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ECOLOGY AND CONSERVATION BIOLOGY OF THE HOMERUS SWALLOWTAIL IN JAMAICA (LEPIDOPTERA: PAPILIONIDAE)

THOMAS C. EMMEL and ERIC GARRAWAY

Department of Zoology, University of Florida, Gainesville, FL 32611 USA, and Department of Zoology, University of the West Indies, Mona, Kingston 7, Jamaica

ABSTRACT.— The Homerus Swallowtail, *Papilio homerus* Fabricius (Lepidoptera: Papilionidae), once inhabited seven of the thirteen parishes on the island of Jamaica. Today, it is found only in two isolated and diminishing strongholds: an eastern population in the parishes of St. Thomas and Portland, and the western population in the rugged Cockpit Country of Trelawny and St. Elizabeth. The ecology of the remaining populations is described, including habitat characteristics, seasonality, altitudinal range, host plants, behavior and other associated biological information. A summary of the stages of life history is illustrated by color photographs. The principal threats to the continued existence of the species are (1) destruction of the virgin wet rain forest habitat, and (2) commercial collecting in the remaining small populations. The establishment of patrolled nature reserves or a national park is recommended for the remaining habitat areas, as well as a possible butterfly farming program to lessen pressures on small wild populations.

KEY WORDS: Agehana, butterfly farming, Hernandiaceae, immature stages, Lauraceae, life history, Ornithoptera, Papilio homerus, population ecology, West Indies.



Fig. 1. Papilio homerus Fabricius, adult female reared from larva collected near Millbank, Jamaica, in August 1986 (emerged 13 Sep 1986 in Gainesville, FL): a) dorsal view; b) ventral view.

The Homerus Swallowtail, *Papilio homerus* Fabricius, is one of the most spectacular butterflies in the world, and is the largest swallowtail in the Americas. With its bold black-and-yellow pattern and huge spatulate tails, no other species can be confused with this gigantic and magnificent swallowtail. It is confined to the Caribbean island of Jamaica, where it once inhabited seven of

the thirteen parishes. Today, it is found only in two isolated and diminishing strongholds: an eastern population in the parishes of St. Thomas and Portland at the junction of the Blue Mountains and the John Crow Range, and a western population in the rugged Cockpit Country of Trelawny Parish. Of the 573 recognized species of Papilionidae, it is listed as one of the four endangered



Fig. 2. Despite the central location of Jamaica in the Caribbean (a), no similar rain forest habitat with 300 inches of precipitation occurs on the other nearby major islands, and the Homerus Swallowtail is thus endemic only to Jamaica. (b) The Homerus Swallowtail, *Papilio homerus*, is the largest swallowtail in the Americas and one of the largest butterfly species in the world. Its bold yellow and black pattern with huge spatulate tails and iridescent blue scaling on the hind wings is clearly visible from hundreds of feet away, and the slow majestic flight thrills the observer. (c) The Corn Puss Gap pass in the John Crow Mts. south of Millbank, where the rain forest and the Homerus Swallowtail are threatened by the same clearing operations taking place closer to Millbank. (d) Dr. Eric Garraway of the University of the West Indies at the Island Spring site near Millbank. (e) Forest vegetation at the edge of the Island Spring study site, where *P. homerus* often come down to bask in the sun on leaves near the water's edge. (Photos © Thomas C. Emmel)

swallowtail species in the IUCN Red Data Book, "Threatened Swallowtail Butterflies of the World" (Morris and Collins, 1985).

With the present rapid rate of destruction of its habitat in Jamaica, the species has attracted recent attention as a candidate for preservation, perhaps through the formation of one or more national parks and nature reserves in the mountains of Jamaica, and also as a candidate for imminent disappearance, raising the value of perfect adults to collectors and commercial dealers who are continuing to take specimens even after the 1988 Jamaican government ban and CITES treaty ban on collecting and exporting them. The present paper summarizes our knowledge of the biology and ecology of this spectacular swallowtail from the literature and from intensive individual and collaborative research projects in Jamaica.

DESCRIPTION OF POPULATION AREAS

PHYSIOGRAPHY AND BIOGEOGRAPHY

A better understanding of the distribution and factors controlling the range for *Papilio homerus* may be obtained by a brief look at the physiography of the island. The following descriptions follow those of Cruz (1977), with additional information from other sources.

Jamaica lies at 18° N latitude in the western Caribbean, approximately 150km south of the nearest point on Cuba and some 200km west of Hispaniola, the only two islands in the West Indies to exceed Jamaica in size. The nearest mainland area is Honduras in Central America, approximately 610km to the southwest. Jamaica has a land area of 11,740 square km and much of the terrain is quite mountainous, with more than half of the island exceeding 305m (1,000ft) in elevation. The Central Upland plateau at 600 - 915m, and the Blue and John Crow mountain ranges to the east, comprise most of the higher mountains.

The Blue Mountains run approximately one-third the length of the island, extending westward from the John Crow Range at the eastern edge of the island to Mt. Telegraph (1,275m). Their maximum height reaches 2,155m. The Central Upland plateau contains the Dry Harbor Mountains (in St. Ann Parish) and the Mocho Mountains (Clarendon Parish), separated by the Main Ridge group. In the western third of the island is the Cockpit Country, where sinkholes from 200 - 600ft deep form the characteristic topography of west-central Jamaica. A succession of cone-like hills with deep pits at the base of each "cockpit" (so named because they resemble cock-fighting pits or arenas) represent typical karst country, with underground drainage, many subterranean rivers, sinkholes and caves. In the Cockpit Country's 400 square miles, there are no flat surfaces nor any easily navigable paths.

Mount Diablo (1,000m elev.), located in St. Catherine Parish in the central portion of the island, is a very precipitous, calcareous plateau, similar in terrain to the Cockpit Country.

CLIMATE

Rainfall varies greatly throughout the island, depending on the local physiography. Moisture-laden easterly tradewinds blow throughout the year. These are uplifted and cooled, with resultant precipitation, as they cross the John Crow Mountains and then the northern flank of the Blue Mountains. Hence the parishes in the northeast of Jamaica, particularly Portland, receive heavy rainfall with an average annual rainfall of 381cm, and actually reach 650cm (300 inches) at the junction of the Blue Mountains and the John Crow Mountains. (In contrast, the dry southern parish of St. Andrew receives only 89cm of rain.) In the Cockpit Country, the area gets 150-200 inches of precipitation a year.

Rainfall here is quite seasonal, with the wet season and heaviest rains occurring in May and June and again from August to November. The major dry season is from January to March. *Papilio homerus* seems to require quite wet sites with heavy rainfall, and Garraway has photographed the larvae actually drinking rain droplets from the surface of a leaf. Both of us have observed that the larvae cannot survive in areas of less than close to 100% humidity.

VEGETATION AND PLANT COMMUNITIES

Of the eight major vegetation communities described by Asprey and Robbins (1953), Papilo homerus habitats include Wet Limestone Forest and Lower Montane Rain Forest. Wet Limestone Forest develops on limestone rock where the rainfall is over 190cm and may be as high as 380 cm. This forest occurs largely inland at elevations from 300-780m. Many tree species are present, together with epiphytes, lianas, aroids, and bromeliads. The canopy is about 20m in height, quite dense, and has emergent trees towering up to 30m or more. For P. homerus habitats, this forest type is present particularly in the Mount Diablo area in St. Catherine Parish and in the Cockpit Country. Some of the characteristic trees include broad-leaf (Terminalia latifolia [Combretaceae]), Jamaican cedar (Cedrela odorata [Meliaceae]), prickly yellow (Fagara martinicensis [Rutaceae]), and figs (Ficus spp. [Moraceae]). In recently cleared areas where secondary succession is occurring, one may find trumpet trees (Cecropia peltata [Urticaceae]), citrus trees (Citrus spp. [Rutaceae]), and pimento (Pimenta officinalis [Myrtaceae]). Some of the species from the preceding plant community extend up into the next zone, but the Lower Montane Rain Forest basically occurs at higher elevations, up to 1,070m. Annual rainfall here normally exceeds 250cm and may reach nearly 700cm. Although, as will be pointed out later, much of this community has been destroyed by human disturbance, this Lower Montane Rain Forest is still present in the Blue and John Crow mountains. Particularly nice forest occurs in Corn Puss Gap, located in St. Thomas Parish, which lies at an elevation of 610 - 686m on the southwestern slopes of the John Crow Mountains. This forest consists of many of the tree species found in the Wet Limestone Forest and has a similar general appearance. Characteristic trees of this plant community also include mountain guava (Psidium montanum [Myrtaceae]), Santa Maria (Calophyllum jacquinii [Guttiferae]), cobywood (Matayba apetala [Sapindaceae]), rodwood (Eugenia sp. [Myrtaceae]), and many others, including tree ferns (Cyathea spp. [Cyatheaceae]).

Above the Lower Montane Rain Forest is the Montane Mist Forest, which covers the upper reaches of the Blue Mountains in the island's eastern end. This region of high atmospheric humidity has a high annual rainfall of over 200cm, and mist

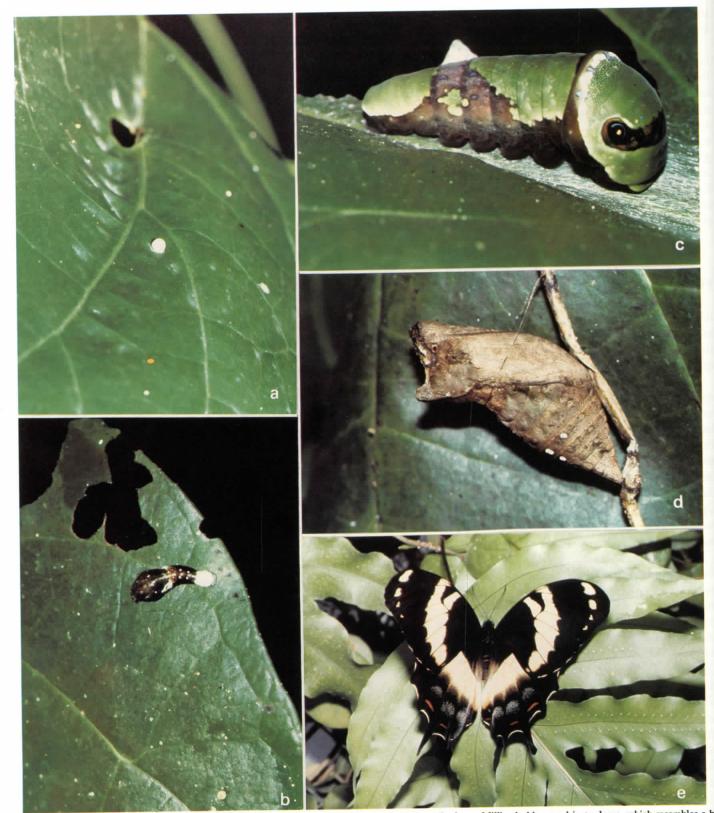


Fig. 3. A brief overview of the life history stages of *Papilio homerus*: a) egg on a *Hernandia* sp. leaf near Millbank; b) second-instar larva, which resembles a bird dropping (the feeding damage is readily visible and makes it easy to find the larvae looking up through the trees); c) the mature larva, showing the lateral pattern of markings; d) the pupa, brown phase (two color phases are known, brown and green, in the eastern population); e) the adult butterfly, freshly emerged. (TCE)



Fig. 4. Life history stages of *Papilio homerus*: a) a mature larva on a *Hernandia catalpaefolia* leaf, showing the huge size of the larva compared to a man's hand and fingers; b) a young seedling of *Hernandia catalpaefolia* in the forest near Millbank; c) an adult showing the underside pattern and the natural twisting of the spatulate tails; d) frontal view of a mature Homerus larva, showing the snake-like markings on the thorax; e) a young seedling of *Hernandia troyiana* in the forest near Elderslie, in the Cockpit Country (this endemic plant serves as the foodplant of the western Homerus population, and has smaller leaves with less-regular margins. Because the larval stages last 45 days and move very little, they can easily be observed on a predictable daily basis and would be interesting to visitors in the proposed national park, in addition to seeing the wild adults. (TCE)

covers the ridges and forest almost continuously. The forest also has a low canopy, seldom exceeding 12m. While *Papilio homerus* does not normally reach these elevations of 1,100m or more, the structural integrity of the higher habitats is important to supply the water flow and atmospheric moisture for the successful survival of *homerus* at lower montane elevations.

The Hernandia (Hernandiaceae) trees that serve as larval host plants for homerus occur primarily in the first zone mentioned above, namely the Wet Limestone Forest. The larval stage, which lasts about 45 days and has five instars, requires very high humidity such as is experienced along montane stream canyons descending through the rain forest. Captive-rearing attempts in both Jamaica and Florida have shown that *Papilio homerus* is extremely sensitive to environmental change in the larval stages, and the present clearing of the forest in its remaining habitat areas, with concommitant decrease in local humidity levels, bodes ill for the species' long-term survival even if a screen of riparian vegetation was left after clear-cutting the surrounding slopes.

DESCRIPTION OF THE ADULT

Papilio homerus is the largest species in the true swallowtail genus Papilio, and it rivals in size some of the birdwings (Troidini) of Southeast Asia as well as Papilio antimachus of West Africa. It has a forewing length of about 75mm, or a wingspread (in some females) that approaches 6 inches (15cm). Its nearest relatives are in Central America and Mexico: P. garamus Hubner and P. abderus Hopffer, neither of which approaches P. homerus in total size or dramatic beauty. Papilio garamus is found from Mexico and Panama. In Costa Rica, P. garamus occurs on east and west slopes of the higher mountain ranges in cloud forest habitats from 1,200-2,800m elevation, somewhat higher than P. homerus in Jamaica (DeVries, 1987). P. garamus flies in the central eastern and western mountains of Mexico from February to November; its larval host is Persea americana (Lauraceae) (Beutelspacher and Howe, 1984). Papilio abderus occurs in the mountains of eastern Mexico, Guatemala and Honduras from March to October; the larvae feed on Lauraceae (Beutelspacher and Howe, 1984).

The sexes of *P. homerus* are similar in coloration and pattern, though the females average notably larger in size. The ground color of the dorsal surface of both the forewing and hindwing is a blackish or very dark brown. A broad yellow discal band extends across both wings. On the hindwing, there are powdery blue, postdiscal spots and brick-red submarginal lunules. The relatively long and widened spatulate tail is quite distinctive among American swallowtails, to be found elsewhere (and exceeded perhaps) only in Asian species such as *Agehana maraho* Shiraki & Sonan of Taiwan. The undersides of the forewing and hindwing are similar to the upper surfaces in their dark brown ground color. However, the yellow-brown discal band is much more narrow on the hindwing ventrally, and it is dusted with blue scales. Dark markings occur between the diffuse red and blue spots (see color figures).

EARLY STAGES OF THE LIFE HISTORY

Papilio homerus was described by Fabricius in 1793, and the species has been avidly pursued on Jamaica ever since. As a result, there is a considerable bibliography for the species. The first person to describe its habits was Rutherford (1878), and the following year Grosse (1879) announced the discovery of its egg and larva. Hampton (1893) described the mature larva, while Taylor (1894) described the mature larva and the pupa. Swainson (1901, p. 77) provided a brief description of the larva as well. Brown and Heineman (1972) summarized the published observations to that year, and Collins and Morris (1985) summarized the life history in brief form, based on unpublished data supplied by Thomas J. Turner. Turner (in press) has prepared a comprehensive report on the life history stages. Garraway and Emmel have each reared the species in Jamaica and in Florida. Our collaborative studies from 1986 to present have produced the color photographs by Emmel which accompany this article. We here present a brief descriptive summary of the life history stages.

EGG: The spherical egg is approximately 1.5mm in diameter and is pale green in ground color. This color changes to a pale yellow and finally dark brown before the egg hatches, eight days after oviposition. The surface of the egg is smooth.

LARVA: The first through third larval instars have a brown head capsule and a light brown ground color across the thoracic and abdominal segments, with the posterior abdominal segments becoming blackish until the last two abdominal segments are reached, which are white dorsally. Each of the first three instars also has a white "saddle" marking with a brown center; this saddle expands diagonally forward down both sides from the dorsal surface of the second, third, and fourth abdominal segments. There are short, simple, black hairs on the head, the sides of the thorax, and the sides of the dorsal and lateral portions of the abdominal segments. Short, stout whitish tubercles are placed in two dorsolateral rows and laterally in the locations that are occupied by bright blue spots in the fourth and fifth instars. Turner (in press) found that the average body lengths of the 51 larvae he studied were 9.0mm at maturity for the first instar, 15.0mm at the end of the second instar, and 26.0mm at the end of the third instar. Each of the first two larval stages lasts five days, while the third larval instar lasts about nine to ten days.

After the larva molts to the fourth instar, the pattern portions that were white in the earlier three instars turn green. The thoracic segments and the first abdominal segments are greatly enlarged at this stage, and give the larva a quite bulbous appearance in contrast with the narrower, normal-sized abdominal segments. Very conspicuous eyespots occur in the vicinity of the tubercles on the third thoracic segment. Also, a white band runs along the posterior edge of this anterior hump and two blue spots occur in it on each side of the dorsal surface. The head is now more-or-less hidden below the anterior thoracic segments and is pale brown in color. Contrary to the negative report by Swainson (1901), the larva does have an osmeterium, which is brick-red in color. The gray, white, and green saddle across the dorsal surface at the front of the abdomen is bordered by two dorsolateral rows of blue spots (one spot per segment on each side), one lateral blue spot midway up from each third proleg abdominal

segment, and green patches on the sides of the fourth proleg abdominal segment and across the dorsolateral surface of all the remaining abdominal segments as in the photographs. Turner (in press) found that this larval instar lasts an average of ten days and reaches approximately 40.0mm in length.

When the fourth instar molts, the fifth instar larva feeds for another 15 to 20 days (sometimes to four weeks) and reaches up to 70mm in length. It is quite heavy, weighing more than any other butterfly larva either of us have ever reared (exceeding even Ornithoptera priamus in mass). The head is grayish-brown, with a brick-red osmeterium that is extended from the prothorax when the larva is annoyed. The conspicuous lateral large eyespots are located at the ends of a broad brown band crossing the green thorax. Posterior to this thoracic region is a white band, bordered posteriorly by brown sweeping down and forward under the thorax and backward under the abdomen. This white band has two bright blue spots on each side of the dorsolateral surface. Green dorsal and lateral markings follow posteriorly over the brown ground color of this larva (see photograph), as in the fourth instar. In all instars, the larva typically rests on the midrib or near the center of a host plant leaf during the day, and feeds primarily at night.

PUPA: Just before changing to the pupal stage, the larva's ground color becomes quite dull green and may turn yellowish, mottled with very light brown. The brown and white bands become purplish black, and as the larva prepares to shed its skin, the entire surface turns dusky. The pupa may occur in several color forms. The most common form in our experience is brown, but the pupa may also be gray or brown mixed with some dull olive green. There are a series of six small white dorsal spots and two lateral spots (one on each side) on this basic ground color of the second and third abdominal segments. The pupal stage lasts from 10 to 14 days.

LENGTH OF LIFE CYCLE: The length of the life cycle varies from about 63 to 78 days from time of oviposition of the egg to emergence of the adult.

HOST PLANTS

The laval foodplants of *Papilio homerus* have been erroneously identified from time to time in published records (Brown and Heineman, 1972). The only verified foodplants that we have are *Hernandia catalpifolia* Britton & Harris (locally known as Water Mahoe, Water Wood), *H. jamaicensis* Britton & Harris (Pumpkinwood, Suck Axe), and *Ocotea* sp., probably *leucoxylon* (Sw.) Gomez Maza (Loblolly Sweetwood). The first two species are in the family Hernandiaceae, which has just four genera worldwide, contains about 65 species, and is pantropical in distribution. Both of the Jamaican species of *Hernandia* are endemics, whereas *Ocotea* is in the Lauraceae and is found throughout the West Indies.

Hernandia catalpifolia is the host plant for the eastern population of *Papilio homerus* and is locally common in Portland and St. Thomas parishes by streams and in damp ravines in submontane woodlands at moderate elevations of 1,500-2,100ft (450700m). It flowers in February and September, and fruits in February to March (Adams, 1972). Garraway has observed that seedlings of *Hernandia* start in secondary-succession patches, where bamboo has sprouted thickly in the regenerating forest.

Hernandia jamaicensis serves as the host plant for the western population of Papilio homerus today. It is locally distributed in the western and northwestern parishes, in woodlands on limestone, where it occurs from 1,200-2,200ft (470-700m). It flowers from July to September, and has fruits from December to March (Adams, 1972). Its use as a host for the *P. homerus* populations in western Jamaica was first discovered by Thomas Turner in October 1971, where he observed oviposition on *H. jamaicensis* in the Cockpit Country.

Oviposition on Ocotea (probably O. leucoxylon) was first observed by Lewis (1949) in the Cockpit Country, and Turner observed oviposition on an Ocotea species at Corn Puss Gap in August 1969. Since this tree also occurs on Mount Diablo in the center of the island, it may have served as a host for the former P. homerus populations there. Another potential foodplant for that former population on Mount Diablo is Hernandia sonora Linnaeus, which was introduced from Mexico into forestry plantations on Jamaica but the species has not become naturalized and is still known in Jamaica today only in cultivation, at sites near Moneague on the northside of Mount Diablo.

DISTRIBUTION AND POPULATION NUMBERS

Since its original description in 1793, *Papilio homerus* has been recorded from seven of the thirteen parishes on the island of Jamaica. It is uncertain from the early records whether *P*. *homerus* was ever continuously distributed through the mountains. Within the last century, it has been found only in three areas; it still survives in two of these, but the populations in each locality appear to be contracting and presently occupy perhaps ten square kilometers of forest or less at these sites. Contrary to one report (D'Abrera, 1981), there are no records for this species on any other Caribbean island.

Eastern Population: The largest population area, and the region from which virtually all of the existing specimens in the museum collections worldwide have come, is the eastern population in St. Thomas and Portland parishes, centering around Corn Puss Gap where the Blue Mountains meet the John Crow Range. The classic locality here is the stream above the old resort center of Bath (full name, Bath of St. Thomas the Apostle) in the Blue Mountain Range. As recently as 1981 through 1986, upwards of 200 adult sightings (probably multiple viewings of many fewer individuals) could be seen in one day in this region, according to one report, and three Peace Corps volunteers were reported to be breeding P. homerus there in 1985-86 in considerable numbers, of up to 86 larvae. The sex ratio in the area of Bath was estimated to be six to seven females per one male (Anonymous report to Emmel, June 1986). One Japanese lepidopterist was said to have purchased 17 P. homerus specimens in a single commercial deal in 1986.

On the other side of the Blue Mountains, local collectors are also appearing more and more frequently in the Rio Grande

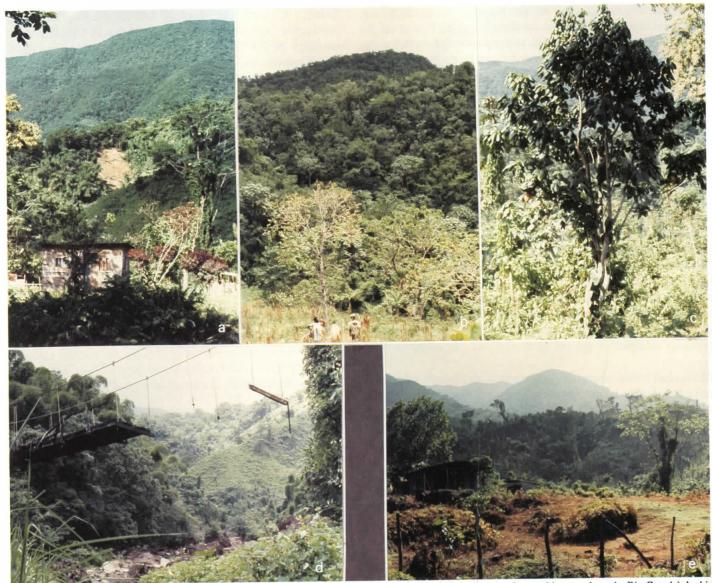


Fig. 5. Habitats and land clearing in the Homerus Swallowtail population areas: a) scene at Millbank (a settlement of several houses along the Rio Grande), looking east at the John Crow Mts., where a new 1986 clearing in the edge of the eastern Homerus population's rain forest habitat above White River is visible; b) the rain forest at the edge of a cleared pasture area near Elderslie in the western population area, where Homerus was present about a half-mile back into the forest along a stream; c) a large *Hernandia catalpaefolia* tree (50ft in height) at Millbank, left behind when the forest was cleared along the Rio Grande; d) the upper Rio Grande river at Millbank, showing the remnants of an old suspension bridge where the trail to the Black Foot Spring site crosses the river (some clearing on the slope is visible in the background); e) a small farm at Millbank in the foreground and cleared hillsides planted in Caribbean pine in the background, representing a scene of the linked fates of all the montane rain forest in Jamaica unless an inviolate reserve area is saved very shortly. (TCE)

Valley, south of Port Antonio. Here, *P. homerus* occurs on the edges of the John Crow Mountains and the Blue Mountains. The John Crow Mountains are essentially a massive slab of limestone sitting on a bed of shale, and where streams emerge at that juncture, *Hernandia* trees occur in abundance. The Rio Grande Valley supports several villages such as Millbank, and many outlying small farms whose owners utilize the steep slopes for subsistence gardens. Thus the forest has been cut extensively here over the years for agricultural purposes, employing slash-and-burn techniques. These small farmers do try to "terrace" the cut slopes, but the run-off from the heavy rains destroys both crops and soil. Thus the patch of land can be used for four to five years by the farmer before it is abandoned. On an optimistic note, the forest is capable of regenerating quickly with the high

rainfall. Bamboo grows very thick during secondary succession, and seedlings of *Hernandia* start in these areas, as long as some *Hernandia* trees have been left immediately adjacent to the watercourses by the farmers. Unfortunately, human population growth in recent decades has reached the point where the forest cannot re-establish itself fully through succession before it is cut and burned again.

Forest Reserve areas were established in the region by the central government and are supposed to be preserved as watershed areas. In actual fact, there is no real enforcement and the local people have ignored the prohibition against cutting. The only remaining uncut Forest Reserve is protected by its distance from a village. Plant diversity is very rich here for Jamaica, with 228 species of vascular plants found in 1.8 sq km (Kelly, 1986).

However, commercial collecting and subsistence agriculture are not the main threats to the survival of the eastern populations of the Homerus Swallowtail. In 1979, FIDCO (Forest Industries Development Company) was formed by the Jamaican government to facilitate involvement with the World Bank and the Food and Agricultural Organization (FAO) in a major project in commercial forestry. The aim was to make Jamaica self-sufficient in wood needs by the year 2000. FIDCO has been cutting 2,000 hectares of rain forest a year to plant Caribbean Pine, Pinus caribbea var. hunduriensis (Pinaceae), and this tree is being planted throughout the Rio Grande area. These pine plantations can grow to maturity in 20 years, hence their attractiveness as a commercial venture. Unfortunately, they present a sterile environment which allows high winds and fire to change the landscape. Whole slopes are bare of any other vegetation, and farming opportunities are destroyed as a consequence. Hurricane Gilbert's direct hit on eastern Jamaica in 1988 also devastated the remaining forest in this eastern population area, rendering it virtually leafless for over three months. There is every evidence (Emmel and Garraway, 1986; Garraway, 1990) that the eastern population area, at least on the northern side of the Blue Mountains and at their junction with the John Crow Mountains, will be destroyed by human forestry activities within several years, unless an inviolate biological reserve or national park is created there almost immediately.

Some idea of the drop in numbers of this species in the eastern population may be had by a review of numbers in the literature. In 1902, a total of 44 specimens of homerus were taken at Cuna Cuna Pass near Corn Puss Gap in ten days between July 10 and 20 (Robinson, 1903). In 1939, Andre Avinoff of the Carnegie Museum and his nephew, Nicholas Shoumatoff, collected about 40 individuals of Papilio homerus in the Blue Mountain range in the vicinity of Bath (Avinoff and Shoumatoff, 1940). Between those two dates, Kaye (1926) found P. homerus to be reasonably common, yet Longstaff (1912) did not encounter this species during his extended December 31, 1906 to March 8, 1907 collecting visit to Jamaica. By 1945, Walker thought that "homerus is rapidly disappearing from the Eastern Blue Mountains." He noted that earlier authors had found the swallowtail abundant at Bath and at Cuna Cuna Pass between 1867 and 1938. The St. Thomas side of Corn Puss Gap was cleared for farming and logging during 1945-46 (Barry, 1945) but over the next 20 years, secondary succession began and T. J. Turner noted a temporary increase in numbers of P. homerus in the Corn Puss Gap area between 1967 and 1969, particularly in 1968. This temporary increase may also have been associated with unusually high rainfalls in those three years. Corn Puss Gap, which separates the John Crow and Blue mountains, has ten streams on its northern side and about five streams on the southern side, creating a rich habitat for the Hernandia catalpifolia hosts of the Papilio homerus population here.

The fragmentation of the habitat in the upper Rio Grande Valley and adjacent Blue Mountains and John Crow Mountains where P. homerus and its host plants have occurred in the past has today led to an extraordinary drop in the population of P. homerus here, noted by all recent lepidopterist visitors, and careful capture-recapture studies are badly needed to assess the

present population size. On our 1986 visit to this area at the supposed height of the season in August, four of us (Emmel, Garraway, James Nation Jr., and Orlando Wilson) saw only one adult *P. homerus* and several larvae in an entire day of careful observation.

Central Mountain Population: The central population is the least known of the three. There is only fragmentary evidence for the population that formerly occurred on Mt. Diablo. Kaye (1926) reported that the butterfly was seen near Ewarton on the north slopes of Mt. Diablo through 1925. None were seen here by Avinoff and Schoumatoff during their 1939 expedition and on five earlier trips by them. This central region was cleared for agriculture and by logging operations earlier than the eastern or western population sites where *P. homerus* still survives at a precarious level today.

Western Population: The western population of Papilio homerus was discovered in the Cockpit Country in 1939 by Avinoff and his nephew, Nicholas Schoumatoff (Avinoff and Schoumatoff, 1940). This wild and remote region, where some virgin forest remains in the midst of extremely rocky terrain, is probably the least disturbed of the sites where the species has been found. The Cockpit Country of Trelawny Parish receives up to 200 inches of rain a year and has a second endemic species of Hernandia (H. jamaicensis) to serve as a host. Emmel and Garraway visited the Cockpit Country in August 1986 and verified that the population there is still surviving. In fact, we saw more adults in this region than in the eastern region. The extraordinarily rough country, lack of roads, and abundance of marijuana farmers who dislike intruding strangers will probably keep this population safe for a few more years than the eastern population, although the marijuana cultivation means that the forest is being slowly cleared for that and other farm crops. The limestone rocks with razor-sharp edges, sinkholes, jagged canyons, perilously slippery clay and wet undergrowth serve to prevent any pursuit of the adults, or at least slow it to such an extent that it is almost impossible to capture any P. homerus in this region. We observed them sailing 30-50ft above the ground at canopy level, wherever a sunlit opening occurred over a valley in the midst of this area. This region likewise needs careful censusing of adults, perhaps by using natural damage to the wings as markers and carrying out close observation of the flying adults via binoculars, to assess population size and sex ratio.

PHENOLOGY AND DAILY ACTIVITY

In the eastern population, *Papilio homerus* has been recorded from January, February, March, April, June, July, August, September, October, November and December. Because of the scarcity of adults in collections, and the lack of extended rigorous observations in the field throughout the year to date, there is a fair amount of controversy over what times of the year that the adults are most abundant. In the vicinity of Bath, in the Blue Mountains, the last week of September through October 15 and December were considered to be the best months in the first half of the 1980's (Anonymous report to Emmel, 1986). Turner (in

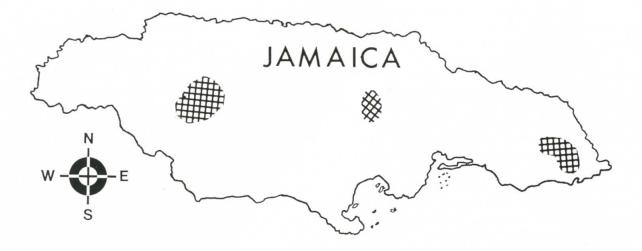


Fig. 6. Map of the island of Jamaica showing the historical range of the Homerus Swallowtail, Papilio homerus Fabricius, according to literature and museum specimen records.

litt.) considers adults to be scarce between December and March, and that the main flight period is between June and August above the Rio Grande Valley. Orlando Wilson, a resident of Milbank who has considerable experience rearing and observing *P*. *homerus* in the wild, believes that August is one of the poorer months to find *P. homerus* in flight.

No information on flight periods was recorded by early lepidopterists visiting the central populations on Mt. Diablo, near Ewarton in St. Catherine Parish.

In the western population, specimens have been seen in June and August. In terms of daily activity, Avinoff, who had considerable experience with this species, noted that "the butterfly is on the wing all day and may be seen from 9:00 in the morning to as late as 6:00 in the afternoon" (Avinoff manuscript, quoted in Brown and Heineman, 1972). He noted that it flies very slowly, usually singly, and frequently alights either on the branch of a high tree, or on broad-leaved shrubs or tree branches near the ground in a clearing. It basks on a sunlit leaf with its wings open flat, but in the evening it sits upright with compactly folded wings. C. B. Lewis (1949) also found the P. homerus population in the Cockpit Country on 2 Aug 1949, following the trail from Quickstep leading westward and more-or-less following the boundary between St. Elizabeth and Trelawny parishes. In the area known as Payne's Patent, he saw at least 20 Papilio homerus but the nature of the terrain was such that although several flew close to him, he was unable to capture any. He observed one female behaving as though it was ovipositing on a Sweet-wood (Ocotea sp.). He also noted that the Cockpit specimens seem to be slightly smaller and to be particularly dark on the wing, compared to those he had seen in St. Thomas Parish in the eastern areas of the Blue Mountains. He noted that people in the Cockpit District said that in 1949, the swallowtails were most abundant during the month of June.

ADULT BEHAVIOR

The typical flight behavior of Papilio homerus males and

females is soaring high overhead in the canopy area, with dark, dull-colored undersides visible as a silhouette against the sky. Occasionally, a butterfly alights on a tree branch or bush at low levels in the forest, such as at the edge of a sunlit clearing along a stream. But more commonly, it alights high in the canopy or on an elevated sunlit branch. Avinoff (quoted in Brown and Heineman, 1972, from an unpublished manuscript) has very accurately described the particular kinds of localities where P. homerus prefers to fly. "The butterfly favors slopes, gullies which form a horseshoe from 30-200ft [9-60m] wide. Such a place may be formed by a stream or by a clearing in the woodland. This butterfly is apparently fond of streams over which it hovers in its leisurely flight. Usually it would sail rather slowly, flapping its wings occasionally. The butterfly is not easily frightened; occasionally, it may not even be disturbed by a faulty swing of the net and would continue a non-hurried flight well within the reach of catching. Nevertheless, this powerful insect is capable of flying quite rapidly, especially when it sails high above the tall trees of the jungles. The regions most readily frequented by P. homerus are from 1,000-2,000ft [300-600m] and within the limits of an altitude of 500ft [150m] as mentioned by Kaye. On Cornpuss Gap, at an altitude considerably above 2,000ft [600m], it is entirely in its native ecology."

Turner (in litt.) has described the seasonal movement of adults down slopes to lower elevations. From April to the end of August, the adults are found in the cooler mountains. When the minimum nighttime temperature reaches about 67° F, the adults seem to move down the mountain slopes. From September to March, he finds that the adults move about 1,000ft lower to warmer temperatures, where there are also more foodplants. Turner (in litt.) has noted that this behavior is concentrated in the afternoon hours, when at about 1300 h, adults begin to move down the mountain slopes at about 4m above the streambed. (In past years, when this butterfly was abundant, this mass movement was quite noticeable and most specimens were noted to be males.) By 1500 h, this daily flight movement largely ceased.

Adults are not observed nectaring very often, but when they do

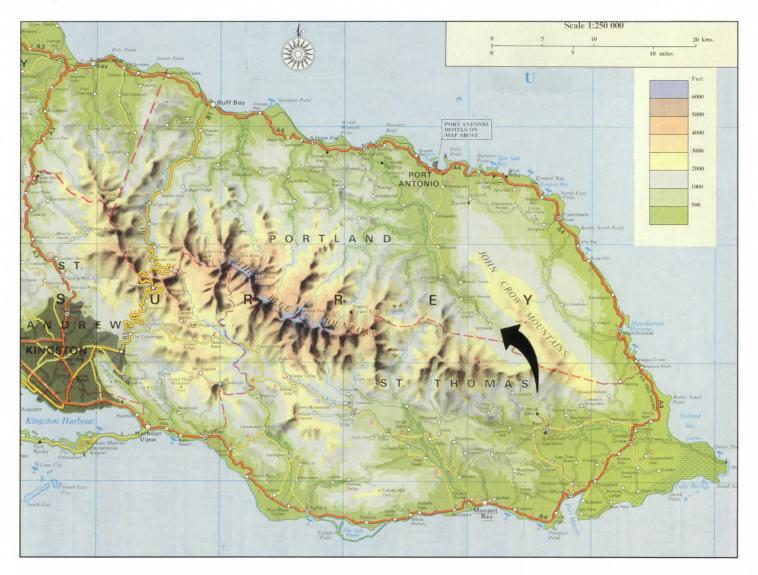


Fig. 7. Map of Jamaica: Eastern end of Jamaica showing the location of the eastern population of the Homerus Swallowtail in the vicinity of Millbank, at the juncture of the John Crow and the Blue mountains.

descend to clearings, they may be seen nectaring on climbing shrubs or small trees in the genus *Cissus* (Vitaceae) (Walker, 1945) and on *Spathodia campanulata* Beauv., colloquially called African Tulip Tree (Bignoniaceae), a common introduced tree that grows up to about 1,500ft elevation (Lewis, 1947).

CONSERVATION BIOLOGY

The plight of *Papilio homerus* has been attracting increasing attention from biologists and naturalists around the world in the last two decades, particularly during the 1980's. John R. Parnell, formerly of the University of the West Indies, produced a film with Eric Garraway in 1984 entitled "*Papilio homerus*, the Vanishing Swallowtail," which documented aspects of the butterfly's biology, ecology, and its threatened extinction resulting from destruction of its habitat. Thomas W. Turner, formerly of the University of the West Indies, has worked extremely hard through the Xerces Society to promote the study of *Papilio homerus* and its conservation. Eric Garraway has studied the biology and ecology of *Papilio homerus* intensively since 1984,

and is currently preparing a joint paper with Parnell which will include details of rearing of this species in cages from early larval stages to adult. In 1985, N. Mark Collins and Michael G. Morris presented a concise summary of the biological and conservationrelated information available on the species in their IUCN Red Data Book, "Threatened Swallowtail Butterflies of the World" (pages 297-298). Much of their information was provided by Thomas W. Turner, who has several important unpublished manuscripts documenting the life history and historical decline of the distribution of this species on the island. After joint field work in August 1986 throughout the range of P. homerus, Emmel and Garraway (1986) presented a detailed report and grant proposal to the World Wildlife Fund, urging that a thorough scientific study be done immediately to survey the distribution and abundance of the Papilio homerus populations and the species' ecological requirements. In 1989-90, Garraway presented a proposal to the Jamaica Agricultural Development Foundation for a study of the conservation of Papilio homerus through commercial rearing on butterfly farms, and collaborative field studies on the species' biology with Emmel and Parnell.

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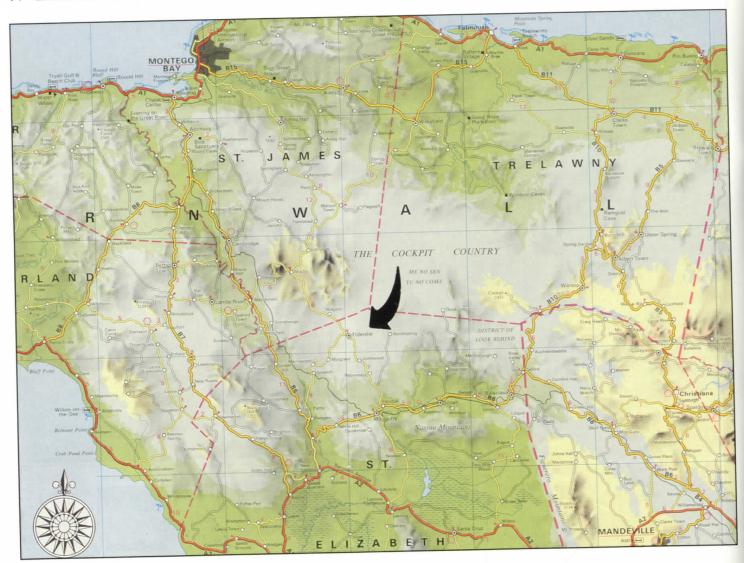


Fig. 8. Map of Jamaica: Western end of Jamaica showing the western population in 1986 in the vicinity of Enderslie, in the Cockpit Country southeast of Montego Bay.

There is no question that this butterfly is presently in a very critical state as regards its continued existence in Jamaica. The government-sanctioned deforestation and pine-replanting program is destroying its unique montane rain forest habitat at an extremely disturbing rate. The Homerus Swallowtail is restricted to virgin forest on mountain slopes and along mountain streams at moderately low elevations, principally from 150m to about 600m above sea level. The two known localities are apparently restricted to a relatively few square kilometers of appropriate habitat where the two verified endemic larval foodplants grow. A third known population in the center of Jamaica is believed to have become extinct in the late 1920's. These remaining two populations, located in unique montane rain forest in areas of exceptionally heavy rainfall (200-300 inches per year) are threatened because of the forest being rapidly cleared for the planting of exotic pine trees, coffee, and cash crops, the latter being primarily involved in the Cockpit Country.

Little hard information is available on the population status and dynamics of the surviving populations. Until an August 1986 scouting trip by Garraway and Emmel, the Cockpit Country site had not been visited by biologists for the preceding ten years and its status was totally unknown. The eastern population was being anecdotally monitored by a local naturalist, Orlando Wilson, who was being prompted by commercial dealers to collect and sell specimens to U.S. and German collectors. Prices abroad have ranged from US\$400 to \$1,500 per specimen in the 1970's and 1980's because of the rarity of available adult Homerus Swallowtails in the marketplace. From all indications, the adults begin to suffer wing damage in the first two or three hours of flight in the forest (they have very soft, fragile wing edges, though possessing strong and resilient venation towards the body, and a number of insectivorous bird species attack them on the wing). Thus collectors worldwide would prefer to secure perfect, reared adult specimens as opposed to tattered wild-caught males and females.

With these factors in mind, then, a strong conservation biology program involving this species should carry out the following objectives:

 an intensive study of the population ecology and present distribution of the Homerus Swallowtail, including a determination of population numbers and the basic environmental parameters characteristic of the chosen habitats where the swallowtail occurs;

- (2) a precise determination of the critical features of the life history that might contribute to increased survival;
- (3) a negotiation of appropriate conservation measures with the Jamaican government to preserve the rich montane forest in and surrounding the known remaining eastern Homerus habitats, at the *least* with the result of altering or suspending the planned cutting schedule for planting of more introduced pine plantations;
- (4) an analysis of the possibilities of a cottage-industry, butterfly-farming program and a captive-breeding program to relieve commercial pressures on the species and to also relieve possible in-breeding depression in the two small isolated wild populations that exist today, through cross-breeding in captivity and release of adults again into nature;
- (5) an undertaking of an international campaign to raise funds for preservation of the montane *Papilio homerus* sites as the core areas of a Jamaican Mountain National Park (of which the Homerus Swallowtail would be an internationally recognized and acclaimed keystone species symbol), thereby preserving not only the butterfly, but also the last significant virgin montane wet forest in Jamaica.

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This summary of the biology and ecology of Papilio homerus in Jamaica has depended on many sources in addition to our personal field work in Jamaica. We would especially like to thank Dr. Thomas W. Turner of Safety Harbor, Florida, for his great encouragement of the study of Papilio homerus, his sharing of much unpublished material over the past five years, and his constant encouragement to pursue sources of funding to preserve this species in the wild. We would also like to thank Dr. John R. Parnell, formerly of the University of the West Indies and now Chief Horticultural Analyst for the City of St. Petersburg, Florida, for his great help in the project and sharing of several manuscripts. James L. Nation, Jr., then Technical Research Assistant in the Department of Zoology, University of Florida, and now of the University of Mississippi, provided invaluable field support on our joint field work in Jamaica and in rearing P. homerus in the greenhouses at the University of Florida in August 1986.

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REFERENCES CITED

Aaron, E. M.

- 1893. New Localities for Papilio homerus. Canad. Ent. (Ottawa), 25:258.
- Adams, C. D.
- Flowering Plants of Jamaica. Kingston: Univ. West Indies. 848 pp.
- Avinoff, A., and N. Shoumatoff
- 1940. Jamaican summer. Carnegie Mag. (Pittsburgh), 14:175-182. Barry, A.
- Butterfly Notes. Nat. Notes Nat., Hist. Soc. Jamaica (Kingston), 11(22):161-163.
- Beutelspacher, C. R., and W. H. Howe.
- Mariposas de Mexico. Fasiciculo I. Mexico City: La Prensa Medica Mexicana. 128 pp.
- Brown, F. M. and B. Heineman.
- 1972. Jamaica and its butterflies. London: E. W. Classey. 478 pp. Collins, M.
- 1986. Butterfly Demand Growing. World Wildlife Fund News (Washington), 42: July - August 1986.
- Collins, N. M., and M. G. Morris.
- 1985. Threatened Swallowtail Butterflies of the World: The IUCN Red Data Book. Cambridge: IUCN. 401 pp.

- 1977. Ecology and behavior of the Jamaican woodpecker. Bull. Fla. St. Mus. (Gainesville), Biol. Sci., 22(4):149-204.
- DeVries, P. J.
- 1987. The butterflies of Costa Rica and their natural history. Princeton: Princeton Univ. Press. 327 pp.
- Emmel, T. C.
- 1975. Butterflies: their world, their life cycle, their behavior. New York: A. A. Knopf. 260 pp.
- Emmel, T. C., and E. Garraway.
- 1986. Conservation of the endangered Homerus Swallowtail in Jamaica. World Wildlife Fund-U.S. [proposal]. 49 pp.
- Fabricius, J. C.
 - 1793. Entomologica systematica emendata et aucta, secundum classes, ordines, genera, species, adjectis, synonymis, locis, observationibus, descriptionibus, 3: pt. I. Copenhagen. 487p.

Garraway, E.

- 1990. The Conservation of the Endangered Swallowtail Butterfly, *Papilio homerus* Fabricius. Conservation of the Species Through Commercial Rearing. Jamaica Agric. Development Foundation [proposal]. 12 pp.
- Gosse, P. H.
- 1879. On Papilio homerus, its ovum and larva. Proc. Ent. Soc. London, 1879:1v-lviii.
- Kaye, W. J.
- 1926. The butterflies of Jamaica. Trans. Ent. Soc. London, 1925: 455-504.
- Kelly, D. L.
- 1986. Native forests on wet limestone in northeastern Jamaica. Pp. 31-42. In, D. A. Thompson, et al. (eds), Forests of Jamaica. Kingston: Jamaica Soc. Scientists Tech. 162 pp.
- Lewis, C. B.
- 1947. Butterfly Notes and Records. Nat. Hist. Notes, Nat. Hist. Soc.

Cruz, A.

Jamaica (Kingston), 3(29-30):91.

Lewis, C. B.

1949. Butterfly Notes. Nat. Hist. Notes, Nat. Hist. Soc. Jamaica (Kingston), IV(39):48.

Longstaff, G. B.

- 1912. Butterfly-hunting in Many Lands. London: Longmans. 729 pp. Panton, E. S.
- 1893. A description of the larva of Papilio homerus. J. Inst. Jamaica (Kingston), 1:375-376.

Swainson, E. M.

1901. Notes on lepidopterous larvae from Jamaica. J. New York Ent. Soc., 9:77-82.

Taylor, C. B.

1894. A description of the larva and pupa of Papilio homerus Fabricius. Trans. Ent. Soc. London, 1894:409-410.

Turner, T. W.

(In Press). Papilio (Pterourus) homerus Fabricius, 1793 (Lepidoptera: Papilionidae) in Jamaica, West Indies: field observations and a description of the immature stages. J. Lepid. Soc. (Lawrence).

Walker, D. J.

1945. Papilio homerus. Nat. Hist. Notes, Nat. Hist. Soc. Jamaica (Kingston), 2(22):161-163.

