaded and impacted native ecosystems is *Icerya purchasi* MASKELL (Homoptera: Margarodidae) on the Galapagos Islands. Commonly known as the cottony cushion scale, *I. purchasi* is native to Australia but has been introduced accidentally to many parts of the world (CALTAGIRONE & DOUTT, 1989). Since its introduction to the Galapagos archipelago in 1982, this species has invaded at least 15 islands causing damage to at least 82 plant species (ROQUE-ALBELO & CAUSTON, 2000, CAUSTON, 2001).

Icerya purchasi causes direct damage to its host plants by sucking phloem sap, which in turn depletes resources intended for new plant growth. Damage can include branch deformation and plant death (BLUMBERG *et al.*, 1992). *Icerya purchasi* also produces large quantities of honeydew, which encourages the growth of sooty moulds that often cover the leaves, blocking the stomata and thus preventing both respiration and photosynthesis (JOHNSON et al. in prep.).

Nutrient and plant resource loss from the impact of *I. purchasi* may also have a direct effect on other insect species, in particular those that have a narrow host range that are restricted to plants that are heavily infested by this introduced scale insect. However, no studies have been published on the impact of *I. purchasi* on others insect populations in the Galapagos archipelago.

In this paper I present data showing the decline of three species of endemic Lepidoptera whose host plant is the endemic composite *Darwiniothamnus tenuifolius* (HOOK. *f.*) a species highly affected by *I. purchasi*.

Material and methods

The study was conducted on the east slope of Volcán Alcedo on Isabela Island from October 1998 to April 2001. Sampling was carried out in the wet (April) and dry seasons (October) at three localities in three different vegetation zones: Arid Zone (300 m) (dry season deciduous forest), Transition Zone (500 m) (evergreen steppe scrub) and Humid Zone (900 m) (evergreen forest).

In each altitudinal zone, ultraviolet light traps were used for 3 hours (1900 h to 2200 h). Moths attracted to the light were collected or counted. Reference specimens are deposited in the Invertebrate collection of the Charles Darwin Research Station, Santa Cruz Island, Galapagos.

Following the arrival of *I. purchasi* to this area, the percentage of infested plants was recorded.

To evaluate the occurrence of *I. purchasi* on *D. tenuifolius* qualitative measures were taken using a value scale from 0 (no occurrence) to 3 (very common and plant mortality observed).

Results

A reduction of population numbers of three species of Lepidoptera associated with *D. tenuifolius* was observed between 1998 and 2001 (Table 1).

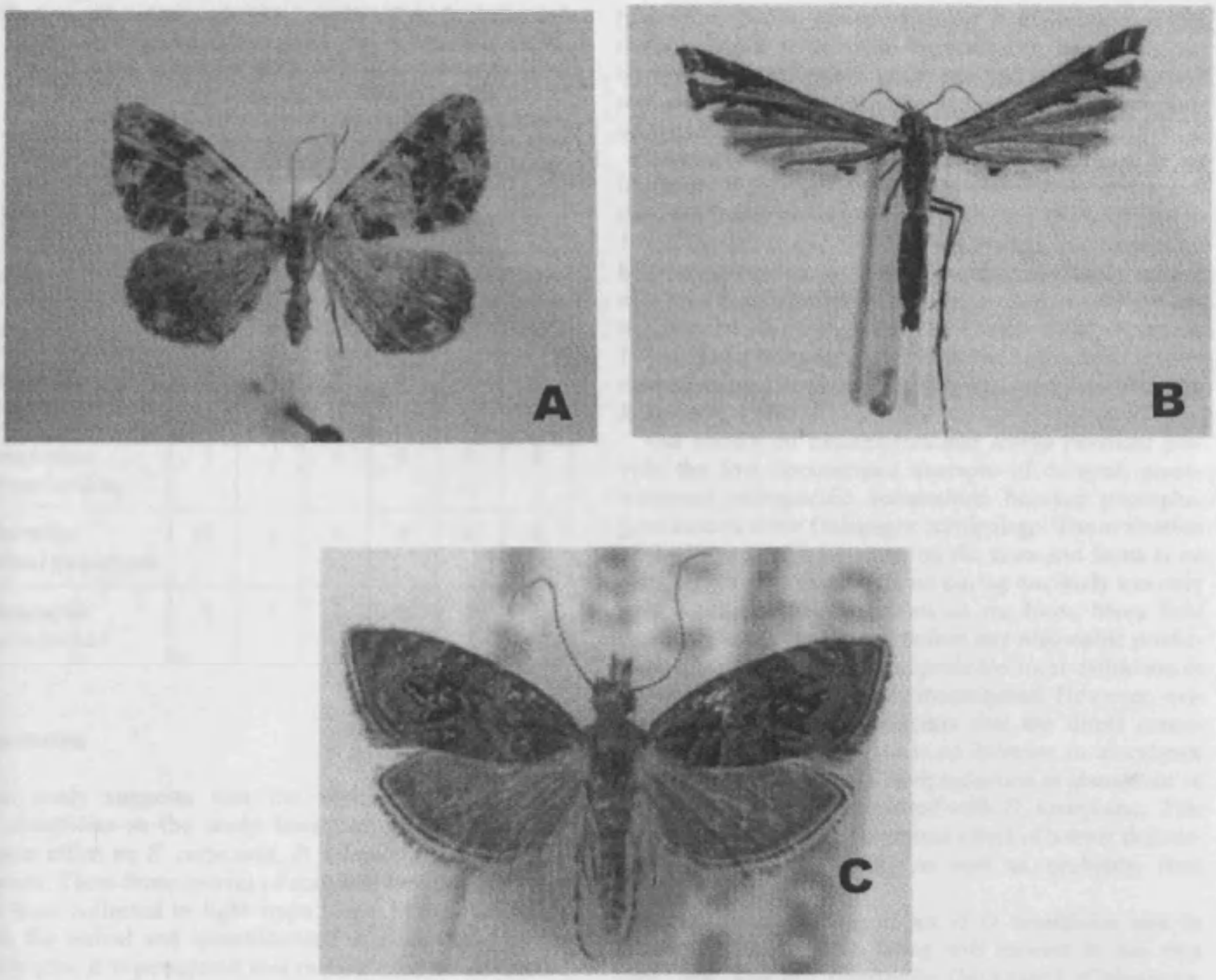

Fig. 1. — Lepidoptera species afected by *Icerya purchasi*. a) *Semiothisa cerussata*, b) *Platyptilia vilema*, c) *Tebenna galapagoensis*.

In contrast, following the discovery of *I. purchasi* on Volcán Alcedo in October 1999, population numbers and *D. tenuifolius* mortality increased markedly from April 2000 onwards.

Semiothisa cerussata Herbulot, 1970 (Geometridae) (Fig. 1 a) was only collected in April 1999 (19 specimens). It was collected at all three altitudes. This is a new distribution record. The larvae were very abundant on leaves and young branches of *D. tenuifolius* in the Arid Zone (300m). Since this date, the species has not been observed. Previously, this species had been reported only from Santa Cruz and San Cristobal islands where adults had been collected only in the wet season (January to June) (Landry & Rindge, 1995).

The large plume moth *Platyptilia vilema* Landry, 1993 (Pterophoridae) (Fig. 1 b) was only collected in small numbers from Volcán Alcedo. In October 1998, five adults were collected and one larva found on leaves of *D. tenuifolius* was reared. Only two adults were collected on alcedo in 1999, and none have been collected since then. This is a new distribution record. This species had been reported only from the volcanoes Darwin and Sierra Negra (Isabela Island) and Pinta in the wet season (Landry, 1993).

A marked reduction of *Tebenna galapagoensis* Heppner & Landry, 1994 (Choreutidae) (Fig. 1 c) was observed during the sampling period. This species was common until 1998. At that time, adults and immature stages were collected from the transition zone (500 m), *T. galapagoensis*, was not collected from 1999 onwards.

In April 1999, *I. purchasi* was recorded for the first time on the east slope of Volcán Alcedo (from 300 m to 600 m). Several plants such as *D. tenuifolius* and *Rhynchosia minima* (L.) DC. were observed with a few individuals of this scale insect. Between then and April 2001 a progressive increase of infestation was observed. Plant death and high levels of infestation were first observed in April 2000.

Table 1 — Abundance of three species of moth associated with *D. tenuifolius* and *I. purchasi* at three altitudinal sites from 1998- 2001. Numbers associated with moth species indicate numbers of specimens collected or observed on plants. Numbers for *Icerya purchasi* indicate: 0: Not observed; 1: Scarse; 2: Common but no *Darwiniothamnus tenuifolius* mortality observed; 3: very common and *Darwiniothamnus tenuifolius* mortality observed.

Family	**1998**	**1999**		**2000**		**2001**
Species	**Oct.**	**Apr.**	**Oct.**	**Apr.**	**Oct.**	**Apr.**
Geometridae *Semiothisa cerussata*	0	19	0	0	0	0
Pterophoridae *Platyptilia vilema*	5	1	1	0	0	0
Choreutidae *Tebenna galapagoensis*	17	0	0	0	0	0
Margarodidae *Icerya purchasi*	0	1	2	3	3	3

Discussion

This study suggests that the virtual elimination of *D. tenuifolius* in the study localities may have had a drastic effect on *S. cerussata*, *P. vilema*, and *T. galapagoensis*. These three species of endemic Lepidoptera have not been collected in light traps since 1999, coinciding with the arrival and establishment of *I. purchasi* in the study area. It is postulated that these moths are restricted to feed on *D. tenuifolius* and therefore, they disappear in its absence.

Data obtained for some indigenous plants in Galapagos showed that the scale insect infestation appear to influence the levels of nutrients and the vegetative growth of the plants (Causton, 2001).

Some plants species appear to be less susceptible to *I. purchasi* attack (Johnson *et al.*, in prep.). However, *D. tenuifolius* is a highly affected species. The IUCN category for this species has been changed recently from non-threatened to vulnerable as a result of damage by *I. purchasi* (A. Tye, pers comm.).

Studies in the Galapagos have shown that it is very difficult to identify in the field whether *I. purchasi* infestations are entirely responsible for plant mortality (Causton, 2003). However, even if *I. purchasi* is not the sole factor responsible for mortality, its effects can be fatal to susceptible plant species that are already stressed by feral goat damage and prolonged dry periods such as those found on Volcán Alcedo.

Interspecific interactions such as competition is an important factor influencing the distribution and abundance of herbivorous insects (Crawley, 1983; Damman, 1993; Denno *et al.*, 1995). Most studies of competition have concentrated on a small number of closely related taxa on the assumption that in these cases resource overlap is most likely to occur (McClure, 1980; Karban, 1986). However competition between herbivorous insects can occur even between distantly unrelated taxa (Blakey & Dingle, 1978).

Our results on Lepidoptera and *Icerya purchasi* provide the first documented example of delayed, plant–mediated interspecific competition between phytophagous insects in the Galapagos archipelago. The evaluation of the impact of *I. purchasi* on the flora and fauna is no easy matter. The data obtained during our study can only give a glimpse into its effect on the biota. More field sampling is clearly needed before any reasonable predictions can be made about the probable local extinction of the species in the localities investigated. However, evidence from this study suggests that the direct consequence of this competition is an increase in abundance of *I. purchasi* and a significant reduction in abundance of Lepidoptera species associated with *D. tenuifolius*. This reduction is due to the combined effect of habitat destruction and food availability as well as, probably, food quality.

It will be interesting to see if *D. tenuifolius* and its associated lepidopteran fauna will recover in this area now that *Rodolia cardinalis* (Mulsant) (Coleoptera, Coccinellidae) has been purposefully introduced as a biological control agent for *I. purchasi*.

Acknowledgements

This paper is dedicated to Charlotte Causton. Her research in the Galapagos Islands greatly enhanced our knowledge of the noxious effect of invasive species. Funding for this research was provided by Alcedo Funds CDF Inc. A special thanks to Charlotte Causton, Bernard Landry, Scott Henderson, Alan Tye and Chris Buddenhagen for providing constructive comments on the manuscript. I thank to V. Cruz, M. Torres, M. Soria, P. Lincango, N. Castillo, R. Boada, G. Estevez, A. Mieles, D. Rosero, C. Calderon, R. Oquendo, S. Rojas and P. Aycart the field assistants at Volcán Alcedo, and our colleagues at the Galapagos National Park Service and the Charles Darwin Foundation for assistance with various aspects of this project.

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Journal of the Lepidopterists' Society
58(1), 2004, 33–43

THE BUTTERFLIES (PAPILIONOIDEA, HESPERIOIDEA) OF THE GALÁPAGOS ISLANDS, ECUADOR: DISTRIBUTION, HOSTPLANTS AND BIOLOGY.

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ABSTRACT. The butterfly fauna of the Galápagos islands is reviewed. Ten species are recorded from the Archipelago. *Leptotes parrhasioides* (Wallengren), *Urbanus dorantes galapagensis* (Williams), and *Agraulis vanillae galapagensis* (Holland) are endemic and the others are Neotropical faunal elements. A number of new island and host plant records are given.

Additional key words: flower visitation, phenology, Neotropical region.

The butterfly fauna of the Galápagos Islands was first discussed by Williams (1911). Six species were then recorded from the archipelago. Previous reports of Galápagos butterflies were published by Wallengren (1860, 1861), Butler (1877) and Holland (1889). Subsequent to Williams' revision, little mention was made of the butterflies in the Galápagos until Beebe (1923) and Parkin et al. (1972) added two species of milkweed butterflies, *Danaus plexippus* (Linnnaeus) and *Danaus gilippus* (Cramer), to the fauna. A literature-based checklist of the insects of Galápagos by Linsley and Usinger (1966) and Linsley (1977) listed eight species and indicated on which island each species occurred. During the last 33 years only two faunistic notes have been published. Onore and Mielke (1988) reported *Calpodes ethlius* (Stoll) and Roque et al. (1997) added *Hemiargus ramon* (Dognin). Additional information such as flower visits and host plant records were given by Linsley (1966), McMullen (1986, 1990, 1993), McMullen and Viderman (1994) and Roque (1998a, b). Finally, Peck et al. (1998) listed the introduced insect species that occur on the archipelago and included *C. ethlius* and *H. ramon*.

This paper reports new information on Galápagos butterflies gathered during 8 years of fieldwork on the Islands. The butterfly fauna of the archipelago includes 10 species and subspecies, three of which are presumed to be endemic.

MATERIALS AND METHODS

From November 1994 to June 2002 the author conducted daytime observations and collections of butterflies in the Galápagos Islands. A total of 387 specimens were sampled and identified, and observations on habitat associations and behavior of each species was noted. The methods included: a) field collections with a light mesh net, b) field observations of adult behavior and visits to food sources, c) collecting and rearing of immature stages.

Immatures were collected and reared in the laboratory. Eggs and larvae were reared in plastic bags at room temperature under the natural day-night photoperiod regime. Fresh leaves were provides at least every other day. Pupae were kept moist until adults hatched.

The majority of this material was deposited in the Invertebrates Collection of the Charles Darwin Research Station (CDRS), Santa Cruz Island, Galápagos Islands. Some of the other specimens are in the following collections: Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador, Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador and California Academy of Sciences (CAS), San Francisco, USA. Additional records of distributions were obtained from the literature and unpublished data from Dr Bernard Landry, whose material is deposited in the Canadian National Collection (CNC), Ottawa, Canada.

The classification adopted here follows Ackery and Vane-Wright (1984) and Ackery et al. (1999). A brief description is given for the immature stages of the endemic species. The nomenclature of the plants follows McMullen (1999).

The following abbreviations were used: FW = fore wings, DFW = dorsal fore wings, VFW = ventral fore wings. HW = hind wings, DHW = dorsal hind wings, VHW = ventral hind wings. DW = dorsal side of the wings, VW = ventral side of the wings. The size of the butterflies in mm refers to their fore wing length.

RESULTS

Doubtful Records

Previous authors reported several species whose occurrence in the Galápagos has not been demonstrated convincingly. It is better to exclude these as probable misidentifications or mislabelling as is explained below.

Actinote sp. (Nymphalidae): Daniel Fitter, a naturalist guide with the Galápagos National Park Service, sent a color photograph to the author for examination. The photograph, taken on Media Luna, Santa Cruz Island, was published in Fitter et al. (2001:115) and was identified as *Actinote* sp. (Nymphalidae). It has not been collected or seen in the archipelago since the picture was taken. The establishment in the Galápagos of this species will be only confirmed or refuted when additional material is found.

Hypolimmnas misippus (Linné), (Nymphalinae): The only notice of the occurrence of this species in the archipelago is from one specimen deposited in the American Museum of Natural History, New York. The specimen has the following label data: "Conway Bay, Indefatigable Is, Galapagos, March 15 1935, Crocker Exped". It is likely that this is a mislabelling or if the record is valid it was a migrant individual. The species has never been seen or collected since.

Agraulis vanillae lucina (C. & R. Felder): This species was reported by Moreno et al. (1997). It is likely a misidentification of the Galápagos's endemic subspecies *Agraulis vanillae galapagensis* (Holland, 1889).

Heteropia sp. (Hesperiidae): One male from Albemarle [Isabela] was reported by Van Duzee (1933), although the author suggested that the specimen had been mislabeled and collected in Mexico.

Erynnis funeralis (Scudder & Burgess), (Hesperiidae): One specimen (as *Thanos persius* (Scudder)) deposited in the CAS is said to have been collected in Chatham [San Cristóbal], 15 IV 1932 by M Willows Jr. However, Van Duzee (1933) suggested the specimen was mislabelled.

Leptotes trigemmatus (Butler), (Lycaenidae): Larsen (1991) mentioned this species from the Galápagos Islands but it is likely a misidentification of the sister taxon *Leptotes parrhasioides* (Wallengren), as noted by Balint and Johnson (1995).

Phoebis agarithe (Boisduval) (Pieridae): Moreno et al. (1997) reported this species from the archipelago. These authors probably misidentified *Phoebis sennae marcellina* (Cramer) as this species which is superficially similar in size and color. *P. agarithe* has never been collected on the Galápagos Islands.

SPECIES ACCOUNTS

HESPERIIDAE

Pyrginae

Urbanus dorantes galapagensis (Williams 1911)

"Galápagos Skipper"

(Fig. 1)

Eudamus galapagensis Williams 1911:303; Draudt 1921:853; Beebe 1923:55; Van Duzee 1933:144.

Urbanus dorantes galapagensis; Evans 1952:93; Linsley & Usinger 1966:137; Parkin et al. 1972:103.

Urbanus galapagensis Williams & Howard 1944:93.

Diagnosis. FW = 15–20 mm. This is the only tailed skipper of the archipelago. FW dark brown with translucent spots and a pattern of lilac and brown bands in VHW. In some specimens, the hyaline spots are smaller. The lilac bands on the VW tend to be pale with lighter brown or yellowish scales. The sexes are similar, but males have coastal folds.

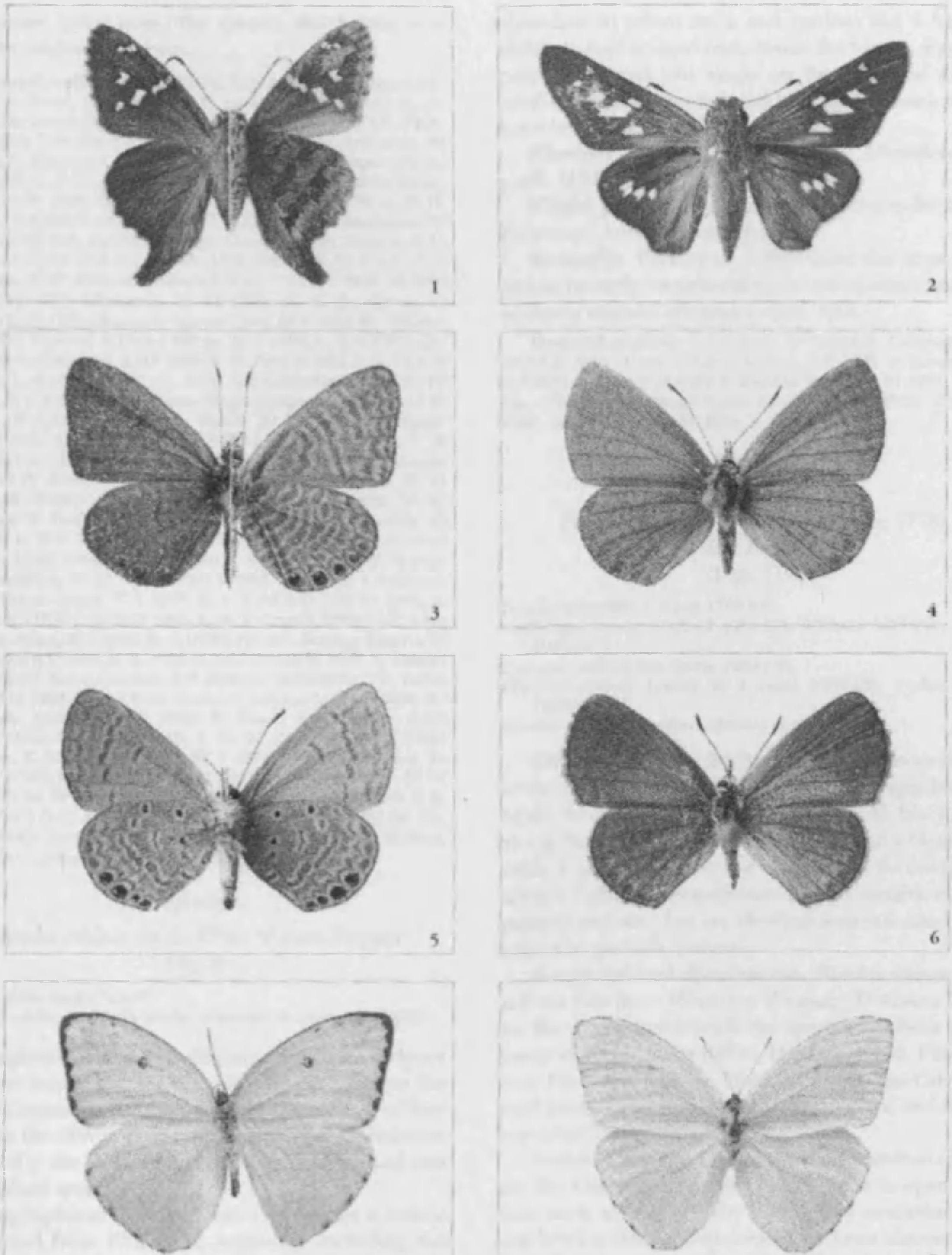
Geographical distribution. Reported from Baltra, Edén, Española, Floreana, Genovesa, Isabela, Pinzón, San Cristóbal, Santa Cruz and Santiago (Linsley & Usinger 1966). Additional records include: Fernandina, Pinta and Rábida.

Natural history. Adults were common in open areas, roadsides, and forests from sea level to the highest elevations. The flight is erratic and low to the ground. Both sexes were seen visiting flowers. Oviposition was observed on leaves and flower buds of various Leguminosae. Eggs greenish laid singly on *Phaseolus atropurpureus* D.C., *P. mollis* Hook, *Desmodium incanum* DC and *Galactia striata* (Jacq). Caterpillar green with the head and prothoracic shield black. In the last instar the body is brown. Pupa pale brown speckled with darker brown.

Flowers visited. Acanthaceae: *Justicia galapagana* Lindau; Asteraceae: *Darwiniothamnus tenuifolius* (Hook. f.) Harling, *Scalesia cordata* Stewart, *Scalesia microcephala* Robins, *Scalesia villosa* Stewart, *Scalesia retroflexa* Hemsley; Boraginaceae: *Cordia leucophlyctis* Hook, *C. lutea* Lam.; Convolvulaceae: *Merremia aegyptica* (L.) Urban, Leguminosae: *Acacia insulaeiacobi* Riley, *P. mollis*; Malvaceae: *Sida rhombifolia* L.; Plumbaginaceae: *Plumbago scandens* L.; Rubiaceae: *Diodia radula* Cham.& Schlecht; Rutaceae: *Citrus limon* (L.) Burn; Solanaceae: *Lycopersicon chesmanii* Riley, *Physalis pubescens* L.; Sterculiaceae: *Waltheria ovata* Cav.; Verbenaceae: *Lantana camara* L., *Lantana peduncularis* Anderss, and *Lippia strigulosa* Mart & Gal.

Flight period. Multivoltine with a peak in January and February.

Remarks. The holotype is in the California Academy of Sciences, San Francisco, USA (CAS); it bears the following label information: Galapagos Is, Chatham I. [San Cristóbal], X 15 06, Coll. By F. X. Williams, California Academy of Sciences Type No. 3209. A specimen deposited on CAS has the following label information: Puerto Vallarta, Jalisco, Mexico, VIII 21 32, M Willow Jr coll, Exp 1932. This could be a mislabelling. Evans (1952) treated it as a subspecies of *Urbanus dorantes* (Stoll, 1790) compared to *Urbanus dorantes santiago* (Lucas, 1856) from Cuba and *U. dorantes dorantes* from mainland Ecuador. *U. dorantes galapagensis* is smaller and has shorter hindwing tails. The male valve is much less dentate and the arms of harpe have few spines. The genus *Urbanus* Hübner 1807, is used provisionally here until revisionary work is undertaken. According to S.



FIGS. 1–8. Galápagos butterflies species. **1,** *Urbanus galapagensis* (DW and VW); **2,** *Calpodes ethlius* (DW); **3,** Male of *Leptotes parrhasioides* (DW and VW); **4,** Male of *Hemiargus ramon* (DW); **5,** Male of *Hemiargus ramon* (VW); **6,** Female of *Hemiargus ramon* (DW); **7,** Female of *Phoebis sennae marcellina* (DW); **8,** Male of *Phoebis sennae marcellina* (DW).

Steinhauser (pers. com.) the species may belong in a separate, undescribe genus.

Material studied. (70♂ and 16♀). ECUADOR, Galápagos. ESPAÑOLA: Hood, 15 V 1899, [R. E. Snodgrass, E. Heller] (CAS) (1♂). Bahía Manzanillo, 24 IV 1992, B. L[andry] (CNC), (2♂). FERNANDINA: 1 IX 1966, (CDRS) (1♂), Cueva Norte, Arid zone, 20 VI 1998, L. R[oque] (CDRS) (1♂). FLOREANA: Arid zone, 130 m, 17 IV 1996, L. R (CDRS) (8♂ and 3♀). Cerro Pajas, *Scalesia* forest, 320 m, 18 IV 1996, L. R (CDRS) (6♂). Cerro Pajas 520 m, 19 IV 1996, L. R (CDRS) (9♂). Charles, 5 X 1899, [R. E. Snodgrass, E. Heller] (CAS) (5♂). ISABELA: Tagus Cove, III 1906, Alotype, F. X. W[illiams] (CAS) (1♀). Cowley Mt. VIII 1906, F. X. W (CAS) (3♂). Albemarle, 27 IV 1932, M. Willows (CAS) (1♂); 28 IV 1932, M. Willows (CAS) (1♀). Albemarle, 12 VI 1899, [R. E. Snodgrass, E. Heller] (CAS) (1♀). Albemarle Iguana Cove, 21 V 1932, M. Willows (CAS) (2♀). V[olcán] A[lcedo] 800 m., 2 IV 1996, L. R (CDRS) (5♂ 2♀). V S[ierra] N[egra], 2 III 1989, S. B. Peck (CNC) (1♂). VSN, 6 IV 1996, L. R (CDRS) (1♂ 1♀). VSN, Las mercedita*s* 120m, 24 IV 1996, L. R (CDRS) (1♂ 7♀). Sierra Negra pampas ferns zone, 24 IV 1996, L. R (CDRS) (1♀). Santo Tomás, 20 III 1995, P. Delgado (CDRS) (3♂); 6 IV 1996, L. R (CDRS) (2♂); 23 IV 1996, L. R (CDRS) (1♂); 23 IV 1996, (CDRS) (1♂). V W[olf], 1200 m, *Scalesia* forest, 19 IV 1996 (CDRS) (7♂ 4♀). Playa Tortuga Negra, 22 VI 1998, L R (CDRS) (1♂). PINTA: Abingdon, 24 VI 1899, [R. E. Snodgrass, E. Heller], (CAS) (1♂). PINZON: Playa escondida, 20 IV 2002, L. R & B. Landry (CDRS) (2♂ 3♀). RABIDA: Sendero turístico, 13 III 1998, L. R, (CDRS) (1♂). SANTA CRUZ: Horneman farm 220m, 18 III 1964, (1♂); 3 V 1964, (2♀). D. Q. Cavagnaro, (CAS). Puerto Ayora, 17 I 1989, B. L (CNC) (1♂); 8 XI 1995, A. Herrera (CDRS) (1♂); 29 X 1995, L. R, V. Cruz (CDRS) (1♂). 4 km N Puerto Ayora, 20 I 1989, B. L (MECN) (1♂). Tortuga Reserve W Santa Rosa, 6 V 1989, S. B. Peck (CNC) (1♂); 6 II 1989, B. Landry (CDRS) (1♂). Cerro Crocker, 9 II 1996, L. R (CDRS) (1♂), Bellavista, 13 II 1999, reared from leaves *D. camum*, L. R (CDRS) (4♂ 1♀); Punta Nuñez, 29 VII 2002, R. Boada (CDRS) (1♀). SAN CRISTOBAL: Chatam, X 1905, F. X. W, (CAS) (3♂); 1 X 1906, Holotype, F. X. W (CAS) (1♂); 23 V 1899, [R. E. Snodgrass, E. Heller], (CAS) (6♂ 1♀); 15 IV 1932, (3♂); 17 IV 1932, (1♂); 18 IV 1932, (2♂), M. Willows, (CAS). Puerto Baquerizo, 17 II 1989, S. B. Peck (CNC) (1♂). Airport 30 m, 6 III 1996, L. R (CDRS) (6♂ 2♀). SANTIAGO: James, 21 IV 1899, [R. E. Snodgrass, E. Heller], (CAS) (2♀). Central 700 m, 9 IV 1992, B. L (CNC) (1♂).

Hesperiinae

Calpodes ethlius (Stoll, 1782) "Canna Skipper"

(Fig. 2)

Papilio ethlius Stoll 1782:212.
Calpodes ethlius; Onore & Mielke 1988:619, Peck et al. 1998:227.

Diagnosis. FW = 19.5–24 mm. The Canna Skipper is a large brown species with translucent spots on the wings. Diagnostic features include a linear row of four spots on the HW and the absence of a tail. Specimens collected in the Galápagos are similar in shape and size to mainland specimens.

Geographical distribution. This species is widely distributed from Florida to Argentina including the West Indies. In the Galápagos Islands it has been reported previously from Isabela (Onore & Mielke 1988) and here from Santa Cruz Island.

Natural history. *Calpodes ethlius* is a powerful flyer that is most active at dawn and dusk, but is also seen at other times of the day. The species is most abundant in urban areas and gardens but it has the ability to find isolated hosts inside the forests. Eggs are pale green and laid singly on the leaves of *Canna edulis* Kerr and *Canna lutea* Mill (Cannaceae), which have been introduced to the Archipelago.

Flowers visited. Verbenaceae: *Clerodendrum molle* HBK.

Flight period. Specimens have been collected in February, April, May and July.

Remarks. Peck et al. (1998) listed this large skipper as recently introduced in the archipelago, and it is a known migrant (Ferguson et al. 1991).

Material studied. (5♂ and 1♀). ECUADOR, Galápagos. ISABELA: VSN, 1 km W Santo Tomás, 12 V 1996, ex larvae, L. R (CDRS) (1♂). SANTA CRUZ: Road to Baltra, 11 VI 1981, Y. Lubin, (CDRS) (1♂). Puerto Ayora, 24 VII 1996, (CDRS) (3♂); 18 II 1998, (CDRS) (1♀); 22 IV 1998, L. R (CDRS) (1♂)

PIERIDAE

Coliadinae

Phoebis sennae marcellina (Cramer, 1779) "Sulfur Butterfly"

(Figs. 7, 8)

Papilio marcellina Cramer 1779:103.
Callidryas eubele; Holland 1899:195; Williams 1911:296; Beebe 1923:55.
Catopsila eubele; Van Duzee 1933:140.
Phoebis sennae; Linsley & Usinger 1966:156; Parkin et al. 1972:103.
Phoebis sennae marcellina; Moreno et al. 1997:146.

Diagnosis. FW = 24–36 mm. Easily recognized, it is the only yellow butterfly on the Galápagos Islands. Male: bright yellow. Female: yellow with black spots along the outer margins of the wings and a black spot with a pale center at the end of the forewing cell above. Galápagos populations are very variable in color pattern and size, but are identical with mainland specimens in genitalic features.

Geographical distribution. *Phoebis sennae marcellina* flies from México to Uruguay (D'Abrera 1981). In the Galápagos Islands the species has been previously reported from Baltra, Daphne, Edén, Fernandina, Floreana, Isabela, Pinta, Santiago, San Cristóbal, and Santa Cruz (Linsley & Usinger 1966) and is here reported from Marchena.

Natural history. One of the most common species on the Galápagos Islands. Adults occur in open habitats such as beaches, dry forests and roadsides from sea level to 900 m. Both sexes have been observed visiting flowers and puddles. The flight is fast and erratic. Beebe (1924) reported a southeast migration of this species from Santiago and Isabela to Santa Cruz, and individuals have been observed commonly flying between islands. Williams (1911) reported *Senna picta* G. Don as a host plant in Galápagos. Females have been observed laying eggs in *Senna tora* L., *Senna bicapsularis* L., and *Senna occidentalis* L. (Fabaceae).

Flowers visited. Acanthaceae: *J. galapagana;* Apocynaceae: *Catharanthus roseus* (L.) G. Don; Asteraceae: *Bidens pilosa* L.; Boraginaceae: *C. leucophlyctis, C. lutea, Heliotropium angiospermum* Murr., *Tournefortia rufo-sericea* Hook. f.; Cactaceae: *Opuntia insularis* Stewart; Convolvulaceae: *Ipomoea pes-caprae* (L.) R. Br., *Ipomoea nil* (L.) Roth; Leguminosae: *S. picta;* Malvaceae: *Gossypium barbadense* var. *darwinii* (Watt.) Hutch, *Hibiscus rosa-sinensis* L., *S. rhombifolia;* Nyctaginaceae: *Bougainvillea spectabilis* Willd. Plumbaginaceae: *P. scandens;* Rubiaceae: *D. radula;* Verbenaceae: *L. camara, Verbena litoralis* HBK.

Flight period. Multivoltine. Specimens have been seen throughout the year.

Material studied. (32♂ and 10♀). ECUADOR, Galápagos. FERNANDINA: Cabo Douglas, 15 IV 1999, P. Polo (CDRS) (1♂). ISABELA: VA, Pega-pega, 6 IV 1999, L. R[oque] (CDRS) (1♂). Puerto Villamil, 2 III 1989, B. L[andry] (CNC) (1♂). Arid Zone, 7 III-1989, S. B. Peck (CNC) (1♂). VSN, 6 IV 1996, L. R (CDRS) (3♂ and 2♀). VSN, Santo Tomás 300 m, 26 IV 1996, L. R (CDRS) (8♂). VSN, Pampas, 24 IV 1996, L. R (CDRS) (1♂ and 3♀). VSN, La Bocanilla 1000 m, 28 IV 1996, L. R (CDRS) (2♂). VSN, Alemania 350 m, 29 IV 1996, L. R (CDRS) (2♂). Playa Tortuga Negra, 22 VI 1998, L. R (CDRS) (3♂). MARCHENA: Playa Negra, 30 IV 2000, L. R, (CDRS) (1♂). SAN CRISTÓBAL: Puerto Baquerizo, 17 II 1989, B. L (CDRS) (2♂); El Porvenir, 15 III 1996, L. R (CDRS) (1♂ and 5♀). SANTA CRUZ: Santa Cruz, 8 VIII 1990, C.K McMullen (CDRS) (1♂). SANTIAGO: Los Jaboncillos, XII 1974, (CDRS) (1♂); Espumilla, 17 III 1998, L. R (CDRS) (1♂).

LYCAENIDAE

Polyommatinae

Leptotes parrhasioides (Wallengren 1860)
"Galápagos Blue Butterfly"
(Fig. 3)

Lycaena parrhasioides Wallengren 1860:37; 1861:355.
Cupido parrhasioides: Williams 1911:300. Beebe 1923:55; Van Duzee 1933:143; Moreno et al. 1997:158.
Leptotes parrhasioides: Bridges 1988:I 268. Linsley & Usinger 1966:157; Balint & Jonhson 1995:9.

Diagnosis. This species and the following are the only lycaenid butterflies in the Galápagos Islands. Both are similar, but the wing pattern and genitalia are distinctive. FW = 8–12.5 mm. Male: DFW and DHW violet blue with two or three black anal spots. VW ground color grayish with a pattern of white markings. VHW with three or four marginal spots, black in the middle, and filled with metallic blue. Female: similar to male but DW ground brown or blue.

Geographical distribution. Endemic to the Galápagos Islands, and reported from the islands of Baltra, Edén, Española, Fernandina, Floreana, Isabela, Pinzón, San Cristóbal, Santa Cruz, Santiago (Linsley & Usinger 1966). It is reported here from Marchena, Pinta and Rábida.

Natural history. Common in the arid zone of the islands. The flight is slow and close to the ground, but may also be rapid and erratic. Both sexes have been seen visiting flowers and were often observed on muddy puddles early in the morning or after rainfall. The pale green eggs are laid singly on the flowers, young fruits, or young leaves of host plants. Williams (1911) reported *Cardiospermum halicacabum* L. as a host plant and indicated *Cardiospermum galapageium* B. L. Rob. & Greenm (Sapindaceae) as another probable food plant. New hostplants records include: *P. scandes, Crotalaria incana* L. and *Rhynchosia minima* (L.) DC. (Leguminosae). The larvae are variable, either green or red with a pattern of dark dorsal marks, depending on the host. The body is covered by short white hairs. Pupae are greenish with brown markings.

Flowers visited. Acanthaceae: *J. galapagana;* Asteraceae: *Darwiniothamnus lancifolius* (Hook. f.) Harling; Boraginaceae: *H. curassavicum, Tournefortia psilostachya* HBK, *T. rufo-sericeae;* Cucurbitaceae: *Momordica charantia* L.; Cyperaceae: *Cyperus ligularis* L.; Leguminosae: *Vigna luteola* (Jacq.) Benth.; Linaceae: *Linum cratericola* Eliass; Lythraceae: *Cuphea racemosa* (L. f.) Spreng.; Malvaceae: *S. rhombifolia,* Plumbaginaceae: *P. scandens;* Nyctaginaceae: *Commicarpus tuberosus* (Lam.) Standl.; Solanaceae: *L. cheesmanii;* Zygophyllaceae: *Tribulus cistoides* L.

Flight period. The species is multivoltine.

Remarks. Wallengren (1860) described this endemic species from at least one male and one female [locality not specified] collected in May 1852 on the Galápagos. However, in 1861 Wallengren redescribed the species with additional material labelled "Puna" [gulf of Guayaquil] and "San Jose island" [Panamá]. Balint and Jonhson (1995) studied a specimen labeled "type" in the Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS). They stated that this specimen belongs to the sister species *Leptotes trigemmatus* (Butler) and that the specimens involved in the redescription (Wallengren 1861) were incorrectly associated with the original series from the Galápagos. The real type of *L. parrhasioides* was not examined, although it is probably located in NRS.

Material studied. (52♂ and 12♀). ECUADOR Galápagos. ESPAÑOLA: Bahía Manzanillo, 25 IV 1992, B. L (CNC) (1♂). FERNANDINA: Narborough, 16 IV 1906, F X W[illiams], (CDRS) (1♀). Near to summit 4800ft, 5 II 1964, D. Q. Cavagnaro, (CAS) (3♂). Cabo Douglas, 21 VI 1998, L. R[oque] and C. C[auston], (CDRS) (3♂ and 2♀). Campamento Perez South Punta Espinoza, 18 VI 1998, L. R and C. C, (CDRS) (7♂ and 4♀). Cueva norte, 20 VI 1998, L. R and C. C, (CDRS) (4♂ and 2♀). North Side 300m, 12 I 2002, L. R and C. C, (CDRS) (1♀). Zona de vegetacion, 20 VI 1996, L. R, (CDRS) (4♂ and 3♀). FLOREANA: Charles, 10 X 1905, F X W, (CAS) (2♀); 23–31 V

1906. F X W. (CAS) (1♀); 1–4 VI 1906. FXW. (CAS) (2♂). Zona costera, 2 IV 1995, L. R and V. Cruz, (CDRS) (1♂). *Scalesia* forest, 4 III 1995, L. R and V. Cruz (CDRS) (12♂ and 4♀). Arid zone 130m, 4 III 1995, in *H. curassavicum* flowers (3♂); in *C. molle* flowers (1♂). L. R and V. Cruz (CDRS). Road to the highland, 4 III 1995, L. R and V. Cruz (CDRS) (3♂). Parte alta, 4 III 1995, L. R and V. Cruz (CDRS) (1♂). Cerro Alieri 340 m, 21 XII 1999, in *Linum cratericola* flowers, L. R. (CDRS) (1♂). ISABELA: Albemarle Banks Bay, 16 X 1906, F X W. (CAS) (2♂). Albemarle Tagus Cove, 22 III 1906, F X W. (CAS) (1♂). V[olcan] S[ierra] N[egra] 1000 m, 1 III 1989, B. L (CNC) (1♀). V[olcan] W[olf], *Scalesia* forest 1700 m, 19 V 1996, L. R (CDRS) (4♂). V W, Upper arid zone, 1250 m, 20 IV 1996, L. R (CDRS) (13♂). Playa Tortuga Negra, 22 VI 1998, L. R, (CDRS) (8♂ and 7♀). PINTA: Playa Ibetson, 14 III 1992, B. L (CNC) (1♂ and 1♀); reared from leaves *R. minima*, 14 III 1992, B. L (CNC) (1♂). 400 m, 17 III 1992, B. L (CNC) (2♂). PINTA: Abingdon green zone, 10 IV 1906, F X W. (CAS) (1♀). PINZON: Summit & upper caldera areas, 7 II 1964, D. Q. Cavagnaro, (CAS) (1♂). SANTIAGO: James bay low altitud, VIII 1932, M. Willows. (CAS) (1♂). SANTA CRUZ: Indefatigable, 8 VI 1932, M. Willows. (CAS) (4♂ and 1♀). Academy Bay CDRS, 5 II 1964, R. O. Schuster, (CAS) (1♂); 25 II 1964, D. Q. Cavagnaro and R. O. Schuster, (CAS) (1♂). Arid Zone, asociated to *Castela galapageia*, 19 I 1989, B. L (CNC) (2♀). Transition zone, 20 I 1989, B. L (CNC) (1♂). SAN CRISTOBAL: Chatam Sapho cove, 9 II 1906, F X W, (CAS) (1♂).

Hemiargus ramon (Dognin, 1887)
"Ramon's Blue Butterfly"
(Figs. 4–6)

Lycaena ramon Dognin 1887:23.
Hemiargus ramon: Roque et al. 1997:29; Peck et al. 1998:227.

Diagnosis. FW = 8.2–11.6 mm. Resembles *L. parrhasioides*, with which it flies, but *H. ramon* has two black dots in the VHW inner costal margin while *L. parrhasioides* has none. Male: DW and DHW violet blue, the outer margins thinly bordered with white. Female: DW and DHW dark with only a touch of blue at the wing base.

Geographical distribution. Distributed on the western slopes of the Andes from northern Chile to the south of Ecuador. This species was listed by Peck et al. (1998) as introduced in the Archipelago. It has been reported from the Galápagos Islands of Baltra, Española, Floreana, Isabela, San Cristóbal, Santa Cruz and Santiago (Roque et al. 1998) and is here reported from Fernandina, Pinzón, Santa Fé, Seymour Norte and Rábida.

Natural history. Common from the low arid zones to the highest elevations. Roque et al. (1997) reported seven leguminous plants as host of the species (*Acacia macracantha* Willd, *S. tora*, *Neptunia plena* Benth, *P. atropurpureus*, *Prosopis juliflora* D.C., *Tephrosia decumbens* (Benth), and one species of Cucurbitaceae: *Cucumis dipsaceus* Her. and one species of Oxalidaceae is reported here: *Oxalis dombeyi* A. St-Hil.

Flowers visited. Asteraceae: *Scalesia gordilloi* Hamann & Wium Anders., *S. pedunculata*; Boraginaceae: *T. rufo-sericeae*; Leguminosae: *T. decumbens*.

Flight period. Observed during all months of the year, but is most common during the rainy season (January to April).

Material studied. (42♂ and 12♀). ECUADOR Galápagos. ESPAÑOLA: Bahía Manzanillo, 24 IV 1992, (1♂); 25 IV 1999 (1♂), B. Landry, (CNC). FERNANDINA: Campamento Perez south Punta Espinoza, 18 VI 1998, L. R[oque] and C. C[auston] (CDRS) (1♂ and 2♀); Cabo Douglas, 21 VI 1998, L. R and C. C, (CDRS) (1♂). Zona de vegetación, 20 VI 1998, L. R and C. C, (CDRS) (1♀). FLOREANA: Zona Costera, 2 IV 1995, L. R and V. C[ruz] (CDRS) (8♂ and 3♀). High arid zone 150m, 4 III 1995, L. R and V. C (CDRS) (5♂). Road to Highland, 4 III 1995, L. R and V. C. (CDRS) (10♂ and 3♀). Parte media, 4 III 1995, in *Heliotropium curassavicum* flowers, L. R and V. C, (CDRS) (5♂). ISABELA: V[olcan] S[ierra] N[egra], 24 IV 1996, L. R (CDRS) (2♂ and 2♀). V S N, Las Merceditas 120m, 24 IV 1996, L. R (CDRS) (1♀). V S N, 2 km W Puerto Villamil, 3 VI 2000, C. Covell (CDRS) (6♂ and 2♀). PINZON: Playa escondida, 20 VI 2002, L. R and B. L, (CDRS) (3♂ and 3♀). SANTA CRUZ: Arid Zone, 8 IX 1999, L. R and C. Covell (CDRS) (2♀ and 4♂), 19 I 1989, B. L, (CNC) (3♂ and 3♀).

NYMPHALIDAE

Danainae

Danaus gilippus thersippus (Bates 1863)
"Queen Butterfly"
(Fig. 11)

Papilio thersippus Bates 1863.
Danaus gilippus: Parkin et al. 1972:103; Linsley 1977:29.
Danaus gilippus thersippus: Ackery & Vane-Wright 1984:208.

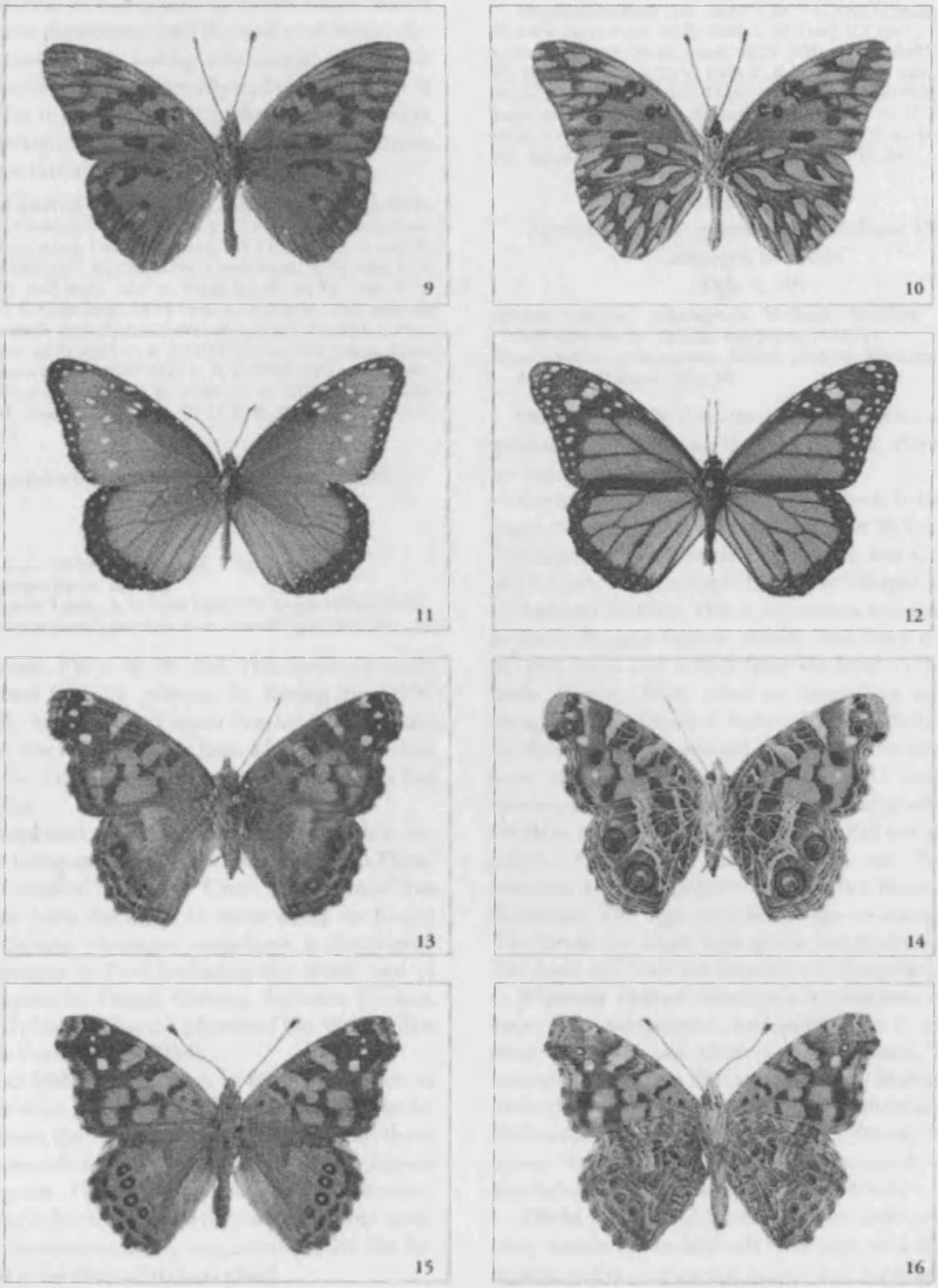
Diagnosis. FW = 36–41 mm. Easily distinguished from *D. plexippus* L. by not having the black inner border, and the black veins on the DFW. Males have a black androconial patch on the DHW. Females are similar to males but without an androconial patch.

Geographical distribution. *Danaus gilippus thersippus* is distributed from the Southern United States to Panamá and is native to the Galápagos Islands. The species has been reported from San Cristóbal (Parkin et al. 1972), and is here reported from Baltra, Floreana, Isabela, Santa Cruz, Santiago, Seymour Norte and Rábida.

Natural history. The queen butterfly is primarily an inhabitant of the arid zones from sea level to 400 m, but its distribution is limited by the occurrence of its foodplants. Adults have been observed flying slowly and frequently visiting flowers in open areas. The pale green eggs are laid singly on young and old leaves of the endemic vine *Sarcostemma angustissima* R. W. Holm. The other milkweed that occurs on the islands, *Asclepias curassavica* L., apparently is used as an alternative food plant.

Flowers visited. Asclepiadaceae: *A. curassavica*, *S. angustissima*; Asteraceae: *D. tenuifolius*; Boraginaceae: *H. angiospermum*; Solanaceae: *P. pubescens*; Verbenaceae: *L. camara*.

Flight period. All available records are from the rainy season.



FIGS. 9–16. **9,** *Agraulis vanillae galapagensis* (DW); **10,** *Agraulis vanillae galapagensis* (VW); **11,** *Danaus gilippus thersippus* (DW); **12,** *Danaus plexippus megalippe* (DW); **13,** *Vanessa virginiensis* (DW); **14,** *Vanessa virginiensis* (VW); **15,** *Vanessa carye* (DW); **16,** *Vanessa carye* (VW).

Remarks. Ackery and Vane-Wright (1984) suggested that this species could have been introduced from California to the islands in recent times. Based on its current distribution and the well-established dispersal potential, and taking into consideration the dates of discovery of the butterfly and its host plants, it is reasonable to assume that *D. g. thersippus* arrived in the Archipelago through natural dispersal mechanisms and was not introduced by humans.

Material studied. (23♂ and 9♀) ECUADOR, Galápagos. FERNANDINA:, Cueva Norte, L. R[oque], (CDRS) (2♂ and 1♀). Campamento Perez south Punta Espinoza, 18 VI 1998, L. R and C. Causton, (CDRS) (1♂). FLOREANA: Cerro Pajas, 20 IV 1996, L. R (CDRS) (1♀). Arid zone, near to Black beach, 22 IV 1996, L. R (CDRS) (2♂). C. Cruz farm, 24 VI 1996, L. R (CDRS) (4♂). Asilo de la Paz 342m, 23 IV 1996, L. R (CDRS) (4♀ and 4♂). ISABELA: Playa Tortuga Negra, 22 IV 1998, L. R (CDRS) (8♂ and 3♀). Volcan Sierra Negra Alemania 350 m, 29 IV 1996, L. R, (CDRS) (10♂ and 6♀). Volcan Sierra Negra pampas, 24 IV 1996, L. R, (CDRS) (1♀). SAN CRISTÓBAL: Puerto Baquerizo, 17 II 1989, B. L, (CDRS) (1♂), (MECN) (1♂).

Danaus plexippus megalippe (Hübner, [1826])

"The Monarch"

(Fig. 12)

Anosia megalippe Hübner [1826]:2, pl. 7, fig. 2.
Danais plexippus; Beebe 1923:55.
Danaus plexippus; Linsley & Usinger 1966:157; Roque 1998a:9, b:10.
Danaus plexippus megalippe; Ackery & Vane-Wright 1984:201.

Diagnosis. FW = 35–50 mm. This species is easily distinguished from *D. gilippus* by having the DFW apex boldly black, a black inner border in DFW and prominent black veins. Males have a black androconial patch on the DFW. Females are similar to males but much darker.

Geographical distribution. The Monarch is native in the Galápagos Islands and reported from Floreana, San Cristóbal and Santa Cruz. The status of this species has been discussed in some detail by Roque (1998a). *Danaus plexippus megalippe* is distributed from Nicaragua to Perú including the North east of Brazil, Venezuela, French Guiana, Surinam, Guyana, Trinidad, Tobago and some islands of the West Indies (Ackery & Vane-Wright 1984).

Natural history. Common in open areas such as fields, roadsides and disturbed sites. In general, the localities where the species occurs are mesic, but there are a few records in arid zones. Galápagos populations do not migrate. The adults fly slowly and visit flowers. Females have been observed ovipositing on the milkweeds *A. curassavica* and *S. angustissima*, but the latter is used as an alternative host plant.

Flowers visited. Asclepiadacea: *A. curassavica;* Malvaceae: *H. rosa-sinensis*; Verbenaceae: *L. camara*, *V. litoralis*.

Flight period. Adults commonly occur only in the rainy season, but are observed sometimes in the dry season.

Material studied. (13♂ and 5♀). ECUADOR, Galápagos. FLOREANA: Cerro Pajas, 20 IV 1996, L. R[oque], (CDRS) (1♂ and 1♀). Arid zone, near to Black beach, 22 IV 1996, L. R, (CDRS) (4♂ and 4♀). Finca de C. Cruz, 24 VI 1996, L. R (CDRS) (1♂). Asilo de la Paz 342 m, 23 IV 1996, L. R, (CDRS) (4♂). SAN CRISTOBAL: Puerto Baquerizo, 17 II 1989, B. Landry (CDRS) (1♂); (CNC) (1♀); (MECN) (1♀). SANTA CRUZ: El cascajo, II 1999, L. R, (CDRS) (1♀). Salasaca, 22 VIII 2000, R. Oquendo, (CDRS) (1♂).

Heliconiinae

Agraulis vanillae galapagensis (Holland 1889)

"Galápagos Fritillary"

(Figs. 9, 10)

Agraulis vanillae galapagensis Holland 1889:194; Williams 1911:298; Beebe 1923:55; Van Duzee 1933:141.
Dione vanillae galapagensis; Stichel 1938:92; Michener 1942:4; Linsley & Usinger 1966:156.

Diagnosis. FW = 19–29 mm. This species is distinguished by its silver markings on the VW. The females are paler than males.

Geographical distribution. Endemic to the Galápagos Islands. It has been collected on Baltra, Edén, Fernandina, Floreana, Isabela, Pinta, San Cristóbal, Santa Cruz, and Santiago (Linsley & Usinger 1966).

Natural history. This is a common species on the larger Galápagos Islands. Adults have been observed in open areas and forests from sea level to the highlands. Beebe (1924) cited an interesting migration along the West Coast of Isabela Island. Adults usually fly slow, low to the ground and frequently have been seen visiting flowers. Williams (1911) mentioned species of the genus *Passiflora* L. as food plants of this fritillary in the Archipelago, but he did not mention which. Oviposition was observed on *Passiflora suberosa* L. and *Passiflora tridactylites* Hook. (Passifloraceae). The eggs were laid singly on young leaves. The larvae are black with green longitudinal stripes. The head and body are covered with long black spines.

Flowers visited. Acanthaceae: *Blechum brownei* Juss. f., *J. galapagana*; Asclepiadaceae: *S. angustissima;* Boraginaceae: *Croton scouleri* Hook. f.; Cannaceae: *Commelina diffusa* Burdm. f.; Malvaceae: *S. hederifolia* Cav., *S. paniculata* L., *S. salviifolia* Presl.; Rubiaceae: *D. radula;* Rutaceae: *C. limon*; Sterculiaceae: *Waltheria ovata* Cav.; Verbenaceae: *L. camara*, *Stachytarpheta cayennensis* (Rich.) M.Vahl.

Flight period. All specimens were collected in the rainy season but individuals were observed during all months of the year except August and September.

Remarks. This species has been treated by several authors as a subspecies of the widely distributed American species *Agraulis vanillae*. Holland (1889) and Williams (1911) stated that the Galápagos taxon should be raised to specific status based on several differences in the wing pattern. Michener (1942) recognized the differences in the wing maculation and size, and mentioned some variation in the male genitalic valvae. Specimens studied here were collected on several localities of the Archipelago.The male genitalia are generally similar to those of mainland specimens of *A. vanillae* but differ consistently in the valva. The apex of the valva is more slender and with fewer denticules in *A. v. galapagensis*. The female genitalia are similar in both forms. *Agraulis vanillae galapagensis* can be separated from the other described subspecies by the smaller size, by the darker and more fuscous color of the basal half of the wings dorsally, by the stronger black markings on the wings, and by the absence of white dots in the black spots of the DFW discal cell. The holotype, collected on Chatham [San Cristóbal], is deposited in the National Museum of Natural History, Washington, DC (USNM). The identity of this species will remain questionable until a revision of the genus makes it more definite.

Material studied. (14♂ and 51♀). ECUADOR. Galápagos. FERNANDINA: Campamento Perez south Punta Espinoza, 18 VI 1998, L. R[oque] and C. Causton, (CDRS) (1♂). FLOREANA: Arid zone 130m, 17 IV 1996, L. R, (CDRS) (1♂). Cerro Pajas, *Scalesia* forest, 18 IV 1996, (9♂ and 5♀); 19 IV 1996, L. R, (1♀); 22 IV 1996, L. R (CDRS) (7♂ and 2♀). ISABELA: V[olcán] S[ierra] N[egra], Santo Tomás, 6 IV 1996, (1♂); 26 IV 1996, L. R, (CDRS) (1♂). V S N, bosque de los niños, 20 III 1995, L. R, (CDRS) (1♂). V S N, pampas 1000m, 1 III 1989, B. L[andry] (CNC) (1♀). V S N, la bocanilla 1000m, 28 IV 1996, L. R, (CDRS) (2♂ and 1♀). V S N, Las mercedi-tas, 30 IV 1996, L. R, (CDRS) (2♂ and 4♀). Volcan Wolf, upper arid zone 1700 m, 19 V 1996, L. R, (CDRS) (13♂ and 4♀). PINTA: 400 m, 17 III 1992, B. L. (CNC) (4♂). SANTIAGO: Playa Espumilla, 4 IV 1992, B. L, (CNC) (1♂). SANTA CRUZ: CDRS, 22 XI 1963, (CDRS) (1♂). Tortugas reserve west of Santa Rosa, 6 II 1989, B. L. (CDRS) (1♂); (MECN) (1♂).

Nymphalinae

Vanessa virginiensis (Drury 1773)
"Painted Lady"
(Figs. 13, 14)

Nymphalis cardui virginiensis Drury 1773:1.
Pyrameis huntera; Williams 1911:299.
Vanessa virginiensis; Linsley & Usinger 1966:156.

Diagnosis. FW = 21.7–29 mm. Differs from *V. carye* by the presence of two blue-centered ocular markings on the VHW. Males and females are similar.

Geographical distribution. This cosmopolitan species was previously reported from Isabela (Volcanoes Darwin and Sierra Negra) (Williams 1911). On Isabela, the species was found at those localities as well as on volcanoes Alcedo, Cerro Azul and Wolf. Other new records include Santa Cruz and Santiago and it probably also inhabits other large islands. The species is distributed from southern Canada to the mountainous region of Colombia, including the West Indies, Hawaii, Azores, Madeira, the Canary Islands, and occasionally Europe (DeVries 1987).

Natural history. This species has only been observed in the open grassy areas of the highlands. All specimens were collected above 900 m in the pampa zone. Although it flies usually under bright and sunny conditions, we have seen it under overcast conditions and even during light rain (Volcán Alcedo, 23.X.1998). Adults fly fast and rest on the ground, flying short distances when disturbed. Eggs, larvae and pupae were found on the leaves of *Gnaphalium purpureum* L. (Asteraceae) on the islands of Isabela and Santiago. The plant can be found on more islands (Lawesson et al. 1987). *Vanessa virginiensis* has resident populations in the Galápagos Islands.

Flowers visited. Rubiaceae: *Borreria laevis* (Lam.) Griseb.

Flight period. Specimens have been collected or observed from January to June.

Material studied. (15♂ and 4♀). ISABELA: Albemarle, 20–31 VIII 1906, F X Williams, (CAS) (1♂). V[olcán] S[ierra] N[egra], rim northwest side, 4 III 1989, B. L[andry], (CDRS) (1♂); (MECN) (1♂). V S N, 1000 m, 4 III 1989, S. B. Peck (CNC) (1♀). V S N, La Bocanilla 1000 m, 28 IV 1996, L. R[oque], (CDRS) (1♂ and 4♀). V S N, Las Mercedditas, 6 IV 1996, L. R, (CDRS) (1♂). Volcán Wolf, high arid zone, 1250 m, 21 V 1996, L. R, (CDRS) (4♂). Volcan Alcedo, top 1100 m, 24 IV 1998, L. R (2♂ and 4♀). SANTA CRUZ: CDRS, 10 VI 1965, (CDRS) (1♂). SANTIAGO: Los Jaboncillos 900 m, 9 IV 1992, B. L, (CNC) (1♀); 16 III 1998, L. R, (CDRS) (1♂). Los Aguacates, 16 III 1998, L. R (CDRS) (1♂). NW slope 600 m, 30 V 1964, D. Q. Cavagnaro, (CAS) (1♀).

Vanessa carye Hübner [1812]
"Western Painted Lady"
(Figs. 15, 16)

Hamadryas carye Hübner [1812]:pl. 45, figs. 1, 2.
Pyrameis caryae; Williams 1911:300.
Vanessa caryae; Linsley & Usinger 1966:156.

Diagnosis. FW = 21–28 mm. Differs from *V. virginiensis* by having four small blue-centered ocular markings on the VHW.

Geographical distribution. This species has been collected on San Cristóbal, Fernandina, and recently observed by the author in Floreana. *Vanessa carye* is distributed in the Andes of Colombia, Ecuador, Peru, Bolivia, Chile, southwestern Brazil, Paraguay, Uruguay, and Argentina. It also occurs on Juan Fernandez island, on Easter island, and the Tuamotu Archipelago.

Natural history. Three out of four specimens collected or observed were from the low arid zone at sea level. Two fresh adults were observed visiting flowers on Floreana (13 I 1995 and 6 II 1995, Puerto Velazco Ibarra) but were not collected. Their fresh condition suggested that they were from a population extant on the island, rather than migrants. The host plant and the immature stages are unknown in the Archipelago.

Members of Asteraceae, Geraniaceae, Malvaceae, and Urticaceae are reported as host plants for the species (Field 1971).

Flowers visited. Verbenaceae: *C. molle*.

Flight period. Adults have been collected or observed in January and February.

Remarks. The only two specimens collected on the Galápagos were deposited in the California Academy of Sciences.

Material studied. (1♂ and 1♀). FERNANDINA: near to summit, 4800 ft, 5 II 1964, D. Q. Cavagnaro, (CAS) (1♀). SAN CRISTOBAL: Chatam, Wreck Bay, 22 II 1906, (CAS) (1♂).

ACKNOWLEDGMENTS

I would like to thank the authorities of the Galápagos National Park and the Charles Darwin Research Station for financial and logistical support in field. The Charles Darwin Research Station and Canacoll Foundation provided financial support for my investigations at the Canadian National Collection of Insects in 1999. I thank the curators Germania Estevez (early curator MECN, Quito, Ecuador), Giovanni Onore and Francisco Piñas (PUCE), Bernard Landry (MHNG, Geneva, Switzerland) for their permission to study the specimens deposited in their collections. I am indebted to Bernard Landry and Charles V. Covell Jr. (University of Louisville, Kentucky, USA) for generosity with their time and knowledge of Lepidoptera, and Stewart Peck (Carleton University, Ottawa, Canada) for his knowledge of Galápagos insects. I am also greatly indebted to Charlotte Causton, Alan Tye, Heidi Snell and Sol Rojas (CDRS), Olaf Mielke and Mirna Casagrande (Universidad Federal de Paraná, Paraná, Brazil), Philip J. DeVries and Carla M. Penz (Milwaukee Public Museum, Milwaukee, USA) and Keith Willmott (NHM London) for their critical review of versions of this manuscript. To Ivan Aldaz (CDRS) for plant identifications, and Zsolt Balint (Hungarian Natural History Museum, Budapest, Hungary) for Lycaenidae literature. To Matts Wedin (CDRS) for producing the plates. Finally I thank to all my field assistants during the years, especially Valentina Cruz.

This research was partially supported by Unesco project #894976.9: Ecological monitoring in the Galápagos Archipelago, Galápagos Conservation Fund, GEF-Natura Project: Monitoring the Galápagos Islands and Darwin Initiative for the survival of species project: Terrestrial Invertebrate Biodiversity in Galápagos (Ecuador): Training and collection rehabilitation.

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Received for publication 19 June 2002; revised and accepted 7 January 2004

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
74, 217 - 226, 2002 (2001)

The Sphingidae (Lepidoptera) of the Galápagos Islands: their identification, distribution, and host plants, with new records

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Two species of Sphingidae (*Perigonia lusca lusca* (FABRICIUS) and *Xylophanes pluto* (FABRICIUS)) are reported for the first time from the Galápagos Islands. Fourteen new host plant records are given for nine of the fifteen species now found in the Galápagos. Forty-one new island records of distribution are given for species already mentioned from the archipelago. An illustrated key to the adults of Galápagos Sphingidae is included and their distribution and host plants are summarized.

Keywords: Sphingidae, Galápagos Islands, faunistics, host plants, illustrated key

INTRODUCTION

The Sphingidae, or hawk moths, are medium-sized to large moths with elongate wings and a large body allowing for powerful flight. They are often seen at dusk hovering and sipping nectar from flowers with their long proboscis. They are present basically everywhere on earth and there are some 1100 described species (HEPPNER 1998). Because hawk moths and their caterpillars can be identified easily, they are prime subjects for ecological and other studies.

The occurrence of hawk moths in the Galápagos Islands was first recorded in a report by BUTLER (1877), in which he mentioned two larvae of "a Sphinx moth" in the collection of Commander W. E. Cookson made during the visit of H.M.S. "Peterel" to the Galápagos in 1875. HOLLAND (1889) made the second mention of Sphingidae from the Archipelago. He reported a series of worn specimens collected by a member of the steamer Albatross in 1887-1888 and described a new endemic species (*Protoparce calapagensis* HOLLAND, 1889). ROTHSCHILD & JORDAN (1903) later considered *calapagensis* a subspecies of *Manduca rustica* (FABRICIUS, 1775). The classic world revision of the Sphingidae family by ROTHSCHILD & JORDAN (1903) and the excellent monograph of the Galápagos hawk moths made by WILLIAMS (1911) mentioned that nine species occurred in the archipelago. Subsequently, BEEBE (1923), CLARK (1926), KERNBACH (1962, 1964), PARKIN *et al.* (1972), HAYES (1975), SCHREIBER (1978) and HICKIN (1979) added new data. LINSLEY & USINGER (1966) and LINSLEY (1977) in their checklist of insects of the Galápagos, list 13 species of Sphingidae in eight genera but one of these, *Pachygonia drucei* ROTSCHILD & JORDAN, 1903, is based on a specimen now presumed to have been taken on Cocos Island (HAYES 1975).

During the last 22 years (1979-2001), only two notes pertaining to the faunistics and taxonomy of the Galápagos Sphingidae have been published. HAXAIRE

(1993) synonymized the subspecies *Hyles lineata florilega* (KERNBACH 1962) under *Hyles lineata* and ROQUE-ALBELO (1999) reported for the first time *Cocytius antaeus* (DRURY, 1773) from the islands. Therefore, prior to the present paper, 13 species in eight genera were known from the archipelago.

There is little additional information available on Galápagos Sphingidae. LINSLEY (1966) and MCMULLEN (1986, 1990, 1993) summarized the known flower-insect relationships in the Galápagos, including some with hawk moths, while KERNBACH (1964) and CURIO (1965a, b) studied the development and behavior of some caterpillars.

This paper reports new information on the distribution of hawk moths in the Galápagos and contains a key to the species of Sphingidae presently known from the islands, as well as new host plant records. The number of Sphingidae known to occur in the Galápagos now totals 15 species in 9 genera. One species, *Xylophanes norfolki* KERNBACH, is endemic to the archipelago.

MATERIAL AND METHODS

We collected the majority of the specimens studied between January 1989 and June 2001 during an extensive survey of the Galápagos butterfly and moth fauna. The study included the majority of the Galápagos islands.

The moths were collected with light traps (mercury vapor lamps (MVL), ultraviolet lights (UL) and fluorescent lights (FL)) and immediately killed with an injection of ethyl acetate. Caterpillars were also collected and reared in the laboratory. The majority of this material is deposited in the Invertebrate Collection of the Charles Darwin Research Station (CDRS), Santa Cruz Island, Galápagos, while some is at the Canadian National Collection of Insects (CNCI), Ottawa. Representative samples are deposited at the Pontificia Universidad Católica del Ecuador (PUCE). Additional records of distribution were obtained from the literature and from specimens deposited in The Natural History Museum, London (BMNH), Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, and the California Academy of Sciences, San Francisco (CAS). The collectors' names are abbreviated below as follows: Charlotte Causton (CC), Valentina Cruz (VC), B. Landry (BL), and Lazaro Roque-Albelo (LRA).

The classification adopted here follows KITCHING & CADIOU (2000). We accept the current nomenclatural status of the Galápagos species although we are not certain that all endemic subspecies are valid. The nomenclature of the host plants follows MCMULLEN (1999).

NEW ISLAND, HOST PLANT AND SPECIES RECORDS

Tables 1 and 2 summarize all known distribution and host plant records of Galápagos Sphingidae.

Sphinginae

Agrius cingulata (FABRICIUS)

New island records. FERNANDINA: Punta Espinoza, 12.V.1992, MVL, BL (1♂, CNCI); Punta Mangle, 13-14.VI.1998, UL, LRA & CC (1♂, 1♀, CDRS); Punta Gavilan, 17.VI.1998, UL, LRA & CC (1♀, CDRS); 4 km S Punta Espinoza, 18.VI.1998, UL, LRA & CC (1♂, CDRS); Zona de vegetación, 19.VI.1998, UL, LRA & CC (1♂, CDRS). MARCHENA: Playa Negra, 12.III.1992, MVL, BL (2♂, CNCI). RABIDA: 13.III.1998, UL, LRA (1♂, CDRS). SANTIAGO: Cerro Inn, 27.III.1992, MVL,

Species	Host plants	References
Agrius cingulata	*Ipomoea pes-caprae* (L.)	Williams (1911)
	Ipomoea habeliana Oliv.	This article
	Ipomoea nil (L.)	This article
	Ipomoea triloba L. [as *I. galapagensis*]	Williams (1911)
	Stictocardia tilifolia (Desr.) [as *I. campanulata*]	Williams (1911)
	Ipomoea spp	Hayes (1975)
Cocytius antaeus	*Annona cherimola* Mill.	Roque-Albelo (1999)
Manduca sexta leucoptera	*Physalis pubescens* L.	Hayes (1975)
	Nicotiana tabacum L.	This article
	Acnistus ellipticus Hook. f.	This article
Manduca rustica calapagensis	*Clerodendrum molle* HBK	Williams (1911), Hayes (1975)
	Cordia lutea Lam.	Williams (1911), Hayes (1975)
	Cordia leucophlyctis Hook. f.	Hayes (1975)
	Tournefortia rufo-sericea Hook. f.	Williams (1911)
	Croton scouleri Hook. f.	Williams (1911)
	Bastardia viscosa HBK	Williams (1911)
	Darwiniothamnus lancifolius (*Hook. f.*) Harling	Williams (1911)
	Commicarpus tuberosus (Lam.) Standl.	This article
	Lantana camara L.	This article
Erinnyis alope dispersa	*Carica papaya* L.	This article
	Manihot esculenta Crantz	This article
Erinnyis ello encantada	*Hippomane mancinella* L.	Williams (1911), Curio (1965), Hayes (1975)
	Psidium guajaba L.	Williams (1911)
	Chamaesyce viminea (*Hook. f.*)	This article
Erinnyis obscura conformis	*Sarcostemma angustissimum* (Andersson) R. W. Holm	Williams (1911), Hayes (1975)
Enyo lugubris delanoi	*Cissus sicyoides* L.	Williams (1911), Hayes (1975)
Perigonia lusca	*Cinchona succirubra* Pav. Ex Klotzsch	This article
Eumorpha labruscae yupanquii	*Cissus sisyoides* L.	This article
Xylophanes tersa	*Diodia radula* (Roem. & Schult) Cham. & Schlecht.	This article
	Clerodendrum molle HBK	Williams (1911)
Xylophanes norfolki	*Psychotria rufipes Hook. f.*	This article
Hyles lineata	*Portulaca oleracea* L.	Hayes (1975)
	Commicarpus tuberosus (Lam.) Standl.	Hayes (1975)
	Boerhaavia caribaea Jacq.	This article

Table 1. Summary of the known Galápagos host plants of Galápagos Sphingidae.

BL (1♀, CNCI); Los Aguacates, 520m, 7.IV.1992, MVL, BL (1♀, CNCI); Central, 700m, 9.IV.1992, MVL, BL (2♀, CNCI); Playa Espumilla, 17.III.1998, UL, LRA (1♂, CDRS).
New host plant records. Convolvulaceae: *Ipomoea habeliana* OLIV., *Ipomoea nil* (L.).

Manduca sexta leucoptera (FABRICIUS)

New island records. ESPAÑOLA: Bahia Manzanillo, 25.IV.1992, MVL, BL (1♀, CNCI). RABIDA: 13.III.1998, UL, LRA (2♂, CDRS). SANTIAGO: Central, 700m, 9.IV.1992, MVL, BL (1♂, CNCI); Los Aguacates, 5.VII.1998, UL, LRA (1♀, CDRS).
New host plant records. Solanaceae: *Nicotiana tabacum* L., *Acnistus ellipticus* HOOK. *f.*

Manduca rustica calapagensis (HOLLAND)

New island records. FERNANDINA: Punta Espinoza, 12.IV.1992, MVL, BL (1♀, CNCI). GENOVESA: Bahia Darwin, 10m, 25.III.1992, MVL, BL (1♂, 3♀, CNCI). MARCHENA: Playa Negra,

12.III.1992, MVL, BL (1♂, 1♀, CNCI). PINTA: Arid Zone, 16.III.1992, reared, BL (1♀, CNCI); 15m, 21.III.1992, MVL, BL (1♂, CNCI); 50m, 20.III.1992, MVL, BL (1♂, CNCI). RABIDA: 8.IV.1992, MVL, BL (1♂, CNCI). SANTIAGO: Cerro Inn, 28.III.1992, MVL, BL (1♀, CNCI); Bahia Espumilla, 4.IV.1992, MVL, BL (1♀, CNCI); 17.III.1998 UL, LRA (2♂, CDRS); 200m, 5.IV.1992, MVL, BL (1♀, CNCI); Los Aguacates, 520m, 6.IV.1992, MVL, BL (1♀, CNCI); 5.VII.1998, UL, LRA (3♂, CDRS); Los Jaboncillos, 900m, 8.IV.1992, MVL, BL (1♀, CNCI); Central, 700m, 9.IV.1992, MVL, BL (1♂, CNCI).
New host plant records: Nyctaginaceae: *Commicarpus tuberosus* (LAM.) STANDL.; Verbenaceae: *Lantana camara* L.

Macroglossinae

Erinnyis alope dispersa KERNBACH

New island records. FLOREANA: Las palmas farm, 130m, 17.IV.1997, MVL, LRA & VC (1♂, CDRS). ISABELA: Puerto Villamil, 2.III.1989, MVL, BL (1♂, CNCI); 8.5 km North Puerto Villamil, 8.III.1989, MVL, BL (1♂, CNCI); V[olcán] Al[cedo], 1100m, 7.VI.1997, MVL, LRA (1♂, CDRS). SAN CRISTOBAL: 4 km SE Puerto Baquerizo, 12.II.1989, MVL, BL (1♂, CDRS).
New host plant records. Caricaceae: *Carica papaya* L.; Euphorbiaceae: *Manihot esculenta* CRANTZ.

Erinnyis ello encantada KERNBACH

New island records. RABIDA: Tourist trail, 3.IV.1992, MVL, BL (1♂, CNCI). SANTA FÉ: Arid zone, 6-9.V.1997, MVL, LRA (2♂, 2♀, CDRS). SANTIAGO: Bahia Espumilla, 4.IV.1992, MVL, BL (1♀, CNCI); Los Aguacates, 520m, 6.IV.1992, MVL, BL (1♂, 1♀, CNCI); Los Jaboncillos, 900m, 8.IV.1992, MVL, BL (1♀, CNCI).
New host plant record. Euphorbiaceae: *Chamaesyce viminea* (HOOK. *f.*).

Erinnyis obscura conformis KERNBACH

New island records. BARTOLOMÉ: 18.III.1998, UL, LRA (1♂, CDRS). FERNANDINA: Punta Espinoza, 12.V.1992, MVL, BL (1♂, CNCI); Zona de vegetación, 19.VI.1998, UL, LRA & CC (1♂, CDRS). GENOVESA: Bahia Darwin, 10m, 25.III.1992, MVL, BL (1♂, CNCI). MARCHENA: Playa Negra, 12.III.1992, MVL, BL (1♂, CNCI). PINTA: Playa Ibbetson, 14.III.1992, MVL, BL (2♂, CNCI); 200m, 16.III.1992, MVL, BL (1♂, CNCI); 50m, 20.III.1992, MVL, BL (1♂, CNCI). SANTIAGO: Cerro Inn, 28.III.1992, MVL, BL (1♂, CNCI); Bahia Espumilla, 4.IV.1992, MVL, BL (1♂, CNCI); 17.III.1998, UL, LRA (1♂, CDRS); 200m, 5.IV.1992, MVL, BL (1♂, CNCI); Los Aguacates, 520m, 6.IV.1992, MVL, BL (2♂, CNCI); Central, 700m, 9.IV.1992, MVL, BL (1♂, CNCI). SEYMOUR NORTE: 29.III.1992, MVL, BL (1♀, CNCI).

Enyo lugubris delanoi KERNBACH

New island records. RABIDA: Tourist trail, 3.IV.1992, MVL, BL (1♂, CNCI). SANTA FÉ: Arid Zone, 6-9.V.1997, MVL, LRA (2♂, CDRS). Seymour Norte: Arid Zone, 23.I.1989, MVL, BL (1♂, CDRS); 29.III.1992, MVL, BL (1♂, CNCI). SANTIAGO: Bahia Espumilla, 4.IV.1992, MVL, BL (1♂, CNCI); 17.III.1998, UL, LRA (2♂, CDRS); Central, 700m, 9.IV.1992, MVL, BL (1♂, CNCI).

Perigonia lusca lusca (FABRICIUS)

New Archipelago record. ISABELA: Volcan Alcedo, pampas, 1150m, 16.IV.2001, UL, LRA (1♂, CDRS). SANTA CRUZ: Barranco, 10m, 14.VII.1999; 8.II.2000, MVL, LRA & VC (3♂, CDRS).
New host plant record. Rubiaceae: *Cinchona succirubra* PAV. EX KLOTZSCH.

Eumorpha fasciatus tupaci KERNBACH

New island record. FLOREANA: Asilo de la Paz, 27.V.1998, MVL, LRA & C. Covell (2♂, CDRS).

Eumorpha labruscae yupanquii KERNBACH

New island record. ISABELA: Volcan Alcedo, Arid zone 10m, 3.VI.1997, MVL, LRA (3♂, CDRS); Volcan Alcedo, pampas, 1100m, 7.VI.1997, MVL, LRA (2♂, CDRS).
New host plant record. Vitaceae: *Cissus sicyoides* L.

Xylophanes pluto (FABRICIUS)

New Archipelago record. SANTA CRUZ: Barranco, 14.VII.1999, MVL, LRA & VC (6♂, CDRS); Puerto Ayora, 5.II.2000, FL, LRA (1♀, CDRS).

Xylophanes tersa tersa (LINNAEUS)

New island records. FLOREANA: Asilo de la Paz, 24.IV.1996, MVL, LRA & VC (1♂, CDRS). ISABELA: Volcan Sierra Negra, Santo Tomás, 23.IV.1996, FL, LRA (4♂, CDRS); Volcan Alcedo, Arid zone, 10m, 3.IV.1997, MVL, LRA (1♂, CDRS); Volcan Alcedo, pampas, 1100m, 7.VII.1997, MVL, LRA (1♂, CDRS). SANTA CRUZ: El cascajo, 7.III.1997, MVL, LRA (1♀, CDRS); Los Gemelos, I.1997, MVL, LRA (4♂, 9♀, CDRS); 27.II.1997, MVL, LRA (2♂, CDRS); 1.III.1997, MVL, LRA (2♂, CDRS); 7.IV.1997, MVL, LRA (2♂, 1♀, CDRS); VI.1997, MVL, LRA (1♂, CDRS); 27.VIII.1997, MVL, LRA (1♀, CDRS); Media Luna, 26.V.1996, MVL, LRA (1♂, 1♀, CDRS); IV.1997, MVL, LRA (2♂, 2♀, CDRS); Transition zone, 5.IV.1997, MVL, LRA (2♂, CDRS).
New host plant record. Rubiaceae: *Diodia radula* (ROEM. & SCHULT.) CHAM. & SCHLECHT.

Xylophanes norfolki KERNBACH

New island records. FERNANDINA: W Side, 1100m 5.II.1964, D. Q. Cavagnaro, (1♂, CAS). ISABELA: Volcan Alcedo, Bursera forest, 3.VI.1997, MVL, LRA (1♂, CDRS); Volcan Alcedo, 850m, 6.VI.1997, MVL, LRA (2♂, CDRS).
New host plant record. Rubiaceae: *Psychotria rufipes* HOOK.*f.*

Hyles lineata (FABRICIUS)

New island records. PINTA: 400m, 17.III.1992, MVL, BL (1♀, CNCI). RABIDA: Tourist trail, 3.IV.1992, MVL, BL (1♂, CNCI). SANTA FÉ: Arid zone, 6-9.V.1997, MVL, LRA (2♀, CDRS). SEYMOUR NORTE: 29.III.1992, MVL, BL (1♂, CNCI).
New host plant record. Nyctaginaceae: *Boerhaavia caribaea* JACQ.

Species	**St.**	**Islands**																
		B	**Bt**	**Es**	**Fe**	**Fl**	**Ge**	**I**	**M**	**P**	**Pz**	**SN**	**SC**	**SF**	**Sg**	**SI**	**R**	**W**
Sphinginae																		
Agrius cingulata	N	X			X	X		X	X				X		X	X	X	X
Cocytius antaeus	N												X			X		
Manduca sexta leucoptera	E			X		X		X					X		X	X	X	
Manduca rustica calapagensis	E	X		X	X	X	X	X	X	X			X		X	X	X	
Macroglossinae																		
Erinnyis alope dispersa	E					X		X					X			X		
Erinnyis ello encantada	E					X		X					X	X	X	X	X	
Erinnyis obscura conformis	E	X	X		X	X	X	X	X	X	X		X		X			
Enyo lugubris delanoi	E					X		X				X	X	X	X		X	
Perigonia lusca	N							X				X	X					
Eumorpha fasciatus tupaci	E					X							X					
Eumorpha labruscae yupanquii	E					X		X					X					
Xylophanes pluto	N												X					
Xylophanes tersa	N					X		X					X					
Xylophanes norfolki	E				X			X					X					
Hyles lineata	N	X		X		X		X		X		X	X	X	X	X	X	

Table 2. Status and distribution of Sphingidae in the Galápagos Islands. St.: Status; N: native, E: endemic; Islands: B: Baltra, Bt: Bartolomé, Es: Española, Fe: Fernandina, Fl: Floreana, Ge: Genovesa, I: Isabela, M: Marchena, P: Pinta; Pz: Pinzón, SN: Seymour Norte, SC: Santa Cruz, SF: Santa Fé, Sg: Santiago, SI: San Cristóbal, R: Rábida, W: Wolf.

KEY TO GALÁPAGOS SPHINGIDAE BASED ON EXTERNAL STRUCTURES

1 Wingspan 50-120 mm 2

\- Wingspan 150-190 mm............................*Cocytius antaeus* (DRURY) (Fig. 2)

2 Forewing outer margin scalloped, wavy or very angular..............................3

\- Forewing outer margin more or less smooth 6

3 Body and wings dark brown; outer margin of forewings strongly scalloped ....*Enyo lugubris delanoi* KERNBACH (Fig. 8)

\- Not as described above 4

4 Forewings gray with dark markings, hindwings reddish-orange with the outer border black 5

\- Forewings dark brown; basal area of hindwings bright yellow....................14

5 Abdomen with black bars...........*Erinnyis ello encantada* KERNBACH (Fig. 6)

\- Abdomen without black bars.. ....*Erinnyis obscura conformis* KERNBACH (Fig. 7)

6 Antenna enlarging toward apex, apically constricted and hook-shaped.......... ....*Hyles lineata* (FABRICIUS) (Fig. 14)

\- Antenna of same width for whole length except for constricted and hook-shaped apex...7

7 Abdomen with 3-6 pairs of yellow spots...8

\- Not as described above..9

8 Abdomen with 5-6 pairs of yellow spots; forewings gray with black and white markings ....*Manduca sexta leucoptera* (FABRICIUS) (Fig. 3)

\- Abdomen with 3 pairs of yellow bars; forewings gray, golden or dark brown with white markings........*Manduca rustica calapagensis* (HOLLAND) (Fig. 4)

9 Abdomen long and pointed; hindwings with row of yellow triangular bars..10

\- Not as described above..11

10 Forewings with a diffuse diagonal whitish line from before middle of dorsal margin to apex.............................*Xylophanes tersa* (LINNAEUS) (Fig. 13)

\- Forewings without diagonal whitish line... ....*Xylophanes norfolki* KERNBACH (Fig. 12)

11 Body and forewing green 12

\- Not as described above..13

12 Hindwing with red, black and blue markings.. ....*Eumorpha labruscae yupanquii* KERNBACH (Fig. 11)

\- Hindwing across with large yellowish-orange band... ....*Xylophanes pluto* (FABRICIUS) (Fig. 15)

13 Forewing dark-greenish brown with sharply defined whitish bands; abdomen dorsally with longitudinal whitish bands ......*Eumorpha fasciatus tupaci* KERNBACH (Fig. 10)

\- Forewing brownish gray; abdomen with 4-5 pairs of pink spots..................... ....*Agrius cingulata* (FABRICIUS) (Fig. 1)

14 Wingspan 80-98 mm; forewing outer margin scalloped................................ ....*Erinnyis alope dispersa* KERNBACH (Fig. 5)

Wingspan 53-68 mm; forewing outer margin curving outward near middle ....*Perigonia lusca* (FABRICIUS) (Fig. 9)

DISCUSSION

The new distribution records mentioned here are believed to reflect better collecting efforts rather than recent expansions of distributions as most Galápagos hawk moths (except the endemic *X. norfolki*) are widely distributed in the New World and good dispersers.

The discovery of the host plant of *X. norfolki* will help in the conservation of this unique species. The host plant (*Psychotria rufipes*) is endemic to the Galápagos and is present on six islands (McMullen 1999). Factors limiting the actual distribution of *X. norfolki* to only three islands should be investigated.

The host plants of the other Galápagos hawk moths are usually not endemic species. Some of these are actually invasive plants on Galápagos landscapes (for ex.: *Cinchona succirubra* and *Psidium guajaba*) but the impact of sphingid caterpillars on their control is not expected to be important as wasps and other predators feed on them extensively (unpublished data). Moreover, sphingid caterpillars are rarely present in large numbers at any given time and place.

ACKNOWLEDGMENTS

We would like to thank the authorities of the Galápagos National Park and Charles Darwin Research Station for financial and logistical support during fieldwork. The Charles Darwin Research Station, Galápagos Conservation Trust (London), and CanaColl Foundation (Ottawa) provided financial support for our investigations at the Canadian National Collection of Insects in 1999, Natural History Museum (2000, 2001), and California Academy of Sciences (2001). We thank curators Germania Estevez (early curator of MECN), Norman Penny (CAS), Martin Honey and David Carter (BMNH) for permission to study the specimens deposited in their collections. We are indebted to Charles V. Covell Jr. (University of Louisville, Kentucky, USA) for sharing his time and knowledge of Lepidoptera and to Prof. Stewart B. Peck (Carleton University, Ottawa, Canada) for his knowledge of Galápagos insects. We are also greatly indebted to Charlotte Causton, Alan Tye, Heidi Snell, Mike Wilson, and Martin Honey for their comments at different stages of this project, and to Ivan Aldaz (CDRS) for plant identifications. Finally we thank all our field assistants during the years, especially Valentina Cruz.

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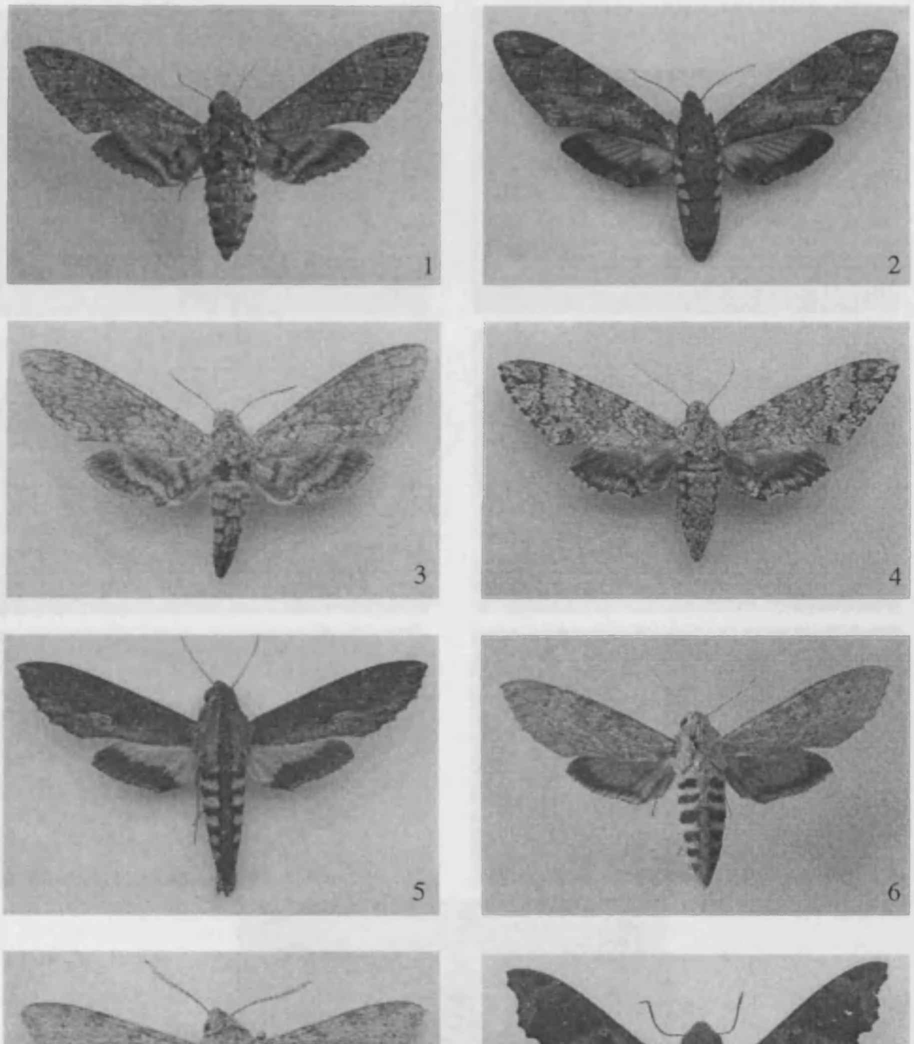
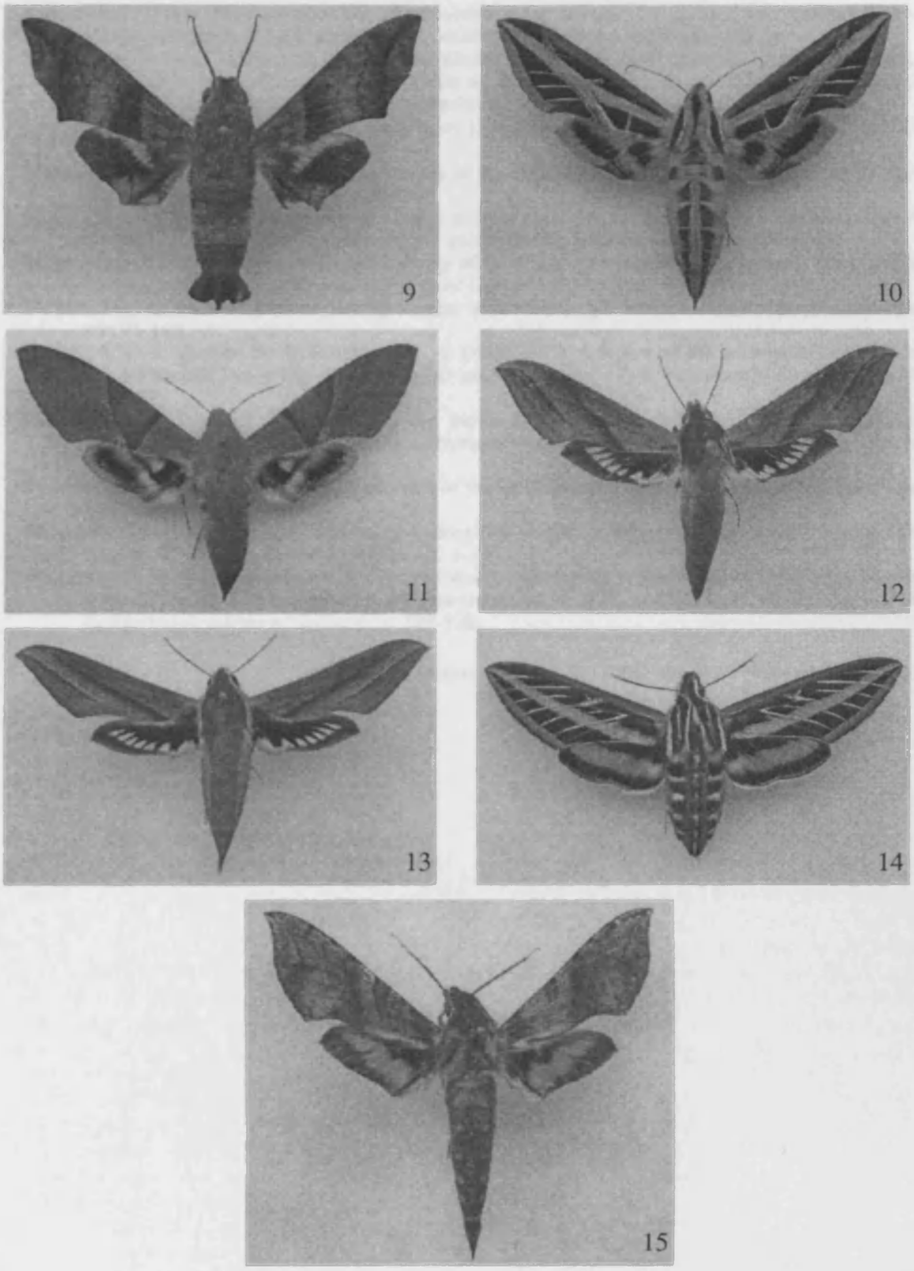


Figs. 1-8. Sphingidae species of the Galápagos. 1: *Agrius cingulata* (Fabricius); 2: *Cocytius antaeus* (Drury); 3: *Manduca sexta leucoptera* (Fabricius); 4: *Manduca rustica calapagensis* (Holland); 5: *Erinnyis alope dispersa* Kernbach; 6: *Erinnyis ello encantada* Kernbach; 7: *Erinnyis obscura conformis* Kernbach; 8: *Enyo lugubris delanoi* Kernbach.



Figs. 9-15. Sphingidae species of the Galápagos. 9: *Perigonia lusca* (Fabricius); 10: *Eumorpha fasciatus tupaci* Kernbach; 11: *Eumorpha labruscae yupanquii* Kernbach; 12: *Xylophanes norfolki* Kernbach; 13: *Xylophanes tersa* (L.); 14: *Hyles lineata* (Fabricius); 15: *Xylophanes pluto* (Fabricius).

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(received October 21, 2001; accepted November 16, 2001)

Chemoecology 12:153–157 (2002)
0937-7409/02/030153-05 $1.50 + 0.20

CHEMOECOLOGY

Chemical defense and aposematism: the case of *Utetheisa galapagensis*

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Summary. The moth *Utetheisa galapagensis* (Lepidoptera, Arctiidae) is an endemic of the Galápagos Islands. Unlike other species of *Utetheisa*, which are gaudily aposematic, it is uniformly grayish in appearance. Our initial presumption that *U. galapagensis* lacks the plant-derived systemic pyrrolizidine alkaloids that account for the aposematism of its congeners was erroneous. *U. galapagensis* feeds on species of *Tournefortia* (Boraginaceae), one of which, *T. rufo-sericeae*, was found to contain pyrrolizidine alkaloids (5% of dry weight). *U. galapagensis* of both sexes contain these compounds. The drabness of *U. galapagensis* may be attributable to the fact that the moth is nocturnal, unlike its aposematic congeners. Two additional species of *Utetheisa* from the Galápagos (*U. devriesi*, and *U. perryi*) are also non-aposematic. Whether the three Galápagos *Utetheisa* are primitively drab, or whether their cryptic condition is secondarily derived from an aposematic ancestry, remains unsettled.

Key words. Chemical defense – Arctiidae – pyrrolizidine alkaloids – Boraginaceae – *Tournefortia*

The genus *Utetheisa* (Lepidoptera: Arctiidae), of primarily Old World affinity, is cosmopolitan in distribution and includes nearly 40 species and subspecies (Strand 1919; Hayes 1975; Holloway 1988), almost all gaudily colored as adults. The coloration, which manifests itself as a sprinkling of yellow, white, and black markings, against a varying background of pink and white, is generally considered to be aposematic. Indeed, *Utetheisa* that have been studied in some detail, such as the New World *Utetheisa ornatrix*, although crepuscular in its mating habits, is as likely to be seen on the wing in the daytime as at night (Hayes 1975; Conner *et al.* 1980). Aposematism in *Utetheisa* is thought to be linked to adult distastefulness, which in turn appears to be a consequence of the larval feeding habits. *Utetheisa* larvae, as far as is known, feed on plants containing pyrrolizidine alkaloids, bitter toxins that they sequester and retain through metamorphosis into the adult stage. In *U. ornatrix*, the larval foodplants are legumes of the genus *Crotalaria* (Fabaceae) (Grossbeck 1911; Pease 1968; Tietze 1972; Newman and Walker 1977). Other species of the genus feed on *Crotalaria* as well, or on species of *Messerschmidia*, *Heliotropium*, *Myosotis*, *Bothriospermum*, *Echium*, and *Trichodesma* (Boraginaceae) (Robinson 1975; Holloway 1988).

It has been known for some time that there exist four species of *Utetheisa* on the Galápagos Islands, of which one is the widely distributed, aposematic *U. ornatrix* (Fig. 1B, C). The other three species – *U. galapagensis*, *U. devriesi*, and *U. perryi* – are endemic to the islands (Hayes 1975), and non-aposematic. They are evenly grayish in appearance and entirely lacking in colored markings. We were interested in securing these drab species for chemical study to check whether they too acquired systemic alkaloid. There were four possibilities. They could be alkaloid-free and diurnal, and therefore cryptic because they could not "afford" to be aposematic, or they could be alkaloid-laden and nocturnal, and hence in no "need" to be warningly colored. Alternatively, they could be alkaloid-free and nocturnal and for both reasons non-aposematic, or alkaloid-laden and diurnal, and non-aposematic possibly because of cryptic behavioral habits. We have now had the opportunity to look into these possibilities with one species, *U. galapagensis*, and were able to show that the second alternative held true. We found both the moth and one of its food plants to be alkaloid-laden, and the moth to be inactive during the day. We here present the data.

Material and methods

The moth

The *U. galapagensis* adult (Fig. 1A) is cryptic in appearance. The forewings are darker than the hindwings, and both wings bear black markings, particularly along the margins. *Utetheisa* typically have a wingspread of about 4 cm; *U. galapagensis*, with a wingspread of about 3 cm, is conspicuously smaller.

The *U. galapagensis* larvae are black and white, unlike the more colorful black-yellow-and-red larvae of other species of the genus (e.g. *U. ornatrix*) (Eisner & Meinwald 1995). *U. galapagensis* differs further from such species as *U. ornatrix* in that it lays its eggs singly rather than in clusters.

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The food plants of *U. galapagensis* are three congeneric species of the family Boraginaceae: *Tournefortia rufo-sericeae, T. psilostachya,* and *T. pubescens.*

U. galapagensis occurs from sea level to the Pampa zone, on the following Galápagos Islands: Baltra, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, Santiago, San Cristóbal, Santa Cruz, and Santa Fe.

Moths were sent in dried condition from their collecting site (Volcano Darwin, Isabela Island) to our Cornell laboratories for analysis.

The plant

Cuttings of *T. rufo-sericeae* (from Santa Cruz Island) were sent in air-dried condition to our Cornell laboratories for analysis.

Chemical analysis (plant)

Powdered leaves and stems (50 g) were extracted with methanol for 24 h. After filtration, the solvent was removed *in vacuo*, and the residue was partitioned between dichloromethane and 0.2 N aqueous HCl. The aqueous phase was separated, basified by the addition of concentrated aqueous NH_3, and extracted with dichloromethane. After evaporation and filtration, the extract was analyzed by electrospray mass spectrometry (MS), using a Micromass Quattro I mass spectrometer, operated in positive-ion electrospray mode. For analyses of the plant's N-oxide content the aqueous phase was acidified with 1 N HCl and treated with Zn dust for 24 h at 25°C. After filtration and adjusting to pH 9 by addition of concentrated aqueous NH_3, the solution was saturated with sodium chloride and then extracted repeatedly with a mixture of dichloromethane and methanol (9/1, *v/v*). Evaporation yielded 1.5 g of a slightly yellowish oil, which was analyzed by ^1H NMR spectroscopy, indicating the presence of large amounts of pyrrolizidine alkaloids. Part of this material (0.4 g) was then chromatographed over a short silica column (length 5 cm) using a mixture of methanol and dichloromethane (1/6, *v/v*) containing 2% aqueous NH_3 as a solvent. The fractions thus obtained were analyzed by ^1H- and ^{13}C-NMR spectroscopy using $CDCl_3$ and acetone-d_6 as solvents, which indicated the presence of four alkaloids, the tetrahydropyrrolizines **1** and **2** and the hexahydropyrrolizines **3** and **4**. NMR spectra were recorded at 298 K using a Varian UNITY+ (500 MHz proton, 126 MHz carbon) spectrometer.

Spectroscopic data of 3 and 4

(1*R*,7*R*,8*R*)-1-({2*R*,3*S*}-2,3-Dihydroxy-2-[1-methylethyl]-propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (tournefortine A, **3**). 1H NMR (500 MHz, acetone-d_6): 2.72 ($J_{1,2a}$ = 8.1 Hz, $J_{1,2b}$ = 7.6 Hz, 1H, 1-H), 1.76 ($J_{2a,2b}$ = 12.0 Hz, $J_{2a,3a}$ = 9.3 Hz, $J_{2a,3b}$ = 7.0 Hz, 1H, 2-Ha), 2.14 ($J_{2b,3a}$ = 7.0 Hz, $J_{2b,3b}$ = 3.3 Hz, 1H, 2-H_b), 2.56 ($J_{3a,3b}$ = 8.9 Hz, 1H, 3-H_a), 3.11 (1H, 3-H_b), 2.67 ($J_{5a,5b}$ = 9.3 Hz, $J_{5a,6a}$ = $J_{5a,6b}$ = 8 Hz, 1H, 5-H_a), 2.95 ($J_{5b,6a}$ = $J_{5b,6b}$ = 4.5 Hz, 1H, 5-H_b), 1.91-1.95 (2H, 6-H_a and 6-H_b), 4.19 ($J_{7,8}$ = 4.5 Hz, $J_{7,6a}$ = $J_{7,6b}$ = 2.8 Hz, 1H, 7-H), 3.13 ($J_{8,1}$ = 5.5 Hz, 1H, 8-H), 3.94 ($J_{9a,9b}$ = 10.6 Hz, $J_{9a,1}$ = 6.0 Hz, 1H, 9-H_a), 4.54 ($J_{9b,1}$ = 4.6 Hz, 1H, 9-H_a), 3.95 ($J_{12,13}$ = 6.5 Hz, 1H, 12-H), 1.11 (3H, 13-H), 2.08 ($J_{14,15}$ = $J_{14,16}$ = 6.9 Hz, 14-H), 0.89 (3H, 15-H), 0.90 (3H, 16-H). ^{13}C NMR (126 MHz, acetone-d_6): 37.0 (C-1), 31.8 (C-2), 55.85 (C-3), 52.6 (C-5), 37.4 (C-6), 70.8 (C-7), 74.0 (C-8), 67.6 (C-9), 175.7 (C-10), 83.5 (C-11), 69.6 (C-12), 17.6 (C-12), 33.05 (C-13), 17.0 (C-15), 17.5 (C-16). Electrospray MS: 302.2 $\{M+H\}^+$.

(1*R*,7*R*,8*R*)-1-({2*R*,3*R*}-2,3-Dihydroxy-2-[1-methylethyl]-propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (tournefortine B, **4**). ^1H NMR (500 MHz, acetone-d_6) [ppm]: 2.76 ($J_{1,2a}$ = 9.3 Hz, $J_{1,2b}$ = 6.0 Hz, 1H, 1-H), 1.75 ($J_{2a,2b}$ = 12.0 Hz, $J_{2a,3a}$ = 10.1 Hz, $J_{2a,3b}$ = 6.7 Hz, 1H, 2-H_a), 2.11 ($J_{2b,3a}$ = 5.8 Hz, $J_{2b,3b}$ = 3.3 Hz, 1H, 2-H_b), 2.54 ($J_{3a,3b}$ = 8.6 Hz, 1H, 3-H_a), 3.04 (1H, 3-H_b), 2.65 ($J_{5a,5b}$ = 9.3 Hz, $J_{5a,6a}$ = $J_{5a,6b}$ = 8 Hz, 1H, 5-H_a), 2.96 ($J_{5b,6a}$ = $J_{5b,6b}$ = 4.5 Hz, 1H, 5-H_b), 1.92-1.96 (2H, 6-H_a and 6-H_b), 4.18 ($J_{7,8}$ = 4.3 Hz, $J_{7,6a}$ = $J_{7,6b}$ = 2.8 Hz, 1H, 7-H), 3.19 ($J_{8,1}$ = 6.8 Hz, 1H, 8-H), 4.11 ($J_{9a,9b}$ = 10.7 Hz, $J_{9a,1}$ = 6.9 Hz, 1H, 9-H_a), 4.20 ($J_{9b,1}$ = 6.6 Hz, 1H, 9-H_a), 3.89 ($J_{12,13}$ = 6.5 Hz, 1H, 12-H), 1.20 (3H, 13-H), 2.15 ($J_{14,15}$ = $J_{14,16}$ = 6.9 Hz, 14-H), 0.85 (3H, 15-H), 0.87 (3H, 16-H). ^{13}C NMR (126 MHz, acetone-d_6) [ppm]: 36.6 (C-1), 32.0 (C-2), 55.75 (C-3), 52.4 (C-5), 37.5 (C-6), 70.45 (C-7), 73.3 (C-8), 67.05 (C-9), 174.8 (C-10), 84.1 (C-11), 71.6 (C-12), 17.8 (C-12), 32.85 (C-13), 16.2 (C-15),18.15 (C-16). Electrospray MS: 302.2 $\{M+H\}^+$.

Hydrogenation of 1 and 2

For comparison purposes, a solution of 50 mg of a 5:2 mixture of compounds **1** and **2** in methanol (2 ml) was hydrogenated at 10 bar for 8 h using palladium on charcoal (10% Pd) as catalyst. Subsequently, the mixture was filtered and evaporated, and the residue analyzed by 1H NMR spectroscopy.

Alkaline Hydrolysis of 1 and 2

A solution of 30 mg of a 5:2 mixture of alkaloids **1** and **2** and 100 mg of potassium carbonate in 20 ml of a 2:1 mixture of methanol and water was stirred for 16 h at 55 °C. After evaporation of the solvent *in vacuo* the semi-solid residue was extracted with dichloromethane. The combined extracts were filtered and evaporated, yielding[1] 1 mg of yellow crystals, which was compared to (+)-retronecine obtained in a similar fashion from (−)-monocrotaline.

Quantification

In order to determine the ratio of these alkaloids on the original extract, a small sample of the mixture of alkaloids obtained after N-oxide reduction was analyzed by ^1H-NMR spectroscopy. Using acetone-d_6 as the solvent, the signals corresponding to the methyl group adjacent to the secondary hydroxyl group in **1-4** are sufficiently separated in order to determine the relative abundance of these compounds via integration.

Chemical analysis (moth)

Air-dried bodies of two female and two male *U. galapagensis* adults were extracted each with 1 ml of a 1:1 (v/v) mixture of dichloromethane and methanol for 12 h at 25 °C. After filtration, the extracts were concentrated and directly submitted to analysis *via* 1H NMR spectroscopy using acetone-d_6 as the solvent.

For HPLC analysis, air dried bodies of two female and two male *U. galapagensis* were extracted for 24 h with 500 ml of buffer solution (2.7 g monopotassium phosphate/2 mL of triethylamine/ 0.4 mL of trifluoroacetic acid in 4 L of water: pH adjusted to 3.0 with phosphoric acid). The samples then were centrifuged for 15 min and the extracts analyzed by HPLC with a Hewlett-Packard 1090 Series II instrument with a diode array detector (column: C-18 BDS Hypersil; 250 4.6 mm: 5-µl particle size). The column was eluted (1 mL/min) with a mixture of buffer solution and acetonitrile (94:6 v/v). The pyrrolizidine alkaloid ridelline served as internal standard.

Results

Plant and moth chemistry

The analyses of *T. rufo-sericeae* plant material revealed the presence of four alkaloids, which were separated by silica gel chromatography into two fractions, containing two tetrahydropyrrolizines (**1**, **2**) and two hexahydropyrrolizines (**3**, **4**), respectively (Fig. 2). The known retronecine derivative indicine (**1**) along with smaller amounts of its epimer morifoline (**2**) were identified through comparison of their proton and carbon NMR spectra with published data (Nishimura *et al.* 1987, Wiedenfeld & Cetto 1998) and

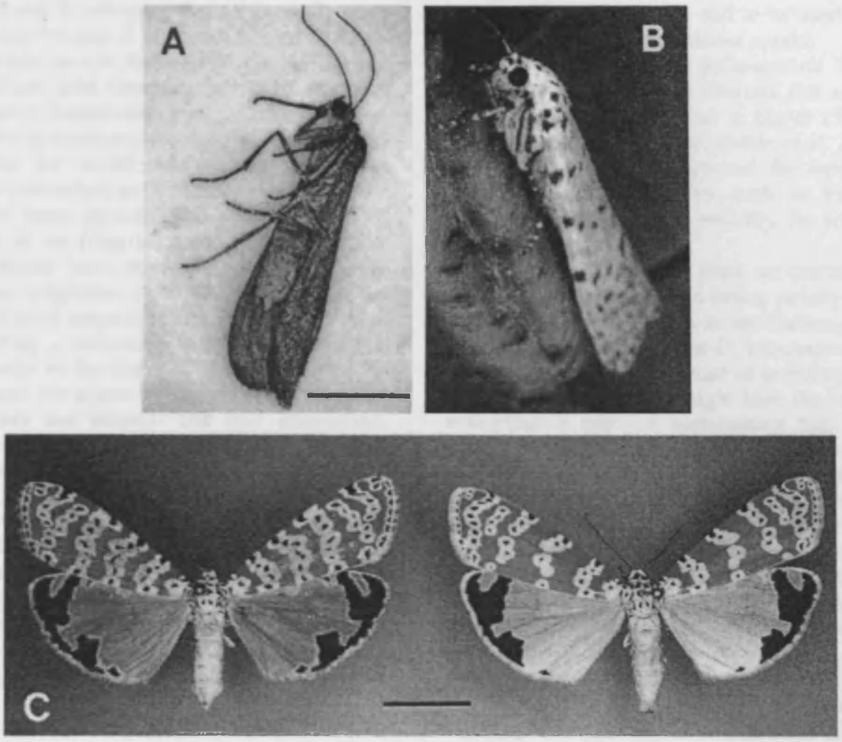
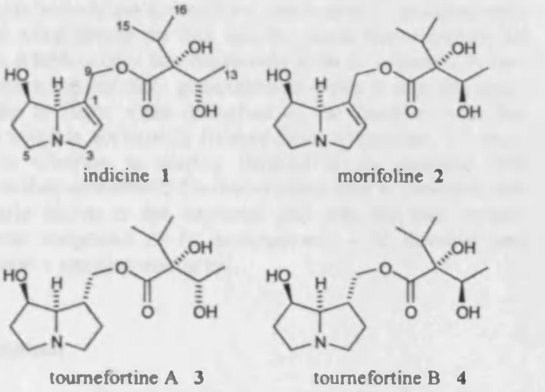


Fig. 1 (**A**) *Utetheisa galapagensis*. (**B**) *Utetheisa ornatrix*, on pod of *Crotalaria mucronata*, its foodplant (Florida specimen). (**C**) *Utetheisa ornatrix*, female and male (right) (Florida specimens). Bars (**A**) 5 mm; (**C**) 10 mm



indicine **1** morifoline **2**

tournefortine A **3** tournefortine B **4**

Fig. 2 Pyrrolizidine alkaloids identified from *T. rufosericeae*

comparison by NMR spectroscopy and HPLC to authentic samples of intermedine and lycopsamine obtained from *Eupatorium* roots (Conner *et al.* 2000). The diastereomers **1** and **2** occurred in a ratio of about 5:2, respectively, as determined by ^{1}H NMR spectroscopy. Their absolute configuration was established through alkaline hydrolysis, which yielded (+)-(7*R*,8*R*)-retronecine.

The unsaturated alkaloids **1** and **2** were accompanied by about equal amounts of their saturated derivatives, **3** and **4**, which were identified through a standard set of two-dimensional NMR experiments, including double-quantum filtered COSY, NOESY, gHSQC, and gHMBC as two diastereomers of 1-(2,3-dihydroxy-2-[1-methylethyl] propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (Fig. 2). The ratio of the relative abundances of **3** and **4** closely resembled that of their unsaturated analogs, **1** and **2**. We anticipated the relative configuration of **3** and **4** at carbons C-7, C-8, C-11, and C-12 to parallel the configuration of the corresponding carbons in **1** and **2**, which was corroborated *via* analysis of NOESY spectra in combination with a hydrogenation experiment. Strong NOE correlation signals observed for the pair of protons (7-H, 8-H) established *cis* orientation for these two protons, whereas NOE signals observed for the pairs of protons (8-H, 9-H_a), (8, 9-H_b), (2-H_a, 9-H_a), (2-H_a, 9-H_b), and (1-H, 2-Hb), indicated *trans* orientation for protons H-8 and H-1 as well as *cis* orientation for H-1 and H-2_b. These assignments were corroborated further by NOE correlation signals observed for the pairs (H-1, 3-H_a) and (H-3_a, H-5_a), which indicates *cis* orientation of H-1, H-3_a, and H-5_a. Therefore, the configuration of the hexahydropyrrolizine unit in **3** and **4** was established as (1*R*,7*R*,8*R*). Hydrogenation of the two tetrahydropyrrolizine derivatives **1** and **2** yielded a mixture of diastereomers of the corresponding hexahydropyrrolizines, among them as two of the major products **3** and **4**, indicating that the naturally more abundant hexahydropyrrolizine **3** is derived from (2*R*,3*S*)-trachelanthic acid, while the less abundant isomer **4** is derived from (2*R*,3*R*)-viridifloric acid. Compounds **3** and **4** represent two hitherto unknown diastereomers of 1-(2,3-dihydroxy-2-[1-methylethyl]propylcarbonyloxymethyl)-7-hydroxy-hexahydropyrrolizine for which we propose the names tournefortine A and tournefortine B, respectively.

The isolation of these pyrrolizidine alkaloids from *T. rufo-sericeae* came as no surprise, given that structurally closely related alkaloids have been identified from other species of the genus (Ogihara *et al.* 1997). However, the sheer amount of alkaloid present in the leaves of *T. rufo-sericeae* is fascinating, considering that the pyrrolizidine alkaloids **1-4** - mostly in the form of their respective N-oxides - make up about 5% of the dry weight of the analyzed plant material (leaves and stems). The four compounds **1-4** occur in a ratio of 5:2:5:2, respectively, as determined *via* integration of the 1H-NMR signal of the protons in position 13.

Analyses of extracts obtained from *U. galapagensis* of both sexes using NMR spectroscopy, HPLC, and electrospray MS revealed the presence of the four alkaloids **1-4** as well as of the corresponding N-oxides. The relative abundances of these compounds varied significantly among the four individuals analyzed. HPLC analysis indicated that the moths contained between 50 and 300 μg of these alkaloids per individual.

Moth habits

Unlike *U. ornatrix*, with which we have field experience, both in Florida and in the Galápagos, and which we know to be active at dusk and during the day, *U. galapagensis* seems to be exclusively nocturnal. One rarely sees *U. galapagensis* on the wing during the day, and the moth flies regularly to lights, which occurs less frequently with *U. ornatrix*. A further characteristic of *U. galapagensis* is that it does not readily take to flight when disturbed in the daytime, with the result that it is not usually flushed from its perches. *U. ornatrix*, in contrast, is readily flushed in the daytime. We assume that aposematic *Utetheisa* other than *U. ornatrix*, are similarly active in the daytime, and that the two cryptic endemic congeners of *U. galapagensis* – *U. devriesi* and *U. perryi* – are also nocturnal.

Discussion

U. galapagensis evidently is unexceptional in that it sequesters pyrrolizidine alkaloids from its larval food plant and stores the compounds systemically. While we did not obtain direct evidence of such sequestration, the presence of the alkaloids in both the moth and one of its *Tournefortia* food plants, leaves little doubt that the moth derives its alkaloid from the larval diet. Since presence of pyrrolizidine alkaloids appears be a common feature of *Tournefortia* (Ogihara *et al.* 1997), we assume the other two food plants of *U. galapagensis* – *T. psilostachya* and *T. pubescens* – to be alkaloid laden as well, and to be used by the moth with equal effectiveness for alkaloid uptake.

We assume that *U. galapagensis* benefits from the possession of its acquired alkaloid, just as *U. ornatrix* does (Dussourd *et al.* 1988, Eisner & Eisner 1991, Hare & Eisner 1993, González *et al.* 1999, Eisner *et al.* 2000), and assume further that by being nocturnal the moth avoids diurnal, visually-oriented predators such as birds and reptiles, providing an explanation, possibly, for why the moth is not aposematic.

One wonders whether there are special advantages for a moth in the Galápagos to being strictly nocturnal. Is bat predation less of an issue in the Galápagos? Whatever the answer, we discovered that *U. galapagensis* has ears (tympanal organs) typical of those of arctiids (Fullard & Barclay 1980), indicating that it might have the capacity to hear the echolocating calls of approaching bats and take evasive action. Moreover we found also that, like other *Utetheisa*, *U. galapagensis* lacks sound producing organs by which to warn pursuing bats of its distastefulness. Aside from the issue of bat predation, could it be that the daytime hours on the Galápagos are fraught with unusual dangers? The possibility certainly cannot be dismissed that some diurnal, visually-oriented predators on the Galápagos are unaffected by *Utetheisa*'s chemical defenses. On the other hand, it should be noted that one species of *Utetheisa*, *U. ornatrix*, does survive in the Galápagos as an aposematic diurnal species.

By the same token one wonders whether drabness in the Galápagos *Utetheisa* is a primitive condition retained unchanged from ancestral times, from before the acquisition of aposematic traits by the *Utetheisa* lineage, or whether it is a secondary condition evolved by divergence from an aposematic ancestry. The former alternative would imply that the Galápagos provided refuge from the selective pressure that forced the evolution of aposematism elsewhere, while the latter alternative would indicate that special adaptive conditions on the islands made retention of aposematism maladaptive. Either way, it is clear that drabness in *U. galapagensis*, as very probably also in *U. devriesi* and *U. perryi*, should the latter two also sequester pyrrolizidine alkaloids, is a correlate of nocturnal habits, not absence of defense.

We are at a loss in explaining why *U. galapagensis* lays its eggs singly, rather than in clusters. In *U. ornatrix*, which does lay clusters, the eggs are protected by parental endowment with pyrrolizidine alkaloid. Being clustered, when thus endowed, provides better protection against some egg predators (chrysopid larvae) than being laid singly (Eisner *et al.* 2000), but this is not to say that the singly laid eggs of *U. galapagensis* are alkaloid free. All in all, there is much that could be learned by further study of *U. galapagensis*. Its courtship alone is deserving of investigation, if for no other reason than to determine whether it is similar, and subject to the same sexual selective strategy on the part of the female, as it is in *U. ornatrix*. In the latter species the female receives pyrrolizidine alkaloid from the male by seminal infusion, a gift that she bestows, together with alkaloid of her own, upon the eggs (Eisner & Meinwald 1995). We had no *U. galapagensis* eggs available for analysis, to see if these too are alkaloid-endowed.

Acknowledgements

Study supported in part by grants AI02908 and GM 53830 from the National Institutes of Health. This is paper no. 184 in the series "Defense mechanisms of arthropods". Paper no. 183 is Smedley *et al.*: Proc Nat Acad Sci USA 99:6822–6827.

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Received 13 February 2002; accepted 8 March 2002.

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SUMMARY

Two new populations and the host plant of the rarely encountered Galapagos endemic moth *Epiplema*
on Isabela Island, on Wolf and Sierra Negra volcanoes, with a sighting on Darwin Volcano. The host
Duranta dombeyana (Verbenaceae). The habitats where all known specimens were collected were *S*
Duranta bushes. To ensure the conservation of *E. becki*, we recommend control of introduced speci

RESUMEN

Distribución, conservación y planta huésped de *Epiplema becki* Hayes (Insecta: Lepidoptera: Uran
Galápagos. Dos nuevas poblaciones y la planta hospedera de la mariposa rara endémica de Galápa
fueron encontradas en la Isla Isabela, en los volcanes Wolf y Sierra Negra, con una avistamiento er
La planta huésped es la nativa *Duranta dombeyana* (Verbenaceae). Los hábitats donde todos los especi
fueron colectados eran bosque de *Scalesia* con arbustos de *Duranta*. Recomendamos control de espe
en su hábitat, para asegurar la conservación de *E. becki*.

INTRODUCTION

Epiplema becki Hayes is a small, inconspicuous moth endemic to the Galapagos Islands, Ecuador where it was first recorded from Fernandina, the type locality, and Isabela islands (Hayes 1975). Hayes (1975) described it from one male and two females. No other records have since been published, and nothing has been published on the host plant or habitat.

We report the host plant and extant populations of *E. becki* on Isabela Island. Because so little is known about the biology of *E. becki*, we provide information on each collecting event and all known localities where the species has been found.

METHODS

We conducted field work from 1994 to 2004 during a survey of Galapagos Lepidoptera. Moths were collected using mercury vapour lamps, ultraviolet lights (UVL), fluorescent lights, and a lightweight mesh net. Specimens are deposited in the Invertebrates Collection of the Charles Darwin Research Station (CDRS), Canadian National Collection, Ottawa, Canada (CNC) and Museum d'Histoire Naturelle, Geneva, Switzerland (MHNG). In addition, Dr Bernard Landry (MHNG) sent data from his extensive survey of Galapagos Lepidoptera since 1989, and further records were obtained from specimens in the Natural History Museum, London (BMNH), and the California Academy of Sciences, San Francisco (CAS).

We used published information (V
1971, Lawesson *et al.* 1987) and materi
Darwin Research Station herbarium (C
the distribution of the host plant.

RESULTS

E. becki has been collected or seen at only si
(Table 1 and Fig. 1).

Fernandina Island

Hayes (1975) selected as holotype a spec
collected by the entomologist F.X. Willi
holotype, now in CAS, is pinned upside
labels: 1 "Holotype"; 2 "Narborough I.
2–5 06"; 3 "Coll. by F.X. Williams"; 4 "C
"Holotype B& *Epiplema becki* Hayes Det
"California Academy of Sciences 13120".
figured by Hayes (1975: 160), and when
was in bad condition, missing the abdom
and with the left hind wing broken and
in the other wings.

These labels, which Hayes (1975) c
appear to indicate that the type locality
Narborough) Island. However, a review o
and related literature (Williams 1920, Sle
that Williams did not visit Fernandina
April 1906, but spent that time aboard the
or collecting on Isabela. Slevin (1931) n

Table 1. Known records of *Epiplema becki*.

Locality	Date	Collector	n	Collection
Fernandina	2–5 Apr 1906	F.X. Williams	1	CAS
N Isabela (locality unknown)	11 Apr 1902	R.H. Beck	1	BMNH
Isabela, Sierra Negra, Corazón Verde, 360 m asl	Jan 1971	R. Perry & T. de Vries	1	BMNH
Isabela, Sierra Negra, Corazón Verde	23–27 Jun 1974	R. Perry & T. de Vries	1	BMNH
Isabela, Sierra Negra, Corazón Verde	Nov–Dec 1974	R. Perry & T. de Vries	7	BMNH, CDRS
Isabela, Sierra Negra, Corazón Verde	19–20 Dec 1975	R. Perry & T. de Vries	2	BMNH
Isabela, Darwin, 1300 m asl, 0.12091°S, 91.18277°W	6 Mar 2000	L. Roque	1	sighting only
Isabela, Sierra Negra, 8.5 km N of Puerto Villamil, 0.88916°S, 91.0074°W	8 Apr 2004	P. Schmitz	3	MHNG
Isabela, Wolf, 1630 m asl(0.04704°N, 91.34734°W)	15 Apr 2004	L. Roque & A. Mieles	14	CDRS
Isabela, Wolf, 960 m asl (0.06536°N, 91.36358°W)	16 Apr 2004	L. Roque & A. Mieles	2	CDRS

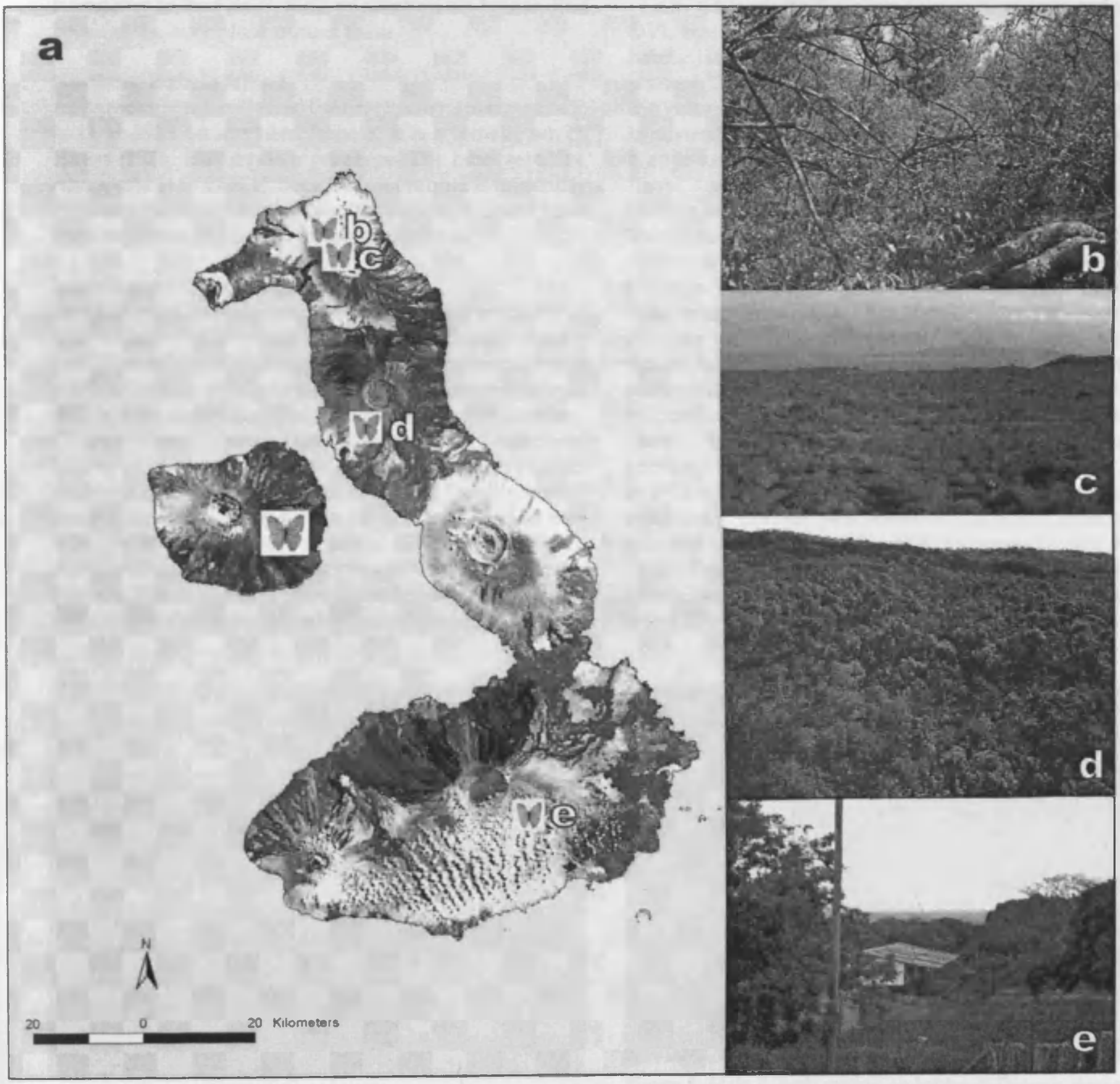

Figure 1. *Epiplema becki* distribution and habitats: (a) distribution; (b) Wolf Volcano 960 m; (c) Wolf Volcano, top locality 1630 m; (d) Darwin Volcano 1300 m; (e) Sierra Negra, Santo Tomás.

Williams and Stewart went inland prepared to camp over night. They made camp at our regular camp tree and were so bothered by mosquitoes they were unable to sleep. Williams spent the night collecting about the camp fire". The "regular camp tree" appears to be midway to the top of Darwin Volcano, and was found by R.H. Beck and Williams on their first trip there on 26 Mar 1906. As described by Slevin (1931: 95): "Part way up the mountain, Beck and Williams, having found a large, green tree with plenty of soil around the base and leaves to shelter them from the sun, made camp."

If Williams did not collect this specimen, perhaps it was collected by Beck, who climbed to the top of Fernandina between 2 and 5 April 1906. It would not be surprising to find an *E. becki* population on Fernandina because the host plant occurs there.

Northern Isabela Island

Apparently, Beck collected the first known specimen of *E. becki*, in 1902 on northern Isabela. It is a female, which Hayes (1975: 152) made a paratype. The label says "N. Abermarle 11 IV 02 R. H. Beck". We were unable to identify the exact location of this collecting event; it could have been on either of Darwin or Wolf volcanoes.

Isabela Island, Wolf Volcano

On 15–16 April 2004, we collected on the top and north side of Wolf Volcano (Fig. 1b, c). We found *E. becki* in abundance at the top (14 specimens collected) and gathered two more specimens at 960 m (Table 1). We also discovered caterpillars under leaves of *Duranta dombeyana* (Fig. 2) a native member of the Verbenaceae. The larvae were encountered singly or in groups of two or three, feeding on old and new leaves. They are green with reddish markings on the last abdominal segments. Developmental observations were not made, but the final instar was 12 mm in length. Some larvae were observed to be preyed upon by adult *Podisus sordidus* (Stal) (Heteroptera: Pentatomidae), a native true bug that is widespread in the archipelago (Froeschner 1985). The moths were observed flying low amongst vegetation early in the morning (6h00–9h00). Two were collected at night with UVL. Adults rest with the wings extended laterally and the antennae folded back below the forewings (Fig. 3).

No signs of goat damage were observed at the sites, but other areas of the volcano have been affected.

Isabela Island, Darwin Volcano

Our field work on Darwin Volcano was carried out in February 1999 and 2000, on the west slope and rim, along an altitudinal transect from Tagus Cove to the western side of the caldera. This way up appears to be similar to that used by the CAS expedition in 1906 and by B. Landry and co-workers in 1992.

On 6 March 2000, one specimen was attracted with UVL but not collected, at the rim camp (Fig. 1d). The habitat is *Scalesia microcephala* forest, and *D. dombeyana* was present. During our 1999 trip very few goats were seen on the volcano, but in 2000, numerous groups were present in several areas but more abundantly in the highlands. Native vegetation appeared to be affected by the goats.

Isabela Island, Sierra Negra Volcano

The second paratype (Hayes 1975) was a female collected by R. Perry & T. de Vries at Corazón Verde, Santo Tomás, Sierra Negra, in January 1971 (Table 1). In 1975, after the publication of his description of *E. becki*, Hayes received a series of specimens from de Vries, which remained undescribed until 1999, when LRA located a Schmidt box containing 11 specimens at BMNH. They were collected between Nov 1974 and Dec 1975 at Corazón Verde, which is the CDRS house in Santo Tomás village in the agricultural zone (Fig. 1e). The area is currently highly modified, mostly pasture and crops, but in 1971 it was less altered, with native vegetation in better condition (J. Gordillo pers. comm.). LRA made Lepidoptera collections there from 1996 to 2004, but never found *E. becki*.

On 8 April 2004, Patrick Schmitz of MHNG collected a male and two females, 8.5 km north of Puerto Villamil, using UVL between 18h30 and 20h00 (Table 1). This

Figure 2. *Duranta dombeyana* at 1630 m on Wolf Volcano, Isabela.

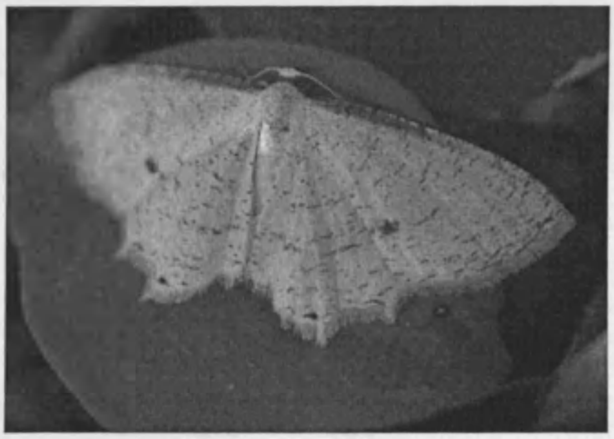

Figure 3. Male *E. becki* resting on leaves of *Duranta dombeyana* at 1630 m on Wolf Volcano, Isabela.

locality is at the lower fringe of the agricultural zone and the vegetation is a mixture of native and introduced plants.

Duranta dombeyana was collected recently at both localities (Table 2), which may indicate that the presence of the larval host plant may not be sufficient to maintain a population of *E. becki*, as shown by its apparent absence at Santo Tomas.

Duranta dombeyana, the larval food plant

Three *Duranta* spp. occur on the islands: *D. dombeyana*, *D. mutisii* and *D. repens*. They are distributed at higher elevations on Isabela, Fernandina, San Cristóbal, and Pinzón islands (Lawesson *et al.* 1987, Table 2).

Only *D. dombeyana* has been found as a host plant for *E. becki*. It is the most widespread of the three species in Galapagos (Table 2), where it has a patchy distribution, mainly on lava slopes and grassy areas from 300 to 1700 m asl, and is abundant at several localities. In 2003, P. Jaramillo reported several individuals along the trail to Volcán Chico (Sierra Negra). Recently, H. Jäger found a numerous population on a hill west of "El Ripioso" on San Cristóbal Island. In March 2004 we found a good population on Wolf Volcano, in an open area above 1700 m. This is in the upper arid zone, a vegetation zone located above 1630 m, with abundant *Opuntia insularis* and other microphilous plants characteristic of the more widespread low arid zone (*sensu* Wiggins & Porter 1971). *D. dombeyana* was also collected at other localities on Fernandina and Isabela, including the agricultural zone of Isabela (Table 2), but it may be less abundant there. The species appears to be highly affected by goats at several places; for example on the rim of Alcedo Volcano (Isabela), it appears to have declined since 1995 (I. Aldaz pers. comm.). The other *Duranta* spp. appear to be less abundant and less widely distributed (Table 2).

DISCUSSION

The discovery of a healthy population of *E. becki* on Wolf Volcano and the occurrence of extant populations on Sierra Negra and probably on Darwin volcanoes was a pleasant surprise. The species was formerly known from only three specimens and presumed to be very rare. However, there is no doubt that the known populations are vulnerable to extinction, and the species has never been recorded on Alcedo Volcano (between Darwin and Sierra Negra), despite our intensive collecting there since 1995.

The introduction of alien species, the alteration of habitats, and the destruction of host plants are considered the main threats for the conservation of Galapagos endemic Lepidoptera (Roque-Albelo & Landry 2004). Different populations of *E. becki* appear to be affected by these three factors, with goats affecting northern Isabela and habitat destruction important on Sierra Negra, both of which may cause loss of host plants.

In 2004, a goat eradication programme began on northern Isabela. The conservation of *E. becki* there depends on the success of this project. On southern Isabela (Sierra Negra) the survival of the known *E. becki* population is uncertain and every effort should be made to protect the host plant and its habitat.

Future studies should investigate the biology of *E. becki* (including the acceptability of other *Duranta* spp.), establish regular monitoring of the known populations, and investigate the distribution of the host plant and the factors affecting its conservation. In addition, a survey on other islands or volcanoes where populations may occur is required. Although *E. becki* has never been collected on San Cristóbal, a survey on the hills around El Ripioso would be useful.

ACKNOWLEDGMENTS

We thank the Galapagos National Park and the Charles Darwin Research Station for financial and logistical support, Felipe Cruz, Karl Campbell, Steve Collins and other colleagues of the "Isabela Project" for their generous help in taking us by helicopter to Wolf Volcano, and Martin

Table 2. Distribution of *Duranta* spp. and recent occurrence of *Epiplema becki*.

	Collection dates	Source	*E. becki* present?
D. dombeyana			
Fernandina, Grass crater. 400 m asl.	1977, 1984	CDS	?
Isabela, Sierra Negra, near Cerro Palomas.	1994	CDS	
Isabela, Sierra Negra, 9 km on road from Puerto Villamil to agricultural zone.	1994	CDS	Yes
Isabela, Sierra Negra, road to Bosque de los Niños [close to Corazón Verde].	1996, 2002	CDS	?
Isabela, Sierra Negra, trail to Volcán Chico.	2003	CDS	
Isabela, Alcedo, top, NE side.	1995, 1996	CDS	
Isabela, Darwin, 1300 m asl, W side.	2000	Pers. obs.	Yes
Isabela, Wolf, 1630 m asl, NE side.	2004	Pers. obs.	Yes
San Cristóbal, hill west of El Ripioso.	2004	CDS	
San Cristóbal, hill east of El Ripioso.	2004	CDS	
D. repens			
Isabela, Sierra Negra, caldera floor, 900 m asl and areas close to rim.	1985	CDS	
Isabela, Sierra Negra, SE of the top.	2000	CDS	
D. mutisii			
Pinzón	1963, 1982	CDS	

Honey (BMNH) and Norman D. Penny (CAS) for permission to study the specimens in their collections. We are also indebted to Bernard Landry and Helmuth Rogg for critical review of this manuscript and to Iván Aldaz and Patricia Jaramillo for help with plant identification. We are especially grateful to Zoran and Leonor Stjepic and Barbara West for hospitality and logistical help during LRA's visits to BMNH and CAS. This research was partially supported by the Galapagos Conservation Fund, Galapagos Conservation Trust (London) and the U.K. Government's Darwin Initiative. This is contribution 1010 of the Charles Darwin Foundation for the Galapagos Islands.

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ARTHROPODS IN THE CHARLES DARWIN RESEARCH STATION HERBARIUM, GALAPAGOS, DURING 1999–2001

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SUMMARY

This paper describes the arthropods found in the Charles Darwin Research Station herbarium from 1999 to 2001. Nineteen species were found from four classes. Most individuals were from the families Formicidae (*Paratrechina longicornis* with 777 individuals), Porcellidae (134), Drosophilidae (43) and Corinnidae (38).

RESUMEN

Artrópodos en el herbario de la Estación Científica Charles Darwin, Galápagos, durante 1999–2001. Este artículo describe los artrópodos encontrados en el herbario de la Estación Científica Charles Darwin desde 1999 a 2001. Se encontraron 19 especies de cuatro clases. La mayoría de los individuos fueron de las familias Formicidae (*Paratrechina longicornis* con 777 individuos), Porcellidae (134), Drosophilidae (43) y Corinnidae (38).

INTRODUCTION

In educational and academic collections such as libraries, museums and herbaria there have been few studies to evaluate periodically the presence and abundance of invertebrate pests. The emphasis has been to remove or eradicate pests, to prevent harm to collections, rather than monitoring the population fluctuations of the pest species.

The invertebrate group that has most impact on herbarium collections is the arthropods, in particular insects, whose effects can be serious. Dry botanical samples, glues, cardboard and newspaper are attractive foods for some of these animals. In tropical regions, continuous high temperatures and humidity favour these organisms and facilitate their population growth (Bridson & Forman 1998). On islands, fewer of these species may occur naturally than in a comparable continental region, although many may be present as introduced species, since they commonly co-occur with humans. Galapagos is a tropical oceanic archipelago, with relatively constant high humidity and seasonally high temperatures (Alpert 1963, Jackson 1993).

REVUE SUISSE DE ZOOLOGIE 111 (3): 599-609; septembre 2004

First report of Tischeriidae (Lepidoptera) on the Galapagos Islands, Ecuador, with descriptions of two new endemic species

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First report of Tischeriidae (Lepidoptera) on the Galapagos Islands, Ecuador, with descriptions of two new endemic species. - The family Tischeriidae is reported from the Galapagos Islands for the first time. The two species found on the archipelago (*Astrotischeria scalesiaella* B. Landry, sp. n. and *A. alcedoensis* B. Landry, sp. n.) are described and illustrated. Both species are presumed to be endemic and their larvae are leaf miners on *Scalesia* species, a group of endemic Asteraceae.

Keywords: Micro moths - *Astrotischeria* - taxonomy - leaf miners - *Scalesia* - Asteraceae.

INTRODUCTION

The Tischeriidae (Tischerioidea) are a group of small, primitive moths belonging to the Monotrysian Heteroneura (Lepidoptera). They may be the sister-group of the Ditrysia (Nielsen & Kristensen, 1996; Kristensen & Skalski, 1998) although Davis (1986) presented an alternative hypothesis of relationships. Some 101 species are described so far, mostly from the Holarctic Region, but species are known also from the Ethiopian, Oriental, and Neotropical Regions (Puplesis & Diškus, 2003). Eleven species have been described from the Neotropics, but the region remains poorly known with regard to its leaf-mining fauna. The region with the most diverse tischeriid fauna is the Nearctic, with 48 described species (Davis, 1983). Larvae mine leaves of Fagaceae, Rosaceae, Asteraceae, Rhamnaceae, Malvaceae, and Tiliaceae, in decreasing order of importance, although Anacardiaceae, Apocynaceae, Combretaceae, Ericaceae, Euphorbiaceae, Hypericaceae, Sterculiaceae, and Theaceae are also used (Puplesis & Diškus, 2003).

For the purpose of documenting the micro-moth fauna of the Galapagos archipelago, BL conducted fieldwork on most of the larger islands in 1989 and 1992. Since 1997, LRA and others at the Charles Darwin Research Station on Santa Cruz Island,

Manuscript accepted 18.11.2003

did more collecting and reared more immature stages, leading to a wealth of new information. This paper is part of a series begun in 1992 (Landry & Gielis, 1992) to describe new species and report on other native and introduced species of micro-moths in the Galapagos to develop a better understanding of this important group of insects for biodiversity management purposes.

MATERIAL AND METHODS

Most of the moths studied here were reared from mined leaves of *Scalesia* species (Asteraceae). Mined leaves were collected by staff of the Charles Darwin Research Station (CDRS), Santa Cruz Island, Galapagos, brought to their quarantine lab, and placed in cages. Emerging moths were collected and mounted. Two other series of specimens were available for study. The larger one was collected by BL in 1992 with a portable generator and a mercury-vapour lamp placed in front of a white sheet (see Landry & Gielis, 1992). The other series was collected at light in 1964 and was borrowed from the California Academy of Sciences, San Francisco, California, U.S.A. (CAS).

The holotype and some paratypes of *Astrotischeria scalesiaella* will be deposited in the Muséum d'histoire naturelle, Geneva, Switzerland (MHNG). The other paratypes of *A. scalesiaella* will be deposited in the CAS, CDRS, National Museum of Natural History, Washington, D.C., U.S.A. (USNM), and The Natural History Museum, London, England (BMNH). The single known specimen of *Astrotischeria alcedoensis* is deposited in the MHNG.

The species described here were determined to be new by comparing specimens with the types of seven of the Neotropical species, with the original and more recent descriptions of four species (Bourquin, 1962; Puplesis & Diškus, 2003), and with the treatment of the North American species published by Braun (1972). The types of six Neotropical species described by Meyrick and Walsingham were examined at the BMNH. The type of *Tischeria unicolor* Walsingham is located in the Naturhistorisches Museum Wien, Vienna, Austria (NMW) and was borrowed for examination.

Genitalia were dissected after the abdomen had macerated in a cold 20% KOH solution overnight. The dissected parts were kept in lactic acid stained with orange G for description purposes. They were subsequently stained with chlorazol black and mounted on slides in Euparal. The head of one male specimen was similarly treated. The right pair of wings of one male specimen was removed, bleached, stained with acid fuchsin, and mounted in Euparal.

Illustrations of the adult head and genitalia were made with the AutoMontage® system using a video camera mounted on a Leica MZ APO stereomicroscope or a Zeiss Axioskop compound microscope. The wing venation was drawn using a camera lucida mounted on a compound microscope.

The descriptions and nomenclature of parts are based on Puplesis & Diškus (2003). Generic characters were not repeated. In the legs, wings, thorax, and abdomen only the lateral or dorsal exposed surfaces are described; the ventral or median surfaces of the legs are uniformly whitish beige.

SYSTEMATIC TREATMENT

Astrotischeria Puplesis & Diškus, 2003

The genus was described to include a monophyletic group of species found only in the New World. Thirty species are known, seven of which were described from the Neotropical Region (Argentina, Chile, Ecuador, Peru).

Species of *Astrotischeria* are characterised by the following synapomorphies: presence of a dorsal arm on the valva; shortened uncus with arms (with some exceptions); long, distally bifurcated aedeagus; strongly developed anellus thickened laterally; enlarged vinculum; stronger development of microtrichia on the female tergite IX; slightly reduced, narrowed ovipositor lobes; greatly elongated mediobasal spur of the hind tibia, which is as long as the tibia; and use of Malvaceae and Asteraceae as hostplants (Puplesis & Diškus, 2003).

Astrotischeria scalesiaella B. Landry sp. n. Figs 1-2, 4-7, 9-12

Holotype ♂. [1] "ECU., GALAPAGOS/ Santa Crúz, Los/ Gemelos, 27.v.1992/ M[ercury] V[apor] L[amp], *leg.* B. Landry" (MHNG). Printed in black ink on white paper. [2] "Tischeria/ det. Davis 1993". Hand-written on white card stock with black border in black ink except for black ink printed "det. Davis 19". [3] "HOLOTYPE/ Astrotischeria/ scalesiaella/ B. Landry". Hand-written in black ink on red card stock. Specimen in perfect condition.

Paratypes, Ecuador: 12 ♂♂, 10 ♀♀ from the Galapagos Islands. FLOREANA: 1 ♂ (dissected, slide BL 1175), Cerro Pajas, 26.xii.1998, ex larva en *Scalesia pedunculata* (L. Roque). SANTA CRUZ: 1 ♀, Los Gemelos, 17.i.2002, [no emergence date], Minador de hojas *Scalesia pedunculata* (R. Boada); 1 ♂ (dissected, BL 1415), same data as holotype; 1 ♂, 1 ♀, Los Gemelos, 2.ix.2001, emergio 10.ix.2001, Minador *Scalesia pedunculata* (L. Roque); 2 ♂, 1 ♀, Los Gemelos, 11.ix.2001, emergio 28.ix.2001, 30.ix.2001 and no emergence date, Criada en hojas *Scalesia pedunculata* (R. Boada); 4 ♂, Los Gemelos, xi.1999, [no emergence date], En *Scalesia pedunculata* (T. Poulson); 1 ♂, 2 ♀ (one dissected, BL 1417), Finca Vilema, 2 km W Bella Vista, 1.iv.1992, M[ercury] V[apor] L[amp] (B. Landry); 1 ♂ (dissected, Wings BL 1416; Head BL 1420), E[stacion] C[ientifica] C[harles] D[arwin], 6.iii.1992, U[ltra] V[iolet] L[ight] (B. Landry); 1 ♀, Steve Devine farm, 31.x.1999, [no emergence date], minador de hojas *Scalesia pedunculata* (C. Causton); 1♂ (dissected, BL 1418), 3 ♀, Horneman Farm, 220 m, 5.iv.1964 (D.Q. Cavagnaro). WOLF: 1 ♀ (dissected, BL 1419), 7.ii.2002, Minador *Scalesia baurii* (L. Roque, C. Causton).

Diagnosis. This species and the next are easily distinguished from other small Galapagos micro-moths with lanceolate wings by virtue of the combination of three characters of the head: 1- the presence of scales on the proboscis, 2- the drooping labial palpi, and 3- the rough vestiture of the vertex. This is a combination of characters found in all Tischeriidae. Gelechioidea have scales on the proboscis as well, and some have lanceolate wings, but their labial palpi are upturned and their vertex is not rough-scaled. *Astrotischeria scalesiaella* can be separated from *A. alcedoensis* by its smaller size (forewing length up to 3.02 mm in *A. scalesiaella* and 4.28 mm in *A. alcedoensis*), more prominent orange colour with more diffuse brown markings, wider, shorter and more angled uncus arms, apically thinner and more pointed dorsal lobes of the valva, and the shorter cucullus. The female of *A. alcedoensis* is unknown.

Description. MALE (n=13) (Figs 1, 4, 6, 7, 9-12). Vertex vestiture a mixture of ochre and brown scales, the ochre scales bicoloured with a paler basal half, the brown scales with white on basal half and apex; frons vestiture (Fig. 4) mostly greyish brown,


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2


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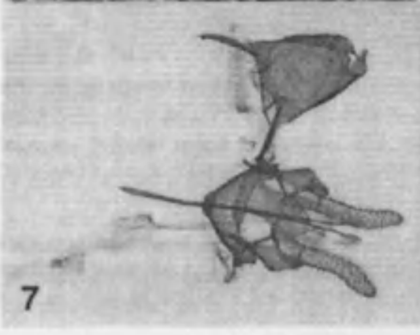
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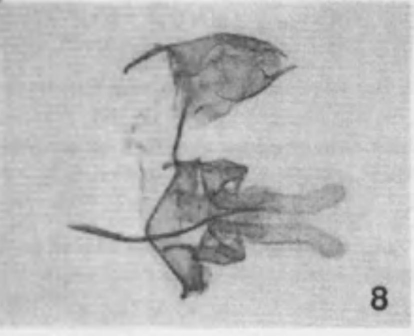
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shining, with row of white or pale ochre scales laterally and apically; interocular index (n=1): 1.76. Antenna 2/3 length of forewing (n=1); with 20 flagellomeres (n=1); scape and slender pecten brown and white, sometimes with some pale ochre scales; with 6 rows of scales on flagellomere I, with 2 rows on other flagellomeres; scales on flagellomeres with brown apex and white basal half; flagellomere I 3X length of flagellomere II; sensillae chaeticae about 1.5X length of flagellomere on flagellomere II, about 2/3 length of flagellomere on last one. Haustellum 3X length of labial palpus; scales on both beige, sometimes with brown laterally on labial palpus. Maxillary palpus 3-segmented, scaled only on third segment. Thorax mostly brown with beige-tipped scales, sometimes with ochre scales at tip of tegulae. Foreleg dark brown. Midleg femur dark brown laterally with pale ochre scales on dorsal edge and beige apically; tibia dark brown with beige on dorsal row of long and narrow scales, and apex; first tarsomere with scales dark brown on apical half and white on basal half; tarsomeres I-V mostly beige with apical dark-brown spot. Hind coxa dark brown with apical row of longer beige scales; femur mostly white; tibia dark brown with beige along ventral margin and on ventral and dorsal rows of long and thin scales, with pale ochre apically; tarsomeres dark brown. Forewing length: 2.46-3.02 mm (holotype: 2.81 mm). Venation (Fig. 9) with only Sc, R, Rs1, Rs4, M1, CuA, and 1A + 2A clearly defined; with a faint indication of Rs3; 1A + 2A not forked at base. Length/ largest width: 0.25. With a patch of microtrichia in anal sector. Colour (Fig. 1) mostly dark brown with ochre scales along dorsal margin beyond middle, along cubital fold, in apical sector, and as a diagonal bar or large spot medially, with darker brown markings as two oblique bands before and beyond middle, first one more inclined than second; sometimes with more ochre scaling (fig. 2); sometimes mostly dark brown with a few ochre scales mostly in apical sector; scales paler on their basal half, white on those with dark-brown apical half; fringe greyish brown. Hindwing venation only with Sc + R and A clearly visible. Sockets of the fringe scales forming spines especially conspicuous on costal margin. Without microtrichia. Colour brownish grey, with concolorous fringe. Abdomen greyish brown.

Male genitalia (n=3) (Figs 7, 10-12). Socii short, with short, slender setae. Uncus arms separate and connecting to tegumen at their most dorsal and most anterior points; each arm elongate, larger in middle, directed downward, flattened and narrowly rounded at apex, with a few short setae on dorsal and ventral edges beyond connection with tegumen. Tegumen hood-like, rounded dorsally and apically, with short setae dorsolaterally, with very narrow and strongly melanised anterior arms connecting with vinculum, with broader and lightly melanised posterior arms connecting with membranous ventral wall of tegumen. Vinculum rather broad, triangular in ventral view, without saccus. Anellus broad, lightly melanised, rectangular, with about five short

FIGS 1-8

Galapagos *Astrotischeria* spp. 1. Holotype of *A. scalesiaella*; 2. Female paratype of *A. scalesiaella* from Santa Cruz, Finca Vilema; 3. Holotype of *A. alcedoensis* from Isabela, Volcan Alcedo, reared from *Scalesia affinis*; 4. Head of male paratype of *A. scalesiaella* from type locality; 5. Leaf of *S. pedunculata* mined by *A. scalesiaella* on Los Gemelos, Santa Cruz; 6. Descaled head of male paratype of *A. scalesiaella* from Santa Cruz, Charles Darwin Station; 7. Male genitalia of paratype of *A. scalesiaella* from Floreana, Cerro Pajas, reared from *Scalesia pedunculata*; 8. Male genitalia of holotype of *A. alcedoensis*.

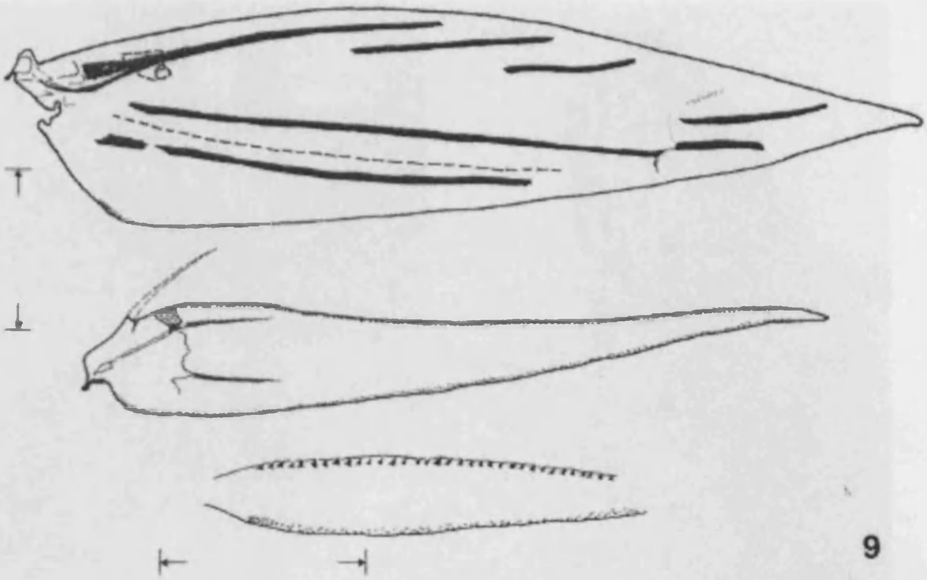
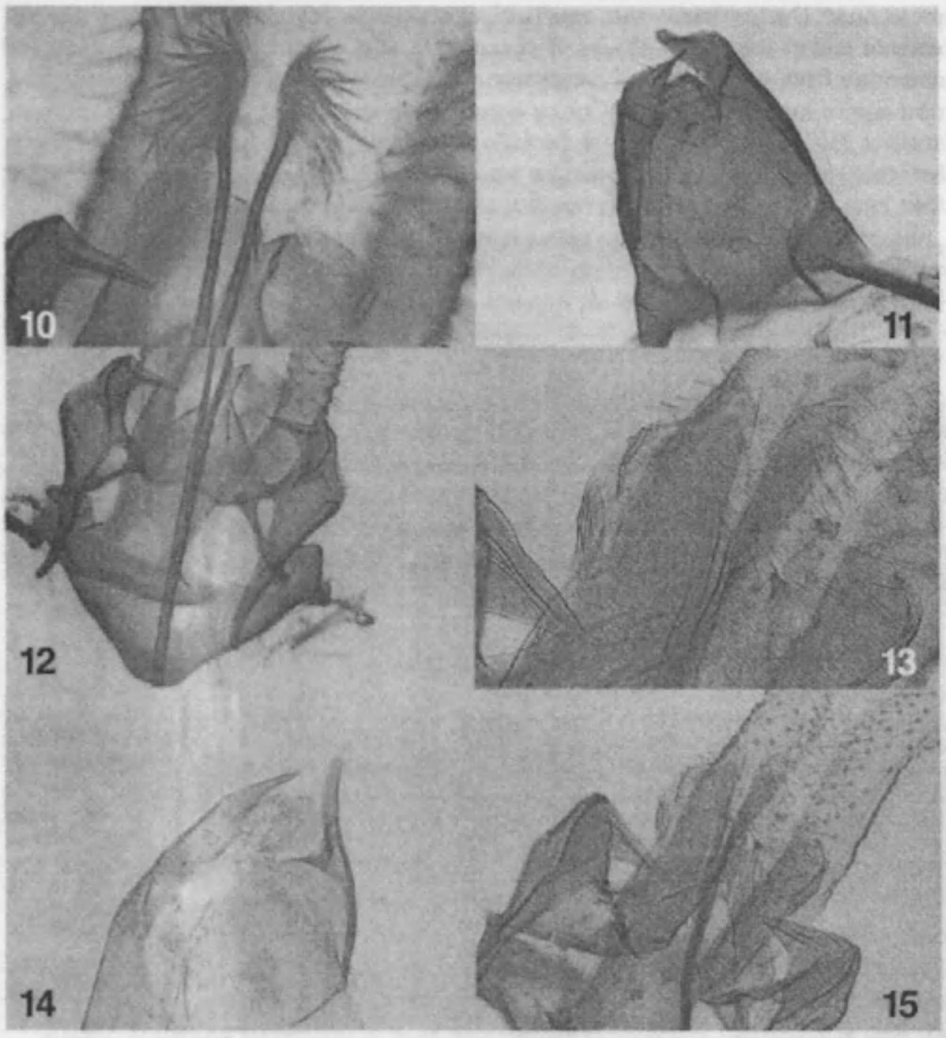


FIG. 9
Wings of paratype male of *Astrotischeria scalesiaella* from Santa Cruz, Charles Darwin Station (frenulum broken) (scale: 0.5 mm) with details of the bases of the costal and inner margins (scale: 0.25 mm).

setae ventrally. Valva with dorsal arm curved inward at right angle, narrowing, apically pointed, and with narrow apodemes projecting directly anteriorly; cucullus slender, slightly curving upward toward apex, with abundant short setation medially, apically not narrowing and rounded, about as long (1.06 X) as dorsal arm inclusive of apodeme. Aedeagus very narrow, slightly longer than vinculum + valva, divided in two divergent branches from about 2/3; each branch apically flattened and with bunch of slender spines and spinules; gonopore from about base of divergent branches.

FEMALE (n=10). Antenna 0.62 length of forewing (n=1). Forewing length: 2.58-2.83 mm. Frenulum with two acanthae. Forewing length/ largest width: 0.25. Female genitalia (n=2) (Figs 16-21). Ovipositor lobes short and round, with rather stout and slightly curved peg setae, the most medially located ones apically bifurcated; median ridge between ovipositor lobes with a series of three pairs of short setae. Tergum IX a more or less triangular plate, slightly convex, with convex lateral margins, emarginated anterior margin, and straight posterior margin, the latter membranous and set with bunch of 3-4 setae on each side of middle, including one much longer than others; with strongly melanised narrow band at anterior and anterolateral margins connecting lateroanteriorly with bases of posterior apophyses; with long and sparse setation dorsally. Posterior lobes of sternum IX somewhat conical, slightly larger than ovipositor lobes, with short and long setae, with long, straight and apically narrow posterior apophyses extending beyond middle of segment VII; anterior lobes of sternum IX very narrow with short setae directed posteriorly; with two pairs of apo-



FIGS 10-15

Male genitalia of *Astrotischeria* spp. 10-12. Paratype of *A. scalesiaella*, same specimen as fig. 7: 10. Posterior end of aedeagus; 11. Tegumen, uncus, and socii; 12. Dorsal arms of valvae, vinculum, anellus. 13-15. Holotype of *A. alcedoensis*: 13. Posterior end of aedeagus; 14. Posterior end of tegumen, uncus, and socii; 15. Dorsal arms of valva.

physes in membranous area anterior to oviporus: dorsal pair narrow, almost reaching as far as posterior apophyses (of sternum IX), apically acute; ventral pair broader, shorter, reaching slightly beyond anterior margin of sternum VIII. Tergum VIII a narrow rectangular and flat plate slightly broader posteriorly, with one anterolateral projection on each side directed ventrally and connected to anterior apophyses of sternum VIII slightly posterad to their middle. Sternum VIII a rather large concave plate extended laterally, with broadly rounded apical margin set with narrow spinelike anterior half. Apex of tergum VII medially with joining pair of median arcs of closely set scale sockets with elongate narrow scales. Sternum VII terminating in small wider than long median lobe set with abundant and rather long setation.

Etymology. The specific epithet refers to the generic name of the host plants.

Biology. Adults were reared from leaf mines found on two species of *Scalesia* (Asteraceae): *S. baurii* Robins. & Greenm. and *S. pedunculata* Hook. filius.

Distribution. Endemic to the Galapagos; found on Floreana, Santa Cruz, and Wolf.

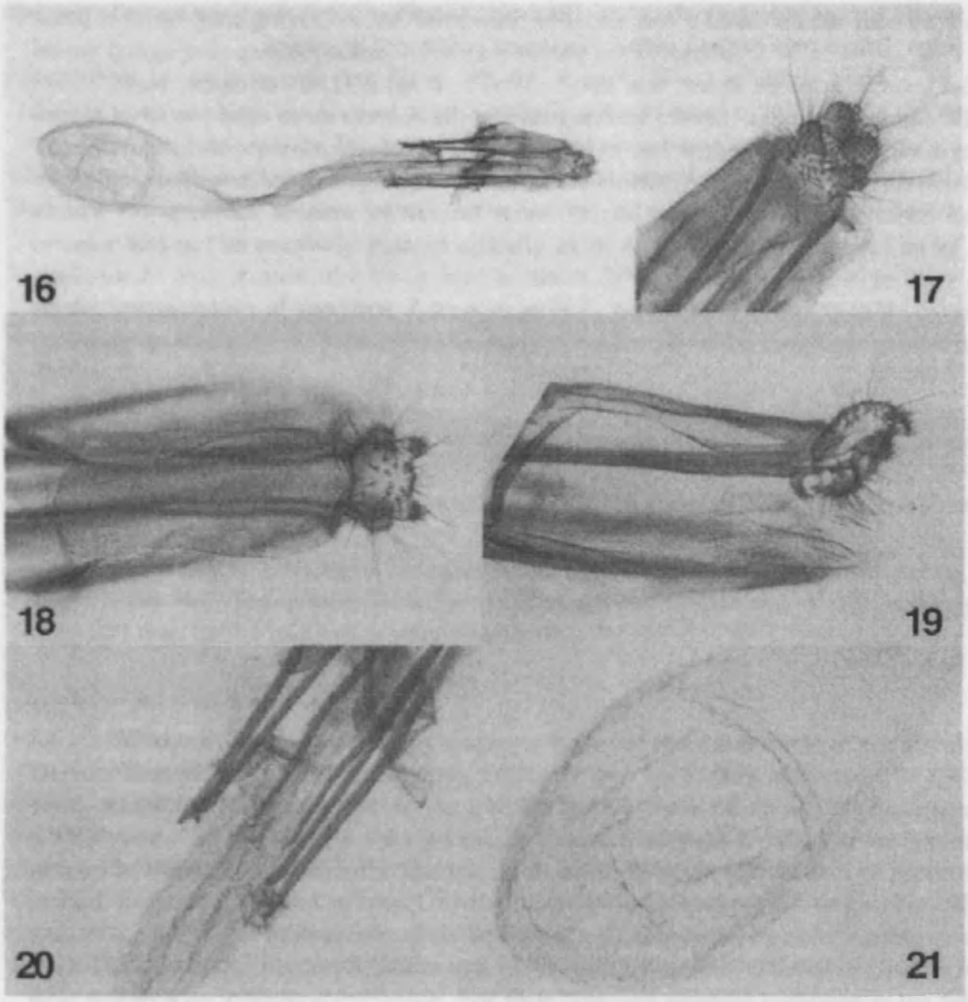
Remarks. In the female genitalia, my interpretation of tergum IX, which I believe is dorsal, between terga VIII and X, differs from that of Davis (1998) and Puplesis and Diškus (2003), who mention that it is ventral from the lobes of tergum X. In my view, tergum IX of these authors is actually sternum IX because of its position. In Davis' (1998, fig. 6.8 N) schematic drawing of the female genitalia of *Tischeria* (now *Coptotriche*) *citrinipennella* (Clemens), there is no sclerite between tergum VIII and the ovipositor lobes of tergum X as in *Astrotischeria scalesiaella* (see Figs 18, 19).

Astrotischeria alcedoensis B. Landry sp. n. Figs 3, 8, 13-15

Holotype ♂. [1] "ECU. GALAPAGOS/ Isabela, V[olcan]. Alcedo, en/ *Scalesia villosa* affinis, 19 X/ 1999, emergio 29 X 1999/ L. Roque" (MHNG). Computer made in black on white paper with black borders on top and bottom. Hostplant species name crossed with pencil and new name added with pencil on last line with an arrow between the two names. [2] "MHNG/ Prép. micr./ No 2724 ♂". Printed black on white card stock except for ink hand written "MHNG", number and male sign. [3] "BL 1423 ♂". Hand-written in black ink on green paper; upside down. [4] "HOLOTYPE/ Astrotischeria/ alcedoensis/ B. Landry". Hand-written in black ink on red card stock. The right midleg and hindleg are in a gelatine capsule attached to the pin. The left hindleg is broken beyond the tibia.

Diagnosis. See Diagnosis of *Astrotischeria scalesiaella* above to distinguish the two species from each other and from all other known micro-moths of the Galapagos.

Description. MALE (n=1) (Figs 3, 8, 13-15). Vertex vestiture with erect scales usually tricolored, pale beige at their base, brown subapically, pale beige at their apex, with a few scales apically shining greyish brown, with appressed scales between antennal bases entirely pale beige; frons vestiture with shorter scales coloured as erect scales of vertex, but scales slightly paler at their base; interocular index not calculated. Antenna about 3/4 length of forewing; approximately 26 flagellomeres (head not mounted on slide); scape brown and white, with greenish-beige narrow pecten; flagellomere I with longitudinal rows of white and brown scales; other flagellomeres with basal scales pale beige and apical scales brown. Haustellum white and brown. Labial palpus dark brown laterally with white apex, pale beige medially. Maxillary palpus scaling probably white (not clearly visible). Thorax mostly with tricolored scales, dirty white at their base, brown subapically, ochre apically. Foreleg coxa with scales bicoloured dirty white at their base and brown at their apex (sometimes with apex a little paler beyond brown area), other parts dark brown except for pale beige



FIGS 16-21

Female genitalia of *Astrotischeria scalesiaella*. 16-17. Paratype from Wolf, reared from *Scalesia baurii*: 16. Segments VIII-X and genitalia; 17. Apex of abdomen. 18-19. Paratype from Santa Cruz reared from *Scalesia pedunculata*: 18. Dorsal view of segments VIII-X; 19. Lateral view of same segments. 20-21. Same specimen as on figs 16-17: 20. Section of ductus bursae; 21. Corpus bursae.

bases of tarsomeres II-IV and all of tarsomere V. Midleg as in foreleg except scales more bicoloured as on coxa and tarsomeres more pale beige except for small patch of brown at apex of tarsomeres II-IV. Hindleg apparently as in midleg, but damaged. Forewing length: 4.28 mm (holotype). Venation not studied. Colour a mixture of beige, brown, and ochre scales, the latter not present in the radial sector, the brown scales usually tricolored with white at base, brown on apical half and beige at apex as a narrow band; without strongly marked pattern in unique and somewhat damaged specimen, but possibly with submedian and postmedian oblique bands as in *A. scale-*

Tegumen as in *A. scalesiaella* except slightly broader and with broader posterior arms. Vinculum narrower, less triangular, than in *A. scalesiaella*. Anellus as in *A. scalesiaella* except for apparent absence of ventral setae. Dorsal arm of valva with distal half broader and not as narrowly pointed apically as in *A. scalesiaella*; cucullus as in *A. scalesiaella* except more distinctly bent at about 2/3 and longer, 1.44 X as long as dorsal arm inclusive of apodeme. Aedeagus as in *A. scalesiaella* except broadly curved (possibly an artefact) and base of two apical branches at about 4/5 length; gonopore not observed.

FEMALE. Unknown.

Etymology. The specific epithet refers to the collecting locality, Volcan Alcedo, on Isabela Island.

Biology. The unique specimen was reared from a leaf of *Scalesia affinis* Hook. filius (Asteraceae).

Distribution. Galapagos endemic; found on Isabela, Volcan Alcedo.

Remarks. The poorly melanised spines of the apical end of the aedeagus (Fig. 13) may be the result of a premature death.

ACKNOWLEDGEMENTS

We thank the authorities of Galapagos National Park and those of the Charles Darwin Research Station for allowing fieldwork and for logistical support in 1989, 1992, and 2002. We are grateful to the Charles Darwin Foundation and the Galapagos Conservation Trust of England for providing financial support for BL's investigations at the BMNH in 2000 and in the Galapagos in 2002. We owe a great deal of gratitude to Prof. Stewart B. Peck, Carleton University, Ottawa, for inviting BL to join his 1989 and 1992 Galapagos expeditions. This fieldwork was supported by an operating grant to Dr Peck from the Natural Sciences and Engineering Research Council of Canada for field research on arthropod evolution. For their help and pleasant company in the field we thank Novarino Castillo, Charlotte Causton, Joyce Cook, Moraima Inca, Ricardo Palma, S. B. Peck, Bradley J. Sinclair, and Eduardo Vilema. We thank curators Don R. Davis (USNM), Sabine Gaal-Haszler (NMW), and Kevin Tuck (BMNH) for their permission to examine specimens in their care. We are thankful to Jean-François Landry, Agriculture and Agri-Food Canada, for his multi-faceted help while BL was in Ottawa working on Galapagos moths. Finally, we thank Florence Marteau (MHNG) for producing the plates and Don Davis, J.-F. Landry, and Rimantas Puplesis for their important comments on the manuscript.

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MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
77, 289 – 310, 2004

Supplemental additions to the Pterophoridae (Lepidoptera) of the Galapagos Islands (Ecuador) with description of a new species of *Adaina* Tutt

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We present descriptions and illustrations for *Adaina scalesiae* **sp. n.**, including larva and pupa, and for the female of *Platyptilia vilema* Landry, both endemic species to the Galapagos. Larvae of *A. scalesiae* were reared from leaves of six species of *Scalesia* and one of *Lecocarpus*, all Galapagos endemic Asteraceae. We give new island records for *Megalorhipida leucodactyla* (Fabricius), *Bipunctiphorus nigroapicalis* (Landry & Gielis), *Postplatyptilia huigraica* Landry & Gielis, *P. minima* Landry & Gielis, *Stenoptilodes brevipennis* (Zeller), *Exelastis pumilio* (Zeller), *Hellinsia cristobalis* (Landry & Gielis), *H. devriesi* (Landry & Gielis), and *H. nephogenes* (Meyrick). We also give a first hostplant record for *S. brevipennis* and a second for *P. huigraica*.

Presentamos descripciones e ilustraciones para *Adaina scalesiae* **sp. n.** (adulto, larva y pupa) y la hembra de *Platyptilia vilema* Landry, ambas especies endemicas de Galápagos. Las larvas de *A. scalesiae* fueron criadas en hojas de seis especies de *Scalesia* y una de *Lecocarpus*, todas ellas Asteraceae endemicas. Presentamos nuevos reportes de islas para *Megalorhipida leucodactyla* (Fabricius), *Bipunctiphorus nigroapicalis* (Landry & Gielis), *Postplatyptilia huigraica* Landry & Gielis, *P. minima* Landry & Gielis, *Stenoptilodes brevipennis* (Zeller), *Exelastis pumilio* (Zeller), *Hellinsia cristobalis* (Landry & Gielis), *H. devriesi* (Landry & Gielis) y *H. nephogenes* (Meyrick). En adicion, presentamos el primer record de planta huesped para *S. brevipennis* y el segundo para *P. huigraica*.

Key words: Lepidoptera, Pterophoridae, Ecuador, Galapagos Islands, larva, pupa, hostplants, taxonomy, new records, new species.

INTRODUCTION

This is the third contribution to our knowledge of the pterophorid fauna of the Galapagos Islands (see Landry & Gielis 1992; Landry 1993). Since 1993, specimens of Pterophoridae have been collected or reared on the Galapagos by LR and other staff members of the Charles Darwin Research Station, Santa Cruz, Galapagos (CDRS). Specimens were also collected by BL in 2002 and 2004 (with P.

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Schmitz, Geneva, Switzerland), and a few more, collected in 1971 were recovered and studied in The Natural History Museum, London, England (BMNH). From these newly available specimens we are able to give the description of a new species of *Adaina* which was misidentified as *Adaina ambrosiae* (Murtfeldt) in Landry & Gielis (1992) and Landry (1993), but which we knew presented some differences in the larvae. Examination of the lectotype and of other North American specimens of *A. ambrosiae* showed that there are also differences in the adults that clearly justified the description of a new species, which is presented below along with descriptions of the last instar larva and pupa. Setal nomenclature and abbreviations for segments follow Stehr (1987) and Heinrich (1916).

In addition, we describe and illustrate the previously unknown female of *Platyptilia vilema* Landry, and we give new hostplant and distribution records for all Galapagos Pterophoridae species except *Lantanophaga pusillidactyla* (Walker), *Stenoptilodes juanfernandicus* Landry & Gielis, and *Stenoptilodes gielisi* Landry. For the island of Isabela, we also give new records from volcanoes Alcedo and Wolf. The distribution data are summarized in Table 1. The number of species in the Galapagos remains at 15. Hostplant names are from Lawesson *et al.* (1987). Previous Galapagos records are from Landry & Gielis (1992) and Landry (1993).

Other than the above-mentioned BL, BMNH, DLM, LR, and CDRS, the following acronyms are used: CNC for Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada; CUIC for Cornell University Insect Collection, Ithaca, New York, U.S.A.; and MHNG for "Muséum d'histoire naturelle de Genève", Geneva, Switzerland. In the list of paratypes of *Adaina scalesiae* sp. n., the information is presented chronologically for each island, which are cited in alphabetical order, and recorded as found on the labels, but abbreviated words are spelled out in square brackets when first encountered, except for cardinal points and distances, which are not spelled out; dates are standardized and all Latin names italicized.

RECORDS AND DESCRIPTIONS

Megalorhipida leucodactyla (Fabricius, 1794)

This is the species reported as *Megalorhipida defectalis* (Walker) in recent Galapagos literature. The synonymy was introduced by Karsholt & Gielis (1995). New island records are: Fernandina, Pinzon, and San Cristobal (CDRS, MHNG). Additional localities on Isabela are the base and NE slopes of Alcedo (March, April, and June, CDRS and MHNG). With specimens collected on 13 islands, *M. leucodactyla* is now the most widespread plume moth species in the archipelago. Fig. 16 shows a mature larva of this species.

Platyptilia vilema B. Landry, 1993

This species has been found only on the islands of Isabela and Pinta, although on the latter, a single specimen was encountered. On Isabela it was known previously from the slopes of Sierra Negra and Volcan Darwin, but additional specimens were collected also on Alcedo (200 and 300 m, March, April, and October) and Volcan Wolf (500 m, May) (CDRS). Specimens were reared from leaves of *Darwinio-*

thamnus tenuifolius (Hook. *f.*) (Asteraceae) on Alcedo (Roque-Albelo 2003), but the voucher specimens were lost. *Platyptilia vilema* is in danger of extinction if the destruction of *Darwiniothmanus* species by *Icerya purchasi* Maskell (Homoptera, Margarodidae) cannot be controlled (Roque-Albelo 2003). The female was previously unknown and we present the following description on the basis of one specimen collected on Volcan Darwin, 300 m, 6.iii.2000, LR (CDRS).

Description (n=1). Habitus as in male (see Landry 1993), but wingspan larger : 24 mm. Frenulum with one acanthus. Female genitalia (Fig. 11). Papillae anales small, moderately setose. Intersegmental membrane IX-X with membranous, rounded sac protruding beyond papillae anales dorsally. Apophyses posteriores slender, extended shortly anterad of posterior margin of tergite VII. Tergite VIII well developed, slightly shorter than wide. Sternite VII extended posteriorly almost to posterior margin of tergite VIII, with lateral margins converging apically. Ostium central, at apical margin of sternite VII. Sterigma a pair of small round plates flanking ostium. Ductus bursae a long and narrow sclerotized tube of almost even girdth reaching segment VI, followed by a shorter membranous section of about 1/3 length of sclerotized section. Ductus seminalis at junction of ductus bursae and corpus bursae. Corpus bursae a large, more or less quadrangular sac, about as long as sclerotized portion of ductus bursae, with a pair of long and slightly curved cornuti set in wide scobinate patches of corpus wall.

Bipunctiphorus nigroapicalis (Landry & Gielis, 1992)

This species was originally placed in genus *Platyptilia*, although that assignment was uncertain. Gibeaux (1994) transferred it to his genus *Bipunctiphorus*, which is otherwise known from Japan, Kenya, Nepal, Réunion, and Tanzania. This generic placement was confirmed by Gielis (2003). The species is here reported as new from the island of Floreana (360 m, BMNH) and from the slope of Alcedo on Isabela (570 m, October, CDRS).

Postplatyptilia huigraica Landry & Gielis, 1992

This widespread Neotropical species had been reported in the Galapagos only from Isabela (Volcan Darwin, Sierra Negra). We report new records from Santa Cruz at the CDRS (november, CDRS), Los Gemelos (May, MHNG), and the transition zone (March, MHNG; September, one reared on *Hyptis mutabilis* (A. Rick) Brig., Lamiaceae, CDRS). The latter hostplant record is new and is the second known for this species, the other being *Hyptis spicigera* Lam. On Isabela the species was also found on Alcedo (400 m, April, MHNG).

Postplatyptilia minima Landry & Gielis, 1992

This Galapagos endemic was known from Isabela (Sierra Negra), and Pinta. We report new records from Santa Cruz (transition zone, 5 km North of Puerto Ayora, September) and from Isabela on Alcedo (292 m, March; 400 m, April; 1100 m, October) and Volcan Darwin (400 and 900 m, March) (CDRS, MHNG).

Figs 1-2. Adults of *Adaina* species: 1, Lectotype of *A. ambrosiae* (Murtfeldt); 2, Holotype of *A. scalesiae* sp. n.

Stenoptilodes brevipennis (Zeller, 1874)

This widespread Neotropical species was previously known in the Galapagos from only five specimens in 1993 (Landry 1993). These had been collected on Isabela (Sierra Negra) and Santa Cruz. The number of specimens available from the Galapagos is now tripled. New island records are Floreana (360 m, January, BMNH; 340 m, May, CDRS), Marchena (April, CDRS), Pinzon (April, MHNG), and San Cristobal (75 and 169 m, March, MHNG). Moths were also collected on Alcedo, Isabela (200 m, April, MHNG; 300 m, October, CDRS). Four specimens collected as larvae on the grounds of the CDRS were reared from *Capraria peruviana* Benth. (Scrophulariaceae) (CDRS). This is the first hostplant record for this species.

Exelastis montischristi (Walsingham, 1897)

In the literature pertaining to the Galapagos, this species was previously known as *Exelastis cervinicolor* (Barnes & McDunnough, 1913). The synonymy of *E. cervinicolor* with *E. montischristi* was made available by Gielis (1993). Although this was not mentioned *per se* by the author it was an unintentional omission (C. Gielis, pers. comm to BL). This species, which is found also in the Antilles and Florida, U.S.A., is the second most widespread plume moth of the Galapagos with records from 11 islands. We have no new island record, but on Isabela, in addition to being known from Sierra Negra and Volcan Darwin, we add Alcedo (lowlands and 1100 m, October, CDRS; 483 m, March, MHNG; beach, April, MHNG) and Volcan Wolf (1220 m, May, CDRS).

Exelastis pumilio (Zeller, 1873)

In March 2004 we collected a specimen of this species on San Cristobal (elev.: 75 m), which represents a new island record. In addition, we collected a specimen on Isabela, near shore at the base of volcan Alcedo.

Adaina ambrosiae (Murtfeldt, 1880) Figs 1, 3, 5, 7, 9, 12, 14, 25, 27

This species was described from Missouri, U.S.A., but it is also known from the Virgin Islands (Gielis 1992) and was mentioned from the Galapagos islands by Gielis (1992), Landry & Gielis (1992), and Landry (1993). However, a closer examination of North American material, including the lectotype, designated by Barnes & Lindsey (1921), showed that the Galapagos material is different and belongs to a new species, described below. The lectotype, deposited in CUIC, bears the following labels: 1- "Type" (hand-written in black ink on white paper); 2- "From/ Ambrosia/ 9/30.96" (hand-written as label no. 1); 3- "Murtfeldt Coll./ Cornell Univ./ Lot 451/ Sub. 1028" (typed, except for hand-written "1028," in black ink on white card stock); 4- "LECTOTYPE/ Cornell U./ No. 541.1" (typed, except for number, in black ink on red card stock); 5- "*Oedematophorus* [sic]/ *ambrosiae*/ Murtf./ Lectotype ♂/ B. + L. Nov. 3, 1920" (hand-written in black ink on white card stock with red double border); 6- "BL 1604 ♂" (hand-written on green paper).

Adaina scalesiae sp. n. Figs 2, 4, 6, 8, 10, 13, 15, 18-24, 26, 28

Adaina ambrosiae (Murtfeldt, 1880): Gielis (1992: 379-381, Figs 3, 20), Landry & Gielis (1992: 19-21, Figs 14, 25, 38), Landry (1993) (misidentifications)

Type material. Holotype: ♂ with the following labels. 1- "ECU[ADOR]., GALAPAGOS/ Isabela, ± 15 km N[orth]/ P[uer]to Villamil, 25.v.1992/ M[ercury] V[apour] L[amp], *leg[it]*. B[ernard]. Landry" (typed on white card stock); 2- "HOLOTYPE/ Adaina/ scalesiae/ Landry, Roque & Matthews" (handwritten on red card stock). Deposited in the CNC.
Paratypes: 30 ♂, 46 ♀ from Ecuador, Galapagos Islands. FERNANDINA. 1 ♀, North side, 1300 m, S 00° 21.862', W 091° 34.308', 15.i.2002, U[ltra] V[iolet] L[ight], L. Roque & C. Causton (CDRS). FLOREANA. 2 ♂ (one dissected, slide BL 1615), Scalesias near Cerro Pajas, GPS: elev. 329 m, S 01° 17.743' W 90° 27.111', 12.iv.2004, uvl, *leg[it]*. P. Schmitz; 1 ♀, Criada en *Scalesia villosa*, 31.vii.1999, M. Gadner; 2 ♂, 1 ♀, Cerro Pajas, ex larva en *Scalesia pedunculata*, 26.xii.1998, L. Roque; 1 ♀, Cerro Pajas, ex larva en hojas de *Scalesia pedunculata*, 27.xii.1998, L. Roque (CDRS, MHNG). GARDNER [near Española]. 1 ♀, Larva criada en *Lecocarpus lecocarpoides*, 30.viii.2001, R. Boada (CDRS). ISABELA. 1 ♂, V[olcan] Darwin. Ex larva en hojas de *Scalesia microcephala*. 13.ii.1999, L. Roque; 1 ♀, V. Darwin, 1200 m, 15.ii.1999, U.V.L., No. 99.19, L. Roque; 2 ♀, V. Darwin, 700 m, Criada en *Scalesia microcephala*, 4.iii.2000, L. Roque; 1 ♀, V. Darwin, 300 m s[obre el] n[ivel del] m[ar], 6.iii.2000, UVL-W[hite] L[ight] Trap, LR #2000-012, L. Roque; 1 ♀, V. Alcedo, North East side, 900 m, Guayabillos camp, 16.iv.2002, uvl, L. Roque & B. Landry; 3 ♀, V. Darwin, 630 m elev[ation]., 16.v.1992 (1 ♀), 17.v.1992 (2 ♀), M[ercury] V[apour] L[amp], leg. B. Landry; 1 ♀, V. Darwin, 1240 m elev., 19.v.1992, MVL, leg. B. Landry; 1 ♂ (dissected, slide BL 1613), 1 ♀, n[ea]r Tagus Cove, 100 m elev., 21.v.1992, MVL, leg. B. Landry; 1 ♀ (dissected, slide BL 1614), same data as holotype; 1 ♂, V. Darwin, 600 m elev., emerg[ed]. 28.v.1992, ex larva on *Scalesia microcephala*, leg. B. Landry (BMNH, CNC, MHNG). PINTA. 1 ♂, 2 ♀, Plaja Ibbeston [sic], 13.iii.1992 (2 ♀), 14.iii.1992 (♂), MVL, leg. B. Landry; 3 ♂, 1 ♀, arid zone, 14.iii.1992 (1 ♂, 1 ♀), 15.iii.1992 (2 ♂) MVL, leg. B. Landry; 1 ♀, 400 m elev., 17.iii.1992, leg. B. Landry; 1 ♂, ± 50 m elev., 20.iii.1992, MVL, leg. B. Landry; 2 ♂ (one dissected, slide BL 1611), ± 15 m elev., 21.iii.1992, MVL, leg. B. Landry (BMNH, CDRS, CNC, MHNG). SAN CRISTOBAL. 2 ♀ (1 dissected, slide MHNG 2852), near Loberia, GPS: elev. 14 m, S 00° 55.149' W 89° 36.897', 16.iii.2004, uvl, leg. B. Landry, P. Schmitz; 2 ♂ (one dissected, slide BL 1536), La loberia, ex larva en hojas de *Scalesia gordilloi*, 12.ix.1998, No 99.28, C. Causton (CDRS, MHNG). SANTA CRUZ. 1 ♂, 1 ♀, Los Gemelos, Ex larva en hojas de *Scalesia pedunculata*, 17.i.1999, L. Roque; 2 ♀, Los Gemelos, En hojas *Scalesia pedunculata*, 17.i.2002, R. Boada; 1 ♀, Los Gemelos, Ex larva en hojas de *Scalesia pedunculata*, 18.i.1999, No. 99.25, L. Roque; 3 ♂ (1 dissected, slide CNC-MIC 3795), 7 ♀ (2 dissected, slides CNC-MIC 3794, 3796), Los Gemelos, 25.i.1989 (1 ♀), 31.i.1989 (3 ♂, 6 ♀), MVL, B. Landry; 1 ♂, 1 ♀, Tortuga Res[erve], W S[an]ta Rosa, 6.ii.1989, MVL, B. Landry; 1 ♂, low agriculture zone, GPS: S 00° 42.132' W 90° 19.156', 13.iii.2004, uvl, leg. B. Landry, P. Schmitz; 2 ♀, Finca S[teve]. Devine, 17.iii.1989, MVL, B. Landry; 1 ♂, C[harles] D[arwin] R[esearch] S[tation] base of El Barranco, GPS: S 00° 44.305' W 90° 18.105', 18.iii.2004, uvl, leg. B. Landry, P. Schmitz; 3 ♂, 2 ♀, Finca Vilema, 2 km W Bella Vista, 1.iv.1992, MVL, leg. B. Landry; 1 ♀, Los Gemelos, 23.v.1981, Y. Lubin; 1 ♀ (dissected, slide BL 1118), Los Gemelos, at light, 25.v.1998, C. Covell, L. Roque; 1 ♂, 4 ♀ (1 dissected, slide MHNG 2853), Los Gemelos, 27.v.1992, MVL, leg. B. Landry; 2 ♂ (one dissected, slide BL 1537), 2 km W Punta Nuñez, 29.vii.2001, Ex larva en *Scalesia retroflexa*, R. Boada; 1 ♂, 2 ♀, Los Gemelos, Criada en *Scalesia pedunculata*, 11.ix.2001, Emergio 6.x.2001, R. Boada (CDRS, CNC, MHNG).

Immature material examined. One vial containing 2 last instar larvae, 3 larval exuviae, and 4 pupae in alcohol. Labels: 1 - "[Galápagos] Pinta, 15.iii.[19]92, larves sur [larvae on] *Scalesia* sp."; 2 - "Foodplant is *Scalesia incisa* Hook. *f.* (Asteraceae)" [wrongly identified, see Life history below]; 3 - "2 pupae 19.iii"; 4 - "Adaina ambrosiae (Murt.), Det. B. Landry 1993" (BL collection (CNC)).

Diagnosis. Adaina scalesiae (Fig. 2) is very similar to *Adaina ambrosiae* (Fig. 1) in wing markings and color, but can be separated from it by its smaller size (5.63 - 6.63 mm in forewing length (n=45) as opposed to 6.88 - 8.44 mm (n=6, lectotype = 8.31 mm), in the male genitalia by its larger and curved harpe on the left valva (compare Figs 5 and 6), and in the female genitalia by the shape of tergum VIII at its base (see Figs 14 and 15). In the Galapagos *Adaina scalesiae* is most similar to *Hellinsia devriesi* (Landry & Gielis), but the latter is a bigger species (forewing

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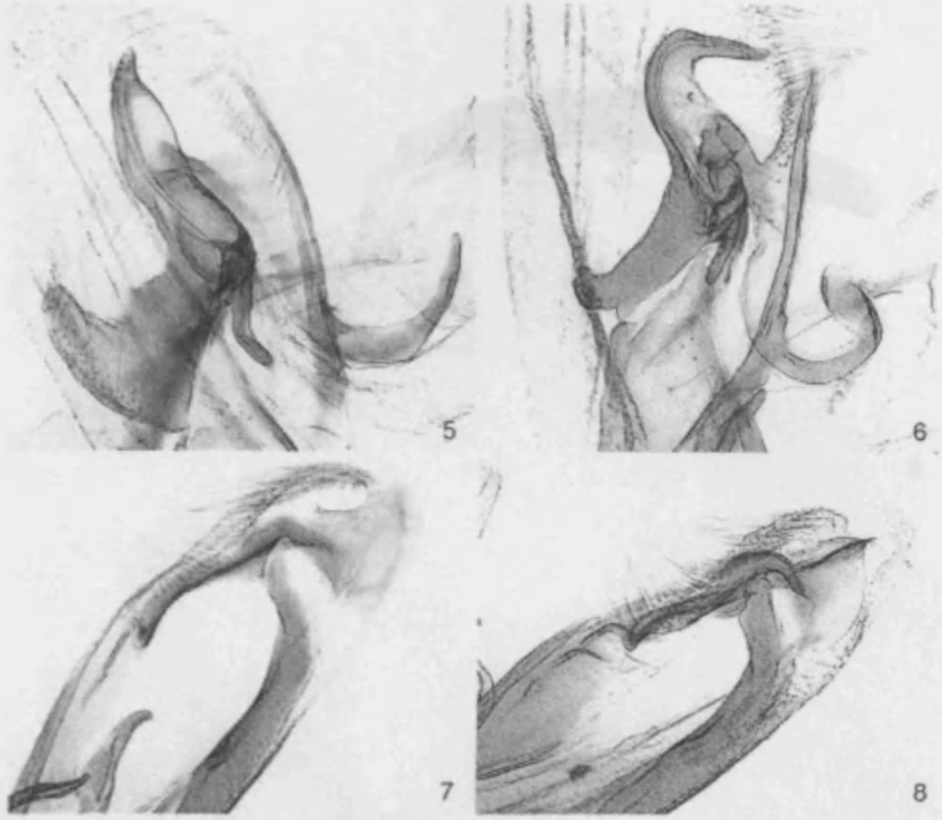
Figs 3-4. Male genitalia of *Adaina* species without aedeagus: 3, *A. ambrosiae* lectotype; 4, *A. scalesiae*, paratype from Santa Cruz (slide BL 1537, CDRS).

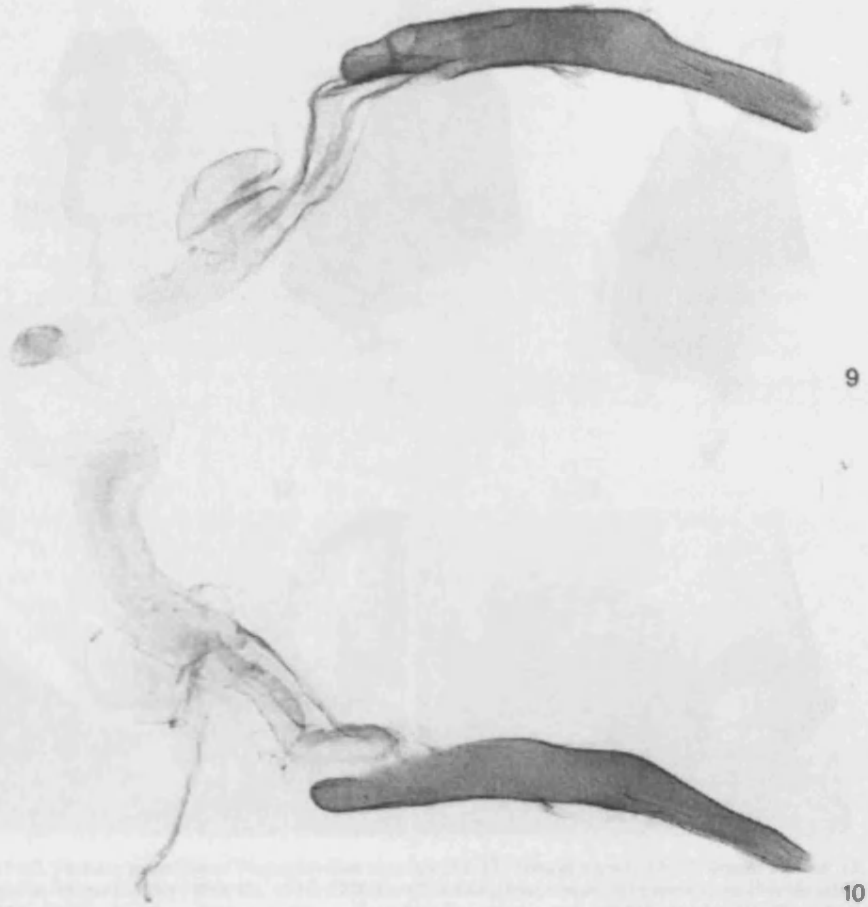
length = 6.88 - 8.44 mm), its forewings have an ochreous tinge, its forewing lobes are apically colored dark greyish-brown, and the abdomen usually bears a dorsomedian dark brown line from the apex of the second segment to the apex of the penultimate segment. In case of doubt, a dissection will provide the answer as the genitalia of *H. devriesi* bear obvious differences (see Landry & Gielis, 1992: Fig. 29 for the female, and Bigot & Deknuydt, 1998: Fig. 1a-b for the male). In the larva, the body plan of *Adaina scalesiae* is similar to that of *A. ambrosiae*, but can be distinguished by having slightly shorter lateral fringe setae relative to body width and distinctly more barbellate as opposed to spiculate lateral setae. The individual barbs on these setae are about 0.1 mm, at least twice the length of those on *A. ambrosiae*. Primary D setae are simple, short, thin, and directed anterad or laterad close to the body in *A. scalesiae* (Fig. 24) as opposed to spiculate, long, robust, and erect in *A. ambrosiae* (Fig. 25). Seta D1 on A8 similar to D1 on A7, not reduced as in *A. ambrosiae*. Sclerites associated with D setae darker and joined or partly joined at midline on A1-A8 in *A. scalesiae* (Fig. 26), lighter and distinctly separate at midline in *A. ambrosiae* (Fig. 27). The dorsal setae are solitary in *A. scalesiae*, while a few minute secondary setae are present on the D tubercles of *A. ambrosiae*. Numerous other less obvious differences include the less prominently exserted spiracles of *A. scalesiae* and differing patterns of minute sclerotized spots and cuticular granulations. The pupa is generally very similar to that of *Adaina ambrosiae*, the differences being much less apparent than those between the larvae of the two species. Primary and secondary setae slightly more spiculate on *A. scalesiae*. Lateral fringe setae of wing and abdomen a bit shorter than on *A. ambrosiae*. Primary setae D1 and D2 erect in *A. scalesiae*, somewhat recurved anterad and posterad in *A. ambrosiae*. Dark markings present on anterior margin of mesothorax, posterior third of mesothorax, and area anterad and surrounding A2 spiracle in *A. scalesiae*, markings faint or absent in *A. ambrosiae* except for a dark circular area immediately surrounding A2 spiracle. Ventral surface of body with secondary setae of thoracic appendages and antenna slightly longer and more abundant on *A. scalesiae* than on *A. ambrosiae*. A longitudinal row of minute secondary setae present on coxal sclerite of foreleg in *A. scalesiae*, absent in *A. ambrosiae*.

Description. MALE (n=31) (Figs 2, 4, 6, 8, 10). HEAD with labial palpi porrect, not extended beyond eye, vestiture mixed brown, dark brown, and white. Fronto-clypeus with short, mostly brown, appressed scales. Vertex scales appressed, whitish beige with greyish brown at their apex. Occiput with short, dark brown appressed scales and thin, long, apically widened and notched, dark brown (longest) and whitish-beige scales. Antenna with slender, erect, and deeply cleft whitish-beige scales except for first few flagellomeres also with some white and dark brown appressed scales. THORAX mostly whitish beige with scales apically tinged with greyish brown at their apex, especially on anterior half. Foreleg coxa pale chestnut-brown with few white and dark brown scales; femur dark brown with thin, white longitudinal stripes, especially on distal half; tibia dark brown with white scales forming small patches laterally near base and middle, thin longitudinal stripe between about 1/4 and 1/2, narrow diagonal stripe near 3/4, and on ventral surface and apex; tarsomere I dark brown with white scales at apex and at base, sometimes forming longitudinal stripes; tarsomeres II-V greyish beige with sometimes darker brown or greyish-brown scales dorsally. Midleg coxa with dark brown and whitish-beige scales; femur dark brown with thin, longitudinal white stripe and some scattered white scales; tibia with dark brown and white stripes, mostly dark brown at



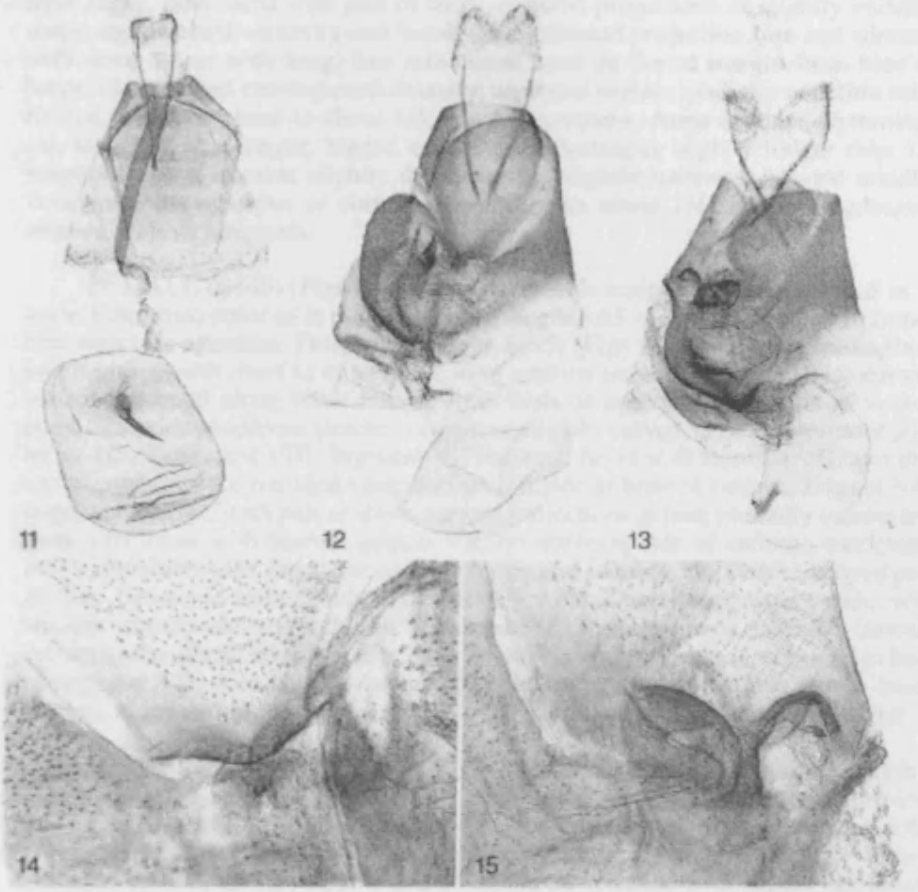
Figs 5-8. Male genitalia of *Adaina* species: 5, details of left valva of *A. ambrosiae*, specimen from Florida (slide BL 1608, CNC); 6, Same for *A. scalesiae*, paratype from Pinta (slide BL 1611, CNC); 7, Details of right valva of *A. ambrosiae*, same specimen as Fig. 5; 8, Same for *A. scalesiae*, same specimen as Fig. 6.

bases of spines, white apically; tarsomere I mostly dark brown on distal half and white with dark brown stripes on basal half; tarsomeres II-V greyish beige with greyish brown mostly on distal half of each tarsomere. Hindleg coxa white; femur appearing speckled with most scales dark brown with their base paler, whitish beige, also with scattered white scales; tibia as femur; tarsomere I mostly dirty white with dark brown at base and dark brown to chestnut-brown mostly toward distal half; tarsomeres II-IV white with few greyish-brown scales at apex of each tarsomere; tarsomere V entirely white. FOREWING length 5.81 - 6.63 mm (Holotype = 6.31 mm); mostly whitish beige with many scales brown at their apex; costa on basal half with row of brown scales with their apex paler; with thin chestnut-brown stripe from wing base to middle of first lobe, sometimes with more extended chestnut-brown along costal half and in first lobe; with dark brown triangular patch before white-lined cleft, rectangular patch along costa at base of first lobe, smaller square patch on costa near middle of lobe, yet smaller patch on costa subapically, and sometimes in middle of wing submedially; sometimes with slightly more extensive dark brown scaling along inner margin before triangular patch, on distal half of second lobe,



Figs 9-10. Aedeagus of *Adaina* species: 9, *A. ambrosiae*, same specimen as Fig. 5; 10, *A. scalesiae*, same specimen as Fig. 4.

and along cubital fold subbasally; fringe of first lobe on inner margin mostly dark brown to greyish brown interrupted by small white areas subapically and apically; fringe of second lobe mostly greyish brown interrupted by very small white areas on inner margin at about 2/3, subapically, and at apex. HINDWING unicolorous greyish brown with concolorous fringe; frenulum with one acanthus. ABDOMEN dorsally whitish beige, with some scales brown or chestnut-brown at their apex, and with dark brown spot medially at hind margin of first six segments, rarely absent on segments I and III-VI; laterally whitish beige with extensive chestnut-brown scaling toward base and dark brown toward apex, including genitalia, or with series of more or less conspicuous chestnut-brown, dark brown and white stripes; ventrally whitish



Figs 11-15. Female genitalia of Pterophoridae species (11-13, ventral views; 14-15, dorsal views): 11, *Platyptilia vilema* Landry (slide BL 1530, CDRS); 12, *Adaina ambrosiae*, specimen from Florida (slide BL 1612, CNC); 13, *A. scalesiae*, paratype from San Cristóbal (slide MHNG 2852, MHNG); 14, *A. ambrosiae*, dorsal connection between segments VII and VIII, same specimen as Fig. 12; 15, *A. scalesiae*, same structures as Fig. 14, same specimen as Fig. 13.

beige with dark brown longitudinal stripe medially, or dark brown median spots at apex of segments, or mostly brown with scales paler at their apex.

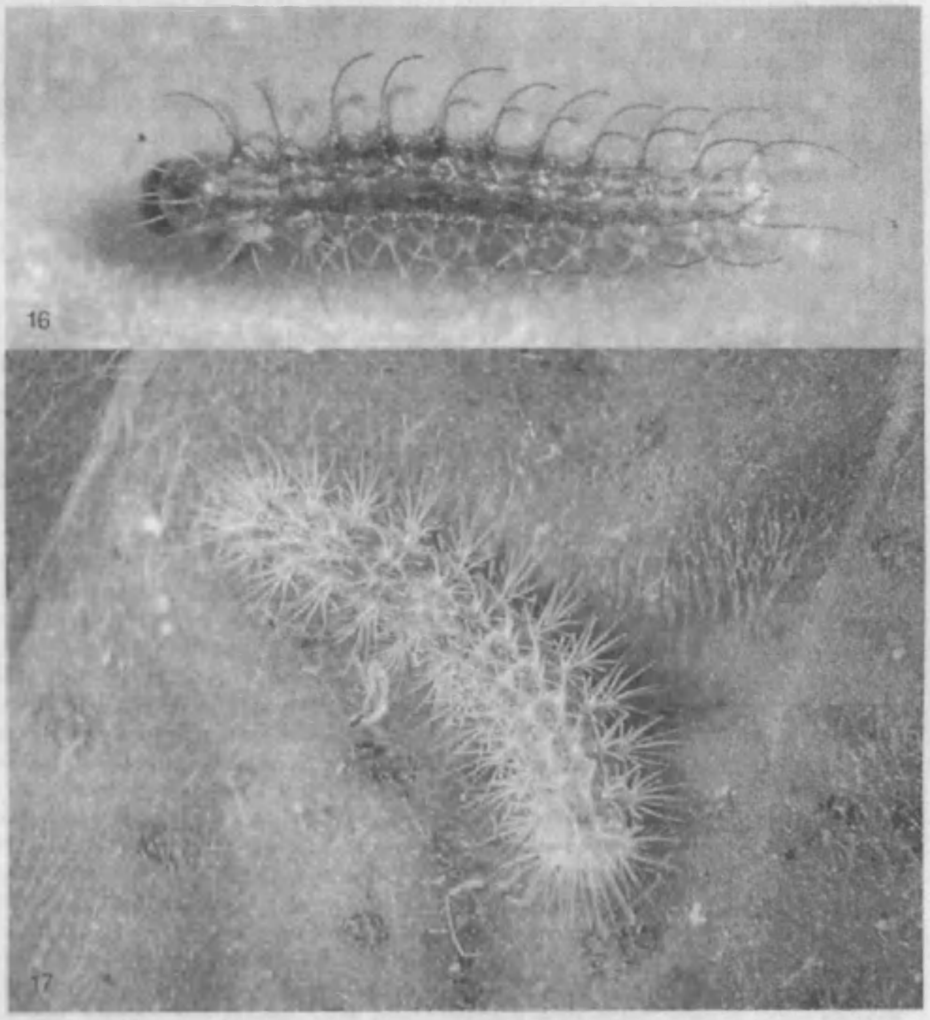
Male genitalia (n=6) (Figs 4, 6, 8, 10). Uncus of medium length, slender, broadly curved ventrad, sharply pointed apically. Tegumen slender, dorsal connection narrow, about 1/2 length of narrow arms. Valvae asymmetrical: right valva narrower, slightly shorter, narrowly rounded rather than broadly rounded, and more darkly sclerotized than left valva. Right valva with inwardly directed, narrow sclerotized crest set with moderately long setae toward and along dorsal margin, from about 2/3 and prolonged subapically by broadly rounded scoop-like projection extended slightly beyond ventral margin; ventral margin with narrow, darkly sclerotized band from before middle and curved subapically toward dorsal margin before scoop-like projection. Left valva with stout, short harpe curved medially at right angle, associated with pair of short, rounded projections of slightly variable shape and directed ventrally and basally, most laterad projection free and adorned with some setae; with long, free sclerotized band on dorsal margin from base of harpe, directed and curving mediobasally; on dorsal surface medially with thin sclerotized band from base to about 4/5. Vinculum narrow. Arms of juxta asymmetrical, the right arm longer, bigger, and curved. Aedeagus slightly longer than 1/2 length of valva, narrow, slightly down-curved, slightly narrowed beyond middle; vesica without spicules or cornuti; coecum penis about 1/4 length of aedeagus, aligned with its long axis.

FEMALE (n=46) (Figs 13, 15). Antenna with scales appressed, colored as in male. FOREWING color as in male; forewing length 5.63 - 6.44 mm. HINDWING frenulum with two acanthae. FEMALE GENITALIA (n=5) (Figs 13, 15). Papilla analis short and rounded with short to moderately long setation on whole surface, with narrow sclerotized band along basal margin from base of posterior apophysis to ventral edge. Posterior apophysis slender, straight or slightly curved, extended to about posterior 1/3 of segment VIII. Segment VII reduced, fused with sternum VIII and distorted, with lip-like rounded extension on left side at base of ostium. Tergum VIII large, shield-like, with pair of short, narrow projections at base medially (where tergum VIII fuses with narrow tergum VII, on opposite side of ostium), associated inside abdomen with short, narrow apophyses and more or less peanut-shaped projection. Ostium to left of middle, moderately wide. Ductus moderately wide, with smooth surface adorned with pair of elongate striae on inside of distal 1/4 (toward ostium), strongly wrinkled on proximal 3/4 (toward corpus busae), extended to base of segment VII, with delicate secondary pouch near ostium. Corpus bursae bean-shaped, about as long as ductus, with ductus seminalis inserted at proximal end.

FINAL INSTAR LARVA (n=2) (Figs 18-21, 22-24, 26). Maximum length 7 mm, width 1.2 mm (excluding setae). Lateral setae on verrucae forming conspicuous fringe around body. Lateral fringe setae long, up to 1.9 mm, 1.6x body width; D and SD setae relatively short, lengths less than 0.5x body width. Primary D and SD setae distinct and solitary; L and SV setae on verrucae with similar secondary setae. Setae clear, primary D and SD setae clear or brownish tinged. Lateral, anterior, and posterior fringe setae conspicuously barbellate, remaining setae simple.

HEAD hypognathous. Anterior aspect round. Width 0.60 – 0.62 mm (n=2) [penultimate instar 0.43 mm (n=1)]. Cranium (Figs 18, 19) uniformly pigmented, light brownish yellow in preserved material; stemmata dark. Adfrontal sclerite extending dorsad to vertex, ventrad to a point just short of anteclypeus. Pore AFa present. Lateral adfrontal suture length about 2x epicranial suture and about 1.5x clypeal width. Setae AF1, AF2, F1, C2, and L1 lengths not exceeding 0.5x clypeal width. Seta P1 length about 0.75x clypeal width; A1 just less than 1x clypeal width. Seta AF1 closer to AF2 than to F1. Seta P1 laterad and slightly ventrad of AF1. Labrum (Fig. 20) with 4 setae, without conspicuous notch, ventral margin slightly concave. Mandible (Fig. 21) 6-toothed, length just exceeding maximum width. Distal seta replaced by pore, proximal seta length about 0.6x mandible width.

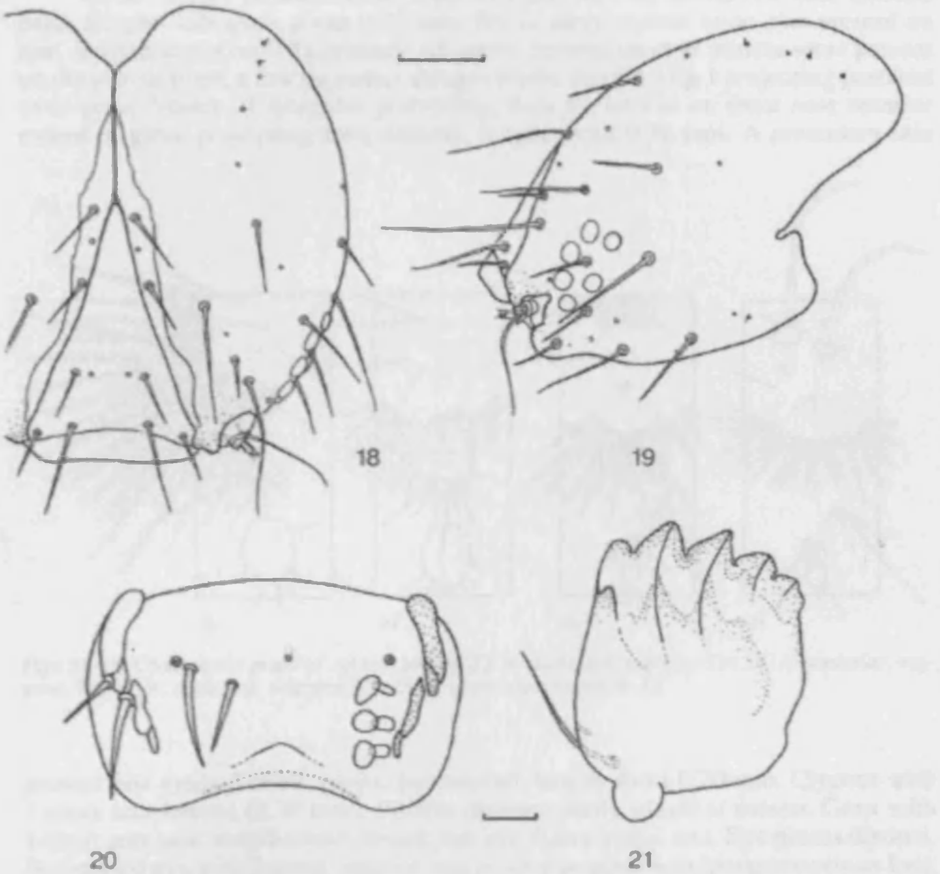
THORAX: Prothorax (Fig. 22) with primary setae XD1, XD2, SD1, and SD2 arranged in a nearly straight, compact, uniform row along anterior margin dorsad of L verruca. Primary XD and SD seta, along with 3 or more shorter secondary setae forming anteriorly projecting fringe, obscuring head in dorsal aspect. Anterior fringe setae barbellate, XD and SD setae lengths about 0.72 mm, 0.7x T1 width (fully developed larva), 1.5x T1 length (anterior-posterior). Setae D1 and D2 solitary. Seta D1 set posterad about 0.25x from anterior margin and closer to midline than relative distance from anterior margin, directed anterad, close but not appressed to body. Seta D1 length about 0.43 mm, form simple, not visibly spiculate (40x magnification); D1 tubercle minute, not distinctly sclerotized. Seta D2 similar to D1 but about 0.3x shorter, positioned about 0.5x from anterior margin and slightly laterad of D1, directed anterolaterad close to body. An aggregate of 3 or more minute, lightly sclerotized spots present along midline near D1. Cuticular granulations also lightly sclerotized along midline posterad of D2, along T1 posterior margin, surrounding spir-



Figs 16-17. Larvae of Galapagos Pterophoridae: 16. *Megalorhipida leucodactyla* (Fab.); 17. *Hellinsia nephogenes* (Meyrick).

acle, and extending anterad in a narrow strip along dorsal base of L. verruca. Lateral verruca crescent-shaped, with anterior bulge exceeding T1 anterior margin. A fan of 40-50 short to very long barbellate setae radiating from verruca. The most dorsal setae on verruca (about 12) arranged in a compact arc-shaped row, projecting laterad in a single plane, lengths reaching 1.8 mm near middle, decreasing at anterior and posterior ends of row. Setae more ventrally placed on verruca decreasing in length, spiculate to smooth. Spiracle dorsally placed posterad of L verruca near T1 posterior margin. Spiracle exserted, tubular with moderately sclerotized collar, peritreme round. Subventral verruca hidden in dorsal aspect, round, slightly elevated, with about 10-15 minute to medium length setae, lengths up to 0.48 mm. Segments T2 (Fig. 23) and T3 with setae D1 and D2 approximate, D2 just posterolaterad of D1. Seta SD2 directly posterad of SD1, SD setae set slightly more apart than D setae. Setae D1, D2, and SD1 lengths subequal, about 0.25 mm, directed anterad; SD2 about 0.14 mm, directed laterad. Dorsum of T1-T2 covered with lightly sclerotized cuticular granulations except for L. verruca, a rectangular hyaline area surrounding D setae, and an oblong hyaline area surrounding SD setae. A tiny dark spot at midline between D1 setae on T2, more developed on T3. A small dark spot also near base of D setae on T2 and another posterad of D setae. Lateral verrucae as on T1 but smaller and with fewer setae, longest setae reaching 1.9 mm. A tiny secondary verruca with a fan of 5 minute to medium barbellate setae present posterad of main L verruca. These setae appearing compressed, with dentate as opposed to setiform barbs. Subventral verruca as on T1.

Abdomen dorsum covered with lightly sclerotized cuticular granulations. Segments A1-A8 (A3, Figs 24, 26) with setae D1 and D2 on separate sclerites but sclerites (D1 and D2 right and left sides) coalesced, forming a dark quadrate patch near the center of each segment. Setal tubercles on sclerites small. Setae D1 and D2 lengths subequal (0.12-0.22 mm); D2 posterad and slightly laterad of D1; D1 directed anterad, D2 posterolaterad. Seta SD1 on hyaline patch laterad of D2, directed anterad, length similar or slightly less than D1. Spiracles as on T1 but more central on segment, about 0.5x from anterior margin, centered dorsad of L verruca, posterolaterad of SD1 on A1-A7, closer and more directly posterad of SD1 on A8. Lateral verrucae as on thorax. Main (L1-L2) lateral verruca shifted more posterad on A8. A small secondary verruca posterad of main L verruca on A1-A7, with about 5 short to minute setae on A1-A5, 2-3 on A6-A7, replaced by 1 or 2 similar type setae at posterior end of main L verruca on A8. Segments A1-A8 with a small round L3 verruca bearing 7-10 short to medium simple setae. Subventral verruca on A1-A8 small, round, 3-12 setae present, dorsad of proleg on A3-A6. Prolegs elongate, length about 2.5x width, with 7-9 crochets arranged in a mesopenellipse. Three minute V setae present mesad at proleg base. Seta V1 solitary or with another shorter seta on remaining abdominal segments. Segment A9 dorsum smaller than A8; D setae closer together on 1 small darkly sclerotized rectangular tubercle on posterior half of segment. Tubercles and sclerites (right and left) not joined at midline. Seta D1 on A9 similar in length to D1 on A8; D2 almost one-third longer on A9 than on A8 and slightly thicker. Segment A9 with both SD1 and SD2 present. Seta SD1 length similar to D1; SD1 laterad of D1 on anterior side of tubercle bearing SD2. Seta SD2 barbellate, thicker than SD1, and very long, reaching 2.4 mm, in plane with lateral fringe setae of A8. Lateral verruca reduced on A9, with setae L1 and L2 barbellate, less than 0.5x SD2 length, with about 5 shorter setae ventrad of L1 and L2. Verruca L3 absent. One small verruca with about 4 short setae present between L. verruca and seta V1 (transversally aligned between L3 and SV verruca

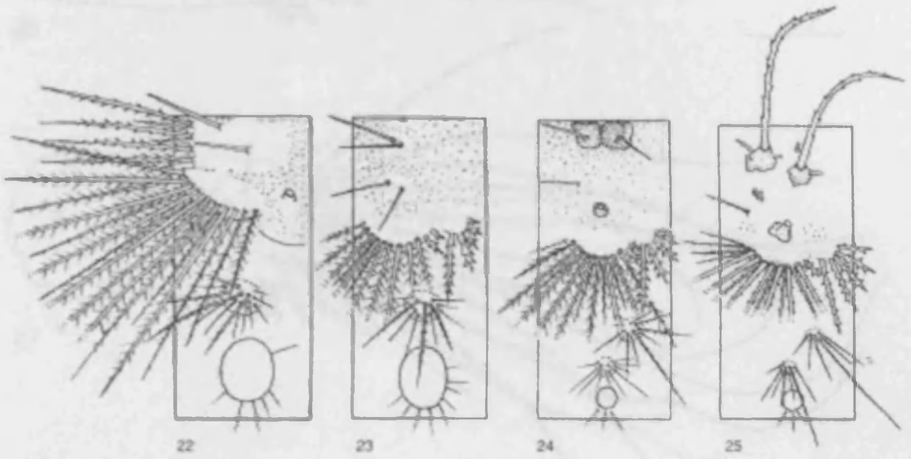


Figs 18-21. Larval head of *Adaina scalesiae*: 18, Frontal view of cranium, scale line = 0.125 mm; 19, Lateral view of cranium, same scale as Fig. 18; 20, Labrum, epipharyngeal surface on right, scale line = 0.03 mm; 21, Right mandible, same scale as Fig. 20.

of A8). Anal plate with several tiny dark sclerotized spots. Seta D1 simple, short, erect, about 0.3x from caudal margin. Remaining primary and secondary setae mostly long, barbellate, forming thick caudal fringe. Anal proleg with 10-12 crochets, several short setae present.

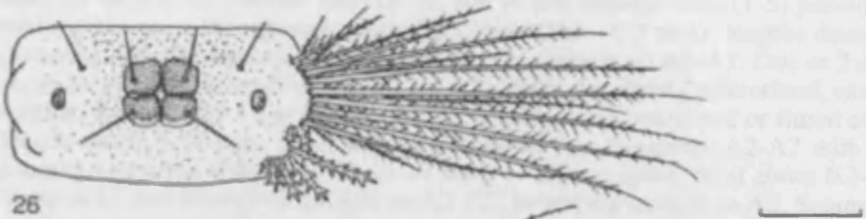
PUPA (n=4) (Fig. 28). Maximum length 7 mm, width (T2) 1.44 mm. Primary and secondary setae present, minutely spiculate, including those on venter. Primary D and SD setae long, reaching 1.25 mm, on verruca-like tubercles with shorter secondary setae. Longitudinal rows of short to minute secondary setae present on wings. Setae on lateral row of moderate length, forming fringe along wing. Abdomen with lateral setae on flange-like verrucae, seta lengths exceeding fringe setae of wing. Spiracle on A2 prominently exserted, tubular with a flared base, darkly sclerotized.

HEAD. Vertex obscure. Front with AF1 and AF2 on lateral rise near antenna base; lengths subequal, about 0.72 mm. Six or more shorter setae also present on rise, lengths less than 0.5x primary AF setae. Several short to minute setae present on dorsum of front, a few on venter along cephalic margin with 1 projecting posterad over gena. Venter of front not protruding. Seta F1 laterad on front near anterior extent of gena, projecting anterolaterad, length about 0.48 mm. A secondary seta present just mediad of F1, projecting anterad, length about 0.20 mm. Clypeus with 1 short seta laterad (0.36 mm). Pilifers distinct, partly joined at meson. Gena with 1 short seta near maxilla base, length just less than clypeal seta. Eye pieces distinct. Sculptured eye with 2 setae; anterior seta as long as genal seta, posterior seta as long as clypeal seta. Maxilla without setae, base extending to about 0.5x T2 leg length, about even with A3 anterior margin. Distal tip of maxilla exposed between T2 legs, extending from foreleg apex to a point even with or just short of midleg apex. Antenna exceeding forewing tip, nearly reaching T2 leg apex, a row of short to minute setae extending along entire length. Setae at antenna base longer (about 2x length at tip), 2 additional rows flanking main row above gena and eye, contributing to cephalic fringe.



Figs 22-25. Chaetotaxic maps of *Aduina* larvae: 22, *A. scalesiae*, segment T1; 23, *A. scalesiae*, segment T2; 24, *A. scalesiae*, segment A3; 25, *A. ambrosiae*, segment A3.

THORAX. Pronotum surface covered with numerous minute to short secondary setae. Three long primary setae present: D1 near midline, 0.5x from anterior margin; D2 laterad and slightly posterad of D1, between D1 and spiracle; 1 SD seta on lateral margin. Seta D1 about 0.65 mm, D2 about 0.60 mm, SD seta about 0.96 mm. Foreleg extending to about 0.92x T2 leg length, reaching anterior 0.3x of A5. Anterior third of foreleg with double row of minute setae, a single row extending to about 0.75x. Coxa of foreleg exposed, with a row of about 8 minute setae. Prothoracic spiracle embedded in T2 anterior margin, slightly exserted, moderately sclerotized. Dorsum of mesothorax villous. Tegular region of mesothorax gently rounded, not producing a noticeable keel or carina. Anterior margin and posterior third sclerotized. Secondary setae arising from sclerotized posterior third also dark. Primary D



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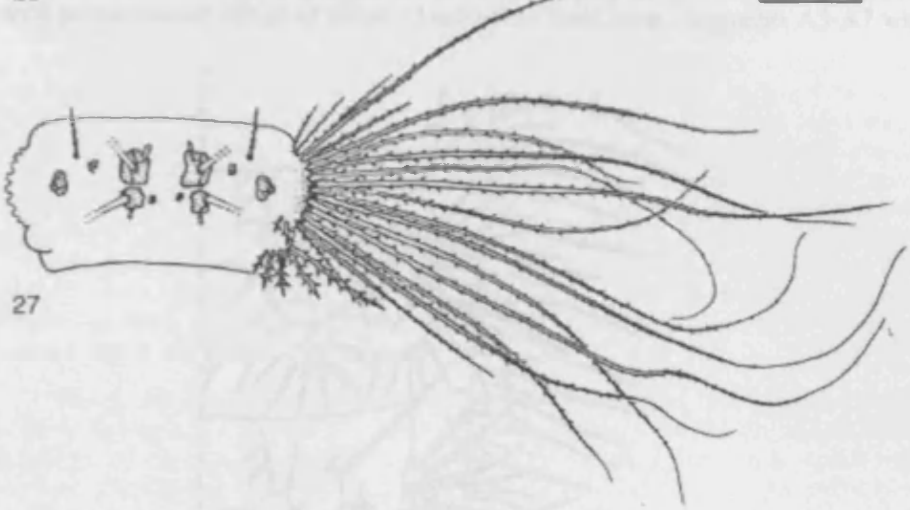

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Figs 26-27. Larvae of *Adaina* species, comparison of A3 dorsum and relative lengths of lateral setae: 26, *A. scalesiae*; 27, *A. ambrosiae*, scale line = 0.5 mm.

and SD setae long. Setae D1 and D2 erect, longitudinally aligned, just laterad of midline. Setae SD1 and SD2 approximate, laterad of D1 near alar furrow, directed laterad. Primary D and SD setae subequal, lengths reaching 1.5 mm. Forewing base with numerous minute setae, a verruca-like cluster of about 4 short setae present anterolaterad. Forewing with several longitudinal rows of minute to short setae marking veins and wing margins. The lateral rows forming fringe with setae up to 0.6 mm, lengths gradually decreasing posterad to A3. Forewing apex reaching anterior third of A5. Midleg nearly reaching A5 posterior margin. Midleg transversally striated, without setae. Metathorax with D1 and D2 moderately long, about 0.72 mm, close together near anterior margin, longitudinally aligned, erect but diverging anterad and posterad. Setae SD1 and SD2 close together, at anterolateral angle, lengths about 0.43 mm. Numerous minute to short secondary setae present on dorsum, especially just laterad of midline; 1 or more setae posterad of D2 distinctly longer than others. Hindwing with longitudinal row of short to minute setae. Hindwing apex about even with A2 spiracle. Hindlegs longitudinally aligned beneath maxilla, tarsal apex exposed where just exceeding maxilla.

Abdomen segments A1-A8 (A2-A3, Fig. 28) with primary D setae on separate verruca-like tubercles, each tubercle bearing up to 10 shorter secondary setae. Seta D2 posterolaterad of D1, directed slightly posterolaterad. Setae D1 and D2 lengths about equal, reaching 0.72 mm, a bit shorter on A1 and A8 with D1 shorter than D2 on A1, D2 shorter than D1 on A8. A few minute setae (1-5) present near midline between D2 tubercles. Seta SD1 short (0.2 – 0.3 mm), lengths decreasing posterad, directed anterolaterad, just anterad of spiracle on A2-A7. One or 2 minute secondary setae posterad of SD1 (4 on A1). Spiracles darkly sclerotized, exserted, tubular. Spiracle on A2 at least 2x length of others and buttressed or flared at base, length about 0.19 mm. Lateral setae absent on A1. Segments A2-A7 with small round L1 verruca with up to about 14 short to minute setae, most about 0.24 mm. Verruca L1 just laterad of spiracle on A2-A7, near wing margin on A2. Segment A2 with posterolateral fringe of about 12 minute to short setae. Segments A3-A7 with

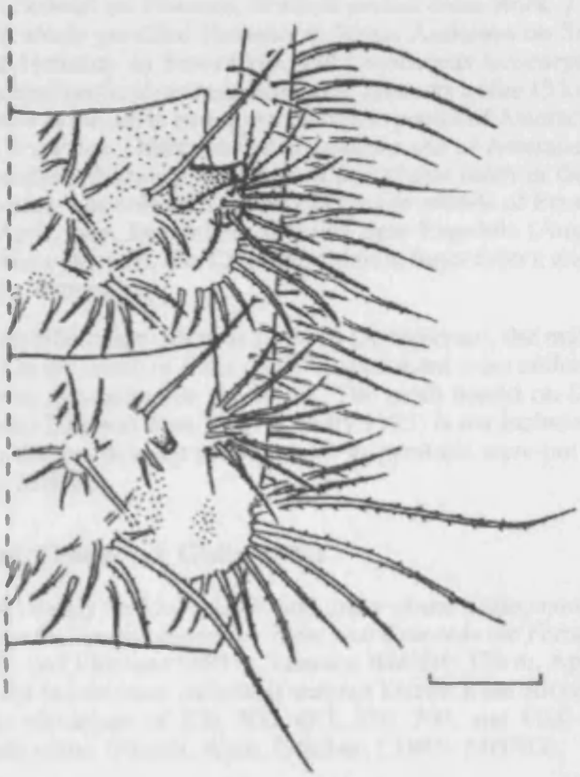

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Fig. 28. Pupa of *Aduina scalesiae*, dorsal view of segments A2-A3, scale line = 0.2 mm.

fully developed L2 flange-type verruca bearing fan of about 16 minute to long setae (longest 0.72 mm). Segments A4-A7 with small round L3 verruca ventrad of L2 lateral flange verruca. One short SV seta on A4, 3 short SV setae longitudinally aligned on A5-A7. Segment A8 with setae generally shorter, spiracle absent. Verrucae L1 and L2 combined on A8, with setae about as long as L1 setae on preceding segments. Venter of A8 with 2 short setae representing L3 verruca, 2 minute SV setae at posterior margin. Posterior margin bordering ventral plate lightly sclerotized. Dorsum of A9 covered with numerous short to minute setae, primary setae difficult to distinguish. Dorsum of A10 with 2 short primary setae directed posterad and with numerous short hooked hamuli. Caudal apex acute. Ventral plate (fused A9/A10 venter) with dense patch of hooked minute to short anterior hamuli centrally placed near A8 posterior margin. Minute hooked posterior hamuli numerous laterad at caudal tip. Scattered hamuli also present between anterior patch and anal slit.

Life history. Larvae of this species have been recorded to feed on leaves of *Scalesia microcephala* Robinson on Isabela and *S. incisa* Hook. *f.* (in fact *S. baurii* ssp. *hopkinsii* (Robinson) Eliasson; C.K. McMullen, pers. comm. to BL, 1994) on Pinta (Asteraceae) (Landry 1993). In addition, the caterpillars skeletonize the leaves of *Scalesia villosa* Stewart on Floreana, *Scalesia pedunculata* Hook. *f.* on Floreana and Santa Cruz, *Scalesia gordilloi* Hamann & Wium Andersen on San Cristobal, *Scalesia retroflexa* Hemsley on Santa Cruz, and *Lecocarpus lecocarpoides* Cronq. & Stuessy (Asteraceae) on Gardner near Española. Thus, six of the 15 known species of the endemic genus *Scalesia*, in addition to another species of Asteraceae, are used as hostplant by *A. scalesiae*. Other species of *Scalesia* and of Asteraceae should be investigated to complete the hostplant range of this plume moth in the Galapagos.

Adaina scalesiae was collected on the Galapagos islands of Fernandina (January), Floreana (April, July, December), Gardner near Española (August), Isabela (February-May), Pinta (March), San Cristobal (March, September), and Santa Cruz (January-May, July, September).

Notes. The specific name refers to *Scalesia* (Asteraceae), the main hostplants in the Galapagos. On the island of Pinta a pair of specimens were collected on Playa Ibbetson, which was misspelled on the labels. The moth reared on *S. baurii* ssp. *hopkinsii* (Robinson) Eliasson from Pinta (Landry 1993) is not included in the type series as its wings did not develop properly and its genitalia were not dissected; it is deposited in the MHNG.

***Hellinsia cristobalis* (Landry & Gielis, 1992)**

Recorded previously on four islands and under genus *Oidaematophorus*, this species is among the Galapagos endemics. New island records are Fernandina (1300 m, January, CDRS) and Floreana (360 m, January, BMNH; 329 m, April, MHNG). Although mentioned before from Isabela, it was not known from Alcedo, where we have records from elevations of 200, 300, 483, 570, 700, and 1100 m, the latter being the rim of the crater (March, April, October; CDRS, MHNG).

***Hellinsia devriesi* (Landry & Gielis, 1992)**

Described from six females in the genus *Oidaematophorus*, this species was presumed to be endemic until Bigot & Deknuydt (1998) found it on Martinique and described the male. New island records are Fernandina (Punta Mangle, June, CDRS) and Santa Cruz (highest elevations, May, June, and CDRS, December, CDRS). On Isabela, in addition to previous records from Sierra Negra, we report this species also from Alcedo (1100 m, CDRS) and Volcan Darwin (beach, June, CDRS). In the key, diagnosis, and description of *H. devriesi*, the dorsal abdominal markings are said to be a single longitudinal dark-brown patch on one subapical segment. However, based on additional specimens, this patch may be longer and may form a median line from the apex of the second segment to the tip of the penultimate segment. This feature more easily separates this species from *A. scalesiae*, which only has small spots at the tip of most segments medially.

Hellinsia nephogenes (Meyrick, 1926)

This endemic pterophorid is newly recorded from Fernandina (June, CDRS). It was reported previously in the genus *Oidaematophorus* Wallengren. Perry & de Vries (2003) record this species as *Pterophorus ?nephogenes* Meyrick. They mention having reared it from *Scalesia affinis* Hook. *f.* (although this had been mentioned already in Landry & Gielis, 1992), but also on *Rhynchosia minima* (L.) DC. (Fabaceae). The *Scalesia affinis* rearing records are correct as they are associated with voucher specimens, but the record from *Rhyncosia minima* must be considered dubious as there are no voucher specimens and this association of hosts from separate families is not very plausible. Fig. 17 represents a larva of this species on a leaf of *Scalesia affinis* for which the specimen was reared and is in the CDRS collection.

Table 1. Summary of the distribution of the Pterophoridae species on the islands of the Galapagos placed in decreasing order of surface area. In parentheses after each name is the number of hostplants known in the archipelago.

Island Species (hostplants)	Isabela	Santa Cruz	Fernandina	Santiago	San Cristobal	Floreana	Marchena	Española	Pinta	Baltra	Santa Fe	Pinzon	Genovesa	Rabida	Gardner at Española
Megalorhipida leucodactyla (2)	+	+	+	+	+	+	+	+	+	+		+	+	+	
Lantanophaga pusillidactyla (0)	+	+					+						+		
Platyptilia vilema (1)	+								+						
Bipunctiphorus nigroapicalis (0)	+	+			+	+			+						
Postplatyptilia huigraica (2)	+	+													
Postplatyptilia minima (0)	+	+							+						
Stenoptilodes brevipennis (1)	+	+			+	+	+					+			
Stenoptilodes gielisi (0)	+														
Stenoptilodes juanfernandicus (0)	+														
Exelastis montichristi (1)	+	+		+	+	+	+	+	+	+	+		+		
Exelastis pumilio (1)	+				+									+	
Adaina scalesiae (7)	+	+	+		+	+			+						+
Hellinsia cristobalis (0)	+	+	+	+	+	+			+						
Hellinsia devriesi (0)	+	+	+												
Hellinsia nephogenes (1)	+	+	+			+									

CONCLUSIONS

We have now found Pterophoridae on 15 different islands of the Galapagos archipelago, the smallest of which being Gardner at Española. As the latter is the 22nd largest island with 0.58 km2, we can expect that some islands of larger size, such as Bartolome or Darwin also have a fauna of Pterophoridae, as undoubtedly do smaller ones, but these have yet to be sampled for micromoths.

In accordance with the theory of island biogeography (MacArthur & Wilson 1967), it is not surprising that Isabela, by far the largest island of the archipelago with 4588 km^2, has the richest fauna of Pterophoridae. In fact, all 15 species known from the archipelago occur on Isabela. Isabela is also the richest island for many other Lepidoptera families (e.g. Arctiidae, Geometridae, Noctuidae).

We have collected only five species of Pterophoridae on the third largest island, Fernandina, no doubt because very little collecting has been performed on this island. Insufficient collecting also accounts for the current status of the known distribution of most other species as exemplified by the situation for *Stenoptilodes gielisi* Landry and *Stenoptilodes juanfernandicus* Landry & Gielis, which remain known from only one and two Galapagos specimens respectively.

ACKNOWLEDGEMENTS

We are very much indebted to the collecting and rearing efforts of CDRS staff Ruth Boada, Charlotte Causton, Yael Lubin, and Walter Simbaña. We thank the authorities of the CDRS and Galapagos National Park for permission to carry field work and for logistical support. For their help in the field we thank Novarino Castillo and Patrick Schmitz. We thank Richard Hoebeke (CUIC), Jean-François Landry (CNC), and Kevin Tuck (BMNH) for the loan of specimens in their care. Finally we extend our gratitude to Cees Gielis and J.-F. Landry for their comments on the manuscript.

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(received 8 October 2004; accepted 14 November 2004)

REVUE SUISSE DE ZOOLOGIE 113 (2): 307-323; juin 2006

Taygete sphecophila (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on *Polistes* wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands

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***Taygete sphecophila* (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on *Polistes* wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands.** - *Taygete sphecophila* (Meyrick) (Lepidoptera; Autostichidae) is reported on the Galapagos Islands. The morphology of the moth, larva, and pupa are described and illustrated in details. Part of the mitochondrial DNA was sequenced and made available on GenBank. The incidence of predation by *T. sphecophila* on nests of *Polistes versicolor* Olivier (Hymenoptera; Vespidae) was measured in four different vegetation zones of Floreana and Santa Cruz Islands. The percentages of infested nests varied greatly (from 13.9% to 66.7% on Floreana and from 20.0 to 100% on Santa Cruz) and no clear ecological trends could be ascertained.

Keywords: Micro moths - Autostichidae - *Taygete* - *Polistes* - Galapagos Islands - mitochondrial DNA - larval predation - morphology - ecology.

INTRODUCTION

Taygete was described by Chambers (1873) to accommodate *Evagora difficilisella* Chambers, 1872 (Nye & Fletcher, 1991). The latter name proved to be a synonym of *T. attributella* (Walker, 1864). The genus appears to be restricted to the

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Manuscript accepted 06.12.2005

New World. Becker (1984) lists 13 names in this genus for the Neotropical fauna while Hodges (1983) lists six species for the North American fauna, including five that are stated to be misplaced in this genus. BL's examination of the type specimens of the Neotropical species at the Natural History Museum, London, points to the possibility that only *T. sphecophila* (Meyrick, 1936) is congeneric with *T. attributella* in this region. However, the types of *Epithectis consociata* Meyrick, *E. notospila* Meyrick, and *E. altivola* Meyrick have lost their abdomen and cannot be assigned to genus, and the type of *E. lasciva* Walsingham, deposited in the USNM, Washington, could not be found.

Taygete Chambers was considered to belong to the Gelechiidae until Landry (2002) moved it to the Autostichidae, Symmocinae sensu Hodges (1998). *Taygete sphecophila* was described from three specimens bred in Trinidad from "bottom of cells of the Hymenopteron *Polistes canadensis*" (Meyrick, 1936). The moth and male genitalia were later illustrated with black and white photography by Clarke (1969). On the Galapagos Islands moths of *T. sphecophila* were first collected in 1989 by BL, but the species probably arrived earlier within nests of *Polistes versicolor* Olivier (Vespidae).

The purposes of this paper are to redescribe and illustrate the moth of *T. sphecophila*, to describe and illustrate the larva and pupa, to present part of its mitochondrial DNA, and to report on a few aspects of its biology, particularly with regard to the incidence of damage to *P. versicolor* nests by larvae.

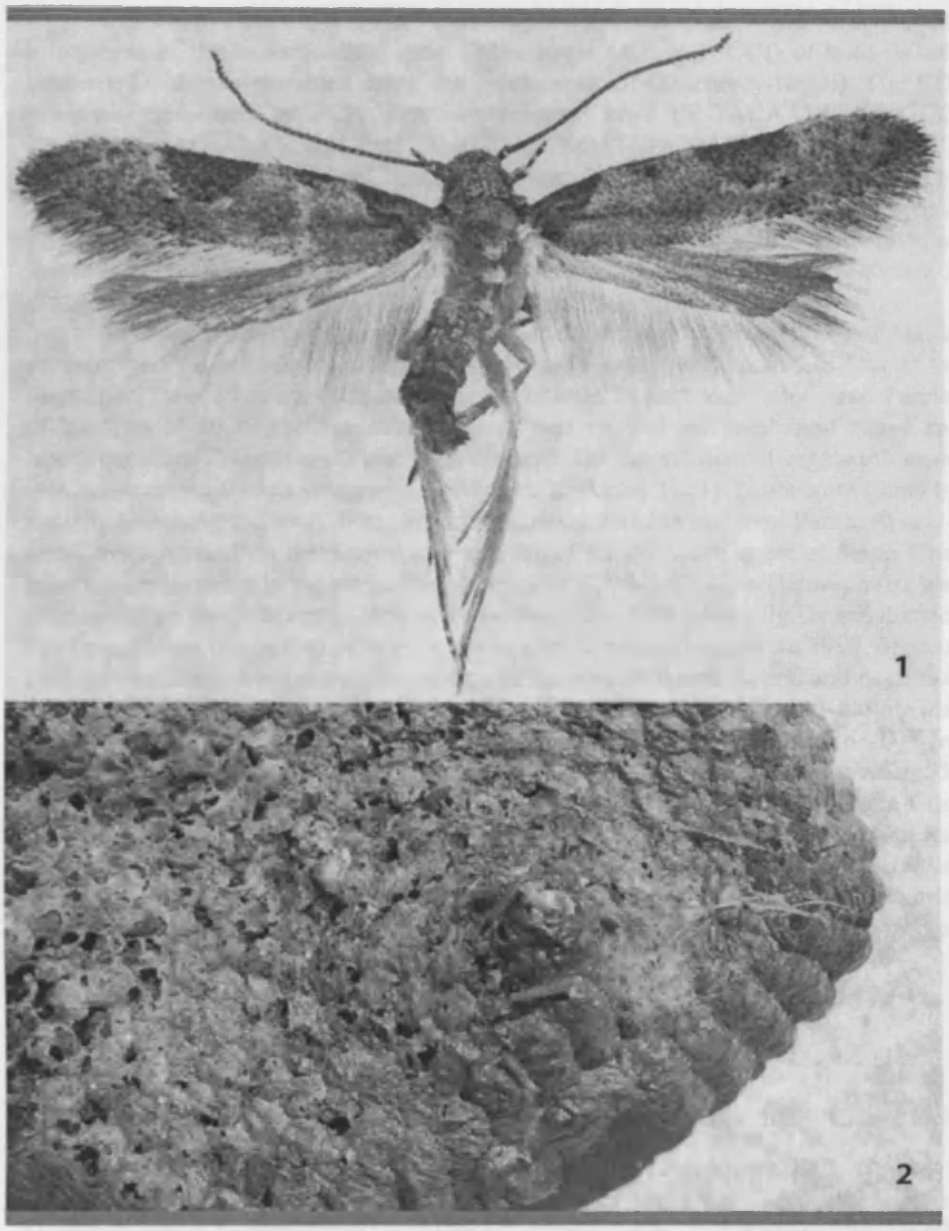
MATERIAL AND METHODS

Moths of *T. sphecophila* were first collected at night with a mercury vapor light set in front of a white sheet and powered by a small generator, and with an ultra-violet lamp powered by a battery. Other adult specimens were reared from contained nests of *Polistes versicolor*. Immature stages were found by dissecting *Polistes* nests and by exposing them to the sun, which causes larvae to exit nests and run away from them (Fig. 2).

Specimens are deposited in the Charles Darwin Research Station (CDRS), Santa Cruz, Galapagos, Ecuador; the Canadian national Collection of Insects (CNC), Ottawa, Ontario, Canada; the United States National Museum of Natural History, Washington, D.C., U.S.A. (USNM), and the Muséum d'histoire naturelle (MHNG), Geneva, Switzerland.

For the study of specimens using electron microscopy, larvae and pupae were first rinsed several times in water, cleaned in 10% EtOH with a camel hairbrush, and then dehydrated in EtOH as follows: 10% EtOH for 15 minutes, 20% for 15 minutes, 40% for 15 minutes, 70% for 1/2 hour, 90% for 1/2 hour, and 100% for 1/2 hour each in two separate baths. After dehydration, specimens were critical-point dried using a Tousimis critical point dryer, mounted on stubs, and coated with gold-palladium (40-60%) using a Cressington sputter coater. The ultrastructure of the larvae and pupa was studied with an Amray scanning electron microscope.

Gross morphological observations and measurements of the larvae and pupae were made using a dissecting microscope (reflected light) with a calibrated micrometer.



FIGS 1-2
1, *Taygete sphecophila*, female; 2, part of an abandoned nest of *Polistes versicolor* exposed to the sun with at least 8 larvae of *Taygete sphecophila* exiting from it.

Maps of the larval chaetotaxy were initially drawn using a WILD dissecting microscope with a camera lucida attachment. Terminology for chaetotaxy follows Stehr (1987).

In order to certify that the larvae corresponded to the adults found we sequenced a fragment of the mitochondrial gene Cytochrome oxidase I (COI) of both. Whole genomic DNA was extracted using the Nucleospin kit (Macherey-Nagel). The COI gene was amplified by PCR with two primers: k698 (5'-TACAATTTATCGCC-TAAACTTCAGCC-3'), and Pat2 (5'-TCCATTACATATAATCTGCCATATTAG-3'). The thermal profile started with an initial denaturation at 95°C for 5 min, followed by 35 cycles at 94°C for 30 s, 47°C for 30 s, and 72°C for 1 min 30 s, and a final step at 72°C for 10 min. The purified PCR product was sequenced in both directions using fluorescent dye terminators in an ABI 377 automated sequencer. The sequence is available from GenBank (Accession No. DQ309437).

In order to determine the distribution and the density of *Taygete sphecophila* as predator on *Polistes versicolor* nests, several study sites were selected in four of the vegetation zones of Santa Cruz and Floreana Islands. In each vegetation zone a series of quadrats of 10 m x 10 m were made at random, and the number of active and inactive nests of *Polistes versicolor* were counted. The delimitation of vegetation zones was based on vegetation composition (Wiggins & Porter, 1971). Nests were found by visually searching the study sites. In addition, nests found in and near Puerto Ayora, a small town located on the littoral and arid zones on the south coast of Santa Cruz Island, were included in the study. The presence of *T. sphecophila* in *Polistes* nests was determined by the presence of little holes on the back of the nests (Fig. 2) and distinctive breaches on the capped cells normally occupied by wasp pupae. In 1999, nests of *Polistes versicolor* were monitored weekly in the area of Puerto Ayora, and nests that were abandoned after being infested by *T. sphecophila* were collected during that period of time. Some adults of *T. sphecophila* that emerged from these nests were preserved dry for taxonomic identification. The ecological observations were made between April and August 1999, February and April 2002 and 2003 on Santa Cruz Island, and between April and August 1999 on Floreana Island. To test for ecological or insular trends in the frequency of parasitism of *P. versicolor* nests by *T. sphecophila*, we performed a G-test for goodness of fit (Sokal & Rohlf, 1995) on each island dataset using the proportion of *P. versicolor* nests in a given zone to infer the expected frequency of parasitism by *T. sphecophila*.

TAXONOMIC TREATMENT

Taygete sphecophila (Meyrick)

Epithectis sphecophila Meyrick, 1936: 624; Gaede, 1937: 113; Clarke, 1955: 290; Clarke, 1969: 63, pl. 31 figs 4-4b; Makino, 1985: 25; Yamane, 1996: 85.

Taygete sphecophila (Meyrick); Becker, 1984: 47; Landry, 1999: 68; Landry, 2002: 818-819.

MATERIAL EXAMINED FOR MORPHOLOGICAL WORK: Moths (13 specimens from the Galapagos Islands, Ecuador): SANTA CRUZ: 1 ♀, C[harles] D[arwin] R[esearch] S[tation], arid zone, 19.i.1989, M[ercury] V[apor] L[amp] (B. Landry); 4 ♀ (two dissected with genitalia on slides CNC MIC 4586 & BL 1196, the latter with right wings on slide BL 1313), CDRS, arid zone, 3.ii.1989, MVL (B. Landry); 2 ♂ (one dissected, slide BL 1126), Barranco, ex larva en nido *Polistes versicolor*, 8.ii.1999 (L. Roque, No. 99.20); 1 ♀, NNW Bella Vista, GPS: 225 m elev., S 00° 41.293', W 090° 19.665', 18.ii.2005, u[ltra] v[iolet] l[ight] (B. Landry, P. Schmitz); 1 ♀ (dissected, slide BL 1195), 2 km W Bella Vista, 27.ii.1989, MVL (B. Landry); 1 ♀, casa L. Roque-Albelo & V. Cruz, GPS: 137 m elev., S 00° 42.595', W 090° 19.196', 27.ii.2005, uvl (B.

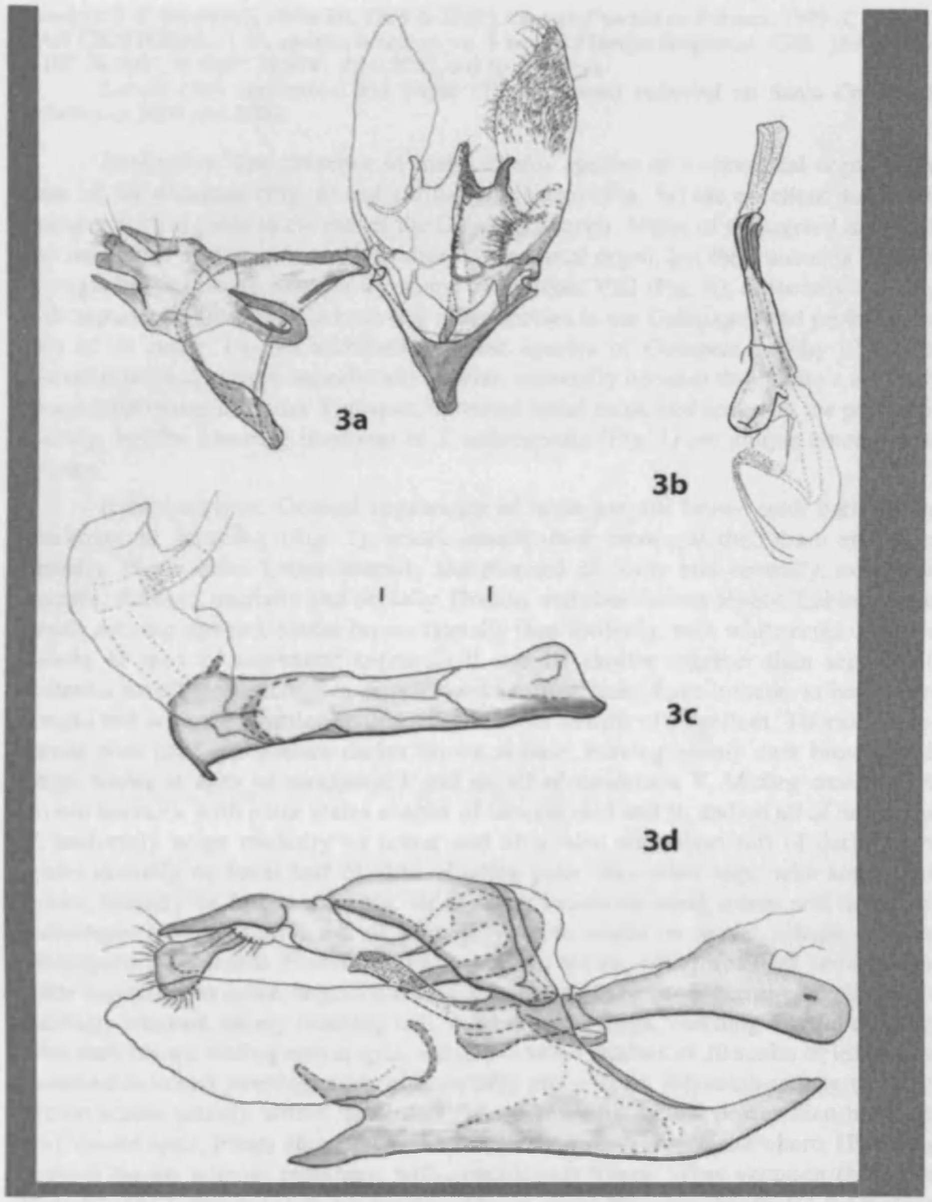


FIG. 3

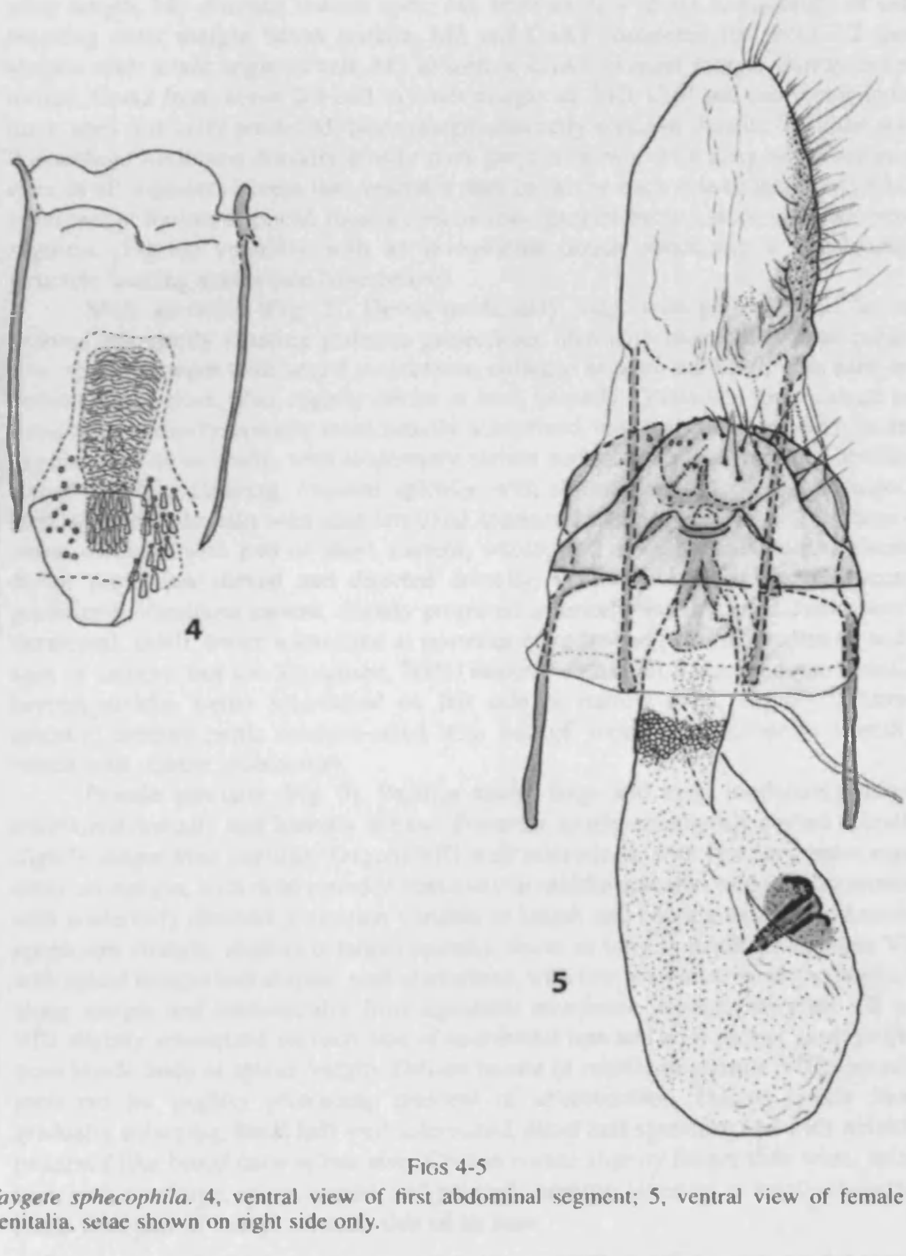
Taygete sphecophila, male genitalia (sizes not proportionate). 3a, dorsal view of valvae + vinculum + juxta and ventral view of tegumen + uncus + gnathos detached on right side and spread on left side, phallus removed, setae shown on right side only; 3b, side view of phallus with vesica everted; 3c, dorsal view of phallus, vesica inverted, scale = 0.1 mm; 3d, lateral view of whole genitalia.

Landry); 2 ♂ (dissected, slides BL 1208 & 1209), émergé d'un nid de Polistes, 1999 (C. Parent). SAN CRISTOBAL: 1 ♂, antiguo botadero, ca. 4 km SE P[uer]to Baquerizo, GPS: 169 m elev., S 00° 54.800', W 089° 34.574', 22.ii.2005, uvl (B. Landry).

Larvae (166 specimens) and pupae (10 specimens) collected on Santa Cruz by P. Schmitz in 2004 and 2005.

DIAGNOSIS: The presence in males of this species of a corematal organ at the base of the abdomen (Fig. 4) and a trifurcated uncus (Fig. 3a) are excellent diagnostic features with regards to the rest of the Galapagos fauna. Males of *Galagete* Landry are the only other Galapagos moths to share a corematal organ, but their uncus is made of a single projection. In females the shape of segment VIII (Fig. 5), especially dorsally, will separate *T. sphecophila* from any other species in the Galapagos and probably the rest of its range. On the archipelago, some species of *Galagete* Landry (2002) or Gelechiidae may appear superficially similar, especially because they share a similarly shaped hindwing, a similar wingspan, upturned labial palpi, and scales on the proboscis basally, but the forewing markings of *T. sphecophila* (Fig. 1) are unique among these groups.

REDESCRIPTION: General appearance of moth greyish brown with dark brown markings on forewing (Fig. 1); scales usually dark brown at their base and paler apically. Head scales longer laterally and directed medially and ventrally, except on occiput, directed medially and dorsally. Ocellus and chaetosema absent. Labial palpus gently curving upward, darker brown laterally than medially, with white rings of scales mostly at apex of segments; segments II and III shorter together than segment I. Antenna mostly greyish brown, darker brown toward base; flagellomeres in both sexes simple and with erect scales ventrally from about middle of flagellum. Thorax concolorous with head, sometimes darker brown at base. Foreleg mostly dark brown, with beige scales at apex of tarsomere I and on all of tarsomere V. Midleg mostly dark brown laterally, with paler scales at apex of tarsomeres I and II, and on all of tarsomere V, uniformly beige medially on femur and tibia, also with short tuft of dark brown scales dorsally on basal half of tibia. Hindleg paler than other legs, with some dark brown laterally on femur and tibia, mostly dark brown on tibial spines and at base of tarsomeres I-IV, also with tuft of long dirty white scales on dorsal margin of tibia. Wingspan: 7.5-9.0 mm. Forewing mostly greyish brown, with three dark brown triangular markings on costa, largest marking at base, reaching inner margin, smallest submedially situated, barely reaching cell, third marking large, reaching middle of wing; with dark brown scaling also at apex and as 1-3 small patches of 10 scales or less below postmedian costal marking; also with variable amounts of yellowish-orange to rusty-brown scales usually within basal dark brown marking, below postmedian marking, and toward apex; fringe dark brown at apex, more greyish brown elsewhere. Hindwing greyish brown without markings, with concolorous fringe. Wing venation (based on slide BL 1313, female) (Fig. 6): Forewing Sc to about 2/5 wing length; R1 from about middle of cell; R2 and R3 separate, both from before upper angle of cell; R4, R5, and M1 from upper angle of cell, connected, R4 and R5 directed toward costa before apex, M1 directed toward outer margin below apex; M2 and M3 separate, M2 from lower angle of cell, M3 from shortly before lower angle of cell; CuA1 and CuA2 separate, both from shortly before lower angle of cell; CuP absent; cell a little more than half



FIGS 4-5

Taygete sphecophila. 4, ventral view of first abdominal segment; 5, ventral view of female genitalia, setae shown on right side only.

wing length; A1 and A2 joined at about 1/5 their lengths. Female forewing retinaculum consisting of anteriorly directed scales at base of cubital stem and posteriorly directed scales at base of Sc. Hindwing Sc closely following costa, reaching it at about 3/5 wing length; Rs connected with M1 after upper angle of cell, Rs reaching costa at about 4/5 wing length, M1 directed toward apex; M2 from slightly above lower angle of cell, reaching outer margin below middle; M3 and CuA1 connected for about 1/2 their lengths after lower angle of cell, M3 to tornus, CuA1 to inner margin shortly before tornus; CuA2 from about 2/3 cell to inner margin at 7/10; CuP and anal veins indistinct; apex distinctly produced; outer margin distinctly concave; female frenulum with 2 acanthae. Abdomen dorsally mostly dark greyish brown, with dirty white scales at apex of all segments except last; ventrally dark brown on each side of large dirty white band except for last segment, mostly concolorous, greyish brown; male first abdominal segment (Fig. 4) ventrally with an invaginated pouch containing a membranous structure bearing scales (see Note below).

Male genitalia (Fig. 3). Uncus moderately long, with pair of fixed lateral, pointed and gently tapering glabrous projections; also with movable median projection, slightly longer than lateral projections, enlarged at apex and bifid, with each end bulbous and setose, also slightly setose at base laterally. Gnathos a long curved rod pointing posteriorly, apically more heavily sclerotized, tapered, glabrous, and rounded. Tegumen broad medially, with moderately narrow pedunculi. Valva with unsclerotized setose cucullus, tapering, rounded apically, with slightly sclerotized setose ridge at base on inner side, also with medium sized apodemes directed anteriorly from base of costa; sacculus with pair of short, narrow, setose, and apically rounded projections, dorsal projection curved and directed dorsally, ventral one straight and directed posteriorly. Vinculum narrow, slightly projected anteriorly and upturned. Juxta poorly developed, small, better sclerotized at posterior edge around phallus. Phallus (= aedeagus of authors, but see Kristensen, 2003) narrow, with shaft flattened dorsoventrally beyond middle, better sclerotized on left side in narrow band, slightly upturned apically; coecum penis medium-sized with pair of very small peduncles laterally; vesica with minute scobination.

Female genitalia (Fig. 5). Papillae anales large and long, moderately setose, sclerotized dorsally and laterally at base. Posterior apophyses slightly curved apically, slightly longer than papillae. Tergum VIII well sclerotized, with few long setae especially on margin, with deep rounded concavity in middle apically; middle of concavity with posteriorly directed projection variable in length and bearing two setae. Anterior apophyses straight, slightly enlarged apically, about as long as papillae. Sternum VIII with apical margin bell shaped, well sclerotized, with few long setae mostly posteriorly along margin and midventrally. Intersegmental membrane between sternites VII and VIII slightly sclerotized on each side of midventral line and with pair of short projections inside body at apical margin. Ostium bursae in middle of sternite VIII, ventrally protected by slightly protruding crescent of sclerotization. Ductus bursae short, gradually enlarging, basal half well sclerotized, distal half spiculose and with wrinkles patterned like brood cells in bee hive. Corpus bursae slightly longer than wide, spiculose, with one large, spiny, curved, and pointed cornutus; latter set in small sclerotized patch with pair of bumps on each side of its base.

DESCRIPTION OF THE LARVA AND PUPA: Larva. (Figs 7-17): Length 5.0-8.2 mm (n = 72), < 5.0 mm (n = 94). Body pale gray, textured with microconvolutions; head capsule amber; prothoracic shield amber, gradually darkening posteriorly; pinacula pale brown; anal plate pale amber; setae with widened, circular, and slightly raised

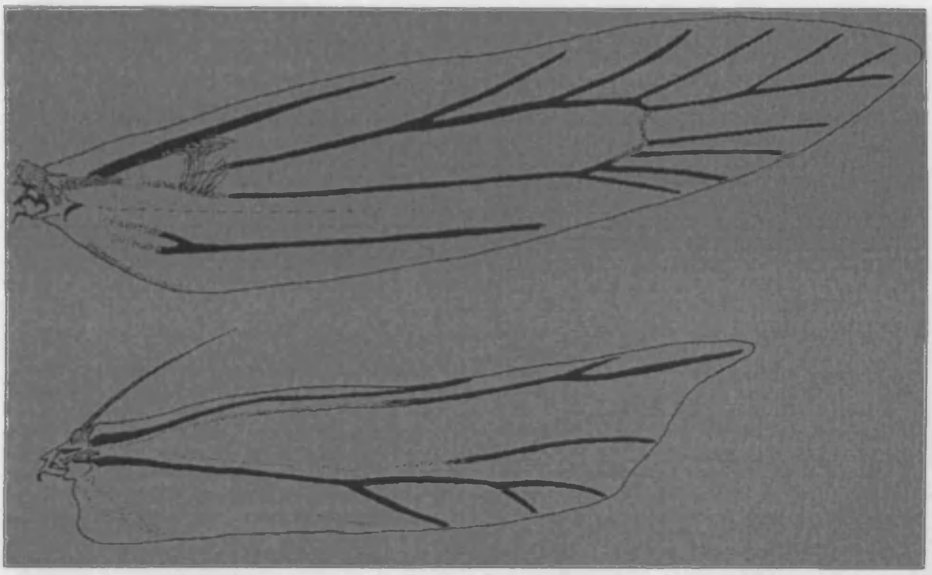
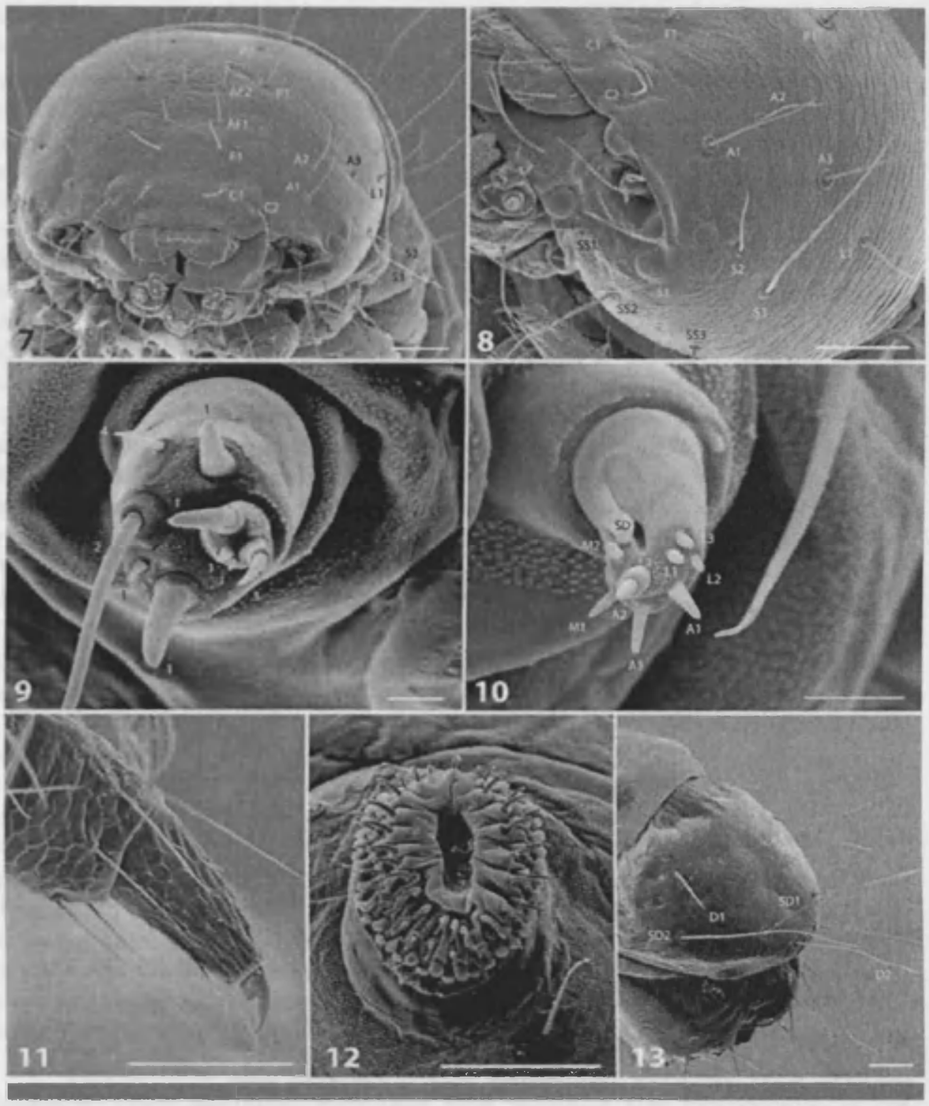


FIG. 6
Wing venation of *Taygete sphecophila.*

sockets. Head (Figs 7-10, 17): hypognathous, textured with slightly raised, confluent, polygonal ridges except on area between adfrontal sclerites (Figs 7-8); adfrontal sclerites widened distally, frontal setae about equal in length, AF2 above apex of frons, AF1 below; F1 slightly closer to AF1 than to C1; C2 at least 2 1/2 times longer than C1; clypeus with 6 pairs of setae, 3 pairs on medial half, 3 on distal half; mandible angular (Fig. 17), shallowly notched subapically forming small apical dentition, bearing pair of subequal setae on outer surface near condyle, and with 1 large dentition on inner surface; sensilla types and arrangement on antenna (Fig. 9) and on maxillary palpi (Fig. 10) similar to those of other Gelechioidea studied by Adamski & Brown (1987), Adamski (1999), Adamski & Pellmyr (2003), Landry & Adamski (2004), and Wagner *et al.* (2004), and other Lepidoptera studied by Adamski & Brown (2001), Albert (1980), Avé (1981), Grimes & Neunzig (1986a, b), and Schoonhoven & Dethier (1966). Three stemmata in genal area, 1 approximate pair above antenna, and 1 stemma below antenna; substemmatal setae about equal in length, arranged as in Fig. 8; S3 and S1 elongate and about equal in length, S2 short; S3 lateroventral to S2, S2 approximate to stemma 3, and S1 approximate to stemma 5 (stemmata 1, 2, and 6 absent); A-group setae above gena, mesal to L1; P1 dorsolateral to AF2, P2 dorsomesal to P1. Thorax (Figs 11, 14): T1 with L-group trisetose, on large pinaculum extending beneath and posterior of spiracle; setae anterior to spiracle; L1 approximate and posteroventral to L2, about 2 1/2 times lengths of L2 and L3; SV-group setae on anterior part of elongate pinaculum; SV1 about 1/3 longer than SV2; coxae nearly touching, V1s very approximate (not shown); segments of leg textured with slightly elongate ridges, many produced distally into hairlike spines, claw single (Fig. 11); shield with SD1 slightly posterior to and about 1/3 longer than XD2 and XD1; XD2, XD1, D1, and SD2 about



FIGS 7-13

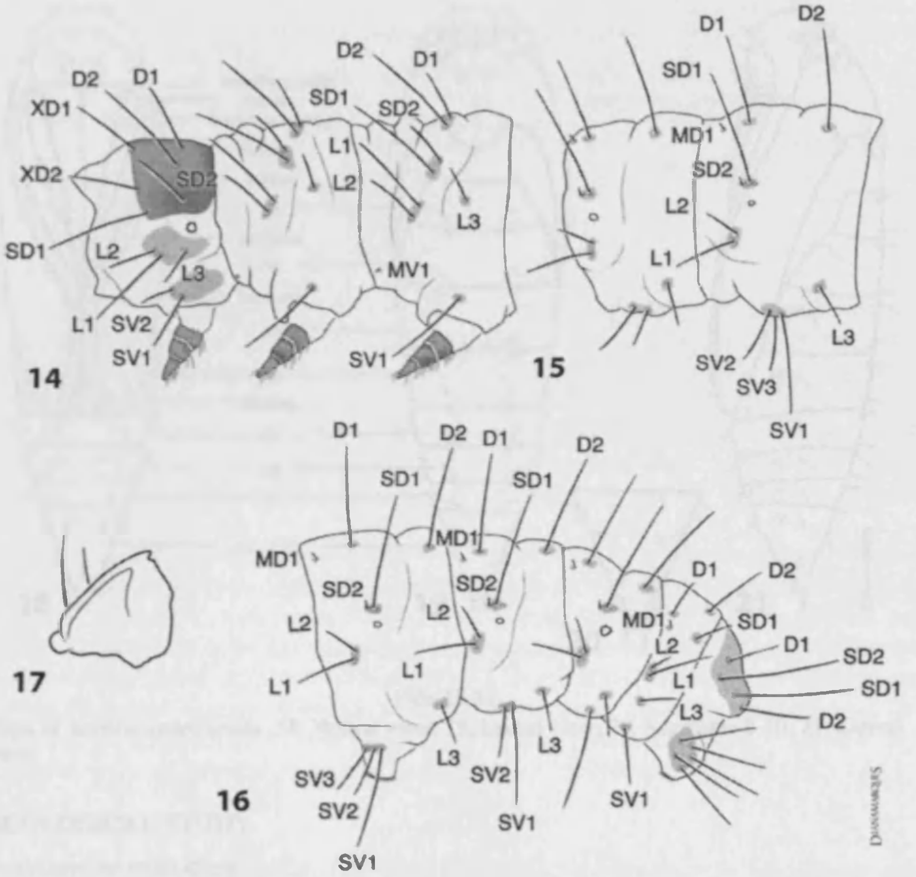
Scanning electron micrographs of larva of *Taygete sphecophila*. 7, Frontolateral view of head capsule, scale = 100 µ; 8, Ventrolateral view of head capsule, scale = 100 µ; 9, Sensilla of antenna: 1 = sensilla basiconica, 2 = sensillum chaetica, 3 = sensillum styloconicum, 4 = sensillum trichodeum, scale = 10 µ; 10, Sensilla of maxillary palpus: A2 = sensillum styloconicum, A1, A3, M1-2, L1-3 = sensilla basiconica, SD = sensillum digitiform, scale = 10 µ; 11, Distal portion of left prothoracic leg showing claw, scale = 10 µ; 12, Left proleg on A4, scale = 100 µ; 13, Anal plate of A10, scale = 100 µ.

equal in lengths, XD2 about twice distance from XD1 than from SD1; D1 in straight line with XD1, slightly posterior to SD2 and D2; D2 about same length as SD1, in straight line with SD2. T2-T3 (Fig. 14): D2 about 2 times length of D1, both on small pinaculum; SD1 about 2 times length of SD2, both on small pinaculum; L1 about 1/3 longer than L2, both on small pinaculum, L3 slightly shorter than L2, posterior to or in vertical line with SV1; MV1 on anterior margin between T2-T3, slightly above SV1 (hard to see); V1s on T2-T3 about equal distance apart, at least 4 times distance between V1s on T1. Abdomen (Figs 12, 13, 15, 16): A1-A2 (Fig. 15): D2 and D1 equal in lengths or D2 slightly longer, MD1 on anterior part of segment anteroventral to D1; SD1 above spiracle, about 1/3 longer than D2, with minute SD2 (anterior part of pinaculum); small opening on ventroposterior margin of pinaculum bearing SD1 and SD2; spiracle on A1 slightly larger than those on A2-A7; L1 2 times length of L2, both on same pinaculum, slightly anterior of spiracle; L3 about same length as L2, anterior to, in vertical line with, or posterior to D2; SV-group bisetose on A1, trisetose on A2, on same pinaculum; V1s equal distance apart (not shown). A3-A10 (Figs 12, 13, 16): A3-A6 with 4 pairs of protuberant prolegs, crochets biordinal, in circle (Fig. 12); setae as above; A7 as above except, SV-group bisetose and on same pinaculum; A8 as above except with spiracle slightly larger than on previous segments and SV-group unisetose; A9 with D2 about 2-2 1/2 times longer than D1; D1 anterior to D2 and SD1, equidistant to both setae; SD1 about same length as D1; L-group setae slightly anterior to D1; L1 about 3 times length of L2, on same pinaculum; L3 slightly longer than L2; SV1 slightly shorter than L1; V1s as previous segments; A10 (Figs 13, 16): anal plate with SD2 and SD1 equal in lengths, about twice length of D2; D1 slightly shorter than D2; crochets of proleg biordinal, in semicircle, gradually shortened mesally and laterally.

Pupa. (Figs 18-21): Length 3.6-4.6 (n = 10): amber, smooth, spiracles protuberant; all dorsal setae apically hooked except long seta associated with axillary tubercle (Figs 19-20). Sclerites of antennae annulated, widely separated anteriorly, gradually convergent from beyond basal 1/3 of sclerites of maxillae, fused for short distance beyond distal apices of sclerites of maxillae, gradually divergent posteriorly, exposing distal part of sclerites of hindlegs; sclerites of midleg not fused distally; paired nodular scars of prolegs on A5-A6 (Fig. 18); A6-A10 fused, rotating as unit; cremaster dorsolaterally flattened, trapezoidal basally, extending posterolaterally into 2 slightly divergent and elongate spine-like processes (Fig. 21).

DISTRIBUTION AND PHENOLOGY: The species was described from Trinidad (Meyrick, 1936) and never mentioned from anywhere else subsequently. In the Galapagos Islands it has been found on Floreana (from the littoral to the humid zones), San Cristobal (in the arid zone), and Santa Cruz (from the littoral to the humid zones). In the Galapagos we have collected live moths of this species in January, February, March, April, September, November, and December.

NOTES: Preliminary phylogenetic analyses, both morphological and molecular, support the placement of *Taygete sphecophila* within Autostichidae (PS, unpublished data). For example, Kaila's (2004) matrix was reanalyzed with *T. sphecophila* data, and the species clusters in Kaila's autostichid assemblage with *Galagete* Landry.



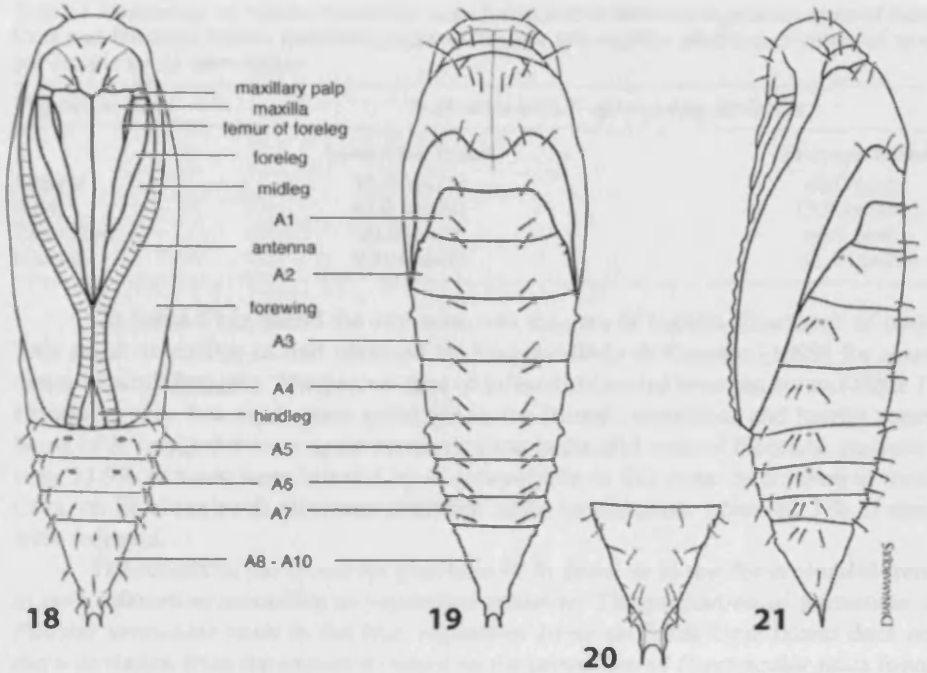
FIGS 14-17

Larva of *Taygete sphecophila*. 14, Chaetotaxy of thorax; 15, Chaetotaxy of abdominal segments 1-2; 16, Chaetotaxy of abdominal segments 6-10; 17, Mandible.

A comparison of a 1283 base pairs fragment (consisting of most of the COI gene except the first 254 base pairs) sequenced for a larva and an adult of *Taygete sphecophila* showed no substitution, which clearly indicates conspecificity.

The larva has only three stemmata, a condition that is highly unusual in Gelechioidea and that may be due to the unique host relationship.

It proved impossible to evaginate the ventro-abdominal pouch (Fig. 4) in several male specimens of this species. However, BL was able to evaginate this corematal organ from a specimen of *Taygete attributella* (Walker). The organ consists of a narrow membranous tube, almost as long as the abdomen, on which narrow scales are connected all around. The membrane of the tube is very thin and the tube collapsed as soon as specimens were transferred to lactic acid for temporary storage. An illustration of this structure for the closely related *Galagete turritella* Landry is provided by Landry (2002: Figs 17, 18).



FIGS 18-21
Pupa of *Taygete sphecophila*. 18, Ventral view; 19, Dorsal view; 20, Segments 8-10; 21, Lateral view.

ECOLOGICAL STUDY

PATTERNS OF PREDATION

Although egg-laying was never observed, it is possible that the female moths lay their eggs within the pupal cells of *P. versicolor* through numerous small holes of 1-2 mm in diameter that we observed on the back of the nests. In a sample of 25 *P. versicolor* nests, the number of *T. sphecophila* moths found per nest varied between 3 and 13. However, 42 *T. sphecophila* larvae were recovered by PS from a rather small nest collected on Santa Cruz in 2004. The food source needed for the development of the moth's larvae are the wasps' pupae which are defenseless because of their isolation in their capped cells. When ready to emerge from the wasp's cell, the moth makes a distinctive breach through the cap covering the top of the cell.

DISTRIBUTION OF INFESTED NESTS

The level of *T. sphecophila* infestation could only be assessed for nests of *P. versicolor* that were abandoned. A total of 103 such nests were found on the different study sites on Santa Cruz Island between 1999 and 2003, and 141 nests on Floreana Island in 1999. The percentages of nests that presented signs of predation by *T. sphecophila* are given in Table 1, along with the vegetation zones in which they were found.

Vegetation Zone	% of nests with *T. sphecophila* predation	
	Santa Cruz Island	Floreana Island
Littoral	35.3 (n=17)	40.0 (n=5)
Arid	43.0 (n=79)	13.9 (n=101)
Transition	20.0 (n=5)	66.7 (n=6)
Humid	100.0 (n=2)	51.7 (n=29)

On Santa Cruz island the arid zone was the area of highest abundance of nests. This result is similar to that obtained by Roque-Albelo & Causton (1999) for abundance of adult foragers. The percentages of infestation varied between zones (Table 1). However, very few nests were collected in the littoral, transition, and humid zones. Nests of *P. versicolor* were again more common in the arid zone of Floreana. However, only 13.9% of them were infested by *T. sphecophila* in this zone. In contrast to Santa Cruz, on Floreana nests also were abundant in the humid zone, where 51.7 % of them were infested.

The results of the G-test for goodness of fit allow us to test for ecological trend in nest infestation according to vegetation zonation. The proportion of parasitism in *Polistes versicolor* nests in the four vegetation zones on Santa Cruz Island does not show deviation from the expected (based on the proportion of *P. versicolor* nests found in each vegetation zone; $G = 4.806$, $df = 3$, $P > 0.05$). However, the situation on Floreana Island appears different as *P. versicolor* nests found in the arid zone are infested by *T. sphecophila* less than expected, and nests found in the transition and humid zones are infested more than expected ($G = 15.482$, $df = 3$, $P < 0.01$).

DISCUSSION

Different factors, including climatic conditions, infestation by nest scavengers and parasitoids, and predation affect the wasp colony cycle (Yamane, 1996). Across its range of distribution, from Costa Rica to Southern Argentina, *P. versicolor* seems to prefer dry forest habitats (Richards, 1978). Data from previous studies suggest that in the Galapagos the wasps are more abundant in the arid zone of the islands (Roque-Albelo & Causton, 1999; Lasso, 1997). This preference in distribution could be associated with climatic conditions (Parent, 2000). In the Galapagos the higher zones of the islands are cooler and receive more rainfall than lower zones, particularly on the southern slopes, and this factor probably affects nest development. Collection data of *T. sphecophila* suggest a similar pattern of distribution. Most moth specimens were collected in the dryer zones of the islands suggesting a close correlation with nest abundance.

On Santa Cruz Island the occurrence of *T. sphecophila* in different vegetation zones is a reflection of the frequency of *P. versicolor* nests. However, *T. sphecophila* seems to be more abundant than expected in the transition and humid zones of Floreana Island and less frequent in the arid zone. Therefore, *T. sphecophila*'s occurrence on Floreana Island is not strictly a reflection of the abundance of *P. versicolor* nests, suggesting that other ecological or climatic factors might influence its distribution. It is not clear why there is such a difference between Floreana and Santa Cruz islands, but one possible hypothesis is that *T. sphecophila* has colonized these two islands at different points in time, so that populations on one of the island have had more time to adapt to the island's ecological and climatic context.

Polistes nests, as in many other social wasps, are scavenged and parasitized by various insects including more than 11 moth species from four families (Makino, 1985). Only *Taygete sphecophila* was found in the Galapagos, where the species apparently prefers to attack large nests, and all infested nests collected were large enough to presume that they were in an advanced stage of the reproductive phase. If predation by *T. sphecophila* is restricted to this stage of the wasp colonies the probabilities for this moth species to be an effective agent of biological control are reduced. These results support the idea of Miyano (1980) that parasitic and scavenging Lepidoptera reduce notably the colony's productivity but are not thought to be a direct cause of colony failure. However, the possibility to use *T. sphecophila* as a biological control agent against *P. versicolor* needs to be evaluated.

We believe that the first individuals of *Taygete sphecophila* probably arrived within a nest of *P. versicolor* built on some human-made structure that would have traveled by boat from the continent. It is actually quite possible that both animals arrived together on the Galapagos. The wasp was first detected in 1988 on Floreana, and is thought to have arrived with a shipment of bananas (Abedrabbo, 1991), but Eduardo Vilema, resident of Santa Cruz, says that he first saw a nest of *Polistes versicolor* near Bella Vista, on Santa Cruz, in 1984 or 1985 (pers. comm. to BL in 2004). And we think it unlikely that the wasps came on banana regimes as they are not known to build their nests there.

ACKNOWLEDGEMENTS

BL would like to thank the authorities of the CDRS and Galapagos National Park Service (GNPS) for providing authorizations and logistical support for sampling micro moths in 1989, 1992, 2002, 2004, and 2005. The first two expeditions were organized by Stewart B. Peck, Carleton University, Ottawa, and benefited from financial support of the National Sciences and Engineering Council of Canada. Professor Peck, as well as Bradley J. Sinclair and several others were excellent field companions. BL is also grateful to Jean-François Landry, Agriculture & Agri-Food Canada, Ottawa, for providing lab space, equipment and technical support in 1999-2000. We are thankful to curator Kevin Tuck of the Natural History Museum, London, for his kind help to BL in London and for providing information on references regarding *T. sphecophila* and on specimens of other species. Financial support for BL's investigations in London in 2000 were provided by the Galapagos Conservation Trust, United Kingdom, and the Charles Darwin Foundation.

PS would like to thank the CDRS and GNPS for allowing field work and providing logistical support in the Galapagos in 2004 and 2005. Research funds to PS were provided by the A. Lombard Foundation, the E. & L. Schmidheiny Foundation, the Swiss Academy of Sciences, and the Department of cultural affairs of the city of Geneva.

CEP would like to thank the CDRS and GNPS for providing logistical support and required permits to conduct field work in Galapagos in 1999. Research funds to CEP were provided by CIDA, the Canadian International Development Agency.

DA thanks Diana Marques, scientific illustrator, for the illustrations (Figs 14-21) of the larva and pupa and the digital production of the plates, and Scott D. Whittaker, Manager of the Scanning Electron Microscopy Laboratory, Smithsonian Institution, Washington, DC, for the help with the preparation of the larval specimens for study.

LR thanks Henry Herrera of CDRS for his help in the field and in the lab.

Finally, we are grateful to Lauri Kaila and Klaus Sattler for reviewing the manuscript.

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