

# CONTRIBUTION TO THE ECOLOGY AND CONSERVATION BIOLOGY OF THE ENDANGERED *PAPILIO HOMERUS* (LEPIDOPTERA: PAPILIONIDAE)

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**ABSTRACT.**— Ecological and biological studies were conducted on the eastern population of *Papilio homerus* Fabricius between January 1991 and September 1992. *Hernandia catalpaefolia* Britton and Harris was the only confirmed larval food plant and only a small portion of the available plants was utilized at any time. Eight adult nectar sources were recorded. Immature stages were recorded throughout the year and there was no indication of distinct broods. Neither seasonal nor daily migration were observed. The ratio of females to males netted in the field was 1:3.5, that for animals reared was 1:1.4. Mating adults were observed in tandem for over 25 minutes. Hymenopterous egg parasitoids caused 76.5% mortality and bacterial infection caused high mortality among the larvae, prepupae and pupae. Population numbers appear to be naturally regulated. The establishment of a National Park system now gives protection to some of the vital habitat.

**KEY WORDS:** Acanthaceae, ants, Araceae, Araliaceae, bacteria, biology, Clethraceae, conservation, Cyatheaceae, Encyrtidae, Eulophidae, Formicidae, Gramineae, Guttiferae, Hernandiaceae, hostplants, Hymenoptera, immature stages, Jamaica, larva, Lauraceae, Leguminosae, lizards, Malvaceae, mating, Mimosaceae, Musaceae, natural control, Papilionaceae, parasitoids, Pinaceae, predation, pupa, Urticaceae, Verbenaceae, Zingiberaceae.

*Papilio homerus* Fabricius is among the four endangered swallowtail butterflies listed in the IUCN Red Data Book (Collins and Morris, 1985) and is considered the largest of the true swallowtail species in the Americas. It is endemic to Jamaica and only an eastern and a western population now exist (Emmel and Garraway, 1990).

Although *P. homerus* has attracted much attention, there has never been a conservation program aimed specifically at the species. The present research project aims at supplying vital information which will allow the development of such a conservation program. Preliminary studies began with the initiative of J. R. Parnell (formerly of the University of the West Indies) who, aided by Garraway, produced in 1984 a film entitled "*Papilio homerus*, the vanishing swallowtail." This film recorded some aspects of the biology and ecology of the butterfly and highlighted the associated conservation problems. Garraway along with Emmel later developed a number of clear objectives necessary for the establishment of a strong conservation program (Emmel and Garraway, 1990). This present paper summarizes some of the findings of an ongoing research program aimed at realizing the suggested objectives.

*P. homerus* occurs in habitats that are remote and with very difficult terrain. Consequently, previous research have been limited to occasional one day trips, for example, the work of Lewis (1948, 1949) and Turner (1991) who spent 123 days in the field over a 19 year period (1962 to 1980). The results of these exercises have been largely restricted to taxonomic descriptions of the immature stages (Turner, 1991; Swainson, 1901), and records of adult sightings and adult behavior (Walker, 1945; Lewis, 1948, 1949; Avinoff, unpublished, quoted in Brown and

Heineman, 1972; Turner, 1991).

This report is based on the findings of the first intensive study of *P. homerus*. Over 1000 man-days of observations were made during the period January 1991 to September 1992 (during which time Garraway and Bailey were based at the Rio Grande Field Station, Portland). This was augmented by observations made by the senior author between 1984 and 1990. Information is presented on food plants, mating and the behavior of the adults and larvae. The importance of developmental mortality in the regulation of the population numbers of *P. homerus* is examined and the conservation status of the species discussed. The descriptions of the immature stages in the present paper augment previous ones and include the first set of color photographs on all immature stages.

## METHODS & STUDY AREAS

The major study site was at Fishbrook in the Rio Grande Valley, in the parish of Portland; other sites were Bowden Pen and Cuna Cuna Pass, also in the parish of Portland, and the Corn Puss Gap region in St. Thomas. Observations were also made in some of the districts in the Rio Grande Valley (Millbank, Comfort Castle, Ginger House and Grey Town). Data were collected at elevations ranging from 150m to 750m, but there were exploratory exercises to higher altitudes.

Fishbrook include a number of streams which descend sharply through deep ravines in the John Crow Mountains to the Rio Grande River. These ravines acted as natural conduits into the forests, thus allowing research at elevations ranging from 170 to 550m. The first two authors and a resident field assistant spent



Fig. 1. Immature stages of *P. homerus*. (a) Recently laid egg on *H. catalpaefolia* leaf. (b) Preserved specimen of first instar larva, lateral view showing scoli and setae. (c) Laboratory reared first instar larva near to the remains of the chorion; when reared in laboratory on small pieces of leaves, larvae have multiple encounters with chorion and consume most of it. In nature, a significant portion of the chorion is generally uneaten. (d) Second instar, dorsal view; the well developed scoli and setae of first instar are now much reduced. (e) Third instar, dorsal view; further reduction of scoli and setae apparent. (f) Third instar, lateral view; head capsule extended, eye spot and saddle marking now well developed. Scale bar = 1mm. (Photos © 1993 E. Garraway).

four days per week at Fishbrook.

Three one-day visits were made to Cuna Cuna Pass during July and August 1991. Due to extensive logging and clearing of the vegetation in the lower regions, observations on the immature stages were made between 490 and 750m on the northwestern slopes along a road leading from Millbank to the Pass. One two-day visit was made to Corn Puss Gap in July 1992. As in the case of Cuna Cuna Pass, there was extensive cutting of the forest on the lower slopes and observations on the immature stages were made between 460 and 630m on the southeastern slopes. Observations were made along a road leading from Bath to the Gap.

The average annual rainfall at Corn Puss Gap is 700cm, that at 400m elevation on the south-eastern slopes to Corn Puss Gap is 390cm, Millbank 630cm, and Cuna Cuna Pass 510cm.

The areas studied were a mixture of primary and secondary forest (large areas having been cleared for shifting agriculture); the forests regenerate rapidly and some of the secondary areas were well developed forests (i.e., approaching primary). The secondary forests occurred at the lower altitudes and typically had a combination of hard woods such as *Clethra alexandri* Griseb (Soapwood) (Clethraceae), *Oreopanax capitatus* (Jacq.) (Woman Wood) (Araliaceae), *Hibiscus elatus* L. (Blue Mahoe) (Malvaceae); shrubs including *Pilea* spp. (Urticaceae), *Bambusa vulgaris* Schrad. (Common Bamboo) (Gramineae) and vines such as *Entada gigas* (L.) (Cacoon) (Mimosaceae), *Philodendron* sp. (Wicker Vine) (Araceae), and cultivated crops such as *Colocasia esculenta* (L.) (Dasheen) (Araceae), and *Musa* spp. (Bananas, Plantains) (Musaceae).

The well developed secondary and the primary forests had the general characteristics of a lower montane rain forest as described by Asprey & Robins (1953) and Emmel and Garraway (1990). Such forest occurred above 300m and were abundant in *Calophyllum calaba* L. (Santa Maria), (Guttiferae). Other plants present included *Ocotea* spp. (Lauraceae) and *Cyathea* spp. (Tree Ferns) (Cyatheaceae).

A monthly census was conducted during which larval food plants were searched up to a height of 3m above ground and the developmental stages recorded. Samples of branches above 3m as well as observations of adult behavior indicated that over 95% of eggs were laid below 3m. The occurrence of immature stages was used as a measure of population activity; this is a better measure than adult count since the immature stages remain on the food plants for relatively long periods and may be more accurately counted.

In the laboratory, larvae were reared in cylindrical plastic cages 30cm high. All cages and leaves fed to the larvae were sterilized using dilute solution of chlorine and general handling procedures were such as to reduce the chance of bacterial infection.

The date, time and location of adult sightings were recorded. Individual adult *P. homerus* could sometimes be identified by marks on the wings which were visible with the naked eye or with the use of a pair of binoculars (8 X 30 or 10 X 50). In order to estimate the size of the adult population, a capture-mark-recapture method was employed. Adults were gently netted, marked with individual numbers on the underside of the wing using waterproof markers, then released at the site of capture within three minutes.

Eggs and first instar larvae were measured using an ocular micrometer and other immature stages measured using a caliper.

## DESCRIPTION OF IMMATURE STAGES

Several authors have contributed to our knowledge on the immature stages of *P. homerus*; these include Taylor (1894), Swainson (1901) and Turner (1991). The descriptions below complement these earlier reports.

**EGG:** Egg shape, texture and developmental changes have been reported by Emmel & Garraway (1990) and Turner (1991). Egg height ranged from 1.6 - 1.9mm with a mean of 1.8mm; the width ranged from 1.9 - 2.1mm with a mean of 2.0mm (n = 30). A recently laid egg is shown in Fig. 1 (a).

**FIRST INSTAR LARVA:** Figs. 1 (b & c). The general appearance of the first instar is like that of a lizard dropping (predominantly black with posterior 20% white). Larval body length ranged from 2 to 8mm (n = 30). The larvae have very prominent dorsolateral scoli on all three thoracic segments and the first abdominal segment. These scoli are largest on the prothorax and smallest on the metathorax, while those on the mesothorax and first abdominal segments are similar in size. The bases of both scoli on the metathorax were bordered by light-blue crescent shaped spots, reported by Turner (1991) as white rings.

The first three abdominal segments are blackish-brown, with segments four, five, and six becoming dark brown. Segment seven is blackish brown anteriorly, becoming white posteriorly. Segments eight, nine and ten are white. Light blue crescent-shaped spots occur at the base of the dorsolateral scoli of abdominal segments one to six.

**SECOND INSTAR LARVA:** Fig. 1 (d). In the second instar, the major scoli become reduced to tubercles (Turner, 1991). The prothoracic segment is black ventrally, becoming reddish-brown laterally and dorsally. This instar can be distinguished from the first instar by the two large round reddish-brown scoli situated dorsolaterally on the prothoracic segment, with very short blunt setae on them. Slight white markings occur around the lateral spiracles and just posterior to the tubercle on the mesothorax. The range of body lengths of the larvae studied was 9 - 15mm (n = 20).

**THIRD INSTAR LARVA:** Fig. 1 (e & f). The coloration of the third instar is similar to that of the second instar, but the tubercles become less prominent except for those on the metathorax. The tubercles (eye spots) become more prominent as the instar grows and are as described by Turner (1991). The scoli on the posterior edge of the prothorax of the second instar are reduced to tubercles and are white. Body length at rest, 1.3 - 2.5cm (n = 40).

**FOURTH AND FIFTH INSTAR LARVAE:** Fig. 2 (a, b and c). Panton's (1893) and Turner's (1991) descriptions of the fourth and fifth instars agree well with our findings. However, there is variation in the non-green areas which can be grayish black, light or dark brown. Fourth and fifth instars are similar in color, but the colors in the fourth are distinctly paler in the immature stage. As the larva matures, the colors become darker, looking more like that of the fifth instar. Fourth instar body length at rest was 2.3-4.0cm (n = 25); fifth instar body length 3.8-5.4cm (the fully extended larva might be over 7cm) (n = 26).

All instars possess osmeteria and these are extruded quite reluctantly (Emmel and Garraway, 1990; Garraway and Parnell, 1993). When abruptly disturbed, a mature larva not only extruded its brick red osmeteria which emitted a musty smell, but raised its anterior region in a defensive posture and moved it to-and-fro in a snake-like manner.

**PUPA:** Ground color of the pupae varied and along with the gray, brown or brown and green reported by Emmel and Garraway (1990) and Turner (1991), green pupae have been observed (Fig. 2, e & f).



Fig. 2. Immature stages of *P. homerus*. (a) Fourth instar larva: green coloration is pale, white and grey areas still prominent. (b) Fifth instar larva: green coloration intensifies. (c) Fifth instar larva at rest. (d) Prepupa. (e) and (f) Pupal skins, showing different color morphs. Scale bar = 1cm. (Photos © E. Garraway).



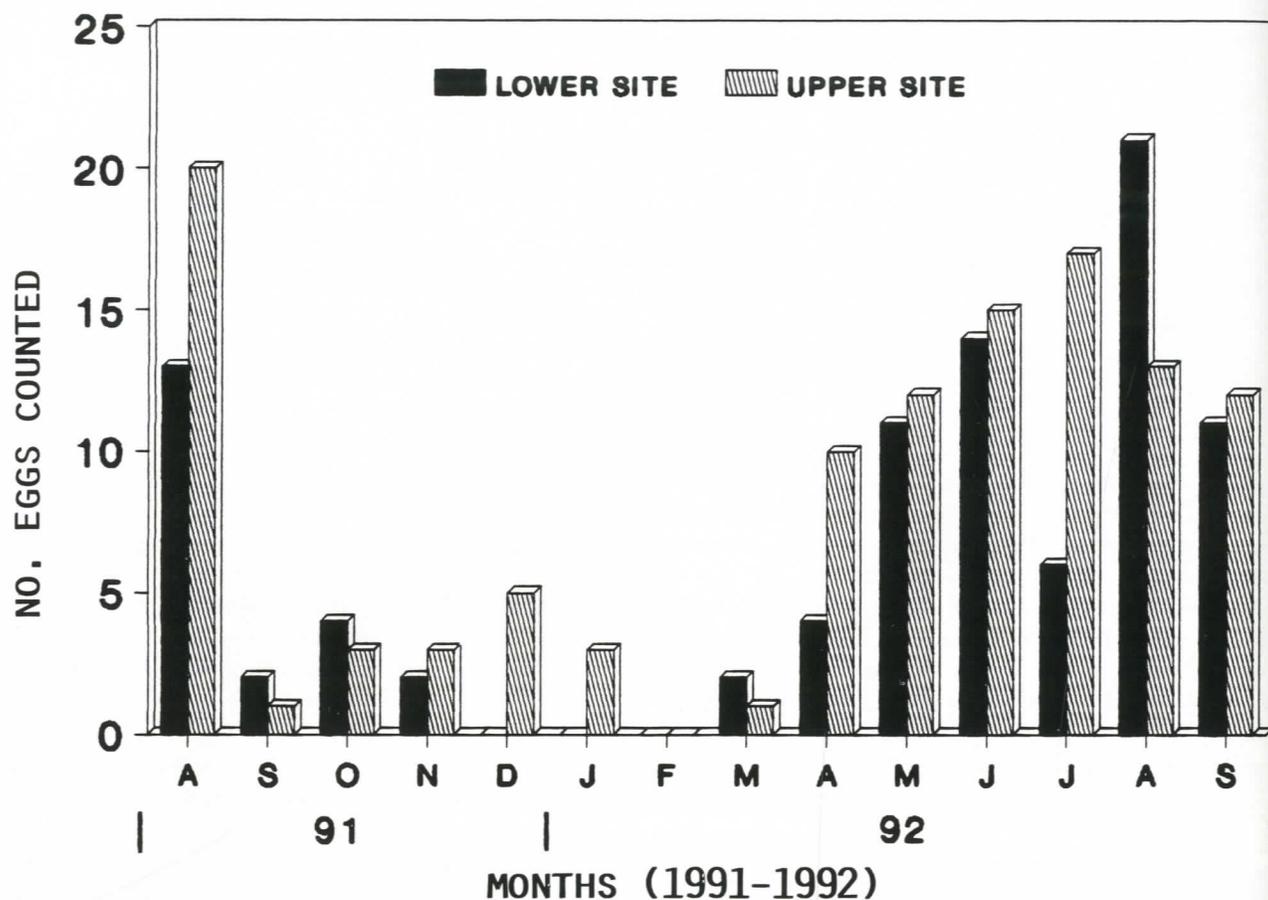


Fig. 4. Number of eggs recorded per month at lower (170 - 380m) and upper (380 - 550m) regions of a Fishbrook stream, August 1991 to September 1992.

ascend or descend over 200m elevation while gliding on air currents or in a single rapid flight. Such is not unusual as the terrain is very steep and a 200m change in altitude can be achieved in a relatively short distance.

It is not uncommon to see different adults along a range of elevations of 150 to 550m in a day. Adults generally rested for the night close to their sphere of daily activity and males often return to patrol the same areas for several days. Turner (1991) reported daily vertical migration which was most noticeable between 1300h and 1500h when the population numbers were high between 1962 and 1968. This daily migration was not observed between 1984 and the present. Such spectacular daily flights as described by Turner must have been a rare occurrence, for as Turner himself pointed out, "usually no more than three different individuals were observed on days with favorable weather conditions."

Females have been observed flying slowly above a wide range of vegetation, apparently in search of larval foodplants. They periodically landed on the leaves of the plants as they investigated them. Females on locating the foodplant, *Hernandia catalpaefolia* Britton and Harris, either oviposited or continued searching the leaves.

Eggs were oviposited on the upper surfaces of mature as well as on the young and terminal leaves of *H. catalpaefolia* and rarely on very old leaves. The eggs were oviposited 1 - 6m above

ground, but more commonly between 1 and 3m. Generally, they were laid singly, but four eggs (three of which were of the same age) were recorded on a single leaf and Turner (1991) recorded as many as five eggs of different ages on the same leaf. Eggs were also laid on leaves with larvae and on leaves that had been partially eaten.

Males have been observed patrolling either up and down streams or in cleared areas. They investigated butterflies and birds flying through the area being patrolled. This behavior of males makes them more susceptible to netting; consequently, the ratio of females to males captured in the field was 1:3.5 ( $n = 27$ ). This would explain the skewed sex ratio for adults in collections. In the laboratory, however, the ratio of females to males emerging was 1:1.4 ( $n = 12$ ).

In April 1991 a pair of adults was observed mating at Fishbrook at 1358 h. The mating pair remained in tandem for twenty-five minutes before taking to flight, the male trailing the female. The pair was perched approximately 3m above ground on the leaves of *Bambusa vulgaris* (Common Bamboo). The duration of the mating is uncertain, as it was already in progress when the pair was sighted. No courtship has been observed.

Adults have been observed nectaring on a wide variety of flowers; some of these are still unidentified while others are listed in Table 1.

## ECOLOGY

Immature stages were observed all year round throughout the study site of Fishbrook (Fig. 3). Turner (1991) reported three overlapping broods between April and October at Corn Puss Gap, and two broods, August to December, at the lower elevations. We found no indication of the occurrence of distinct broods at any elevation, but rather, continuous breeding with overlapping generations.

An estimate of the size of the population is not yet available. Several attempts by the authors using capture-mark-recapture methods have failed due to low numbers. The highest number of adults marked was nineteen in April 1991; the only recapture was a male which was recaptured within half an hour of his release and at the site of his first capture.

**HABITAT:** Contrary to previous reports (Turner 1983, referred to in Collins and Morris, 1985), *P. homerus* is not restricted to virgin forests but rather breeding populations occur in secondary forests and in cleared areas. Immature stages were observed on isolated food plants even in the midst of agricultural plots although moist, shaded areas near to streams are the preferred habitats.

**LARVAL FOODPLANT:** The only confirmed foodplant in the study sites was *H. catalpaefolia*, which was recorded as low as 150m (Garraway and Bailey, 1992) though Adams (1972) recorded the plant between 450 and 640m.

The question of larval foodplant remains a controversial issue and has been reviewed by Emmel and Garraway (1990) and Turner (1991). To date, larvae have only been observed feeding on *H. catalpaefolia* (Emmel & Garraway, 1990; Turner, 1991) and have been fed *H. jamaicensis* (Turner, 1991). Although ovipositional behavior on *Ocotea* has been observed (Lewis, 1949; Turner, 1991), until larvae are found feeding on this species or have been fed this plant and found responsive to it, its suitability as a larval foodplant remains questionable. Moreover, a mature larva returns to a specific leaf after feeding and consequently a distinctive silken mat and a depression develops on such a leaf; such silken mats and depressions were never observed on *Ocotea* during this study.

Only a small proportion of the *H. catalpaefolia* trees available at Fishbrook was used at any time. In August 1992 when a relatively high number of eggs were recorded, only 27% (n = 205) of the trees at Fishbrook had eggs oviposited on them, although, 82% had been used at least once during the study period. Defoliation of a tree by larvae was recorded once, when two larvae developed on a small tree, about 0.75m in height. Generally, only a small fraction of the leaves on any tree is utilized.

## DEVELOPMENTAL MORTALITY

**Egg mortality:** Egg mortality was due primarily to three parasitoids which were first observed in May 1991 (Garraway and Bailey, 1992). The parasitoids were two species of the genus *Chrysonotomyia* (Eulophidae) and one species of *Oencyrtus* (Encyrtidae). These caused 76.5% mortality (n = 444) between

TABLE 1. Nectar sources recorded for the eastern population of *P. homerus*.

Botanical names	Common names	Family
<i>Entada gigas</i> (L.)	Cacoon	Mimosaceae
<i>Hedychium coronarium</i> Koenig	Ginger Lily	Zingiberaceae
<i>Hernandia catalpaefolia</i> Britton & Harris	Water Mahoe	Hernandiaceae
<i>Hibiscus rosa-sinensis</i> L.	Hibiscus	Malvaceae
<i>Lantana camara</i> L.	Orange Sage	Verbenaceae
<i>Pachystachys coccinea</i> (Aubl.)	Black Stick	Acanthaceae
<i>Psophocarpus palustris</i> Desv.	—	Papilionaceae
<i>Urena lobata</i> L.	Bur Mallow	Malvaceae

July and October 1991 (Garraway and Bailey, 1992). Parasitization of eggs was observed throughout May 1991 to September 1992 at Fishbrook.

In the Corn Puss Gap region, ten eggs were observed at elevations between 490 and 580m: three were parasitized and both species of *Chrysonotomyia* observed. *Chrysonotomyia* spp. were also observed at Cuna Cuna Pass (750m). Turner (1991) collected 23 eggs at Corn Puss Gap but recorded no parasitoids. It is not clear if our record represents the discovery of newly introduced mortality factors or the expansion of the range of the parasitoids.

Other factors included fungus-caused death of a further 10.9% of the eggs, resulting in a total of 87.4% egg mortality. On one occasion, an unidentified, small, black and red ants were observed attacking an egg of *P. homerus* at Fishbrook. Turner (1991) noted attacks on eggs by a large ant at Corn Puss Gap. No other egg predator has been recorded.

**Larval mortality:** Larval mortality was caused by three species of bacteria, *Bacillus* sp., *Enterobacter* sp. and *Clebsiella* sp. (Garraway and Bailey, in press). All larval stages were affected by one or more of the bacteria. It is uncertain whether any of the disease-causing organisms are secondary invaders. First to third instar larvae succumbed more quickly to the bacterial infection than older larvae. An infected larva shows clear symptoms of septicaemia; it becomes sluggish, stops eating and tends to wander, brown fluid exudes from the anus twenty-four hours after showing the above symptoms, the larva becomes flaccid and finally dies.

The prevalence of bacterial infection among larvae collected in the field and reared in the laboratory varied greatly. For example, larvae reared during April and May 1991 (n = 5) showed no signs of bacterial infection; however, all larvae reared in November and December 1991 (n = 8) as well as May and June 1992 (n = 16) died from a bacteria-related disease.

Mortality due to predators was not estimated. Body fluids dripping from leaves from which larvae had vanished indicated the occurrence of a predator which consumes larvae on the leaves. The only possible predators recorded were lizards and birds; however, only the first is likely to consume larvae on the surfaces of the leaves. Vogel (personal comm.) found that lepidopteran larval-remains made up a high percentage of the gut contents of lizards (*Anolis* spp.) which he analyzed. Larval disappearance was most marked during the third instar. During this stage, larvae partially lose their faecal-dropping appearance but have not yet developed the protective coloration of the later instars; their size also make them relatively conspicuous.

Attack by ants was recorded only once; *Campanotus* sp. was observed attacking a first instar. The body wall of the larva was slashed open, after which the ant lost interest, suggesting unpalatability. No larval parasitoids have been observed. Mortality due to molting failure was recorded in first and second instar larvae.

**Prepupal and pupal mortality:** Pupal deaths have been recorded and in each case, one of the following symptoms was observed: (1) incomplete metamorphosis in which case either the abdomen or thorax and head remained larval; (2) the entire pupa or part of it became black and on dissecting, the body fluid was found to be brown and foul-smelling; (3) larva did not spin a silken girdle, and on pupating, deep clefts were observed at the base of the wing and along the mid-dorsal line, body fluid oozed from the clefts; (4) deformed pupa, with clefts along the antennal line; (5) pupa dried out and appeared woody; indications are that at least the first three of these symptoms are related to bacterial infection.

#### NATURAL REGULATION OF NUMBERS

The under-utilization of available larval food plant and the high availability of adult nectar sources indicate that the population is being controlled by some factor(s) at a level below which these resources become limiting. Possible key factors include parasitoids in the egg and bacteria in the larval stages; that is, the population is probably naturally regulated.

The 76.5% mortality caused by egg parasitoids is significant for an animal with extremely low densities. This suggests that the parasitoids are exceedingly efficient in their search for *P. homerus* eggs, or the possible existence of alternate hosts that maintain the population of parasitoids at high levels. As pointed out by Parsons (1984), parasitoids breeding in a common alternate host may adversely affect the survival of a rare species.

Bacterial mortality is well known in the Lepidoptera and *Bacillus* has been used extensively for decades as a biological control agent (DeBach and Schlinger, 1964; Kumar 1984). While the work on bacterial mortality in *P. homerus* is just beginning, indications are that it has the potential to cause large-scale mortality among larvae and pupae and is thus an important part of the complex of natural controlling agents.

#### CONSERVATION STATUS

While no actual counts of *P. homerus* was done over the decades, evidence that there has been a reduction in numbers was reviewed by Emmel and Garraway (1990).

In the John Crow and Blue Mountains, the habitat of *P. homerus* suffered major modification during the 1980's through the establishment of commercial plantations of *Pinus caribea* More. which extended over the 650m elevation mark in some areas. There were further modifications by Hurricane Gilbert in 1988, which not only ruined the natural forests but devastated the commercial plantations. These commercial plantations have not been replanted. *H. catalpaefolia* recovered rapidly and is now common in both the regrown natural forest as well as in some of the previously pine forested areas. Local farmers continue shifting cultivation, especially on the lower slopes; *H. catalpaefolia* is also found among these farms.

Legal protection for sections of its habitat is now becoming a reality with the implementation of the Blue Mountain/John Crow Mountain National Park Project in 1990. The geographic range of the butterfly, however, extends outside the park into the area used by the local farmers and plans are now being developed for an extensive public awareness campaign.

The illegal international trade in *P. homerus* continues on a limited basis. Most poachers are local "opportunistic collectors" and organized poaching is limited to a single town. Organized poaching has become more difficult since *P. homerus* has been protected under CITES, Appendix I, 1987, and under the Jamaican Wild Life Act of 1988. The chances of enforcement of the Jamaican Wild Life Act are likely to increase with the establishment of the National Park.

There is need to continue protection of the unique habitat, especially in the higher elevations since the lower regions are unstable due to agricultural usage; however, further research into the factors limiting the population density is essential.

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