

Butterflies of the Golfo Dulce Region Costa Rica

Corcovado National Park
Piedras Blancas National Park
,Regenwald der Österreicher'

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The 'Tropical Research Station La Gamba'

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The main building of the Tropical Research Station

In 1991, Michael Schnitzler, a distinguished musician and former professor at the University of Music and Performing Arts in Vienna, founded the 'Association Rainforest of the Austrians' (*Verein Regenwald der Österreicher*). Over many years, he collected contributions in Austria and forwarded the funds to the Costa Rican government. With the money, the government purchased large tracts of forest from landowners and placed it under the control of the 'Parque Nacional Piedras Blancas', thereby preserving the Esquinas Rainforest in southwestern Costa Rica. It soon became apparent that this protected area



Scientists at work in La Gamba

also provided ideal conditions for promoting Austrian research and teaching programmes in rainforests. To make the area more accessible, the 'Association Rainforest of the Austrians' bought an old farmhouse (a *finca*) in 1993. This formed the nucleus for a tropical field station, located directly on the border of the National Park near the small village of La Gamba. With the support of the 'Association Rainforest of the Austrians', the Ministry of Science and Research and the University of Vienna, the 'Tropical Research Station La Gamba' flourished and grew. It now comprises several buildings and includes comfortable living and research facilities for more than 30 visitors as well as a botanical garden. In 2008 an airconditioned laboratory was constructed with the support of the Faculty of Life Sciences of the University of Vienna. With its infrastructure, the field station is currently on the threshold of becoming an internationally established research institution and education centre, focussing on the exploration and conservation of Neotropical rainforests. Since its foundation, many scientists have carried out field research in the Esquinas rainforest and many visitors have admired its beautiful surroundings. As well as supporting research and teaching activities, the station helps the inhabitants of La Gamba by means of a series of applied projects to improve their living conditions. These projects are partly run in

collaboration with the nearby 'Esquinas Rainforest Lodge', another brainchild of Michael Schnitzler, which represents an Austrian example of sustainable ecotourism. Indeed, the lodge was awarded some years ago the official Costa Rican 'Three-Leaf Certificate of Sustainable Tourism'. We are particularly proud that the former European Commissioner for Agriculture, Dr. Franz Fischler, has been a patron of the 'Society for the Preservation of the Tropical Station La Gamba' (*Verein zur Förderung der Tropenstation La Gamba*) since 2006. Numerous scientific publications have resulted from research performed at the Tropical Research Station La Gamba, including about 70 doctoral and diploma theses. The scientific work initially focussed on the flora and vegetation of the Esquinas forest but it has now broadened to include a wide range of other topics, such as animal-plant interactions, herpetology, ornithology, entomology (especially studies of butterflies), limnology, chemical eco-physiology, bio-geochemistry, geography and sociology. About 60 field courses and excursions have been organized, enabling students and scientists from universities all over the world to visit the Piedras Blancas National Park.

Our Society is particularly interested in providing all our visitors, and beyond that the many friends and admirers of the tropics, with information on the biology and ecology of the local and regional rainforests and of the adjacent cultural land. Following the publication of an internationally acclaimed 'Field Guide of Flowering Plants of the Golfo Dulce Rainforests' in 2001, seven colourful brochures have to date

been published: 'Amphibians and Reptiles of the Golfo Dulce Region', 'The Birds of the Golfo Dulce Region, Costa Rica', 'Das Leben hier und dort - La vida aquí y allá', 'Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica)', 'Fruits in Costa Rican Markets', 'Corbiculate Bees of the Golfo Dulce Region, Costa Rica', 'Dragonflies of the Golfo Dulce Region, Costa Rica'. Additionally, a scientific monograph 'Natural and Cultural History of the Golfo Dulce Region, Costa Rica' has been published in 2008.

We are now proud to offer a further colorful issue dealing with a group of animals - the butterflies - which on the one hand belong to the most eye-catching insect groups, and can be encountered on the other hand due to their behaviour usually more frequent by rain forest visitors as some other insect groups. We hope that this booklet - as all our former brochures and books - will be a source of information and joy to lovers of tropical life, to scholars and students, to teachers and researchers at the University and - finally - to all the friends of the 'Rainforest of the Austrians' and the 'Tropical Research Station La Gamba'.

For further information see:

www.lagamba.at

and

www.regenwald.at



The 'Comedor'



Martin Wiemers with students in the laboratory

The rainforests of the Golfo Dulce region

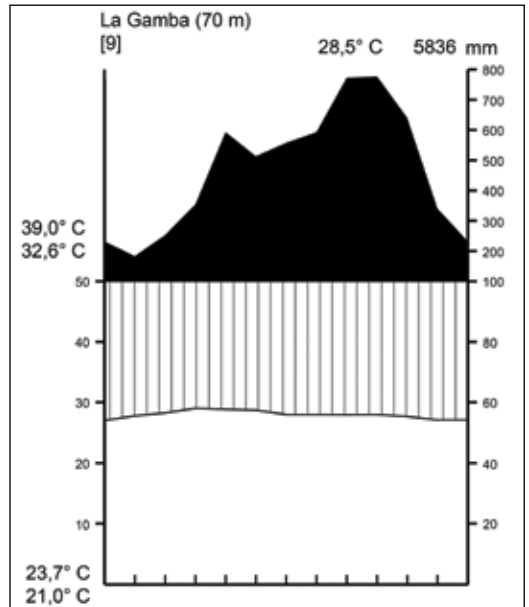
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The Golfo Dulce region is located in the southern corner of the Pacific coast of Costa Rica, near the border with Panama. Within this region are the Corcovado and Piedras Blancas national parks. The forests of the region are the only moist or wet evergreen lowland forests that still exist on the Pacific coast of Central America. The elevations range from sea level to 745 m on the Cerro Rincón, Peninsula de Osa; the annual precipitation is up to 6,000 mm with a short or almost nonexistent dry season from December until March; the relief is strongly structured at the landscape level and contains many microhabitats



Morning clouds above the forest



Climatic diagramm, La Gamba

and niches; and the soil types are diverse and the vegetation highly dynamic. All of these factors, coupled with the biogeographical position of the Golfo Dulce, have led to a very species-rich forest: about 2,700 species of higher plant have been recorded from the area.

The tallest trees in the moist and wet evergreen lowland forests grow up to 60 m high (e.g.



Waterfall on the Quebrada Chorro



The Río Bonito in the NP Piedras Blancas

Anacardium excelsum, *Parkia pendula*, *Carapa guianensis*, *Brosimum utile* and *Caryocar costaricense*). Most trees retain their foliage throughout the year. Palms (about 45 species) such as *Socratea exorrhiza*, *Iriartea deltoidea*, *Welfia regia* and *Asterogyne martiana* are typical features of the forest. *Heliconia* herbs are obvious near streams and in gaps. Lianas (e.g. *Bauhinia* and *Entada*), vines and epiphytes (Bromeliaceae, Orchidaceae) are found on many trees. About 100 species of orchid (e.g. vanilla) and 40 species of bromeliad are distributed in the region.

Hemi-epiphytic plants of the genus *Clusia* are abundant in the very wet parts of the forest while fig trees (*Ficus*) are more frequent in the drier regions (on the Corcovado plains). On the coast, the coconut palm (*Cocos nucifera*) and the “tropical almond tree” (*Terminalia catappa*) are the most conspicuous plants; in the mangroves this position is taken by red mangrove (*Rhizophora*

mangle) and mangle pinuela (*Pelliciera rhizophorae*). In addition to the various types of primary and secondary forest, the area also features other types of habitat such as pastures, pools, rivers, cultivated land and various kinds of plantation (e.g. oil palm, teak and manioc). Bees are very abundant and are found in all habitats.

Costa Rica’s geographic location on the ‘bridge’ between North and South America and the fact that the country formed a kind of refuge for tropical animals and plants during the last ice age has led to remarkable biogeographical patterns. Restricted-range plants and animals are abundant and many reach their northern limits in southern Costa Rica. The region is an excellent place for naturalists to enjoy tropical nature. An extensive system of trails in the Corcovado and Piedras Blancas national parks (La Gamba) offers wonderful insights into tropical rainforests.



Interior of the forest of the NP Piedras Blancas

Butterflies of the Golfo Dulce Region Costa Rica

Introduction

The butterflies of Costa Rica are extraordinarily diverse and rich in species. They are one of the most thoroughly studied butterfly faunas of the Neotropics. At least 1,323 species of true butterflies and skippers (Papilionoidea and Hesperioidea) have been identified in the various habitats of the country, according to the study of DeVries (1983). It is estimated that about 5% of the total number of butterfly species of the world live in Costa Rica (Wiemers & Fiedler 2008).

The preliminary checklist of the surroundings of the Tropical Research Station La Gamba accounts for a total of 216 butterfly species (202 Papilionoidea and 14 Hesperioidea, Appendix 1). The list summarizes the results of four standardized one-week-surveys which were carried out from 2006 to 2010 (mainly in February), and includes species, which were encountered outside of the time period of the studies. Additional species were added from two longer surveys carried out by Hellena Binz (December 2008 - January 2009 and November 2009 - February 2010) who also employed fruit baiting for her second study. The results of the first two surveys in 2006 and 2007 were published by Wiemers & Fiedler (2008), who list 144 butterfly species (130 Papilionoidea and 14 Hesperioidea) and estimate at least 156-204 species of Papilionoidea for the area of La Gamba within the Esquinas Rainforest. An additional 64 species (49 Papilionoidea and 15 Hesperioidea) were reported from the Corcovado National Park. Thus, a total of 280 butterfly species (251 Papilionoidea and 29 Hesperioidea) are currently known from the Golfo Dulce region of the Costa Rican province Puntarenas.

The habitats surrounding the research station can be divided into three types with varying degrees of land use: the natural forest, the secondary forest and the intensively used land systems. The natural forest consists of primary forests which are located mainly in the Piedras Blancas National Park. This habitat type contains the highest number of butterfly species. It is followed by the secondary forest habitat, which borders the protected areas of the National Park. The habitat

type characterized by intensive land use consists of pastures, oil palm plantations, roadsides, and gardens and shows the least number of butterfly species (Wiemers & Fiedler 2008). Typical for the natural forests are the nymphalid species *Philaethria dido*, *Heliconius sapho*, *H. cydno*, *Eueides lybia* and the lycaenid species, *Arumecla galliena*. In the intensively used habitats, the nymphalids *Hermemythia hermes*, *Anartia jatrophae*, *A. fatima* and the pierid butterfly *Pyrisitia nisa* are most common (Wiemers & Fiedler 2008).

Diurnal butterflies, unlike moths, are active during the daytime. They are presently classified into two superfamilies: Papilionoidea and Hesperioidea. The Papilionoidea (or true butterflies) are split into five families: Papilionidae (swallowtail butterflies), Pieridae (sulphures and whites), Nymphalidae (brush-footed butterflies), Lycaenidae (blues) and Riodinidae (metalmarks). Of these, the Nymphalidae is the group richest in species. The Hesperioidea includes only one family, Hesperidae (skippers).

This booklet includes the most frequent and most conspicuous butterflies in the examined region. A short description is given for each of the selected species along with general information about aspects of its natural history. In addition to the scientific names of the butterflies, we provide common English and Spanish names, in as much as they are available. Most species in the booklet can be seen during the whole year; however, the frequencies of the species will vary over the seasons. Typical for tropical biodiversity is that a high number of species may be present but the number of individuals is usually low. Thus, on a brief visit, one should not expect to be able to see all the butterflies mentioned in the book.

This guide book is a product of a field course in tropical biology for students of the University of Vienna (Austria) during August and September 2009 and is based on results of similar student courses of previous years. Determination of the butterfly species was based on the two volumes of 'The Butterflies of Costa Rica and their Natural History' (DeVries 1987, 1997) and the recent field guide 'Mariposas de Costa Rica - Butterflies and moths of Costa Rica (Chacón

& Montero 2007). The nomenclature, systematic classification and order in the book follow Lamas (2004) and the preliminary checklist of the Papilionoidea and Hesperioidea of the Tropical Research Station La Gamba (Wiemers & Fiedler 2008). English common names were taken from the internet site: www.neotropicalbutterflies.com. For comprehensive information on the biology of butterflies, see DeVries (1987, 1997) and Janzen (1983). Aspects of climate, habitats and biodiversity are well summarized in 'Natural and cultural history of the Golfo Dulce Region, Costa Rica' (Weissenhofer et al. 2008).

The best time to observe butterflies is from morning to noon. In these hours, most butterflies are active and searching for food or mates. The best opportunity to closely observe and photograph these beautiful insects is while they are occupied with feeding. Most butterfly species can be found on or near flowering plants. Some are attracted to rotting fruits and others take up fluid from wet ground. The photographs and the text in this guidebook should be helpful in identifying some of the most frequent species and in becoming more acquainted with their natural history.

Life cycle of butterflies

The life cycle of a butterfly can be divided into four stages: egg, larva (caterpillar), pupa (chrysalis) and adult (imago).

Adult females lay individual eggs or clusters of eggs on surfaces of leaves, flower buds or stems of the host plants. The eggs undergo embryonic development until they hatch from the chorion shell, after which begins the larval stage.

The larvae of butterflies are known as *caterpillars*. Most are voracious herbivores and make good use of their biting-chewing mouthparts. They generally feed on more or less closely related host plants or exceptionally on a single plant species. Some are able to feed from a relatively wide variety of plant species. Caterpillars increase their size over one hundredfold. In the process, they molt four to seven times. The phases between successive molts are called *instars*. Many caterpillars assume different shapes and appearances from instar to instar. Not all instars are easy to find in nature.

During the pupal stage, larval tissues are broken down, and the new organs of the adult become differentiated (i.e., metamorphosis). Fi-



Eggs of *Heliconius melpomene*



Larva of *Heliconius melpomene*



Pupa of *Heliconius melpomene*



Imago of *Heliconius melpomene*

nal adjustments for adult life are made while the butterfly is still emerging from the pupal encasing. The wings unfold, and the adult feeding organ or *proboscis* becomes fully assembled.

As adult insects, butterflies take flight, consume liquid nutrients and reproduce. Many butterflies display special courtship behavior. After mating, the females search for host plants on which to lay their eggs.

Morphology of adult butterflies

Like all insects, the body of a butterfly is composed of three main parts: head, thorax and abdomen. The *head* contains the brain, the major sensory organs, mouthparts (*proboscis*) and the suction pump of the frontal alimentary tract. The proboscis is a long coil that can be extended to suck on fluids such as nectar, the juice of rotting organic matter or water. The large spherical compound eyes form the visual organs. The two elongate and club-tipped antennae on the head serve primarily tactile and olfactory functions. They are used to locate food and mates, as well as the appropriate site on the host plant to lay eggs. In addition, antennal movements help the butterfly keep its balance when flying. The *thorax* bears the locomotory organs, i.e., three pairs of legs and two pairs of wings. The fore and hind-

wings fold vertically over the body when the butterfly is at rest. The wings vary in color, size and form in the different groups and species. They are exceedingly thin structures, yet with an immensely large surface area in comparison to the actual body. Inside the wings is a network of supporting veins. The hind part of the body, the *abdomen*, contains the major organs for digestion, excretion and reproduction. The morphology of the male sex organs is complex. The genitalia are thus not only useful in taxonomic studies but often they provide the distinguishing traits, which unambiguously identify the species.

Wing pattern and defense mechanisms

Butterflies are among the most popular insects, mainly because of their beautifully colored wing patterns. The wing surfaces are coated with minute cuticle scales, each capable of a single color. Some scales reflect light and appear silvery. When iridescent hues are present, it is because the scales produce a particular blue or green color by physical diffraction of light. Not all patterns are visible to human eyes since we are unable to see UV-reflected or polarized light, which many butterflies can. The wing pattern may serve multiple biological functions. In many species, the underside of the wings is dark and cryptically colored so that the butterfly is hardly

detectable when sitting still with its wings closed. The upperside of the wings is often colorful and functions as a signal enabling the butterflies to recognize members of their own species as either sexual partners or co-rivals. The wings of some butterflies display eyespot patterns, and others sport a short process (tail) on the hindwing. It is postulated that eyespots and tails steer the attention of an attacking bird away from the delicate body to the wing margins thereby better enabling a butterfly to escape. In many cases, particularly colorful wing patterns are aposematic and warn potential predators of the toxicity or distasteful properties of the butterfly.

A great number of butterflies defend themselves with chemical compounds, which they acquire as larvae when feeding on toxic host plants and which they transfer via the pupae to the adults. Toxic or unpalatable butterflies often have conspicuous patterns on the wings. A bird which has eaten a poisonous butterfly may be forced to vomit it out. If it can remember the color pattern, it may avoid eating similar looking butterflies. The success of such chemical defenses has led many species to resemble closely each other in behavior and wing color pattern. In other words, they imitate each other. Two types of mimicry are distinguished.

In Batesian mimicry, a non-toxic edible butterfly looks like a toxic or distasteful species. The non-toxic species profits because an experienced predator will associate the conspicuous color pattern with the distastefulness of the toxic butterfly. However, if non-toxic mimics are too common, predators will not make the association. Thus for Batesian mimicry to be maintained, it is important that non-toxic mimics are present in lower frequency in the habitat than toxic model species.

In the second type, Müllerian mimicry, all involved butterflies are more or less distasteful and have evolved a similar color pattern of the wings. They profit from the mimetic resemblance since a predator will learn faster when the warning color pattern is more frequent. This type of mimicry is much more common, and it is considered to be a more stable evolutionary strategy.



Mimicry ring with *Mechanitis lysimnia* (top), *Heliconius hecale* (bottom, left) and *Lycorea halia* (bottom, right)



Mimicry ring with *Dismorphia theucharila* (Pieridae) (top), *Greta oto* (Nymphalidae) (bottom, left) and *Phanoptis vitrina* (Notodontidae) (bottom, right)





Rainforest gap in the Piedras Blancas National Park. In natural rainforests, gaps are regularly produced by fallen trees. Many butterfly species such as those of the Swallowtail genus *Parides* are most easily observed in light gaps.



Papilio larva with everted osmaterium



Mud puddling swallowtail (*Heraclides thoas*)



Papilionidae

Swallowtail Butterflies

The Papilionidae include many large and impressive butterflies. Some, but not all, have typical short tails on their hindwings that lend the entire group the name *swallowtails*. One feature, which uniquely characterizes all caterpillars of Papilionidae, is the osmaterium, a stink-producing organ that delivers an odious smell when it is extruded, and probably serves as a defense mechanism against predators. The host plants of the Costa Rican swallowtail caterpillars belong to the plant families Aristolochiaceae, Annonaceae, Rutaceae, Piperaceae and Umbelliferae. Swallowtails are conspicuous insects and can be seen in all habitats of Costa Rica. They are fast fliers and quite active in the sunshine. In many species, the males and females hardly resemble each other in appearance. In such cases, their wing patterns are described as being sexually *dimorphic*. Normally, both sexes visit flowers to feed on nectar, but males are often encountered on moist sand or around puddles. They use their proboscis to suck up mineral substances from the water to supplement their diets. This behavior is called 'mud puddling'.

Parides crithalion (Variable Cattleheart)

Forewing length: 38 - 43 mm

The sexes of this butterfly are conspicuously dimorphic. The males have a green band of variable size on the forewing and they are distinguished by having very reduced white spots on the forewing. Both sexes have large red areas on the hindwings. The species is restricted to rainforest. Both sexes visit flowers in the morning and remain active until late afternoon. Like many other *Parides* species, these butterflies flutter and move their forewings while feeding nectar on flowers, yet at the same time, they keep their hindwings open and motionless. The flower visiting butterflies of this genus are thus very conspicuous, even from a great distance. Females lay their eggs during midday on host plants of the genus *Aristolochia* that may grow along forest edges and in light openings of the forest.

Three other species of *Parides* can be found in the Piedras Blancas National Park. One of the most common ones is *Parides iphidamas*, which is tolerant of disturbed habitats. The males of these species can be distinguished from each other mainly by the shape of the green band. However, the females are extremely similar to each other and often cannot be reliably identified.



Parides larva on *Aristolochia*



Parides erithalion male



Parides erithalion female

Heraclides thoas (Thoas Swallowtail)

Forewing length: 57 - 61 mm

Heraclides thoas is a large and conspicuous swallowtail. The hindwing tail is rather long. The black wings are marked with oblong yellow spots. *Heraclides thoas* appears very similar to its sibling species, *Heraclides cresphontes*, and can be distinguished from it by a notch in the genital region of the male and the yellow spot on his tail. Swallowtails are very fast fliers, which help them avoid predation by birds. Both species of *Heraclides* are regularly seen in moist and wet forests, such as forest edges, clearings or along streams where sunlight penetrates the forest canopy. They are frequently encountered in gardens and parks to which these marvelous butterflies are attracted. There they find flowers rich in nectar, such as *Stachytarpheta* and *Lantana*. The mineral substances, which the males take up from wet sand or muddy roads, are necessary for production of the spermatophore, which is transferred to the female genital tract during copulation. The eggs are laid singly on pepper trees (*Piper* sp.). The caterpillars resemble bird droppings, which

represents a very effective camouflage and discourages birds from eating them. If a caterpillar is disturbed, the stink organ (*osmaterium*) is turned inside out and projects like a fork shaped orange antenna. It exudes a nasty smell, which is presumed to act as a repellent against predatory birds.



Heraclides thoas caterpillars on *Piper* leaf



Heraclides thoas



Pasture near the research station. Open habitats such as pastures are the preferred habitat for many Sulphures and Whites. Some species of the genera *Phoebis* and *Pyrisitia* can reach high abundances at those places.



Pieridae

Sulphures and Whites

Pieridae are small to medium-sized butterflies usually with white, yellow or orange wings. Many species present a simple pattern consisting of few small black or brown dots, lines or dark wing margins on the otherwise uniformly colored wing. In addition, the wing pattern of many species reflects UV-light, which is invisible to human eyes, but important for conspecific butterflies in courtship display. All species of Pieridae are flower visitors. They can be observed readily when they are nectar feeding. In many species, the color pattern on the underside of the wings is cryptic. When they close their wings, they remarkably resemble a leaf.

Most important host plants for the larvae are species of Mimosaceae, Fabaceae, Caesalpiniaceae, Brassicaceae, Capparidaceae and Loranthaceae. Many of these plants contain chemical toxins, which have been shown to be important cues for egg laying and feeding stimulus. The caterpillars are smooth; many are green or brown and very inconspicuous when on a plant. For pupation, the caterpillars spin a silk girdle that attaches the pupa at a 45° angle to a twig or other part of a plant. The pupae are cryptic, some look like young leaves, buds or even bird droppings.

Pyrisitia nise (= *Eurema nise*) (Mimosa Yellow)

Forewing length: 16 - 19 mm

Pyrisitia nise is a small butterfly; the wings are yellowish; black markings are present along the front margin of the forewing, which is arched from the costa to the tornus. The underside of the wings is dull yellow and lacks the black markings along the margin. The butterflies fly low to the ground and visit a variety of flowers to feed on nectar. This is one of the most common butterflies in disturbed habitats near the station. Although they are small, they are known as fast fliers and are not easily caught by predators. The larvae feed on leaves of the Sensitive Plant (*Mimosa pudica*).

Similar and related species from the genus *Pyrisitia* inhabit open areas and are especially common where human activity has created pasture and farmland. All species of this genus are easily recognized due to their small size and the yellow, orange or white wing coloring with a black margin. The males often are brighter and

may aggregate on wet ground to take up mineral substances.



Pyrisitia nise

Phoebis sennae (Cloudless Sulphur)

Forewing length: 29 - 36 mm

Phoebis sennae is a medium-sized butterfly with yellow wings. Those of the male are clear yellow with lighter yellow distal margins. Those of the females are usually lighter yellow with a black wing margin. On the underside of the wings are brown dots and spots. The butterflies fly rapidly in the sunlight and are regularly seen along roads, in gardens, pastures, and open fields. They have a long proboscis and can gain

access to the nectar in long tubular flowers, such as *Stachytarpheta*. *Phoebis sennae*, like all species of the genus *Phoebis*, is a migratory butterfly. They regularly travel long distances to colonize new habitats.

The larvae of *Phoebis sennae* are green and astoundingly cryptic. Their host plants belong to the family Caesalpiniaceae. When not feeding, the caterpillars often rest beneath leaf petioles.



Phoebis sennae male



Phoebis caterpillar

Dismorphia theucharila (Clearwing-Mimic White)

Forewing length: 25 - 27 mm

This butterfly species is encountered in wet natural forests where it flies in low densities. *Dismorphia theucharila* is the only pierid butterfly in Costa Rica that has partly transparent wings. The species is difficult to separate from some nymphalid butterflies because of the close resemblance in wing coloration and flight behavior. The resemblance is an amazing example of Batesian mimicry, which includes toxic model

species and edible mimicking butterflies. *Dismorphia theucharila* is palatable to bird predators, in contrast to the distasteful and/or toxic model species of nymphalid butterflies, such as *Mechanitis polymnia* (mentioned below). Nonetheless, *Dismorphia theucharila*, like all Pieridae, can be distinguished from the nymphalids because it stands and walks on six legs, while the nymphalids use only four legs.



Dismorphia theucharila



Rainforest creek near La Gamba. Creeks and rivers often produce gaps in the rainforest which are used for patrolling male butterflies, e.g. the Longwings of the genus *Heliconius*, in search of food or females.



Nymphalidae

Brush Footed Butterflies

Nymphalidae contain a large number of species exhibiting amazing life history traits. The family includes species of different sizes from small to very large. The shape, coloration and pattern of the wings are highly diverse. Likewise, the feeding preferences of the adults vary greatly. Some representatives of this group feed on floral nectar, others suck on rotting fruits or tree sap. In several species, the adults have never been observed feeding on flowers or other plant sources, rather only on fresh dung, urine or decaying carrion.

Despite the great diversity of life histories and the unresolved phylogeny of these butterflies, all adult Nymphalidae can be recognized by the fact that they stand and walk on four legs only. The greatly reduced forelegs bear sensory organs, which probably detect larval host plants. The caterpillars, too, show a great variety of sizes, shapes and feeding preferences. Most pupae hang with their head down, anchored with special hooks to a silk web, which was spun by the caterpillar.

Subfamily Danainae

Lycorea halia (= *cleobaea*) (Tiger Mimic-Queen)

Forewing length: 44 - 51 mm

Lycorea halia is a medium-sized butterfly with an orange to brown wing coloration and white dots along the black wing margins. The color pattern is named 'tiger-stripe'. It is a conspicuous warning coloration (aposematic) and strongly resembles that in several distasteful and/or toxic Neotropical butterflies. All these co-mimic species take advantage of imitating each other since predatory birds learn to avoid unpalatable species more rapidly if butterflies displaying the same warning coloration occur in greater number in a given habitat.

In comparison to other tiger-stripe butterflies, *Lycorea halia* can be identified by the rather short yellow antennae. The butterflies are found in the forest and open areas where they feed on nectar from a variety of flowers or where males wait for females. The males perch in the morning under the subcanopy and chase away conspecific males. Occasionally, they extrude the hair pencils on the abdomen and send out pheromones to attract females.

The preferred host plants of the larvae belong to *Papaya* and *Asclepias*, both of which contain milksap. The larvae cut a ring into the leaf tissue or veins and wait for about an hour before feeding. The behavior presumably prevents mobilization of defensive plant compounds. Later instars are white with black rings and have a

pair of movable filaments behind the head. The caterpillars are probably distasteful to birds due to the toxicity of the host plants. The larvae store the secondary chemical compounds and transfer them to the adults via the pupal stage. The substances are used by the adult butterflies as a means of chemical defense. Together with toxic pyrrolizidine alkaloids, which the butterflies gather from other plants, the substances are essential precursors for the production of the male sex pheromone.



Pupa of *Lycorea halia*



Lycorea halia (right) and co-mimic *Heliconius hecale* (left)

Lycorea halia larva

Danaus plexippus (Monarch)

Forewing length: 41 - 48 mm

The Monarch butterfly has a large global distribution and is most famous for its extraordinary migrations across North America. The butterflies of the last generation of the summer will travel up to 3,600 km south to their overwintering sites. The populations in eastern North America migrate to the Central Mexican highlands. There millions of individuals congregate among the conifer trees. However in Costa Rica, the species is found all year round in small numbers, usually in open areas. The caterpillars feed on poisonous milkweeds (*Asclepias* sp.). They are able to sequester cardiac glycosides from their food plant, which renders them unpalatable for most predators. This protection extends into the adult

stage, and the conspicuous orange color pattern signals to potential predators that the butterflies are unsuitable as food.



Danaus plexippus larva on *Asclepias*



Danaus plexippus

Subfamily Ithomiinae

Mechanitis polymnia (Polymnia Tigerwing)

Forewing length: 34 - 38 mm

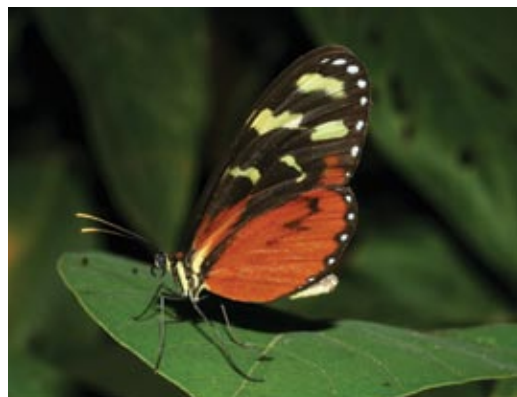
Mechanitis polymnia has wings that are largely orange with black stripes and white dots. It is another abundant member of the tiger-stripe mimicry complex, which includes several unrelated distasteful and toxic butterflies. *Mechanitis polymnia* can be distinguished by the rather small eyes and the round orange spot on the upperside of the forewing margin. It is very common and widespread in Costa Rica. It flies in sunny open areas where it feeds on the flowers. Males settle in the shade of the forest and wait for females. The males are known to use their proboscis to acquire precursor substances to produce their sex pheromones (pyrrolizidine alkaloids) from the wilted leaves of particular species of Boraginaceae and Asteraceae. The females are attracted by the male sex pheromone. During copulation, the poisonous alkaloids are transferred via the

spermatophore of the male to the female. In addition to floral nectar, female butterflies have been recorded to feed from bird droppings, presumably as a source of nitrogen. The butterfly has received the name 'ant butterfly' because of its habit of following birds, which hunt insects trying to escape the procession of army ants.

The larvae feed on the poisonous plant genus *Solanum*, and they possess a chemical similarity between their cuticular lipids and those of the host plant which protects them from predatory ants.



Mechanitis polymnia larva



Mechanitis polymnia

Aeria eurimedia

(Black-and-Yellow Prestonian or Eurimedia Clearwing)

Forewing length: 22 - 25 mm

The wing pattern of this species is black and yellow. A red stripe is evident behind the head. This small butterfly is commonly encountered as a solitary individual flying in deeply shaded forests close to the ground, usually near watercourses. In primary forests, both sexes visit flowers, such as *Psychotria* and *Cephalis*, during the morning. The larvae feed on *Prestonia portabellensis*. First, they cut veins in older leaves to stop the flow of toxic milksap. After briefly waiting, they are able to feed on the leaves without becoming poisoned.



Aeria eurimedia

Hyposcada virginiana (Virginia's Ticlear)

Forewing length: 32 - 35 mm

Hyposcada virginiana is widespread in Costa Rica and one of the more common Ithomiines in the rainforests around the station. It also inhabits secondary forests. It usually flies in the deep shade. The females lay their large white eggs on woody, hemiepiphytic species of *Drymonia*, which belong to the Gesneriaceae, a plant family that is not used by other butterflies in Costa Rica. The caterpillars cut round holes into the interior of the leaf blades, a behavior which is also found in other Ithomiines, whereas most caterpillars feed at leaf margins. Several butterflies from other subfamilies are very similar in wing pattern and form a mimicry ring. Among them are *Heliconius hecale*

(Heliconiinae) and *Eresia ithomioides* (Nymphalinae) in its color form *melaina*. *Hyposcada virginiana* can be distinguished by the rounded shape of the outer forewing.



Hyposcada virginiana

Ithomia celemia (Celemia Clearwing)

Forewing length: 30 - 33 mm

Ithomia celemia belongs to the tiger-stripe mimicry complex and is most similar to *Hypothyris eulea*, a common Ithomiine, as well as to the light color morph of *Eresia ithomioides* (Nymphalinae). Its range extends from Costa Rica southwards to Venezuela. In Costa Rica, it rarely appears outside the Golfo Dulce Region, and is only found in rainforests on the Pacific side. The larval food plant is *Witheringia riparia*, a member of the family Solanaceae, which is the major host plant family for species of the subfamily Ithomiinae.



Ithomia celemia

Subfamily Charaxinae

Consul fabius (Tiger Leafwing)

Forewing length: 36 - 40 mm

Consul fabius is a member of the subfamily Charaxinae, which is most diverse in the Afro-tropical Region. At rest, this butterfly looks like a dead leaf. The upperside, however, is not cryptic but bright orange and resembles members of the tiger-stripe complex, such as *Mechanitis polymnia* from the subfamily Ithomiinae. It is probably one of the best examples of Batesian mimics in Costa Rica. The butterflies also imitate the slow flight of their models, but when alarmed, they can fly very fast, like other members of the subfamily. The butterflies do not visit flowers but are attracted to rotten fruits. They are often observed along forest trails where the males perch in the subcanopy. The females lay their eggs on numerous species of *Piper*, the larval host plant. The mature caterpillars hide inside rolled tubes at the end of the leaves.



Consul fabius

Fountainea eurypyle (Pointed Leafwing)

Forewing length: 28 - 34 mm

Fountainea eurypyle belongs to a large group of similar-looking species, which have previously been placed in the genus *Memphis*. All of them have a cryptic underside resembling dead leaves, and are therefore difficult to spot when resting in the trees. The upperside, however, is more colorful, ranging from orange brown (as in *Fountainea eurypyle*) to an iridescent blue or green. Like other Charaxinae, adult butterflies do not visit flowers, but are attracted to fruits. Most species occur in primary and secondary rainforests. *Fountainea eurypyle* is one of the more common species, which has been observed in the garden of the station. Its caterpillars feed on leaves of *Croton* (Euphorbiaceae).



Fountainea eurypyle

Subfamily Satyrinae

Morpho helenor (= *peleides*) (Peleides or Helenor Morpho)

Spanish name: Celeste común, morfo

Forewing length: 64 - 78 mm

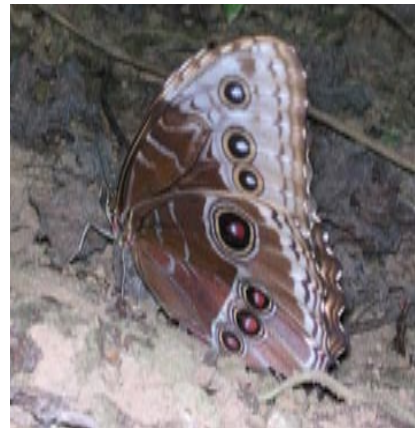
This *Morpho* butterfly is one of the most famous in the rainforest. It seems to be depicted in nearly every book about the natural wildlife of Costa Rica. It has iridescent blue wings and flies with a low frequency of wing beat. The large wings of the males have a clear shiny blue hue and black margins. In females, the blue is reduced and the black margin is broader. *Morpho helenor* is regularly seen along forest trails and woodland streams, but also in plantations. The butterflies are very popular in butterfly gardens and nurseries since they can be easily bred in captivity.



Morpho helenor, male



Morpho helenor, female



Morpho helenor

Although the appearance of the butterfly is very conspicuous, their fast and erratic flight makes them difficult to catch, even for birds. This behavior is an appropriate strategy, since *Morpho* butterflies do not store toxins in their body as many other butterflies.

Morpho helenor is peculiar since it does not visit flowers. Instead, the butterflies feed on rotting fruits, such as bananas and fruit peels. Also, they drink tree sap, which flows from cuts in the bark. Their proboscis is relatively short and has long sensory structures near the tip. The shape of these structures is important for sucking liquids from moist surfaces, since they serve to acquire

liquids by adhesion at the tip of the proboscis. When feeding, they always close their wings and show their cryptic underside. A row of eyespots along the wing margins probably serve to distract potential predators.



Morpho helenor larva

Morpho menelaus (= *amathonte*) (Menelaus Morpho)

Forewing length: 73 - 87 mm

The sexes of this large butterfly are very distinct from each other in appearance. The males have an iridescent light blue on the upperside of the wings, while the females have wide brown margins and two rows of white spots. The underside of the wings in both sexes is washed reddish brown, and the eyespots are reduced. The bright blue of the upperside of the wings in the males is the result of light diffracting from the wing scales. Diffraction colors are produced by a series of parallel grooves or ridges on the scales. The grooves are separated from each other by the distance of the particular wavelength of light. Light reflecting from such parallel structures interferes with the reflectance from neighboring parallel structures.

Thus, at particular angles, the light of a given wavelength will be either reinforced or cancelled out. Flying male *Morpho* butterflies are easily identified by the blue reflection of their wings, even when they fly through the dark forest with their typical low frequency of wing beat. The underside of the wings is cryptic, and when the butterfly rests, it closes its wings over the bark of a tree and becomes nearly undetectable.



Morpho menelaus with wing damage

This butterfly is regularly found in rainforest habitats. The males actively patrol along forest edges and rivers during the early morning soon after sunrise. By late morning, they become less active and feed on fleshy fruits, as do the females. At midday, the females search for oviposition sites. Just before dusk, both sexes slowly flutter along the forest ridge tops and settle on the undersurfaces of leaves to sleep for the night.

Caligo eurilochus (Owl Butterfly or Forest Giant Owl)

Spanish name: Buhito pardo

Forewing length: 77 - 91 mm

The *Caligo* species are among the largest butterflies in Costa Rica. Their wingspan can reach up to 18 cm. The dark wings of the males show a dull iridescent blue. The underside of the hindwing is cryptic and has a large eyespot, which resembles a large pupil with a light-colored iris. Probably, it distracts predators for a moment. When a predator attacks, the conspicuous eyespot is often the target, and the butterfly can escape. Due to its large wings, the butterfly is still capable of flight, even if large parts of the wings are missing. *Caligo* butterflies are most active at dusk and dawn. In the daytime, they rest with closed wings on tree bark. Adults feed exclusively on rotting fruits, tree sap and mammal droppings.

The caterpillars are considered a pest in banana plantations. Late instars can measure about 10 cm in length. Astoundingly, a single caterpillar

can consume an entire banana leaf in a few days. The natural host plants of the larvae in Central America are species of the plant genus *Heliconia*.



Caligo eurilochus caterpillars on a banana leaf

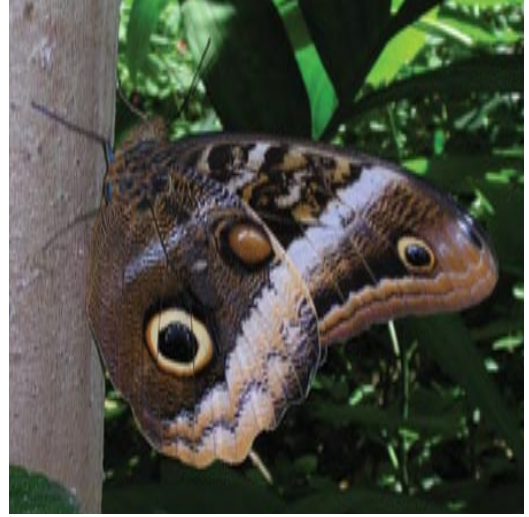


Caligo eurilochus

Caligo atreus (Yellow-Edged Giant-Owl or Arteus Owl)

Forewing length: 73 - 85 mm

Caligo atreus is an inhabitant of the Costa Rican rainforests; the larvae feed on plants from genus *Heliconia*, *Musa* and different genera of the family Cyclanthaceae. Its wings are gray to brown with large eyespots on the underside of the hindwings (similar to that of *C. eurilochus*, mentioned above) and small eyespots on the forewings. The butterfly can be easily identified. When it is startled, it reveals a conspicuous dull blue shimmer on the upperside of the forewing that contrasts to the yellow stripe of the hindwing. When in flight, the huge size, low frequency of wing beat and blue and yellow coloration on the upperside of the wings are revealing of the species. However, the butterfly is difficult to notice when resting on a tree trunk with closed wings because of the cryptic coloration on the underside of the wings.



Caligo atreus

Catoblepia orgetorix (Orange-rimmed Owl-Butterfly)

Forewing length: 48 - 55 mm

Apart from the Giant Owl-Butterflies of the genus *Caligo*, several smaller Owl-Butterflies occur in Central America, most of which belong to the genera *Eryphanis*, *Opsiphanes* and *Catoblepia*. All are butterflies of the forest understory and are rarely observed due to their crepuscular behavior. In contrast to their camouflage wing pattern on the underside, the upperside is often bright

orange or marked with iridescent blue. *Catoblepia orgetorix* is a species which can be found in the Piedras Blancas National Park. The upperside of the wing is dark brown with an orange marginal band. The underside bears prominent eye spots and a pinkish hue. The butterflies feed on fallen fruits, the caterpillars feed on the leaves of various species of palms (family Arecaceae).



Catoblepia orgetorix

Hermeuptychia hermes (= *Cissia hermes*) (Hermes Satyr)

Forewing length: 16 - 20 mm

Hermeuptychia hermes is one of the most common butterflies in the garden of the station and along the roads of La Gamba. The butterfly is small, and the wings have a grayish hue on both sides. On the hindwings are several small eyespots, three of which are darker. On the forewings are three small spots, as well. The butterflies feed on fruits and dung; occasionally they are seen on flowers drinking nectar.

Hermeuptychia hermes can be distinguished from similar looking species of the genus and

related genera *Cissia* and *Magneuptychia*, by its smaller size, number and arrangement of the eyespots. Most of the other species are only found singly along forest tracts. More common is *Magneuptychia libye*, a large species with a forewing length of 22-23 mm, which occurs in secondary forests around the station.

The caterpillars of most species are nocturnal and feed on various grasses from the family Poaceae.



Hermeuptychia hermes



Magneuptychia libye



Hermeuptychia hermes

Pareuptychia ocirrhoe
(= *Cissia hesione*) (White Satyr)

Forewing length: 18 - 21 mm

Unlike most related satyrines, this Central American species has a pearly white upperside and a striped underside. It is often encountered in secondary bush and along waysides near the station. The females lay their eggs on grasses of the genus *Eleusine* at the base of trees.



Pareuptychia ocirrhoe

Pierella luna
(Quiet Diaph or Moon Pierella)

Forewing length: 33 - 39 mm

Pierella luna has a dark brown color on the upperside of the wings. The hindwings are conspicuously large and have two black dots on the front margin. One spot has a white dot in the center that resembles an eyespot. The underside of the wings is lighter.

The butterfly is characteristic of primary forest habitats. It is often encountered on forest trails flying low to the ground. Because of its dark coloration, it is difficult to see in the low light of a rainforest. Especially when it sits on the ground with closed wings, the butterfly seems to vanish before our eyes. With some patience, male territorial behavior can be observed in this species.



Pierella luna

The males defend the boundaries of their territory against rival males by chasing them away. Remarkably, the butterflies have never been observed to visit flowers. Instead, they feed almost entirely on matter exuded by fungi.

Cithaerias pireta (= *menander*)
(Pink-Tipped Satyr)

Forewing length 30 - 33 mm

Cithaerias pireta occurs in wet rain forest habitats. It flies close to the forest floor in deeply shady areas. The wings of this medium-sized butterfly are transparent. The hindwings are characterized by a reddish hue and an eyespot. Male butterflies have been observed over a period of several weeks to visit consistently the same perching site in light openings of the rain forest.



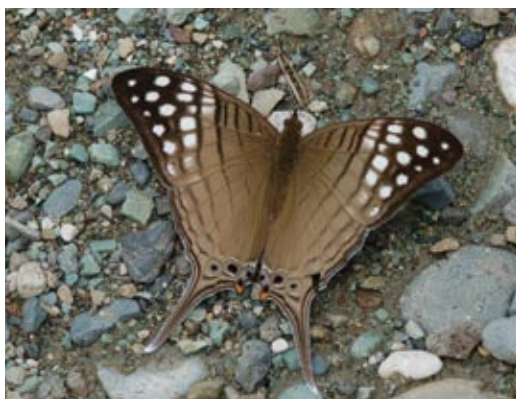
Cithaerias pireta

Subfamily Cyrestinae

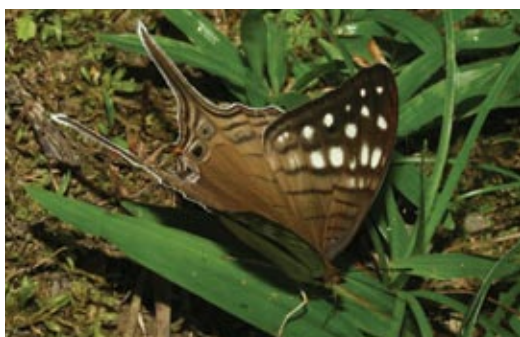
Marpesia merops (Merops Daggerwing)

Forewing length: 29 - 33 mm

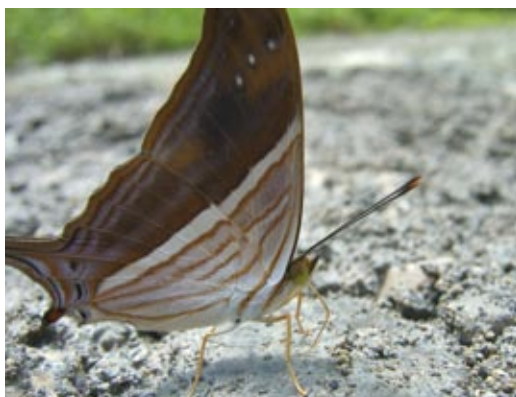
The butterfly is regularly encountered on unpaved roads near the station, usually with its proboscis in the wet sand (sucking in mineral substances). The brown-gray wing coloration of *Marpesia merops* blends in very well with ground textures. The butterfly is nearly impossible to see from a distance. It resembles a brown swallowtail because of the long tail on each hind wing. Near the tip, on the upperside of the forewing are several small white spots. The underside of the wings is grayish white with brown streaks. *Marpesia chiron* is similar but bears a conspicuous red mark near the tornus of the hindwing. More different is *Marpesia petreus* which has a bright orange upperside coloration. *Marpesia* species have never been seen on flowers.



Marpesia merops



Marpesia merops



Marpesia chiron



Marpesia petreus

Subfamily Biblidinae

Dynamine tithia (= *salpensa*) (Tithian Sailor)

Forewing length: 16 - 18 mm

The genus *Dynamine* encompasses several small-sized butterflies, which have a similar orange-banded pattern on their undersides, sometimes with silver spots. Among them, *Dynamine tithia* is characterized by its reflective blue upper-side. In Costa Rica, this species is only found in the southernmost part. It is most easily encountered at mud puddles along river banks. The females lay their eggs on the buds of *Dalechampia triphyllia* (Euphorbiaceae), and the caterpillars feed on the flower parts or bore into the developing ovary.



Dynamine tithia

Hamadryas feronia and *Hamadryas arinome* (Cracker Butterflies)

Forewing length: 35 - 38 mm

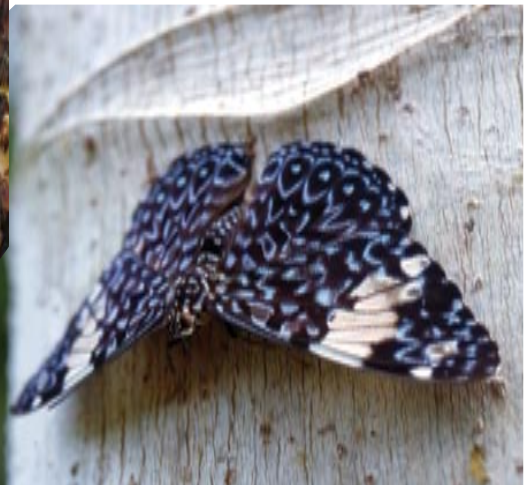
Hamadryas species of the *feronia*-group are famous for the crackling noises that individuals produce in interaction with other individuals. The interactions are mostly male-to-male and represent territorial fights. Resident males immediately fly from their perch site in their territory toward any intruding male to prevent it from entering. The mechanism of sound produc-

tion involves movements of the wings, but is incompletely understood.

Two species have been identified in the garden of the station. The males can regularly be seen perching on trees trunks with the head characteristically in a downward position and the wings spread open. *Hamadryas feronia* is distinguished from *Hamadryas arinome* by the grayer color and by the black zigzag lines on the upper-side of the wings. *Hamadryas arinome* can be identified by the blue color of the wing pattern and the white band on the forewing.



Hamadryas feronia



Hamadryas arinome

Subfamily Nymphalinae

Anartia fatima (Banded Peacock)

Spanish name: Cocinera

Forewing length: 27 - 30 mm

Anartia fatima is the most common butterfly in Costa Rica. It can be seen in the garden of the station throughout the entire year where it comes to feed on nectar from various flowers. The wings are dark brown except for a white or yellow band. On the inside of their hindwings are red dots, which enable one readily to recognize the species. Males start out with yellow bands, but over time, the color of the bands fade to white. The discoloration has allowed studies to be conducted on age structure in various populations. The adults store no defensive chemical substances in the body or wings. Lacking chemical protection, the butterflies are a welcome meal for many predators, such as spiders, frogs, lizards, birds and certain mammals. That some individuals can escape and survive an attack is occasionally evident in butterflies with pieces of the wings missing.

The larvae of *Anartia fatima* feed on plants of the family Acanthaceae. The caterpillars are abundant yet very difficult to find in nature.



Anartia fatima

Anartia jatrophae (White Peacock)

Forewing length: 28 - 30 mm

A second member of the genus, *Anartia jatrophae* is likewise very common and can be observed daily on flowers in the garden of the station. It prefers to drink nectar from *Lantana*, which is abundant in the surroundings of the station. The wings of *A. jatrophae* are grayish-white with brown streaks all over.

Actual flower visiting behavior of both *Anartia* species can readily be observed on *Lantana camara*, for example. The butterfly often sits in the middle of the inflorescence (i.e. a flower cluster). It uncoils the proboscis and quickly begins to probe for a flower opening. The tip of the proboscis is inserted into a single flower by lowering the entire proboscis. Sensory organs at the tip help detect the presence of nectar in the corolla of a flower. After taking up nectar, the butterfly withdraws from the flower by raising the proboscis as a whole and turns to the next flower of the inflorescence. By repeating this sequence of feeding movements, a butterfly can exploit rapidly and effectively an inflorescence with numerous small flowers, like that of *Lantana camara*.

The caterpillars are known to feed on different herbs of the plant families Acanthaceae, Scrophulariaceae and Verbenaceae.



Anartia jatrophae

Junonia evarete (Mangrove Buckeye)

Forewing length: 26 - 29 mm

This middle-sized butterfly is distinguishable by the orange wing pattern of the upperside, an eyespot on each forewing and two on each hindwing. *Junonia evarete* occurs in disturbed habitats, such as cattle pastures and along beaches. The butterfly visits various flowers to feed on nectar. Males occasionally alight on the ground to obtain mineral substances from mud puddles. Without these minerals, they cannot successfully mate. The larvae feed on Acanthaceae, such as *Ruellia*.



Junonia evarete

Siproeta stelenes (Malachite)

Forewing length: 45 - 48 mm

Siproeta stelenes is common in a variety of habitats – forest edges, secondary forests and cultivated lands. It is easy to recognize because of the pale green on the upperside of the wings, the broad black wing margins and the small tail on the hindwing. It probably is a Batesian mimic of the very similarly colored nymphalid butterfly *Philaethria dido*. *Siproeta stelenes* is frequently seen in open areas and gardens, where they feed on floral nectar or squashed fruits. The larvae feed on plants of the family Acanthaceae.



Siproeta stelenes

Anthanassa frisia (= *tulcis*) (Cuban Crescent)

Forewing length: 16 - 19 mm

This is a small and inconspicuous butterfly, which can be recognized by the indented margin of the forewing and the brown coloration with light dots and lines on both wings. The upperside of the wings is darker than the underside. It is a very common butterfly in fields, pastures, along roadsides, and even in oil palm plantations. *Anthanassa frisia* flies close to the ground and often visits small flowers in the low vegetation to feed on nectar. *Dicliptera* and possibly other genera of Acanthaceae are used as larval hostplants.



Anthanassa frisia

Chlosyne janais (Crimson Patch)

Forewing length: 21 - 30 mm

Chlosyne janais is a common butterfly in Central America and one of several similar looking species. All are characterized by scattered white spots on the black forewing and an orange patch on the hindwings. Fertile females may be so weighted down with eggs in their abdomen that they can barely manage to take flight. Nonetheless, they lay eggs in large clusters on various host plants from the families Asteraceae, Acanthaceae and Amaranthaceae. The caterpillars bear many small black spines on the body and occur in two color morphs (red and black). They feed gregariously on the host plants.



Chlosyne janais larva,
black and red morph



Chlosyne janais



Chlosyne janais pupa

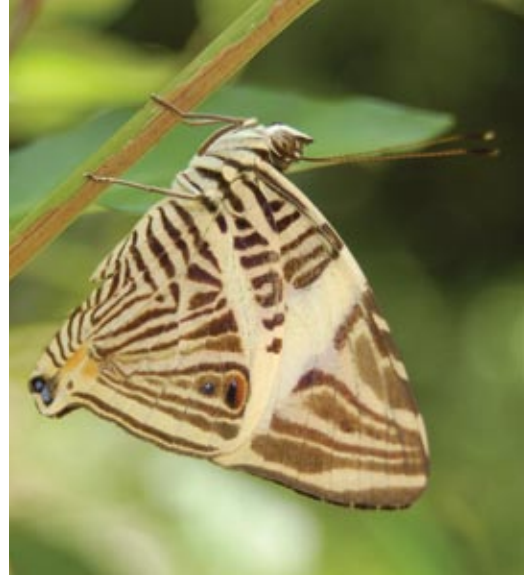


Chlosyne janais

Colobura dirce (Small Beauty, Zebra Mosaic)

Forewing length: 35 - 37 mm

The wings of this butterfly are black with a large yellow band on the upperside of the forewing; the hindwing is brown in color. The underside is cryptic and has zebra-like markings. The host plants of the larvae are *Cecropia* trees, which live in symbiosis with *Azteca* ants. Although the ants vigilantly protect against other insects, the caterpillars manage to feed on this plant. Females also frequently oviposit on plants without ant colonies. The adults of *Colobura dirce* feed on rotting fruits, carrion, dung and abstain entirely from floral nectar. A very similar sibling species, *Colobura annulata*, which was described and separated from *C. dirce* only a few years ago, has now also been found in La Gamba. It merely differs in the form of the stripes on the forewing underside. The third dark brown submarginal line narrows in the direction of the costa in *C. dirce*, whereas it is uniformly thick throughout its length in *C. annulata*.



Colobura dirce

Historis odius (Orion Cecropian)

Forewing length: 50 - 55 mm

This large species resembles members of the subfamily Charaxinae, although it is not closely related to them. The underside of the wings resembles dead leaves; the upperside bears an extensive orange patch. The butterfly is distinguished from its congener, *H. acheronta*, by the

single white spot at the forewing apex. The butterflies are attracted to rotten fruit. Although they usually spend most of their time in the canopy, they are easily observed at baits placed near the ground. The caterpillars feed on *Cecropia* (Moraceae).



Historis odius feeding on rotten bananas

Subfamily Limenitidinae

Adelpha cytherea (Smooth-Banded Sister)

Forewing length: 22 - 25 mm

The butterflies of the genus *Adelpha* are medium-sized and typically have dark brown wings with an orange and white pattern. In Costa Rica, the genus contains a number of very similar looking species, some of which are difficult to identify at the species level. Species of *Adelpha* occur in all habitats from sea level to mountainous regions. In most *Adelpha* butterflies, the dark brown upperside of the forewing has a prominent orange patch or band, and it is aligned with a continuous white band on the underside of both wings. Otherwise, the undersides have a light brown color and white bands across both wings. *Adelpha cytherea* is the most common *Adelpha* species in cultivated lands and secondary forests where it can be observed to feed on flowers and fruits. Its larvae feed on the Woolly Woodvine (*Sabicea villosa*). Other similar looking members of the genus occur in the natural rainforest habitats around the station. They are usually seen perching on the top of the trees and hardly ever come close to the ground. The larval food plants of many *Adelpha* species are still unknown, but those which are known belong to a wide range of plant families. *Adelpha boeotia* feeds on *Cecropia* (Moraceae), as well as *Luhea seemani* (Tiliaceae), while the larval host plant of *Adelpha salmoneus* belongs to the genus *Sabicea* (Rubiaceae).



Adelpha cytherea



Adelpha boeotia



Adelpha salmoneus



Adelpha salmoneus

Subfamily Heliconiinae

Dryas iulia (Julia)

Forewing length: 41 - 45 mm

Dryas iulia is easily identified by its bright orange color and elongate forewings. The butterfly is a graceful flier with its long wings and low frequency of wing beat. It occurs at the edge of the forest, in the forest canopy and openings along forest roads and trails. The adults frequently visit many flowers for nectar such as *Lantana*. They can be readily observed in all times of the year in the garden of the station and along roads in the vicinity. The caterpillars of *Dryas iulia* are light brown with white bands and bear long spiny extensions on each body segment. They feed on passion vines (Passifloraceae).



Dryas iulia larva



Dryas iulia

Eueides lybia (Sharp-edged Longwing)

Forewing length: 29 - 31 mm

Eueides lybia is associated with rainforest habitats. This species rarely flies in direct sunlight and does not occur in secondary vegetation growth. The color of the wings is orange with a

black forewing apex and broad black hindwing margins. *E. lybia* is one of the butterfly species which sleep gregariously. The caterpillars feed on *Passiflora vitifolia*.



Eueides lybia

Philaethria dido (Green Longwing)

Forewing length: 49 - 54 mm

Philaethria dido is a common butterfly in the lowland primary forests around the station. However, it is rarely seen because this butterfly mainly flies above the forest canopy. The females visit light openings and the forest edges to

oviposit on their host plants of the plant genus *Passiflora*. *P. dido* is one of the few examples of a butterfly with a green color pattern on the upperside of the wing. It is mimicked by *Siproeta stelenes*.



Philaethria dido

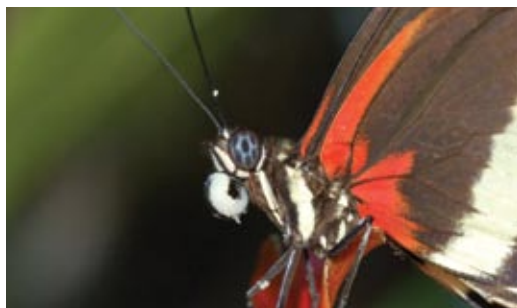
Heliconius (Longwing Butterflies or Passion Vine Butterflies)

In our region of Costa Rica, eight species have been recorded from the genus *Heliconius*. All are characterized by the elongate forewings, the long and club-tipped antennae, their slow flight and unique mode of pollen feeding. Most species are very colorful. They have stimulated considerable biological interest, which has led to studies on mimicry, feeding ecology and evolution. The host plants of the caterpillars are passion vines (Passifloraceae). The plants contain toxic cyanogenic glycosides, which protect them against many herbivore insects. However, the caterpillars of *Heliconius* and other butterflies have evolved the ability to process the poisons and put them to use for their own protection.

Extraordinary is the fact that *Heliconius* species are able to feed on pollen, aside from nectar. The butterflies actively gather pollen from flowers onto the shaft of the proboscis and mash it together with saliva. Afterward, they ingest the liquid, which is rich in extracted amino acids. The special pollen feeding behavior is crucially tied together with their remarkable longevity (up to nine months!), the ability to constantly produce eggs and to mate on multiple occasions.

Ultimately, the chemical defense mechanisms of the adults benefit from the extra nitrogen as well.

A further remarkable feature of the life history of some *Heliconius* species is *pupal mating*. Male butterflies claim female pupae by sitting on them. Mating occurs invariably in the early morning immediately upon eclosion (i.e., emergence from pupal case) or beforehand with the pupa. One knows that female pupae are present, when several males are seen flying in the low vegetation, trying to chase each other away from the female pupae.



Heliconius butterfly processing pollen with its proboscis

Heliconius sapho (= *hewitsoni*) (White-Patched Longwing)

Forewing length: 34 - 41 mm

Heliconius sapho is one of the most abundant butterflies in the forests near the station. It has black wings with yellow bands. Viewed from the underside, remarkable red areas become visible at the base of the wings. The butterfly greatly resembles another species that is common in the

region, *Heliconius cydno*. The species are members of a Müllerian mimicry complex – in which both species are distasteful and profit from looking like each other, since predatory birds learn quickly to avoid potentially unpalatable prey.



Heliconius sapho



Heliconius sapho

Heliconius cydno (= *pachinus*) (Cydno Longwing)

Forewing length: 38 - 43 mm

In our region of Costa Rica, *Heliconius cydno* is almost identical in appearance to *H. sapho*. The two species can be distinguished by looking closely at the yellow stripe on the forewing close to the body. In *Heliconius pachinus*, five wing veins cross the stripe, whereas in *H. sapho* only two to three veins do. The close resemblance of

the butterflies probably serves to protect both. If a predatory bird learns to associate the yellow-black coloration with a distasteful prey, butterflies of both species will be attacked less often. The butterflies emit a pungent smell that arises from the abdominal glands. The odor can be used as a field character for species identification.



Heliconius cydno

Heliconius hecale (Hecale Longwing)

Forewing length: 42 - 50 mm

Heliconius hecale is one of the most common members of the tiger-stripe mimicry complex. Other *Heliconius* species and numerous butterflies from various groups belong to this complex, as well. They all have black, orange and yellow wing coloration. In general, bright colors serve as a warning to birds that prey may be unpalatable or toxic. *Heliconius hecale* occurs in all habitats of Central and South America. It has been subdivided into a number of different looking

subspecies. Both sexes obtain nectar from a variety of flowers, but pollen collection is restricted primarily to flowers of *Psychotria* (Rubiaceae), *Psiguria* and *Gurania* (both Cucurbitaceae). Sometimes individuals aggressively defend flowers against other butterflies. Several individuals of *H. hecale* spend the night in low forest vegetation close to each other in a small group. Similar to *H. cydno*, the larvae of *H. hecale* feed on a variety of *Passiflora* species.



Heliconius hecale



Heliconius hecale

Heliconius sara (Sara Longwing)

Forewing length: 30 - 35 mm

Heliconius sara is a black butterfly with white or yellow wing bands and a blue shining hue. It is most commonly found along forest edges or in secondary vegetation. The species lives in close association with its larval host plant, *Passiflora*

auriculata. Host plant specificity is a major factor limiting the distribution of *H. sara*, and is one of the reasons why this *Heliconius* species is always associated with rainforest habitats



Heliconius sara

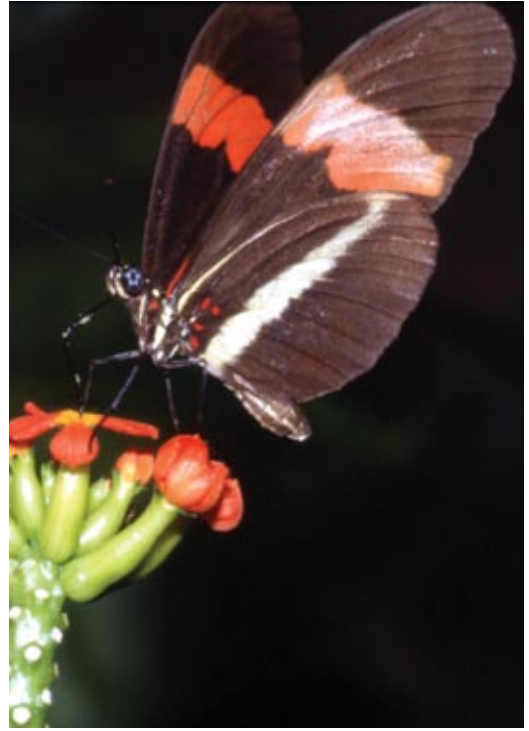
Heliconius melpomene (Postman Butterfly, Melpomene Longwing)

Forewing length: 35 - 39 mm

Like many other species of the genus *Heliconius*, *H. melpomene* is subdivided into various subspecies each with a different coloration, particularly in other regions of Central and South America. In Costa Rica, *Heliconius melpomene* is black with a red band across the forewings and a longitudinal light yellow stripe on the hindwings. The butterfly is very conspicuous and single individuals can be encountered along shady forest trails and in the garden of the station. Its co-mimicking species, *H. erato*, is rare in La Gamba, and is usually encountered in the sunshine. The two species can only be told apart by counting the number of small red dots on the underside of the forewing upon close examination.



Larva of *Heliconius melpomene*



Heliconius erato



Heliconius melpomene

Heliconius ismenius (Tiger-striped Longwing)

Forewing length: 38 - 48 mm

Heliconius ismenius is a member of the Tiger-striped mimicry complex, but can be distinguished from similar species by its large eyes. In wing pattern it looks almost identical to *Melinaea lilis* from the subfamily Ithomiinae. It inhabits

rainforest habitats and prefers to feed on the flowers of *Psiguria* and *Gurania*, which are also excellent pollen sources. The females lay their eggs singly on seedlings of different *Passiflora* species.



Heliconius ismenius

Laparus (= *Heliconius*) *doris* (Rayed Longwing)

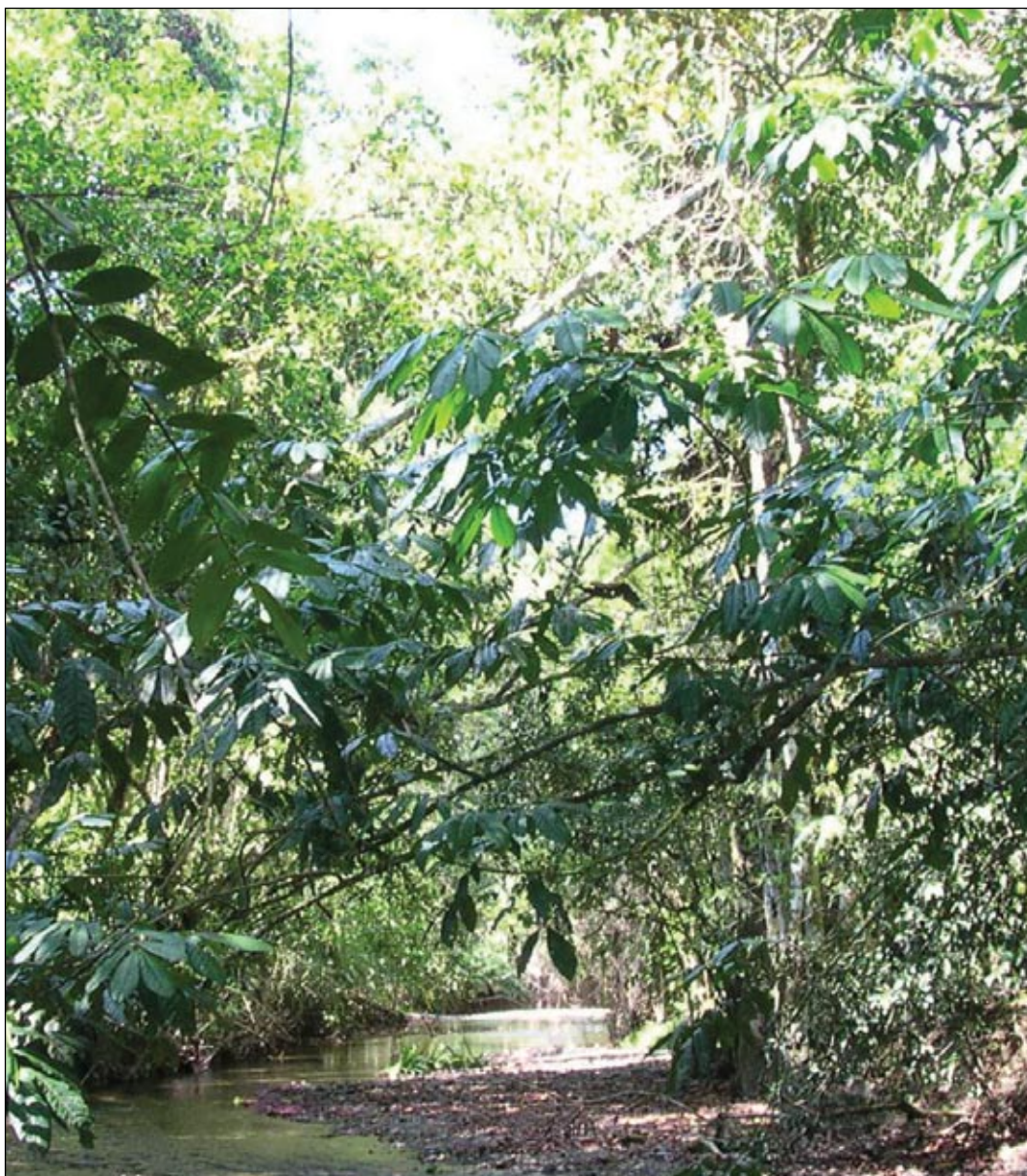
Forewing length: 34 - 45 mm

This Longwing was placed in a separate genus due to differences in chromosome numbers, but recent molecular phylogenetic results do not confirm this splitting from the genus *Heliconius*. This is a variable species which can appear in different color forms but can be readily identified by the ray pattern on the hindwings. It is found

in different forest habitats and regularly seen around the station. Its larvae are highly gregarious and feed on old leaves of *Passiflora ambigua*. Sometimes large numbers of pupae can be found on the tree trunks which hosted the passion vine.



Laparus doris



Gallery forest near the research station. Gallery forests are often the only remains after clearance of surrounding forests for agricultural development. They can provide important habitats for some species, including *Calephelis* and other Metalmarks, and might also function as corridors to connect remaining rainforest fragments.

The larva of the Molpe Metalmark (*Juditha molpe*) is polyphagous and can feed on many different plant families. However, it has obligate associations with the ant species *Dolichoderus bispinosus*, which appears to mediate the hostplant choice of the ovipositing female butterfly.



Juditha molpe larva feeding on a *Passiflora* vine



Riodinidae

Metalmarks

The butterflies of the family Riodinidae are small to medium-sized. The group is characteristic throughout the Neotropics for its great diversity of species. The females, like most insects, walk on all six legs, however the males use only four. Their forelegs are too small to serve for locomotion, but are probably connected with mating. Their wing patterns show extraordinary diversity among species, most of which mimic members of other butterfly or moth families. The metalmarks differ also in behavior from other butterflies. Most species perch on the underside of leaves and are therefore easily mistaken for moths. Their peak time of activity is often in the early morning or in the late afternoon, whereas most other butterflies are most active during midday. In certain genera the larvae live symbiotically with ants (*myrmecophily*). The ants are attracted to and feed on a glandular secretion of the larvae. In return, the ants care for the butterfly larvae by defending them against parasites. In some species, the caterpillars produce a vibration sound by rubbing their head against a special organ. The sounds are not audible to humans but serve as important signals to the ants.

Euselasia regipennis (Purple-topped Sombermark)

Forewing length: 16 - 20 mm

This local Central American species, which is found singly in rainforest habitats, resembles satyrines of and related to the genus *Cissia* (family Nymphalidae). The sexes are dimorphic: In the males, the upperside of the wings is black with a shining deep purple iridescence. The females occur in two color morphs. One of them possesses a white band on the upperside, as in *Pareuptychia ocirrhoe*. The other morph is brown, as *Cissia*, *Hermeuptychia* and *Magneuptychia*. The early stages of this butterfly are still unknown



Euselasia regipennis

Eurybia lycisca (Blue-Winged Sheenmark)

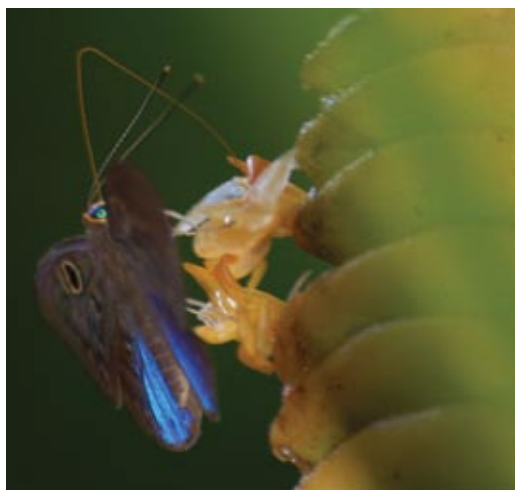
Forewing length: 24 - 27.5 mm

The proboscis of *Eurybia lycisca* is one of the longest among all butterflies. It measures up to 45 mm and is almost twice as long as the body. The upperside of the forewing is brown and has two eyespots with iridescent centers; the upperside of the hindwing is remarkably metallic blue across the entire distal area. The sexes appear similar. However, the blue hues are less conspicuous in females. When the butterfly settles on a plant, it opens the wings, and the blue coloration is noticeable from a distance at particular angles. *Eurybia lycisca* is a medium-sized butterfly. It flies

fast and erratically in the shade of vegetation. In the garden of the station, it is common and can be found near its preferred nectar and larval host plant, *Calathea* (Maranthaceae). Nectar feeding predominantly occurs in the morning; in the afternoon, female butterflies can be observed to lay eggs frequently on the inflorescences of *Calathea* plants. The caterpillars feed on the inflorescence and live in association with ants.



Eurybia lycisca



Eurybia lycisca

Ancyluris jurgensenii (Costa-spotted Beautymark)

Forewing length: 22 - 25 mm

Ancyluris jurgensenii is distributed throughout Central America but is uncommon in Costa Rica. Single specimens have also been observed along forest tracts near the station. In the early morning, males perch on the underside of leaves, and chase any approaching butterfly. The females are more active during midday. The wing patterns of

the sexes are dimorphic. The males have a red band; the females have a white band and their hindwings lack the beautiful blue iridescence along the margins. The caterpillars are known to feed on *Hyeronima oblonga* which belongs to the family Euphorbiaceae.



Ancyluris jurgensenii

Calephelis laverna (Small Scintillant)

Forewing length: 9 - 10 mm

Calephelis laverna is one of many similar looking species, but is distinguished by the red-brown underside and its small size. In Costa Rica, it is only found in the South of the Osa Peninsula but its range extends to Brazil. The butterflies can be seen in the gallery forests close to the station. The life history of this small but pretty species in Costa Rica is still unknown, but in Trinidad the larvae feed on Asteraceae (e.g. *Chromolaena* and *Eupatorium*).



Calephelis laverna

Charis anius (= *aius*) (Anius Metalmark)

Forewing length: 12 - 14 mm

The genus *Charis* comprises several similar looking species which can be abundant in open areas along forest edges or along streams where they fly close to the ground and are therefore easy to observe. Little is known about their life histories, but most species appear to be detritivorous, feeding on dead leaves on the ground. This is the case for *Charis anius*, where egg-laying was observed on dead leaves. The caterpillars are extremely hirsute, which is very unusual in butterflies and much more typical for



Charis anius

Mesenopsis melanochlora (Orange-striped Metalmark)

Forewing length: 15 - 18 mm

Mesenopsis melanochlora is an excellent mimic of day-flying moths from different families, for example, *Josia ligata* (Notodontidae) and various *Josiomorpha* species (Arctiidae). However, due to its slightly club-tipped antennae it can be differentiated from them. It is encountered along forest tracts in the Piedras Blancas National Park, where the males perch several meters above the ground on the upperside of leaves during the morning. The butterflies visit flowers of various Asteraceae and the females deposit their eggs singly in the leaf axils or in the bark of the tree *Miconia argentea* (Melastomataceae). The caterpillars usually feed on sapling plants where they fold the edge of the leaf into a tube.



Mesenopsis melanochlora

Nymphidium ascolia (Creamy Metalmark)

Forewing length: 19 - 20 mm

Nymphidium ascolia is a medium-sized butterfly with white coloration of the wing and body. Both wings have broad brown margin with a blue zigzag band. On the hindwing are orange markings. The butterfly visits flowers, for example *Lantana*, to fill up on nectar. It is common at the biological station, on the surrounding trails and in forest gaps. Morning is the best time to search for the species. Legumes of the genus *Inga* are used as larval food plants. The caterpillars are attended by different ants of the subfamilies Formicinae and Myrmicinae.



Nymphidium ascolia



Light gap in the Esquinas rainforest. Many rainforest butterflies fly in the canopy and are therefore difficult to observe. Natural gaps provide the best opportunity to find such species, including many Hairstreaks.



Lycaenidae

Blues

The Lycaenidae are predominantly small-sized butterflies. In number of species, they are the second largest butterfly family with about 6,000 species worldwide. Three main groups are recognized: the blues, coppers and hairstreaks. Almost all species from Central and South America are hairstreaks; many of them possess small tails on the hindwings. Most hairstreaks are dependent on trees as larval food plants. The butterflies spend most of the time in the tree canopy and therefore are difficult to observe. Little is known about their biology. Like metalmarks, the caterpillars of many blues live in symbiotic relationship with ants (*myrmecophily*). The caterpillars offer the ants a honeydew secretion. In return, the ants protect the caterpillars from parasites. Caterpillars of some species are even transported by the ants into the ant nests, where they are cared for and fed like ant brood. In a few species, the caterpillars become predators and attack ant larvae.

Arawacus lincoides

Forewing length: 15 - 18 mm

Arawacus lincoides is a species of hairstreak with an unusual striped pattern on its underside reminiscent of small satyrines (e.g. *Pareuptychia ocirrhoe*). It has often been confused with its sibling *Arawacus togarna*, which occurs on the Atlantic slope of Costa Rica and further north to Mexico, whereas *A. lincoides* is only found on the Pacific slope of Costa Rica and further south to Panamá and Columbia (Robbins 2010). *A. lincoides* differs from its sibling by genitalia characters and a white marginal spot at the distal end of the hindwing underside between its two tails (Robbins, pers. comm.). The tails of hairstreaks are thought to distract potential predators from essential body parts (false head hypothesis). If a bird or lizard bites off the tail, the butterfly survives essentially unharmed. This hairstreak can be seen quite often in the garden of the station and along waysides usually sitting on small bushes. The caterpillars feed on plants of the family Solanaceae.



Arawacus lincoides

Arumecla galliena (Red-Based Groundstreak)

Forewing length: 12 - 15 mm

Arumecla galliena is found in Central and northern South America. It is one of the most common hairstreaks in the primary and secondary rainforests of the Golfo Dulce region. It is usually encountered in small groups, flying around the treetops. The butterflies are most easily observed in forest gaps around smaller trees. Males are territorial and spend their time chasing away other males. *Arumecla galliena* belongs to a group of hairstreaks which is detritivorous. The females lay their eggs on dead plant material and the caterpillars then feed on leaf litter.



Arumecla galliena

Strymon megarus (= *Tmolus basilides*) (Scrub-Hairstreak, Pineapple Fruit Borer)

Spanish name: Taladro de la Piña
Forewing length: 11 - 14.5 mm

This hairstreak is rare in its natural habitat, but can become a serious pest in pineapple plantations. The females lay their eggs on pineapple flowers and the larvae bore into the fruits. In its natural habitat, various other bromeliads and heliconias are used as food plants. In the garden of the station, females have been observed laying eggs on the flowers of *Heliconia*.



Strymon megarus

Hemiargus hanno (Hanno Blue)

Forewing length: 9 - 11 mm

Not all tropical butterflies are large and colorful. This tiny blue is among the smallest butterflies in Costa Rica. It is most common on pastures with woody legumes, such as plants of the genera *Cassia* or *Acacia*, which constitute the food plants of the caterpillars. They are quite polyphagous and also feed on plants of the families Mimosaceae and Oxalidaceae. Like many other blues, the caterpillars possess three types of myrmecophilous organs (the pore cupola, dorsal nectary and tentacle organ) to entice ants, which in turn guard the caterpillars. The butterfly-ant association is known from Brazil, where the ants were identified as belonging to the formicine genus *Brachymyrmex*.



Hemiargus hanno



Secondary forest near the research station. The larvae of many Skippers feed on grasses which grow better in lighter places than in the deep shade of primary rainforests. Therefore secondary forests can be a suitable habitat for many species of this family. However, only a small fraction of rainforest species can survive in those degraded forests.



Hesperiidae

Skippers

Skippers are characterized by a large head, a compact body, and relatively small wings compared to their body, which helps them to attain their quick and darting flight pattern. The short antennae are club-tipped, but unlike other butterflies the clubs are hooked backwards like a crochet hook. The family is probably the sister group to the remaining 'true' butterflies, but their phylogenetic position is still debated. Many species have a resting position which is very unusual for butterflies: only the hindwings are spread out flat, whereas the forewings are angled upward, producing a 'v' shape. Other skippers (e.g. from the genus *Urbanus*) usually fold their wings over the body giving it a triangular shape. These butterflies are frequent flower visitors. They possess remarkably long mouthparts in comparison to their rather small body so that they are able to extract nectar even from long tubed flowers like *Stachytarpheta*. Many skippers are also fond of dung or carrion, or can be observed taking up minerals at mud puddles. Unfortunately, this species-rich family is the least well known among all butterfly families and there is no identification guide available for species of Costa Rica. The many species are usually dull brown or gray and very similar to each other. Genitalia examination is often necessary for reliable identification.



Skipper in the typical resting position



Skipper feeding on flowers of *Stachytarpheta*

Urbanus teleus (Teleus Longtail)

Urbanus teleus is widespread throughout Central and South America. The butterflies are regularly seen in the garden of the station. The brown and medium-sized butterfly is distinguished by the elongate hindwings which are reminiscent of the tails in swallowtail butterflies. The females lay their eggs on the food plant, i.e. different kinds of grasses. The young caterpillars construct shelters of folded leaf blades.



Urbanus teleus

Pyrrhopyge thericles (= *pseudophidias*) (Thericles Firetip)

Unlike most other groups of skippers, the genus *Pyrrhopyge* contains many beautiful species with an entirely black color or often with red or white wing patterns. One of them, *Pyrrhopyge thericles*, is distributed throughout tropical South America. Some authors, however, consider the Central American populations to represent a different species (*P. pseudophidias*). *P. thericles* has been observed flying in gallery forests along the river near the station. Nothing appears to be known about its life history.



Pyrrhopyge thericles



Appendix

Preliminary checklist of the Butterflies of the Golfo Dulce Region (Papilionoidea & Hesperioidea)

The table includes our own data (La Gamba) as well as published data from Corcovado National Park (Corcovado). The checklist from DeVRIES (1978) excludes six species which appear to represent misidentifications because they are not listed in DeVRIES (1987).

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)	
Hesperiidae:		
<i>Achlyodes mithridates</i> (FABRICIUS, 1793)		
<i>Antigonus nearchus</i> (LATREILLE, 1817)		
<i>Autochton bipunctatus</i> (GMELIN, 1790)		
<i>Autochton neis</i> (GEYER, 1832)		
<i>Celaenorrhinus monartus</i> (PLÖTZ, 1884)		
<i>Celaenorrhinus stallingi</i> FREEMAN, 1946		
<i>Cogia calchas</i> (HERRICH-SCHÄFFER, 1869)		
<i>Helias cama</i> EVANS, 1953		
<i>Heliopetes arsalte</i> (LINNAEUS, 1758)		
<i>Hylephila phyleus</i> (DRURY, 1773)		
<i>Mnasilus allubita</i> (BUTLER, 1877)		
<i>Molo mango</i> (GUENÉE, 1865)		
<i>Nisoniades rubescens</i> (MÖSCHLER, 1877)		
<i>Nyctelius nyctelius</i> (LATREILLE, 1824)		
<i>Ouleus fridericus</i> (GEYER, 1832)	<i>Ouleus panna</i>	
<i>Panoquina ocola</i> (EDWARDS, 1863)		
<i>Pompeius pompeius</i> (LATREILLE, 1824)		
<i>Pyrgus oileus</i> (LINNAEUS, 1767)		
<i>Pyrgus orcus</i> (STOLL, 1780)		
<i>Pyrrhopyge thericles</i> (MABILLE, 1891)	<i>Pyrrhopyge pseudophidias</i>	
<i>Pythonides jovianus</i> (STOLL, 1782)		
<i>Remella vopiscus</i> (HERRICH-SCHÄFFER, 1869)		
<i>Timochares trifasciata</i> (HEWITSON, 1868)		
<i>Urbanus dorantes</i> (STOLL, 1790)		
<i>Urbanus procne</i> (PLÖTZ, 1880)		
<i>Urbanus proteus</i> (LINNAEUS, 1758)		
<i>Urbanus simplicius</i> (STOLL, 1790)		
<i>Urbanus teleus</i> (HÜBNER, 1821)		
<i>Xenophanes tryxus</i> (STOLL, 1780)		
Lycaenidae:		
<i>Arawacus lincoides</i> (Draudt, 1917)	<i>Arawacus togarna</i>	
<i>Arumecla galliena</i> (HEWITSON, 1877)	<i>Thecla galliena</i>	
<i>Brangas caranus</i> (STOLL, 1780)		
<i>Calycopis atrius</i> (HERRICH-SCHÄFFER, 1853)	<i>Thecla atrius</i>	
<i>Calycopis demonassa</i> (HEWITSON, 1868)	<i>Thecla demonassa</i>	
<i>Calycopis isobeon</i> (BUTLER & DRUCE, 1872)	<i>Thecla beon</i>	
<i>Calycopis pisis</i> (GODMAN & SALVIN, 1887)	<i>Thecla pisis</i>	
<i>Calycopis trebula</i> (HEWITSON, 1868)	<i>Thecla trebula</i>	
<i>Cupido comyntas</i> (GODART, 1824)	<i>Everes comyntas</i>	
<i>Eumaeus godartii</i> (BOISDUVAL, 1870)		
<i>Hemiargus hanno</i> (STOLL, 1790)	<i>Hemiargus ceraunus</i>	
<i>Iaspis talayra</i> (HEWITSON, 1868)	<i>Thecla talayra</i>	
<i>Ocaria thales</i> (FABRICIUS, 1793)	<i>Thecla thales</i>	
<i>Panthiades bathildis</i> (FELDER & FELDER, 1865)		
<i>Panthiades phaleros</i> (LINNAEUS, 1767)	<i>Cydno phaleros</i>	
<i>Pseudolycaena damo</i> (DRUCE, 1875)		
<i>Pseudolycaena marsyas</i> (LINNAEUS, 1758)		

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)
<i>Siderus leucophaeus</i> (HÜBNER, 1813)	<i>Thecla leucophaeus</i>
<i>Strymon megarus</i> (GODART, 1824)	
<i>Theorema eumenia</i> HEWITSON, 1865	
<i>Theritas hemon</i> (CRAMER, 1775)	
<i>Theritas lissus</i> (STOLL, 1790)	<i>Thecla hisbon</i>
<i>Theritas mavors</i> HÜBNER, 1818	
<i>Ziegleria syllis</i> (GODMAN & SALVIN, 1887)	<i>Strymon syllis</i>
Nymphalidae:	
<i>Actinote lapitha</i> (STAUDINGER, 1885)	
<i>Adelpha basiloides</i> (BATES, 1865)	
<i>Adelpha boeotia</i> (FELDER & FELDER, 1867)	
<i>Adelpha cocala</i> (CRAMER, 1779)	
<i>Adelpha cytherea</i> (LINNAEUS, 1758)	
<i>Adelpha heraclea</i> (FELDER & FELDER, 1867)	
<i>Adelpha iphiclus</i> (LINNAEUS, 1758)	
<i>Adelpha justina</i> (FELDER & FELDER, 1861)	
<i>Adelpha salmoneus</i> (BUTLER, 1866)	
<i>Adelpha serpa</i> (BOISDUVAL, 1836)	
<i>Aeria eurimedia</i> (CRAMER, 1777)	
<i>Agraulis vanillae</i> (LINNAEUS, 1758)	
<i>Anartia fatima</i> (FABRICIUS, 1793)	
<i>Anartia jatrophae</i> (LINNAEUS, 1763)	
<i>Anthanassa frisia</i> (POEY, 1832)	<i>Anthanassa tulcis</i>
<i>Antirrhoea philoctetes</i> (LINNAEUS, 1758)	<i>Antirrhoea tomasia</i>
<i>Archaeoprepona demophon</i> (LINNAEUS, 1758)	
<i>Archaeoprepona demophoon</i> (HÜBNER, 1814)	
<i>Caligo atreus</i> (KOLLAR, 1850)	
<i>Caligo eurilochus</i> (CRAMER, 1775)	
<i>Caligo telamonius</i> (FELDER & FELDER, 1862)	<i>Caligo memnon</i>
<i>Callicore lyca</i> (DOUBLEDAY, 1847)	
<i>Callicore texa</i> (HEWITSON, 1855)	
<i>Callicore tolima</i> (HEWITSON, 1852)	<i>Callicore pacifica</i>
<i>Callithomia hezia</i> (HEWITSON, 1854)	
<i>Castilia eranites</i> (HEWITSON, 1857)	
<i>Catoblepia orgetorix</i> (HEWITSON, 1870)	
<i>Catonephele numilia</i> (CRAMER, 1775)	
<i>Catonephele nyctimus</i> (WESTWOOD, 1850)	<i>Catonephele mexicana</i>
<i>Ceratinia tutia</i> (HEWITSON, 1852)	
<i>Caerois gerdrudtus</i> (FABRICIUS, 1793)	
<i>Chloreuptychia arnaca</i> (FABRICIUS, 1776)	<i>Chloreuptychia arnaea</i>
<i>Chlosyne hippodrome</i> (GEYER, 1837)	
<i>Chlosyne janais</i> (DRURY, 1782)	
<i>Chlosyne lacinia</i> (GEYER, 1837)	
<i>Chlosyne theona</i> (MÉNÉTRIÉS, 1855)	<i>Thessalia ezra</i>
<i>Cissia confusa</i> (STAUDINGER, 1887)	
<i>Cissia pompilia</i> (FELDER & FELDER, 1867)	<i>Cissia usitata</i>
<i>Cissia pseudoconfusa</i> SINGER, DeVRIES & EHRlich, 1983	
<i>Cithaerias pireta</i> (STOLL, 1780)	<i>Cithaerias menander</i>

	La Gamba				Corcovado	
	Intensive land use	Secondary forest	Natural forest	TOTAL	DeVRIES (1978)	KUNTE (2008)
			●	●		
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Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)	
<i>Colobura annulata</i> WILLMOTT, CONSTANTINO & HALL, 2001	previously confused with <i>Colobura dirce</i>	
<i>Colobura dirce</i> (LINNAEUS, 1758)		
<i>Consul fabius</i> (CRAMER, 1776)		
<i>Danaus gilippus</i> (CRAMER, 1775)		
<i>Danaus plexippus</i> (LINNAEUS, 1758)		
<i>Diaethria astala</i> (GUÉRIN-MÉNEVILLE, 1844)		
<i>Diaethria clymena</i> (CRAMER, 1775)	<i>Diaethria marchalli</i>	
<i>Dione juno</i> (CRAMER, 1779)		
<i>Dione moneta</i> (HÜBNER, 1825)		
<i>Dircenna dero</i> (HÜBNER, 1823)		
<i>Dryadula phaetusa</i> (LINNAEUS, 1758)		
<i>Dryas iulia</i> (FABRICIUS, 1775)		
<i>Dynamine agacles</i> (DALMAN, 1823)		
<i>Dynamine tithia</i> (HÜBNER, 1823)	<i>Dynamine salpensa</i>	
<i>Eresia clio</i> (LINNAEUS, 1758)	<i>Eresia clara</i>	
<i>Eresia eunice</i> (HÜBNER, 1807)	<i>Eresia mechanitis</i>	
<i>Eresia ithomioides</i> HEWITSON, 1864	<i>Eresia eutropia</i> & <i>Eresia melaina</i>	
<i>Eryphanis automedon</i> (CRAMER, 1775)	<i>Eryphanis polyxena</i>	
<i>Eueides aliphera</i> (GODART, 1819)		
<i>Eueides isabella</i> (STOLL, 1781)		
<i>Eueides lineata</i> SALVIN & GODMAN, 1868		
<i>Eueides lybia</i> (FABRICIUS, 1775)		
<i>Eunica alpais</i> (GODART, 1824)	<i>Eunica excelsa</i>	
<i>Eunica chlororhoa</i> SALVIN, 1869	<i>Eunica mira</i>	
<i>Eunica sydonia</i> (GODART, 1824)	<i>Eunica caresa</i>	
<i>Eunica volumna</i> (GODART, 1824)	<i>Eunica venusia</i>	
<i>Euptoieta hegesia</i> (CRAMER, 1779)		
<i>Euptychia insolata</i> BUTLER & DRUCE, 1872		
<i>Euptychia jesia</i> BUTLER, 1869		
<i>Euptychia westwoodi</i> BUTLER, 1867	<i>Euptychia mollis</i>	
<i>Fountainea eurypyle</i> (FELDER & FELDER, 1862)	<i>Memphis eurypyle</i>	
<i>Godyris zavaleta</i> (HEWITSON, 1855)	<i>Godyris zygia</i>	
<i>Hamadryas amphinome</i> (LINNAEUS, 1767)		
<i>Hamadryas arinome</i> (LUCAS, 1853)		
<i>Hamadryas feronia</i> (LINNAEUS, 1758)		
<i>Hamadryas guatemalena</i> (BATES, 1864)		
<i>Heliconius charithonia</i> (LINNAEUS, 1767)	<i>Heliconius charitonius</i>	
<i>Heliconius cydno</i> (DOUBLEDAY, 1847)	<i>Heliconius pachinus</i>	
<i>Heliconius erato</i> (LINNAEUS, 1758)		
<i>Heliconius hecale</i> (FABRICIUS, 1776)		
<i>Heliconius hecalesia</i> (HEWITSON, 1854)		
<i>Heliconius ismenius</i> LATREILLE, 1817		
<i>Heliconius melpomene</i> (LINNAEUS, 1758)		
<i>Heliconius sapho</i> (DRURY, 1782)	<i>Heliconius hewitsoni</i>	
<i>Heliconius sara</i> (FABRICIUS, 1793)		
<i>Hermeuptychia hermes</i> (FABRICIUS, 1775)	<i>Cissia hermes</i>	
<i>Historis acheronta</i> (FABRICIUS, 1775)		
<i>Historis odius</i> (FABRICIUS, 1775)		
<i>Hypoleria lavinia</i> (HEWITSON, 1855)	<i>Hypoleria cassotis</i>	

	La Gamba				Corcovado	
	Intensive land use	Secondary forest	Natural forest	TOTAL	DeVRIES (1978)	KUNTE (2008)
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Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)	
<i>Hypocada virginiana</i> (HEWITSON, 1855)		
<i>Hypothyris euclea</i> (GODART, 1819)		
<i>Ithomia celemia</i> HEWITSON, 1854		
<i>Ithomia patilla</i> HEWITSON, 1852		
<i>Janatella leucodesma</i> (FELDER & FELDER, 1861)		
<i>Junonia evarete</i> (CRAMER, 1779)		
<i>Laparus doris</i> (LINNAEUS, 1771)	<i>Heliconius doris</i>	
<i>Lycorea halia</i> (HÜBNER, 1816)	<i>Lycorea cleobaea</i>	
<i>Magneptychia gomezi</i> (SINGER, DeVRIES & EHRLICH, 1983)	<i>Cissia gomezi</i>	
<i>Magneptychia libye</i> (LINNAEUS, 1767)	<i>Cissia libye</i>	
<i>Marpesia berania</i> (HEWITSON, 1852)		
<i>Marpesia chiron</i> (FABRICIUS, 1775)		
<i>Marpesia furcula</i> (FABRICIUS, 1793)	<i>Marpesia iole</i>	
<i>Marpesia merops</i> (DOYÈRE, 1840)		
<i>Marpesia petreus</i> (CRAMER, 1776)		
<i>Mechanitis lysimnia</i> (FABRICIUS, 1793)		
<i>Mechanitis polymnia</i> (LINNAEUS, 1758)		
<i>Megeptychia antonoe</i> (CRAMER, 1775)		
<i>Melinaea liliis</i> (DOUBLEDAY, 1847)	<i>Melinaea scylax</i>	
<i>Memphis forreri</i> (GODMAN & SALVIN, 1884)		
<i>Memphis glauca</i> (FELDER & FELDER, 1862)	<i>Memphis centralis</i>	
<i>Memphis oenomais</i> (BOISDUVAL, 1870)		
<i>Memphis proserpina</i> (SALVIN, 1869)		
<i>Memphis xenocles</i> (WESTWOOD, 1850)		
<i>Morpho cypris</i> WESTWOOD, 1851		
<i>Morpho helenor</i> (CRAMER, 1776)	<i>Morpho peleides</i>	
<i>Morpho menelaus</i> (LINNAEUS, 1758)	<i>Morpho amathonte</i>	
<i>Morpho theseus</i> DEYROLLE, 1860		
<i>Nessaea aglaura</i> (DOUBLEDAY, 1848)		
<i>Nica flavilla</i> (GODART, 1824)		
<i>Oleria paula</i> (WEYMER, 1883)		
<i>Oleria rubescens</i> (BUTLER & DRUCE, 1872)		
<i>Opsiphanes cassina</i> FELDER & FELDER, 1862		
<i>Opsiphanes invirae</i> (HÜBNER, 1808)		
<i>Opsiphanes tamarindi</i> FELDER & FELDER, 1861		
<i>Pareptychia metaleuca</i> (BOISDUVAL, 1870)		
<i>Pareptychia ocirrhoe</i> (FABRICIUS, 1776)	<i>Cissia hesione</i>	
<i>Perophtalma lasus</i> WESTWOOD, 1851		
<i>Philaethria dido</i> (LINNAEUS, 1763)		
<i>Pierella helvina</i> (HEWITSON, 1859)	<i>Pierella helvetia</i>	
<i>Pierella luna</i> (FABRICIUS, 1793)		
<i>Posttaygetis penelea</i> (CRAMER, 1777)	<i>Taygetis penelea</i>	
<i>Prepona laertes</i> (HÜBNER, 1811)	<i>Prepona omphale</i>	
<i>Pteronymia alcmena</i> (GODMAN & SALVIN, 1877)	<i>Eunica alcmena</i>	
<i>Pteronymia aletta</i> (HEWITSON, 1855)	<i>Pteronymia agalla</i>	
<i>Pyrrhogyra crameri</i> AURIVILLIUS, 1882	<i>Pyrrogyra crameri</i>	
<i>Pyrrhogyra otolais</i> BATES, 1864		
<i>Siproeta stelenes</i> (LINNAEUS, 1758)		
<i>Taygetis laches</i> FABRICIUS, 1793	<i>Taygetis andromeda</i>	

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)	
<i>Taygetis virgilia</i> (CRAMER, 1776)		
<i>Tegosa anieta</i> (HEWITSON, 1864)		
<i>Temenis laothoe</i> (CRAMER, 1777)		
<i>Temenis pulchra</i> (HEWITSON, 1861)		
<i>Thyridia psidii</i> (LINNAEUS, 1758)		
<i>Tigridia acesa</i> (LINNAEUS, 1758)		
<i>Tithorea tarricina</i> HEWITSON, 1858		
<i>Yphthimoides renata</i> (STOLL, 1780)	<i>Cissia renata</i>	
<i>Zaretis ellops</i> (MÉNÉTRIÉS, 1855)		
Papilionidae:		
<i>Battus lycidas</i> (CRAMER, 1777)		
<i>Battus polydamas</i> (LINNAEUS, 1758)		
<i>Eurytides orabilis</i> (BUTLER, 1872)		
<i>Heraclides androgeus</i> (CRAMER, 1775)	<i>Papilio androgeus</i>	
<i>Heraclides cresphontes</i> (CRAMER, 1777)	<i>Papilio cresphontes</i>	
<i>Heraclides thoas</i> (LINNAEUS, 1771)	<i>Papilio thoas</i>	
<i>Mimoides ilus</i> (FABRICIUS, 1793)	<i>Eurytides ilus</i>	
<i>Parides childrenae</i> (GRAY, 1832)		
<i>Parides erithalion</i> (BOISDUVAL, 1836)		
<i>Parides eurimedes</i> (STOLL, 1782)	<i>Parides arcas</i>	
<i>Parides iphidamas</i> (FABRICIUS, 1793)		
<i>Parides panares</i> (GRAY, 1853)	<i>Parides lycimenes</i>	
<i>Protesilaus protesilaus</i> (LINNAEUS, 1758)	<i>Eurytides protesilaus</i>	
<i>Protographium calliste</i> (BATES, 1864)	<i>Eurytides calliste</i>	
<i>Protographium thyastes</i> (DRURY, 1782)	<i>Eurytides marchandi</i>	
<i>Pterourus menatius</i> (HÜBNER, 1819)	<i>Papilio cleotas</i> & <i>Papilio victorinus</i>	
Pieridae:		
<i>Anteos clorinde</i> (GODART, 1824)		
<i>Aphrissa boisduvalii</i> (FELDER & FELDER, 1861)		
<i>Aphrissa statira</i> (CRAMER, 1777)		
<i>Archonias brassolis</i> (FABRICIUS, 1776)	<i>Archonias tereas</i>	
<i>Ascia monuste</i> (LINNAEUS, 1764)		
<i>Dismorphia theucharila</i> (DOUBLEDAY, 1848)		
<i>Enantia melite</i> (LINNAEUS, 1763)	<i>Enantia licinia</i>	
<i>Eurema albula</i> (CRAMER, 1775)		
<i>Eurema daira</i> (GODART, 1819)		
<i>Ganyra phaloe</i> (GODART, 1819)	<i>Ascia limona</i>	
<i>Glutophrissa drusilla</i> (CRAMER, 1777)	<i>Appias drusilla</i>	
<i>Perrhybris pamela</i> (STOLL, 1780)	<i>Perrhybris pyrtha</i>	
<i>Phoebis argante</i> (FABRICIUS, 1775)		
<i>Phoebis neocypris</i> (HÜBNER, 1823)	<i>Phoebis rurina</i>	
<i>Phoebis philea</i> (LINNAEUS, 1763)		
<i>Phoebis sennae</i> (LINNAEUS, 1758)		
<i>Pyrisitia lisa</i> (BOISDUVAL & LE CONTE, 1830)	<i>Eurema lisa</i>	
<i>Pyrisitia nise</i> (CRAMER, 1775)	<i>Eurema nise</i>	
<i>Pyrisitia proterpia</i> (FABRICIUS, 1775)	<i>Eurema proterpia</i>	

	La Gamba				Corcovado	
	Intensive land use	Secondary forest	Natural forest	TOTAL	DeVRIES (1978)	KUNTE (2008)
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Species (LAMAS 2004)	Differing taxon names according to DEVRIS (1987 & 1997) D'ABRERA (1995) or WARREN (in litt.)	
Riodinidae:		
<i>Ancyluris jurgenseni</i> (SAUNDERS, 1850)		
<i>Anteros allectus</i> WESTWOOD, 1851		
<i>Anteros chrysoprasta</i> HEWITSON, 1867	<i>Anteros chrysoprastus</i>	
<i>Anteros formosus</i> (CRAMER, 1777)		
<i>Calephelis browni</i> McAlpine, 1971		
<i>Calephelis iris</i> (STAUDINGER, 1876)	<i>Charis iris</i>	
<i>Calephelis laverna</i> (GODMAN & SALVIN, 1886)		
<i>Calospila cilissa</i> (HEWITSON, 1863)		
<i>Charis anius</i> (CRAMER, 1776)	<i>Charis auius</i>	
<i>Chimastrum argentea</i> (BATES, 1866)	<i>Chimastrum argenteum</i>	
<i>Comphotis ignicauda</i> (GODMAN & SALVIN, 1878)	<i>Phaenochitonina ignicauda</i>	
<i>Detritivora gynaea</i> (GODART, 1824)	<i>Charis gynaea</i>	
<i>Esthemopsis clonia</i> FELDER & FELDER 1865		
<i>Eurybia elvina</i> STICHEL, 1910		
<i>Eurybia lycisca</i> WESTWOOD, 1851		
<i>Eurybia patrona</i> WEYMER, 1875		
<i>Eurybia unxia</i> GODMAN & SALVIN, 1885		
<i>Euselasia aurantia</i> (BUTLER & DRUCE, 1872)		
<i>Euselasia aurantiaca</i> (SALVIN & GODMAN, 1868)		
<i>Euselasia procula</i> (SALVIN & GODMAN, 1885)		
<i>Euselasia regipennis</i> (BUTLER & DRUCE, 1872)		
<i>Juditha molpe</i> (HÜBNER, 1808)		
<i>Leucochimona lepida</i> (GODMAN & SALVIN, 1885)		
<i>Menander pretus</i> (CRAMER, 1777)		
<i>Mesene phareus</i> (CRAMER, 1777)		
<i>Mesene viz.phareus</i> (CRAMER, 1777)		
<i>Mesenopsis melanochlora</i> (GODMAN & SALVIN, 1878)		
<i>Mesosemia asa</i> HEWITSON, 1869		
<i>Mesosemia hesperina</i> BUTLER, 1874		
<i>Mesosemia telegone</i> (BOISDUVAL, 1836)		
<i>Mesosemia zonalis</i> GODMAN & SALVIN, 1885		
<i>Napaea eucharila</i> (BATES, 1867)		
<i>Nymphidium ascolia</i> HEWITSON, 1853		
<i>Perophtalma lasus</i> WESTWOOD, 1851		
<i>Perophtalma tullius</i> (FABRICIUS, 1787)		
<i>Pheles strigosa</i> (STAUDINGER, 1876)	<i>Lepricornis strigosa</i>	
<i>Pirascca arbuscula</i> (MÖSCHLER, 1883)	<i>Stichelia arbuscula</i>	
<i>Pseudonymphidia clearista</i> (BUTLER, 1871)		
<i>Sarota chrysus</i> (STOLL, 1781)	<i>Sarota dematira</i>	
<i>Sarota gyas</i> (CRAMER, 1775)		
<i>Setabis cleomedes</i> (HEWITSON, 1870)		
<i>Theope acosma</i> STICHEL, 1910		
<i>Theope thestias</i> HEWITSON, 1860		
<i>Theope virgilius</i> (FABRICIUS, 1793)		
<i>Thisbe lycorias</i> (HEWITSON, 1853)		
Total number of species		

Acknowledgements

We thank Hellena Binz for contributing unpublished data from her diploma thesis (currently in preparation), Robert K. Robbins and Jim Miller for help in Species determination, and Konrad Fiedler for providing information on the biology of several species.

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Picture credits

Werner Huber: The main building of the Tropical Research Station, Scientists at work in La Gamba, The 'Comedor', Martin Wiemers with students in the laboratory, Waterfall on the Quebrada Chorro, Interior of the forest of the NP Piedras Blancas, The Río Bonito in the NP Piedras Blancas

Harald Krenn: Eggs of *Heliconius melpomene*, Larva of *Heliconius melpomene*, Pupa of *Heliconius melpomene*, Imago of *Heliconius melpomene*, *Papilio* larva with everted osmaterium, Mud puddling swallowtail (*Heraclides thoas*), *Parides iphidamas* female, *Heraclides thoas* caterpillars on *Piper* leaf, *Pyrisitia nise*, *Phoebis sennae* male, *Lycorea halia* (right) and co-mimic *Heliconius hecale* (left), *Lycorea halia* larva, *Morpho helenor*, female, *Caligo eurilochus* caterpillars on a banana leaf, *Catoblepia orgetorix*, *Hermeuptychia hermes* (bottom), *Marpesia merops* (top), *Marpesia chiron*, *Hamadryas arinome*, *Anartia fatima*, *Junonia evarete*, *Siproeta stelenes*, *Colobura dirce*, *Dryas iulia*, *Dryas iulia* larva, *Heliconius* butterfly processing pollen with its proboscis, *Heliconius sapho* (both), *Heliconius cydno*, *Heliconius hecale* (both), *Heliconius sara*, *Heliconius melpomene*, *Heliconius erato*, *Eurybia lycisca* (both), *Nymphidium ascolia*, Skipper feeding on flowers of *Stachytarpheta*

Peter Weish: Morning clouds above the forest

Martin Wiemers: *Mechanitis lysimnia*, arctiid moth, Rainforest gap, *Parides erithalion* male, *Parides* larva on *Aristolochia*, *Heraclides thoas*, Pasture, *Phoebis* caterpillar, *Dismorphia theucharila*, Rainforest creek, Pupa of *Lycorea halia*, Pupa of *Lycorea halia*, *Danaus plexippus* larva on *Asclepias*, *Mechanitis polymnia*, *Mechanitis polymnia* larva, *Aeria eurimedia*, *Hyposcada virginiana*, *Ithomia celemia*, *Consul fabius*, *Fountainea euryppyle*, *Morpho helenor*, male, *Morpho helenor*, *Morpho helenor* larva, *Morpho menelaus*, *Caligo eurilochus*, *Caligo atreus*, *Hermeuptychia hermes* (top), *Magneuptychia libye*, *Pareuptychia ocirrhoe*, *Pierella luna*, *Cithaerias pireta*, *Marpesia merops* (bottom), *Marpesia petreus*, *Dynamine tithia*, *Hamadryas feronia*, *Anartia jatrophae*, *Anthanassa frisia*, *Chlosyne janais* (both), *Chlosyne janais* larva (black morph), *Chlosyne janais* larva (red morph), *Historis odius* feeding on rotten bananas, *Adelpha cytherea*, *Adelpha boeotia*, *Adelpha salmoneus* (both), *Eueides lybia*, *Philaethria dido*, Larva of *Heliconius melpomene*, Gallery forest, Riordinid caterpillar, *Euselasia regipennis*, *Ancyluris jurgensenii*, *Calephelis laverna*, *Charis anius*, *Mesenopsis melanochlora*, Light gap in the rainforest, *Arawacus togarna*, *Arumecla galliena*, *Strymon megarus*, *Hemiargus hanno*, Secondary forest, Skipper in the typical resting position, *Urbanus teleus*, *Pyrrhopyge thericles*

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