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Evaluation of the present conservation status of three endemic butterflies, *Atlantea pantoni* (Kaye, 1906) (Nymphalidae: Nymphalinae), *Pterourus homerus* (Fabricius, 1793) (Papilionidae: Papilioninae), and *Protographium marcellinus* (Doubleday, 1845) in Jamaica, West Indies

by Thomas Turner and Vaughan A. Turland

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Front cover: Female *Atlanta pantoni* nectaring on *Asclepias curassavica* in the Cockpit Country, Jamaica (photo by V. Turland).
Inside back cover 1: Male *Pterourus homerus* nectaring on *Bauhinia divaricata* in the Cockpit Country, Jamaica (photo by V. Turland).
Inside back cover 2: Male *Atlantea pantoni* just emerged in the Cockpit Country, Jamaica (photo by V. Turland).
Back cover: Freshly emerged male *Protographium marcellinus* in the Cockpit Country, Jamaica (photo by V. Turland).

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The conservation status of *Atlantea pantoni* (Kaye, 1906) (Nymphalidae: Nymphalinae: Melitaeini: Chlosynina) in Jamaica, West Indies

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Abstract: The conservation status of the endemic Panton's Fritillary, *Atlantea pantoni* (Kaye 1906), one of Jamaica's most attractive butterflies, is evaluated. This species is confined to the rugged, mostly impenetrable, forested landscapes of west central Jamaica which include the southern Cockpit Country. Land clearance has divided what was a single small population into four smaller known fragments with a loss of approximately 91% of former estimated occupied territory. This habitat is threatened by further loss of territory from ongoing deforestation and bauxite mining activities.

Key words: Cockpit Country, deforestation, endemic species, field surveys, habitat fragmentation, Jamaica, type locality Kellits.

INTRODUCTION

The Greater Antillean genus *Atlantea* (Higgins, 1958 [1959]; Higgins, 1960; Higgins, 1981; Wahlberg *et al*., 2005) is represented by just four species (Miller & Miller, 1989): *A. perezi* (Herrich-Schäffer, 1862) occurs on Cuba; *A. cryptadia* Sommer & Schwartz, 1980 is found in Hispaniola; *A. tulita* (Dewitz, 1877) on Puerto Rico; and *A. pantoni* (Kaye, 1906) on Jamaica. The female of the Hispaniolan species, *A. cryptadia*, was unknown as of 1994 and still has not been described (Smith *et al*., 1994).

Adults of the Jamaican species, also known as Panton's Fritillary (figures 1, 2 and 3) were first observed by E. Stuart Panton while feeding on *Bidens pilosa* L. (Compositae), near the town of Kellits in northern Clarendon Parish after forest was cleared for planting coffee (Panton, 1893). Brown & Heineman (1972) note, "On Jamaica and Puerto Rico, and probably on Cuba, these butterflies have their stronghold in the rugged karst of the limestone country, an area of high rainfall but of such thorough drainage that the vegetation, except in the sinks, is xerophytic." We agree with this observation. In Jamaica, this species preferred habitat are the drier areas of the low to mid-level moist broadleaf forests. Most observations have been between elevations of 525-750 m with the lowest elevation at 100 m in northern Trelawny Parish near Windsor.

A. tulita from Puerto Rico is the only species of *Atlantea* whose immature stages have been discovered as noted by Stuart Ramos (Smith *et al*., 1994), studied by Juan E. Carrión Cabrera (2003), and illustrated by Alejandro Sanchez at https://www.butterfliesofamerica.com (Warren *et al*., 2024).

The larval food plants in Jamaica are unknown but *A. tulita* of Puerto Rico has been reared on *Oplonia spinosa* (Jacq.) Raf., (Acanthaceae). There are four species of *Oplonia* in Jamaica, all endemic. The distribution of *O. armata* (Sw.) Stearn, found at elevations between 150 m and 855 m, best matches the distribution of *A. pantoni*, but other plants from the same family including *Drejerella jamaicensis* (Britton) S. Moore, and *Neriacanthus purdieanus* Benth., also occur where the butterfly is found (Adams, 1972).

From the limited collection records available as documented in Brown & Heineman (1972), *A. pantoni* once occupied a large area of central Jamaica. This attractive endemic species has never been the focus of any conservation measures, a position which needs urgent reconsideration. Recent surveys by the authors have determined that this species is now found in just four small forest fragments in west central Jamaica each threatened by continuing deforestation. This publication seeks to bring attention to this omission, provides information from the surveys conducted, and determines the IUCN conservation status. The species should be considered Critically Endangered and is in need of urgent conservation measures.

Figure 1. Male *Atlantea pantoni*, Litchfield Mountain, Trelawny Parish, September 2018.

Figure 2. Female *Atlantea pantoni*, Cockpit Country, Trelawny Parish, November 2014.

Figure 3. *Atlantea pantoni*, mating in Cockpit Country. Female right. November 2010.

MATERIALS AND METHODS

Field surveys in and around the southern Cockpit Country were conducted between 1966 and 2009 by Turner and continued by Turland and Turner 2009-2014 with continuing field surveys by Turland between 2014 and 2022. Surveys were conducted along available forest trails between 1000 h and 1600 h.

The primary site for observations was along the Crownlands trail in the Cockpit Country in west central Jamaica. Observations have been made in all months and species abundance has been recorded. The exact coordinates where *A. pantoni* was observed have been withheld in keeping with the Jamaican National Environment Planning Agency (NEPA) permit requirements. No specimens were collected in any recent survey. Specimens in the Natural History Museum of Jamaica collection, Institute of Jamaica, were examined.

The adult insects depicted in this publication were photographed using Nikon D800 and latterly a Nikon D850 camera with a Micro Nikkor AF-S 105 mm lens.

RESULTS AND DISCUSSION

General habitat description. *Atlantea pantoni* is only found in west central Jamaica. Primary habitat for this species is humid limestone forest (figure 4) with dryer hilltops and dryer openings or trails within humid broadleaf evergreen forest (T. Turner, pers. obs.). With the exception of a very few cleared forest trails, the terrain of the Cockpit Country is largely impenetrable. Following the insect off any trail is therefore virtually impossible.

A. pantoni is an obligate forest dweller willing to cross clearings within the deep forest but not found crossing long distances of open ground beyond the forest fringe. Somewhat similarly, *A. tulita* of Puerto Rico will not fly more than 1 km from the very small, forested locations to which it is now confined (Carrión-Cabrera, 2003).

Figure 4. Typically dense, Mesic Broadleaf Forest habitat beside a forest trail, preferred by *Atlantea pantoni* in southern Trelawny Parish, July 2011.

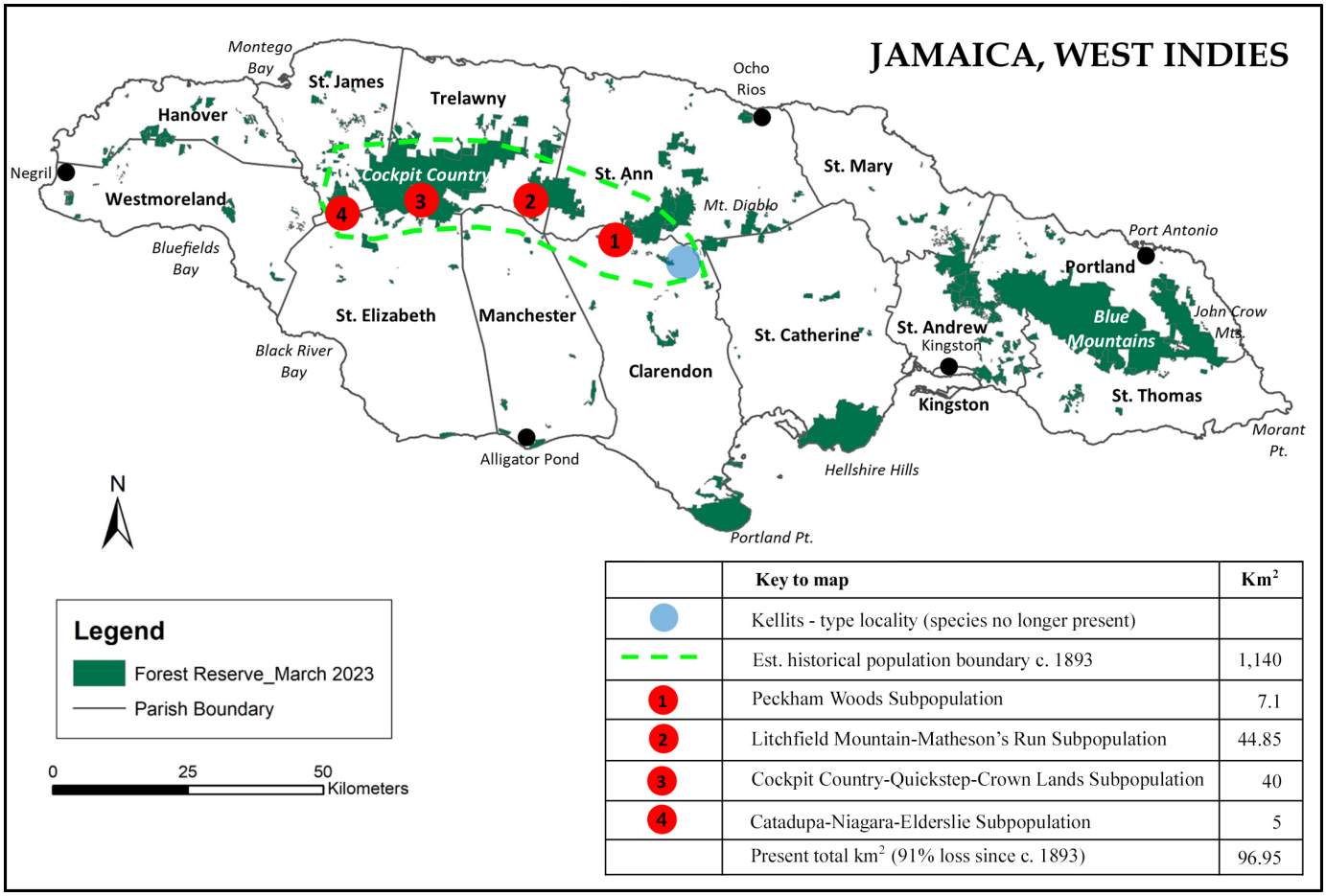
The subpopulations

Based on its present fragmented distribution, resulting from forest clearance, the once single population originally occupied territory within an area from Elderslie in northern St. Elizabeth Parish, and Niagara in Trelawny Parish in the west, extending across the Cockpit Country in Trelawny Parish to the Dry Harbour Mountains of southern St. Ann and northern Clarendon Parishes as far east as Kellits in northeastern Clarendon Parish (figure 5).

The species now exists as four isolated subpopulations which are referred to as the (1) Peckham Woods Subpopulation, (2) Litchfield Mountain-Matheson's Run Subpopulation, (3) Cockpit Country-Quickstep-Crownlands Subpopulation, and (4) Catadupa-Niagara-Elderslie Subpopulation. All four subpopulations are within areas that have been recognized as biological hotspots and are the focus of ongoing studies supported by the Critical Ecosystem Partnership Fund, (CEPF), Phase II, Caribbean Islands, beginning in 2021.

Approximate locations of the known subpopulations are shown in figure 5. Seasonal abundance for survey sites at Crownlands and near Quickstep, Trelawny Parish, and near Niagara, St. James Parish are shown in figures 6, 7 and 8.

Distribution and abundance records for the subpopulations have been compiled from an accumulation of observations since 1893 when E. Stuart Panton discovered the species, from label data attached to previously collected specimens, and from



	Key to map	Km²
	Kellits - type locality (species no longer present)	
	Est. historical population boundary c. 1893	1,140
1	Peckham Woods Subpopulation	7.1
2	Litchfield Mountain-Matheson's Run Subpopulation	44.85
3	Cockpit Country-Quickstep-Crown Lands Subpopulation	40
4	Catadupa-Niagara-Elderslie Subpopulation	5
	Present total km² (91% loss since c. 1893)	96.95

Figure 5. Former and present known distribution of *Atlantea pantoni* (Kaye).

field research by the authors since 1966.

The area originally occupied by this insect in historic times is conservatively estimated at a minimum of 1,140 km², from Elderslie in northern St. Elizabeth Parish, and Niagara in Trelawny Parish in the west, extending across the Cockpit Country in Trelawny Parish to the Dry Harbour Mountains of southern St. Ann and northern Clarendon Parishes as far east as Kellits in northeastern Clarendon Parish.

(1) Peckham Woods Subpopulation. Peckham Woods is located in northwestern Clarendon Parish approximately 20 km direct distance west northwest of the town of Kellits, the type locality for *Atlantea pantoni*. Since the species was described by Kaye (1906), there has been no other mention in the literature of its presence in Clarendon Parish. However, during a field survey of the fauna of Peckham Woods in July 2014, fifteen adults, including both sexes, were recorded here for the first time, and in a second survey in November of the same year another thirty-five adults were seen although no adults were seen during a third survey in August 2015 (V. Turland, pers. obs.).

The topography of this area consists of rugged karst formation, comprising numerous steep hills with deep depressions between; terrain similar to that of dryer parts of the Cockpit Country. The site includes a forest reserve managed by the Forestry Department. This little explored location has long been recognized as a biological hotspot where botanist W. H. Harris collected specimens of *Oplonia armata* (Acanthaceae), as early as 1910 (C. V. Starr Virtual Herbarium, New York Botanical Garden). Later, Jamaican botanists George Proctor and Dennis Adams (1972) collected a number of endemic plants from the area and proposed Peckham Woods be included as a protected reserve as early as 1969, but until very recently little progress had been made in this regard. Although the site covers just 7.1 km² Proctor noted it has "one of the highest densities of site-specific endemic plants" in the island (Proctor, 1983 [1986]). However, the natural vegetation has suffered badly from clearing for forestry projects, cultivation for farming, and from local incursions to cut yam sticks even within the forest reserve.

Since 2015 considerable interest has been generated in the flora of Peckham Woods in projects fostered by the Clarendon Parish Development Committee with the support of botanist Alan Franck formerly of the University of South Florida working in partnership local botanists from the University of the West Indies, Mona, and the Institute of Jamaica. However, there has been relatively little study of the fauna.

The Peckham Woods subpopulation is now geographically isolated from the other populations by deforested countryside. The area estimated to be occupied by the butterfly within the Peckham Woods habitat is very small, comprising only 2.4 km² so this subpopulation should be regarded as being most in danger of extirpation. Immediate threats include continuing loss of the natural forest as a result of human incursions. Only

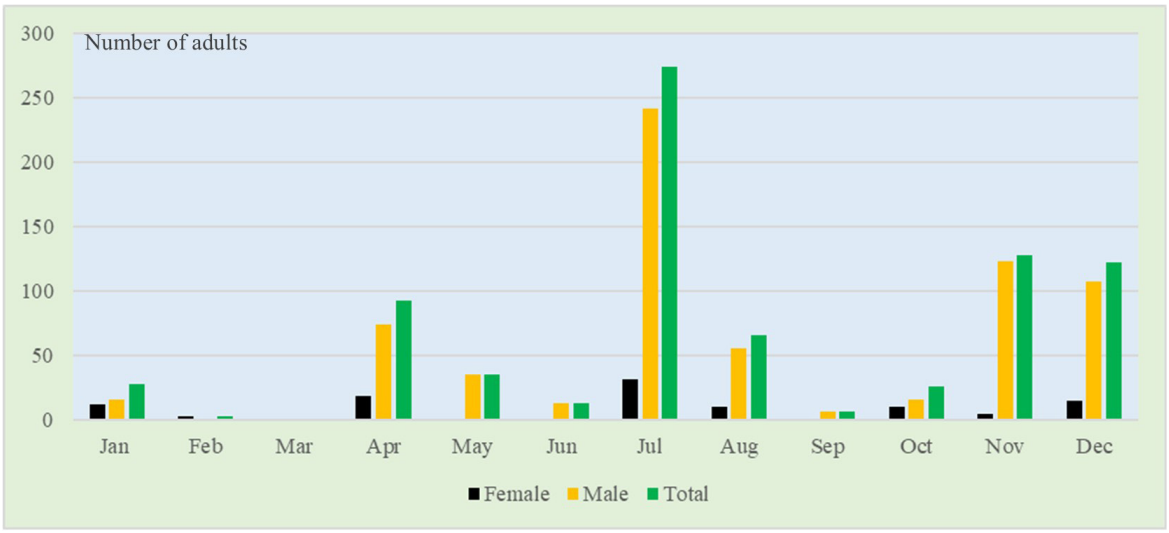


Figure 6. *Atlantea pantoni* surveys at Crownlands, Trelawny Parish, 1966-2015. Data: 33 surveys: adults seen 28 times; total number of adults 796; females 106; males 690.

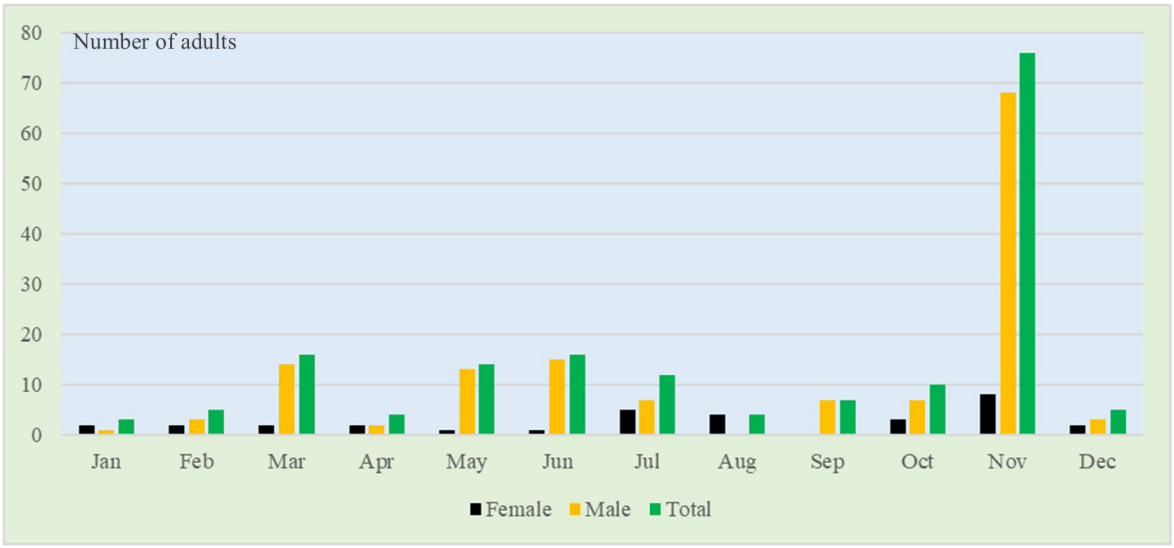


Figure 7. *Atlantea pantoni* surveys near Quickstep in Trelawny Parish, 2007-2022. Data: 120 surveys: adults seen 53 times; total number of adults 155; females 32; males 123.

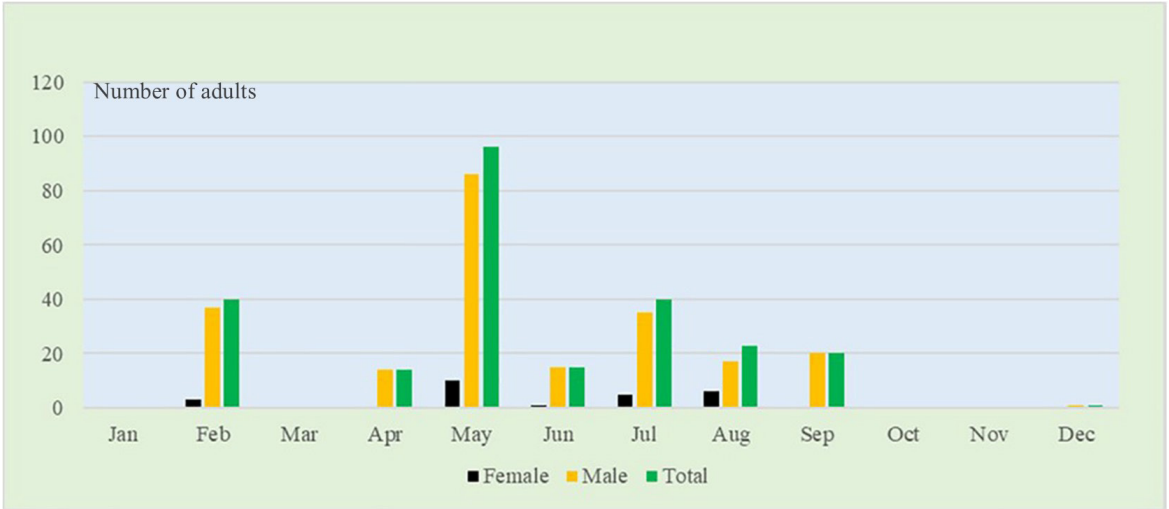


Figure 8. *Atlantea pantoni* surveys near Niagara, St. James Parish, 2009-2018. Data: 31 surveys: adults seen 19 times; total number of adults 249; females 25; males 225.

the three faunal surveys mentioned above have been conducted at this site so far.

(2) The Litchfield Mountain-Matheson's Run Subpopulation. This subpopulation was discovered on September 11, 2018, during a field survey of the southern segment of this forest near Litchfield Mountain (V. Turland, pers. obs.). This subpopulation is located approximately 15 km direct distance northwest of Peckham Woods in southwestern St. Ann Parish and eastern Trelawny Parish. It is separated from the main body of the Cockpit Country proper along the western boundary by a north-south Jackson Town to Wait-a-Bit cleared corridor.

The terrain consists of tower karst limestone with accumulation of soil in the cockpit bottom lands, some of which have been cleared of forest by nearby communities for agriculture. The area occupied by Panton's Fritillary is within the Litchfield Mountain-Matheson's Run Forest Reserve is approximately 44.85 km^2 (V. Turland, pers. obs.). There are two smaller adjacent forest reserves, Hyde Hall with 6.62 km2 and Brislington Crown Land with 2.32 km2 but these have not yet been surveyed. Apart from selective logging of larger trees within the forest reserves and ongoing agricultural-related activities in the valleys between the forested hills, the primary threat to the area is from ongoing bauxite mining operations. No evidence of the insect was found in the northeastern section of this forest area near the town of Gibraltar on the western side of the Dry Harbour Mountains where there was extensive destruction of the habitat from this mining (T. Turner & V. Turland, pers. obs., 2015). The Litchfield Mountain-Matheson's Run forests are also regarded as an Important Bird Area (IBA) by BirdLife International (2022). Only one survey has been completed so far and three males were seen. The epicenter of this subpopulation and precise area of occupancy remains unknown.

(3) The Cockpit Country-Quickstep-Crownlands Subpopulation. The Cockpit Country Protected Area (CCPA) is approximately 780 km^2 and includes the localities of Quickstep and Crownlands (Koenig, 2021).

The terrain is tower karst with cockpits in between numerous small limestone hills with only a few access points. However, field studies from all sides of this preserve over many years have determined that colonies of *Atlantea pantoni* are to be found primarily in relatively dryer locations along the southern borders of this lowland broadleaf forested area. This eastern boundary of this subpopulation is separated from the Litchfield Mountain-Matheson's Run subpopulation not only by the north south Jackson Town to Wait-a-Bit corridor but by a second north south corridor between the town of Kinloss in the north to Burnt Hill in the south.

The center of this subpopulation appears to be close to Crownlands, which is to the north of Wilson's Run, where adults have been observed, over time, in all months of the year. Largest numbers appear between April-May, July-August, and November-December suggesting three main breeding periods. More than 150 individuals were seen at this location on July 12, 2012. Burnt Hill, 14 km direct distance to the northeast, where an occasional adult is seen, may be the eastern extent of this subpopulation, and Spring, north of Quickstep, approximately 12 km to the west, where fewer numbers of adults are seen, may be close to the western boundary. However, Jason Weintraub observed "hundreds of these butterflies" along this trail in September 1980 (Smith *et al*., 1994).

The northern boundary lies within the dense karst terrain of the Cockpit Country with occasional specimens found approximately 9 km to the north, but without permanent presence, in the more humid northern edge of these forests, providing an estimate of 40 km^2 of occupied territory. The forest margin is subject to incursions to cultivate soils accumulated at the bottom of cockpits and for the removal of saplings for use as supports for growing yams (Dioscoreaceae) (Barker, 1998; Barker & Beckford, 2003). Destruction along existing forest trails occurs with periods of forest clearing followed by periods of relative stability, but at an average rate estimated as 0.6 km per year over the last decade (T. Turner, pers. obs.). Along the Crownlands trail this destruction is within a few kilometers of reaching one of Jamaica's most biologically important locations where not only is found the largest numbers of *A. pantoni* but also the least disturbed subpopulation of *Protographium marcellinus* Doubleday, a breeding site for *Pterourus homerus* Fabricius, and the type locality of the endemic butterfly *Troyus turneri* A. Warren & Turland (Hesperiidae: Hesperiinae) (Turland, *et al*., 2012).

It should be noted that *A. pantoni* is not seen in every monthly survey and may be absent in the same localities visited along the same trails in any given month regardless of seasons. Between 1966 and 2015 along the Crownlands trail 33 surveys were conducted during which adults were seen 28 times. Between 2006 and 2022 along the Quickstep trail numbers of adults seen were far fewer and only on 53 occasions in 120 surveys but reflecting only slightly different monthly fluctuations in adult appearances as shown for Crownlands as one might expect if both Quickstep and Crownlands were segments of the same subpopulation. Survey results are shown in figures 6 and 7.

(4) The Catadupa-Niagara-Elderslie Subpopulation. The town of Catadupa lies on the western fringe of the Cockpit Country forests, separated from the main forests of the Cockpit Country by clearings created by human incursions along the road running north-south from Spring Vale in Trelawny Parish to Retirement in northern St. Elizabeth Parish. The forest, known for its large number of endemic species is recognized as the Catadupa Key Biodiversity Area (KBA) as documented by the Windsor Research Centre (Schwartz & Fowler, 1973; Koenig, 2015). The forests are again divided into north, central and southern sectors by east to west roads along which the forest has been cleared. Panton's Fritillary has so far only been recorded from the south eastern part of the central Catadupa KBA between Elderslie and Niagara in the Fyffe and Rankin Forest Reserve. Periods of monthly abundance are slightly different to those of the Crownlands subpopulation with largest numbers seen in February, April-May, and then for a more extended period between June and September, these small differences in times of appearances reflecting the probable isolation of this subpopulation from the subpopulation at

Crownlands (V. Turland, pers. obs.). The area known to be occupied is approximately 5 km^2 in area. A total of 31 surveys have been completed so far with adults observed on 19 occasions. Additional surveys, particularly between September and January are needed. Survey results are shown in figure 8.

Assessment of conservation status of *A. pantoni*

Here we apply the IUCN Red List Criteria (2023) to determine the current conservation status of *A. pantoni*.

Population size reduction. Loss of an estimated 91 percent area of occupancy in the last 125 years; loss of suitable forest habitat irreversible. **Assessment: Critically endangered (A2(c))**

Geographic range. B1: Extent of occurrence: 96.95 km^2. B2(a)(b): Area of occupancy: 96. 95 km^2. Original single population reduced to four subpopulations; continuing loss of forest habitat. **Assessment: Critically endangered (B1, B2(a)(b)).**

Population size and decline. More than 60 but less than 250 individuals estimated in all subpopulations combined between July-August and September-December. Less than 60 individuals in all subpopulations combined estimated between January and March. C1: At the continuing average rate of decline of suitable habitat for all subpopulations during the last 125 years of approximately 8 km^2 pa. which, if continued at the same rate, could mean this species would be lost within the next 15 years. However, the remaining subpopulations now occur in very difficult terrain which has already slowed the rate of forest decline and the insect has demonstrated the ability to persist in territories as small as 2.4km^2-5 km^2. Realistic estimates are that remaining habitats occupied will be substantially reduced or lost within the next 50 years. This time frame could be rapidly shortened by existing bauxite mining activities and incursions into existing subpopulation habitats for local farming and forestry projects. The largest subpopulation in the Cockpit Country Preservation Area may be more protected. However, it should be noted that while species are listed as being protected in Jamaica, their habitats and hence larval food plants are currently not protected in law from human incursions for cultivations, cutting of saplings for growing of yams, for housing materials, and selective logging. This is also true of forest reserves where enforcement of regulations has been limited. C2b. Extreme fluctuations in numbers of adults throughout the year. **Assessment: Endangered (C, C1, C2(b)).**

Very small or restricted population. Four subpopulations are known, the two smallest occupying just 2.4 km^2 and 5 km^2. The third subpopulation occurs in a forested area 44.85 km^2 in size but the area occupied by the insect within this area is still undetermined. Females are only found in small, secluded locations, presumably close to areas where the still undiscovered larval food plants are to be found, while males are found more widely. Although the largest estimated number of both sexes seen in a single day is 150 individuals, 70 percent of visits to the largest subpopulation at Crownlands in the Cockpit Country result in sightings of less than five individuals in a day. Sixty percent of all surveys in the same locations find no adults present. Numbers seen here have been steadily falling since the mid 1960s. **Assessment: Vulnerable (D2).**

Quantitative analysis. Quantitative analysis has not been possible due to the difficulties in obtaining data from an insect occupying extreme karst terrain. However, very conservative estimates based on the present rate of decline of forest habitat, at least 50 percent of remaining forest in suitable condition for occupancy will be lost within the next 50 years. **Assessment: Endangered.**

Overall Assessment. Panton's Fritillary, *Atlantea pantoni*, a reclusive forest species, has not been assessed or IUCN Red Listed before. This species has lost an estimated 91% of original territory occupied (AOO), and the extent of remaining occurrence (EOO) is less than 100 km^2. Irreversible loss of suitable forest habitat is ongoing, though small but apparently vigorous breeding populations are capable of surviving in very small and extremely inaccessible microhabitats in the karst limestone terrain. Population numbers have not been fully assessed but clearly fluctuate from a maximum of approximately 150 individuals in favorable periods to just a few individuals in less favorable times. The numbers and extent of the subpopulation in the Litchfield Mountain-Matheson's Run forests in particular still require further study. This forested area is currently threatened by expansion of bauxite mining lease # SML 165 (Koenig, 2015). Importantly, because of their inaccessibility, this attractive insect's subpopulations do not appear to have been impacted to any great extent by commercial collecting. Specimens are only rarely offered for sale.

On average, one in six specimens seen in the field are female, though fewer females have been seen in the Catadupa-Niagara-Elderslie subpopulation where surveys have not been completed through all months of the year. The larval food plant and the immature stages are still unknown

Taking all these aspects into consideration, but subject to possible change resulting from further field surveys, present evidence strongly indicates that this endemic species should be added to the IUCN Red List initially as **Critically Endangered.**

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A review of factors threatening the continued survival of Jamaican Giant Swallowtail or Homerus Swallowtail, *Pterourus* (*Pyrrhosticta*) *homerus* (Fabricius, 1793), with recommendations for mitigating threats

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Abstract: This paper documents the major threats to each of the two remaining subpopulations of Homerus Swallowtail *Pterourus* (*Pyrrhosticta*) *homerus* (Fabricius, 1793), evaluates the insect's present conservation status, examines the limitations of current conservation measures, and documents the need to implement additional protections. Evaluations presented here of deteriorating habitat conditions of this endemic swallowtail and its small population size lead to the conclusion that the IUCN conservation status of the Homerus Swallowtail should be upgraded from Endangered to Critically Endangered.

Keywords: Cockpit Country, forest fragmentation, Homerus Swallowtail, Jamaica, John Crow Mountains.

INTRODUCTION

There are at least 241 species of New World swallowtail butterflies (Tyler *et al*., 1994). As the biology of the immature stages and distinguishing characters of the adults has become better known over time, the classification of the group has continued to evolve, especially with the application in recent years of DNA sequences (Condamine *et al*., 2023). Homerus Swallowtail may still be commonly known as *Papilio homerus*, but recent subdivisions of the large worldwide genus *Papilio*, confirmed by DNA studies, now place Homerus Swallowtail in the genus *Pterourus* Scopoli, which includes the *troilus* group of New World swallowtails (Miller & Brown, 1981; Tyler *et al*., 1994; Shiraiwa *et al*., 2014). The *troilus* group is further subdivided into two subgenera, *Pterourus* Scopoli, to which *Pterourus* (*Pterourus*) *troilus* Linnaeus, and some other North American species belong, and *Pyrrhosticta* Butler, a more tropical, mostly Central and South American group which includes *Pterourus* (*Pyrrhosticta*) *homerus* (Fabricius, 1793) Homerus Swallowtail (Tyler *et al*., 1994).

Homerus Swallowtail (Figs. 1, 2, 3, 9) is the largest butterfly in the western hemisphere. In size, it is second only to the Asian birdwing butterflies, and rightfully recognized as Jamaica's national butterfly (Garraway *et al*., 2017). This insect is found only in mesic broadleaf forest which originally stretched east to west across most of Jamaica, until the arrival of the first Europeans in 1494 (Sloane, 1725; Long, 1774; Asprey & Robbins, 1953; Beard, 1955). Since the first description of this endemic butterfly in 1793 the biology of the species has been investigated and much information about the life stages is now known. While the knowledge gained is essential for conservation planning and some ideas for conservation have been defined, a comprehensive conservation program for Homerus Swallowtail (also known as Jamaican Giant Swallowtail) has yet to be initiated.

Jamaica is a small island with a landmass of 10,992 km^2, with the original distribution of Homerus Swallowtail probably extending over most of the island between elevations of 150 m and 1,050 m as recently as 600 years ago. However, the original area of occupancy will never be truly known. Suitable habitat for Homerus Swallowtail within existing forests at present is less than 8% of the total landmass of Jamaica. Present conservation data is based on the two remaining subpopulations: a subpopulation in the John Crow Mountains of eastern Jamaica and a second subpopulation in the Cockpit Country, a rugged, forested, wilderness area in west central Jamaica. These two subpopulations now occupy a combined area of approximately 700 km^2 (Turner, 1991). During the last 60 years much life history information has been gathered. This now contributes substantially to planning and implementing the much-needed protection of Homerus Swallowtail. Nevertheless, additional research is still urgently required.

While notable progress has been made with the designation of a Cockpit Country Protected Area (CCPA) closed to bauxite mining along with enhanced public awareness for protection of the butterfly, many of the recommendations made for preservation of Homerus Swallowtail during the last forty years have not been implemented. In particular, the continuing removal or thinning of the forest in and around the areas containing the two subpopulations has never been effectively addressed. Forest preservation and restoration is now stated as a priority, not just for the preservation of this species, but for

Figure 1. Male Homerus Swallowtail in southern Cockpit Country, March 2023.

Figure 2. Male Homerus Swallowtail in southern Cockpit Country, June, 2008.

the entire plant and animal communities where the swallowtail occurs.

The last official evaluation of this insect's IUCN Red List conservation status was in 1996, when Giminez Dixon concluded that the conservation status should remain as Endangered, a status unchanged since Collins & Morris (1985). There have been suggestions that this species might now be Critically Endangered (Lehnert *et al*., 2017), but this proposed status has not been evaluated. Understanding Homerus Swallowtail's requirements for survival in the habitats which it occupies defines which areas and any adjacent areas that must be preserved. There is a need for immediate action to preserve

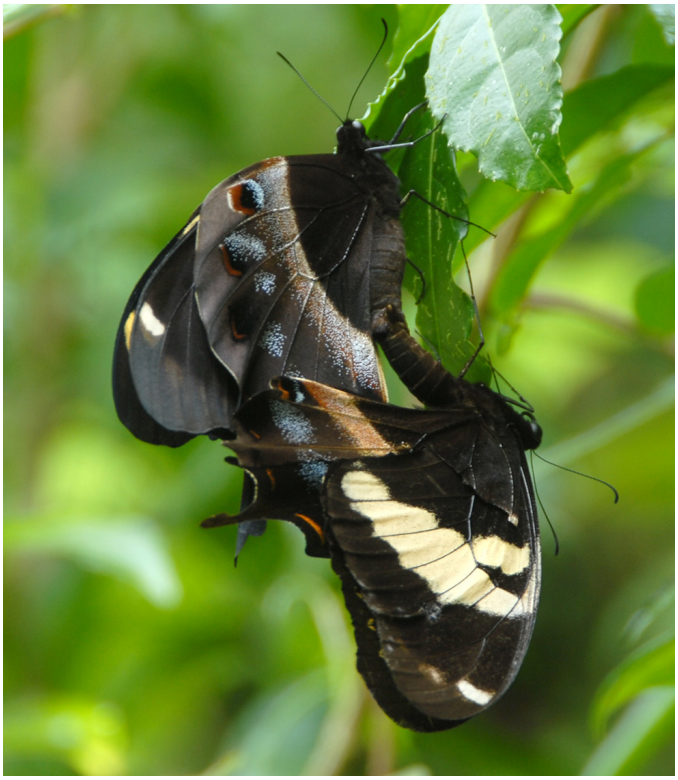
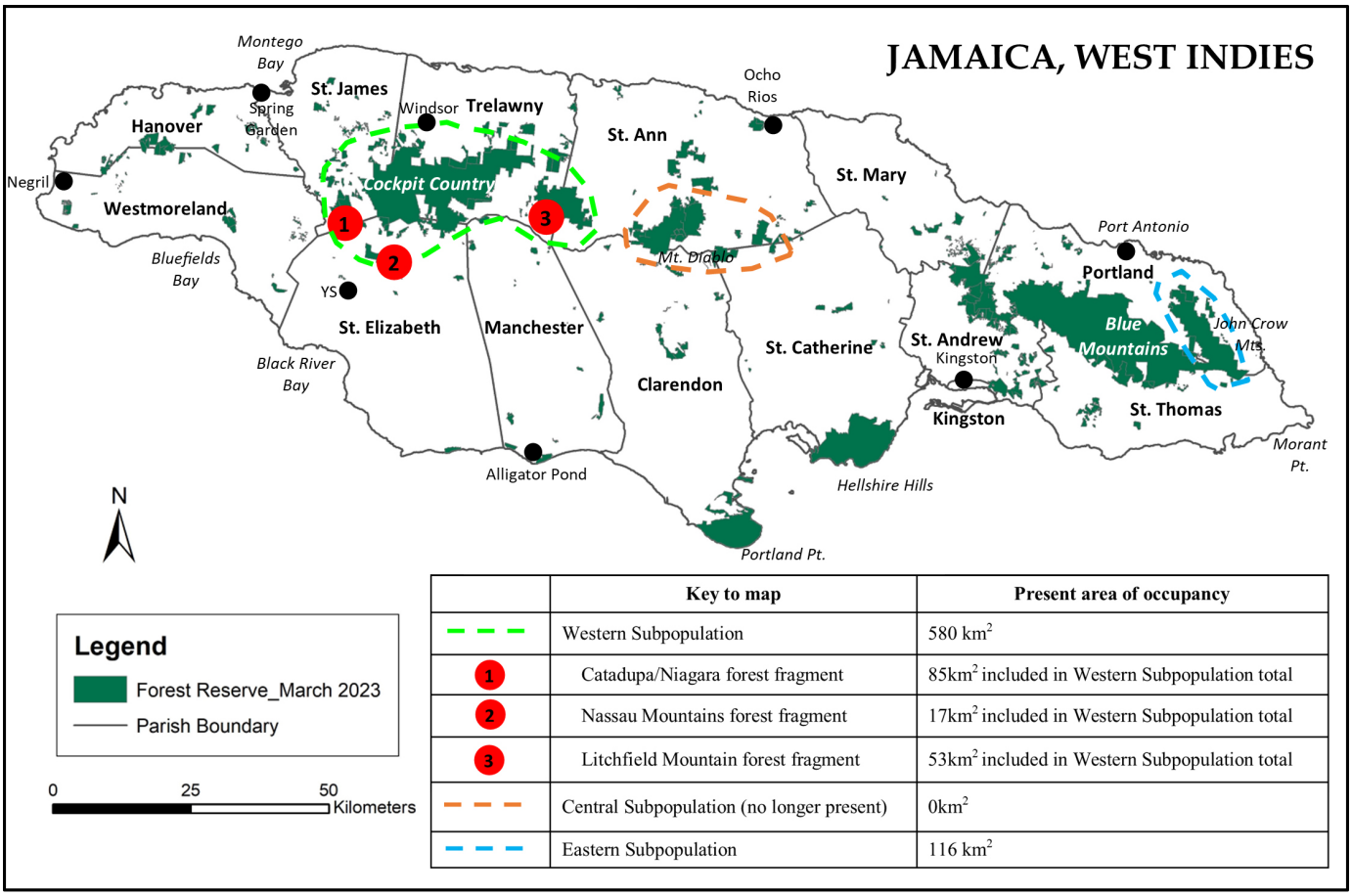


Figure 3. Homerus Swallowtails mating in the southern Cockpit Country. Female above. July 2010.

the remaining habitat without further fragmentation, reduction in size, or degradation through any form of adverse human encroachment.

HISTORICAL ASPECTS

A brief modern history of Homerus Swallowtail in the island begins with large-scale removal of the lowland forest starting with Spanish settlement in 1509. After the arrival of the English in 1655, large expanses of forest were cleared for habitations and interconnecting roads, and also for the extraction of timber and fuelwood, planting of sugarcane and coffee, and creation of pastures for livestock (Long, 1774; Craton & Walvin, 1970). There was also increased movement of people into the interior after the abolition of slavery in the British Commonwealth in 1833 (Füllberg-Stolberg, 2010). By the mid-1800s the once contiguous mesic broadleaf forest across the island had become discontinuous (Gosse, 1851; Craton & Walvin, 1970). Along with this fragmentation, the once single population of Homerus Swallowtail was permanently subdivided, leaving three subpopulations, each isolated within smaller areas of primary forest (Garraway & Emmel, 1990; Turner, 1991) (Fig. 4). These locations have been referred to as the Eastern, Central, and Western Subpopulations: the Eastern Subpopulation, centered in the southwestern John Crow Mountain range of eastern Jamaica in the parishes of Portland and St. Thomas; the Central Subpopulation, centered on Mount Diablo, primarily in the Parish of St. Ann; and the Western Subpopulation, located in the Cockpit Country and adjacent limestone forest landscape in the parishes of Trelawny, St. James, St. Elizabeth, and Manchester (Garraway & Emmel, 1990; Turner, 1991).



	Key to map	Present area of occupancy
– – –	Western Subpopulation	580 km^2
1	Catadupa/Niagara forest fragment	85km^2 included in Western Subpopulation total
2	Nassau Mountains forest fragment	17km^2 included in Western Subpopulation total
3	Litchfield Mountain forest fragment	53km^2 included in Western Subpopulation total
– – –	Central Subpopulation (no longer present)	0km^2
– – –	Eastern Subpopulation	116 km^2

Figure 4. The three subpopulations of the Homerus Swallowtail [map courtesy of Windsor Research Centre, 2021].

Because the butterfly is an obligate forest dweller unwilling to leave the contiguous forest habitat, these subpopulations were effectively isolated from each other.

As a result of continued deforestation, the Central Subpopulation has been extirpated. Little useful data can be obtained from examination of this subpopulation because there are too few records, but at one time the insect occupied a known area of no more than 225 km^2 (22,500 ha) (Kaye, 1926). Specimens obtained by early collectors, who, reportedly, often stayed at the former Moneague Inn or in nearby Claremont, were mostly from the Union Hill and Hollymount area of Mount Diablo (E. M. Swainson, in Brown & Heineman, 1972). Although approximately 82.5 km^2 (82,500 ha) of natural forest remains around Hollymount (839 m) (2,754 ft), this is evidently insufficient to support a population of Homerus Swallowtail. Average annual rainfall for the area based on records between 1870 and 1965 was between 1,270-2,540 mm, seasonally distributed with less than 127 mm per month between January and March, but apparently still capable of supporting a subpopulation of the insect. However, clearance of the forest for agriculture evidently included loss of the assumed larval foodplant, *Hernandia jamaicensis* Britton & Harris. This tree, known to occur only in discrete locations scattered through mesic broadleaf forest, has not been found there in recent years (Turner, pers. obs.). Adams (1966, pers. comm.) had suggested that the congener *H. sonora* L., introduced from Central America and growing near Moneague, could have been used as a larval foodplant, but no large-scale plantings exist to support this suggestion. The last record of Homerus Swallowtail documented from this location was in 1925 (Kaye, 1926). The species is now present only in the Eastern and Western Subpopulations, each presently threatened by decreasing humidity as a result of rising global temperatures and further loss of forest habitat (Turner, 1991; Stephenson *et al*., 2014; Planning Institute of Jamaica, Climate Studies Group, 2015).

POPULATION STUDIES

To accurately determine seasonal fluctuations in numbers of this insect in its natural surroundings requires continuous long-term studies, in part because it is unusual to see more than three adults on any given day. Accumulating meaningful data requires frequent visits to the habitat over consecutive years. Such studies have been conducted or overseen, for example, by Turner (1968-1970) and Garraway (1990-1993) in the Eastern Subpopulation, and M. Schwartz (2012-2013), Turland and Turner (2006-2016), and Lehnert (2008; Lehnert *et al*., 2017) in the Western Subpopulation. However, the data collected during such studies has to be assessed carefully to avoid unintended biases from anomalous records which can be unexpected or opportunistic, or rarely, the unusual occurrence of many specimens seen at once (Turner, 1991). Opportunistic sightings occur when visiting new or rarely visited locations outside the known population centers, when a single Homerus Swallowtail might be seen flying over the forest or along a watercourse. Any such sightings are important but these records were not

included in monthly tallies. Such sightings are noted for further investigation but so far these have been regarded as occasional strays.

In the Eastern Subpopulation there have been instances of multiple sightings in a single day within study areas. Walker (1945) noted that in 1902 Colonel Wirt Robinson collected fifteen specimens in one day, and an average of just over four more per day during the next nine days, for a total of forty-four specimens during ten days at Cuna Cuna Pass. Exceptional counts were also observed at Corn Puss Gap, with the early afternoon descent of adults along stream courses during summer as reported by Ronald Bengry and Thomas Farr (Institute of Jamaica, pers. comm.) in the early 1950s. Turner also observed this phenomenon in August 1962 just south of Corn Puss Gap, when eighteen adults descended one stream course during a 1.5 h period (Turner, 1991). This phenomenon was never observed again at this site and Garraway (pers. comm.) advised that he had never observed this behavior in streams feeding the upper Rio Grande valley north of Corn Puss Gap. Such records are of great interest but atypical.

THE EASTERN SUBPOPULATION

Geographic and climatic conditions. The northeast trade winds cross a very narrow band of coastal limestone, often no more than 5 km wide, before meeting the John Crow Mountain range, which is aligned southeast to northwest, parallel to the east coast of Jamaica, rising to a height of 1,143 m (Murray, 1952). Over the millennia the rain on the eastern slopes has removed much of the topsoil, leaving vast limestone blocks with deep crevasses and sinkholes over and between which dense forest has grown. The terrain here is so rugged and inhospitable that the primary forest has remained largely intact. From the eastern aspect of this mountain range there are three larger tributaries which flow east into Drivers River. This river flows southeast into Manchioneal Harbour. Priestmans River drains northward from the John Crow Mountains to enter the sea at Priestmans River Bay, approximately 12 km to the north of Manchioneal. Several smaller rivers or short streams are also present along the east coast. However, for reasons still unknown, the larval foodplant for Homerus Swallowtail has not been found in any of these waterways, although surveys, because of the difficult terrain, are still incomplete. Because the insect flies over these eastern slopes in summer it is possible that the butterfly also breeds here, but this has not yet been documented.

After rising to the highest elevation, the moisture laden clouds cross a narrow plateau with a plant community known as Saltwater Wood, resulting in almost daily rain falling on the west side of the mountain. Here, the clay capping on the western scarp face has largely eroded away at higher elevations, exposing layers of harder limestone or shale, but the clay soils have accumulated at lower elevations where high rainfall initiates large landslides from time to time. There is a spring line at elevations between 750 m and 850 m, from which no less than eleven streams, some branching, fall precipitously down in a general westerly direction until they encounter the east to west aligned Blue Mountain chain whose eastern end abuts the John Crow Mountains at Corn Puss Gap. At this juncture the streams are diverted to flow either southeast into the Plantain Garden River drainage or northwest into the Rio Grande River valley.

Corn Puss Gap experiences early morning mists, and rainfall occurs nearly every day throughout the summer, providing high humidity. The area where Homerus Swallowtail is known to breed receives not less than 380 mm of rain each month between May and December. In the upper reaches of the Rio Grande there is less frequent rainfall between January and March, but still not less than 250 mm per month, although average temperatures are lower (Nancoo *et al*., 1963; Turner, 1991).

In April 1961, a few kilometers north of Milbank in the Rio Grande Valley, customary daily showers were absent for the entire thirty days resulting in severe wilting of many plants which are adapted to normally wet conditions. This suggests that lack of even monthly distribution of adequate rainfall in this watershed can have a greater negative impact on plants growing in areas of normally high rainfall than has generally been recognized. However, streams descending the west side of the John Crow Mountains do remain flowing all year, albeit sometimes reduced to a trickle, and most of the larval foodplants for this subpopulation are found beside these streams. Temperatures at Milbank ranged between 27ºC and 29ºC during the day and 22ºC to 23ºC at night, but at Corn Puss Gap, near the upper limits for presence of the larval foodplant, the temperature at night falls below 20ºC from the end of September until the following March, and marks the descent of the butterfly from higher elevations to lower elevations which they occupy until favorable temperatures return the following April (Turner, 1991) (Fig. 5). In September, barometric pressure also falls from 1,016 mb to 1,012 mb and hours of cloud cover increase significantly, with many days with little sunshine. It is probably a combination of these factors, and possibly the shortening day length, that initiates this movement of adults to lower elevations.

The primary study area selected by Garraway and collaborators extended from the tributaries of the upper Rio Grande valley to higher elevations along the trail to Cuna Cuna Pass west of Corn Puss Gap, where weather conditions may be less extreme between November and March (Garraway *et al*., 1993; Garraway *et al*., 2008a). At elevations between 170 m to 550 m no seasonal vertical population shifts were detected, although a reduction in adults present between September and April in the upper Rio Grande valley was also noted as shown in Figure 6 (Garraway *et al*., 1993).

Number of generations. The life history from egg to adult can be completed in as few as 74 days or as many as 84 days and is expected to take longer to complete between November and February when conditions are both cooler and dryer (Turner, 1991; Garraway *et al*., 2008a) (Fig. 7). Fluctuations in monthly numbers of adults in the Eastern Subpopulation were compiled from egg counts, and from monthly counts of adults over consecutive years. The number of eggs found on foodplant leaves correlated closely with the seasonal numbers of adults seen in the field when plotted monthly (Turner 1991; Garraway *et al*., 1993; Garraway *et al*., 2008a; Turner & Turland, 2017).

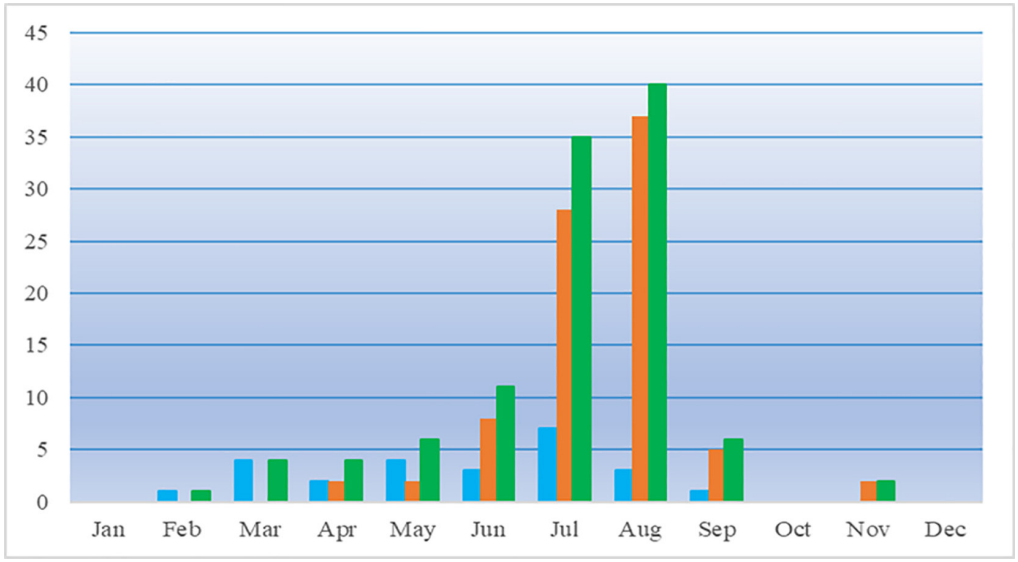


Figure 5. Numbers of adults observed monthly in the Eastern Subpopulation between upper Rio Grande valley and Corn Puss Gap 1968-1970 [After Turner, 1991].

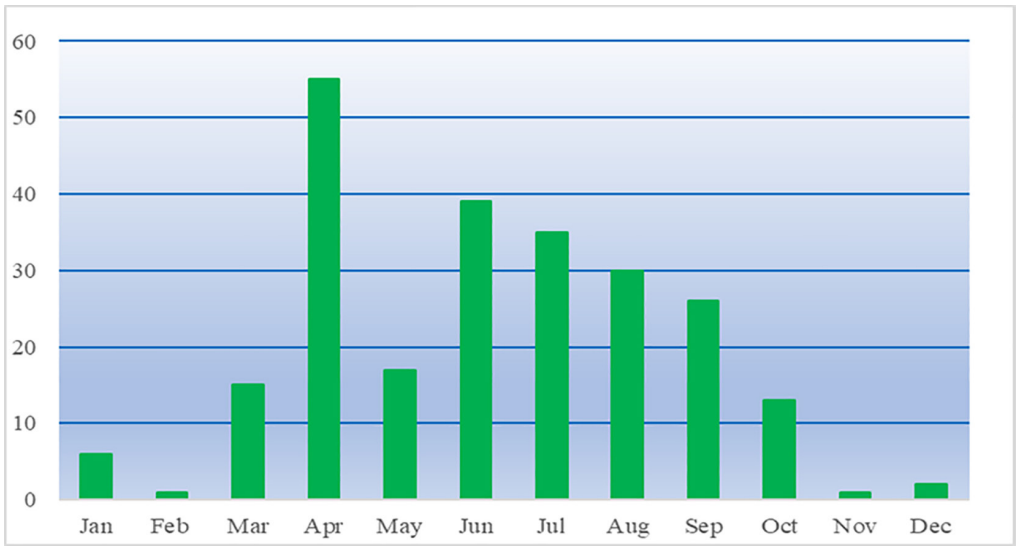


Figure 6. Numbers of adults observed monthly in the Eastern Subpopulation between the upper Rio Grande valley and Cuna Cuna Pass 1991-1993 [After Garraway *et al*., 1993].

Data collected from the number of immatures, and adults present in any given month, and their wing condition, were used to estimate the number of annual generations and to examine factors that might be modulating the abundance of adults in the field (Turner, 1991; Garraway *et al*., 1993; Garraway *et al*., 2008a; Turner & Turland, 2017).

There is no doubt that generations overlap (Fig. 8), with the adults from the first life cycle, for example, contributing to the third generation and those from the second generation contributing to the fourth generation and so on. There are two overlapping generations between October and February, three overlapping generations between February and late September, the generations between October and February marking a critical period in the life history when adults and immature stages are at their lowest numbers. Between November and February very few adults are seen, yet survival of the adults and any immature stages during this time is essential for the origination of the next generation leading to increased numbers of adults seen in later generations when conditions become more favorable. Pupal diapause, a possible way of overcoming adverse conditions evident in some groups of swallowtails, has not been found in any studies of Homerus Swallowtail so far (Garraway & Emmel, 1990; Turner, 1991; Garraway *et al*., 1993; Garraway *et al*., 2008a). In Figure 8, the first two overlapping generations combined give rise to the increase in numbers of adults produced at lower elevations between February and April. Adults from these generations then ascend the valleys to produce the generations observed at Corn Puss Gap after temperatures become more favorable at higher elevations (Turner, 1991). The information obtained from these studies was then compared with monthly abundance of adults seen in the far less studied Western Subpopulation (M. Schwartz, 2013; Turner & Turland, 2107). The monthly numbers of adults present during the year vary greatly, but with a similar pattern in each subpopulation with fluctuations appearing to be influenced mostly by climatic conditions (Fig. 11).

Figure 7. Life cycle stages of the Homerus Swallowtail. Key: a. Egg; b. First instar larva; c. Third instar larva, lateral aspect; d. Third instar larva, dorsal aspect; e. Final instar larva, dorsal aspect; f. Final instar larva, lateral aspect; g. Pupa.

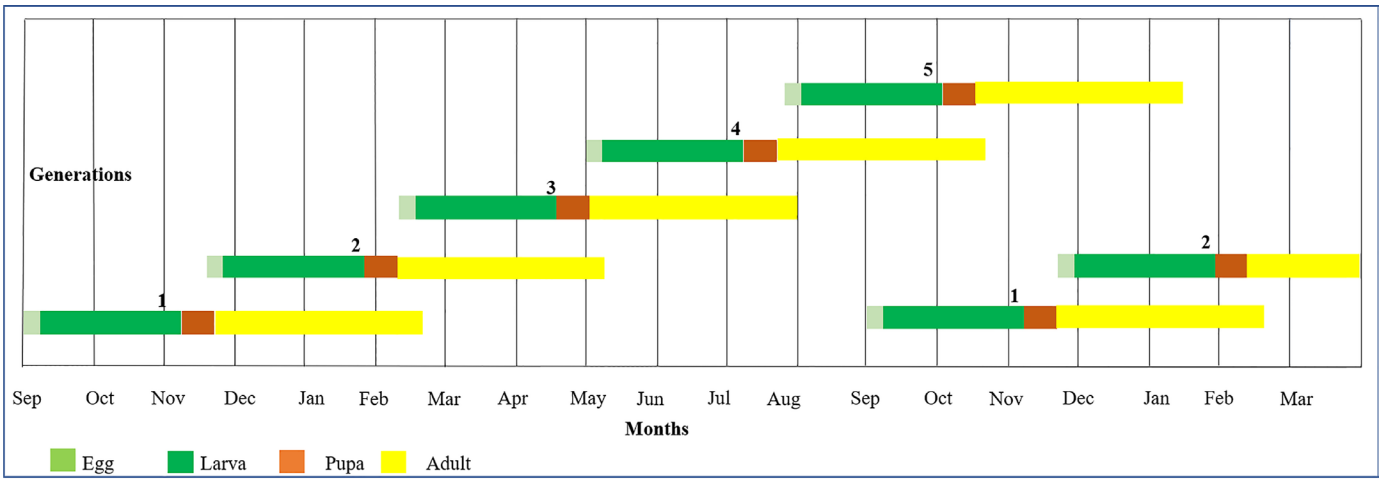


Figure 8. Estimated number of generations of Homerus Swallowtail, twelve-month period [Turner, 2021].

Longevity of the adult. Based on observations over time of individual territorial males at Corn Puss Gap, some adults appear to live as long as twelve weeks during summer as indicated by identifiable wing damage. Garraway noted adults live "for a few weeks in the field" but that adults in shade houses in Gainesville, Florida, were kept alive for a "maximum of only six days" (Garraway *et al*., 2008a). Additional research is required to understand these differences.

Distribution of larval foodplant. Another factor affecting distribution of adults in the Eastern Subpopulation is the distribution of *Hernandia catalpifolia* Britton & Harris, the larval foodplant. The distribution of *H. catalpifolia*, the only fully documented larval foodplant in the Eastern Subpopulation, is determined by topography, elevation, the amount and distribution of annual rainfall, and the amount of groundwater, usually in the form of streams. While male Homerus Swallowtail are sometimes seen at the periphery of contiguous forest, the females appear to be more closely associated with areas where the larval foodplant occurs. *Hernandia catalpifolia* is an understory tree which grows primarily along streams in a narrow band of forest at elevations from approximately 150 m up to an elevation of 640 m (Adams, 1972). Between elevations of 380 m and 640 m there is usually a closed primary forest canopy 24-28 m in height (Kelly, 1986). At an average elevation of approximately 300 m on either side of the Blue Mountain divide are patches of abandoned fields or active cultivations. This leaves a narrow band of relatively undisturbed forest between elevations of 300 m and 640 m, approximately 22 km^2 in area, where most *Hernandia* can be found. The present known distribution of this plant closely matches the area which receives between 250 mm and 380 mm of rainfall each month, based on data from 1870 to 1960 (Nancoo *et al*., 1963). Density of larval foodplants in the Eastern Subpopulation, where most trees grew within 30 m of streams, varied between 55.5 per km^2 and 80.8 per km^2 depending upon degree of forest disturbance (Garraway *et al*., 2008a).

Seasonal availability of nectar sources. A further requirement for the successful survival of the adult is the ready availability of nectar sources, but observations indicate that nectar sources in the forests where the insect flies are limited. Plants within the forest flower sporadically and adults appear to accept nectar from any available source. Nectar plants can be divided into three categories: native flowering plants found within undisturbed forest; nectar plants introduced accidentally into the forest along trails; and plants introduced into secondary

Figure 9. Female Homerus Swallowtail nectaring on *Psychotria* sp., southern Cockpit Country, July 2012.

forest along the primary forest margins including cultivated plants, with one native species *Entada gigas* (L.), F. & R., found climbing over other plants along riverbanks at lower elevations (Table 1). These plants have specific flowering times during the year and are not continuing sources of nectar, but when in flower are visited by adults (T. Turner pers. obs.).

Individual adults visited flowers of native species of *Cissus* and *Nectandra* for up to 10 minutes at a time (Turner, 1991). Adults were also observed visiting flowers introduced to the forest habitat along open trails feeding close to the ground on species of *Asclepias*, *Biden*s, *Urena*, and *Lantana*. Such visits were brief. However, adults spent considerable time nectaring on introduced *Spathodea* tree flowers (Turner, 1991).

In lower river valleys and disturbed areas, the native vine *Entada*, introduced Manila Bean, *Psophocarpus*, Ginger Lily, *Hedychium*, Black Stick, *Pachystachys*, and *Hibiscus*, as well as *Lantana*, *Urena*, *Bidens*, *Asclepias*, and *Spathodea* are also nectar sources (Turner, 1991; Garraway *et al*., 1993). Some of these species growing at the forest margins are the source of those plants introduced along trails through primary forest by man and animals. Others are associated with habitations present just beyond the forest margin.

Although the list of flowering nectar plants includes several species, most of the observations are from isolated records accumulated over time, often with a single plant species being the only flowering plant present at any one time. The behavior of opportunistic feeding on any available flowering plant representing many different families suggests that nectar sources within the forest, as observations confirm, are actually in limited supply from time to time resulting in the insect flying to the forest margins where introduced flowering plants are also available. Native flowering plants were probably in greater abundance before the upper Rio Grande valley forests were cleared for small-scale agriculture. Now, a number of introduced garden plants have become available at these lower elevations.

This apparent shortage of nectar plants is further borne out during the summer months when adults will fly beyond the primary forest to the periphery of their territories in localities as far away as Ecclesdown on the east side of the John Crow Mountains (M. Partridge, pers. obs.) and south of Corn Puss Gap in the Plantain Garden River watershed to access flowering African Tulip trees, *Spathodea*, with as many as eight adults of either sex feeding together at a single flowering tree (Lewis, 1947; Turner, 1991).

Table 1. Nectar sources for Homerus Swallowtail.

Native Nectar Plants in Undisturbed Forest	
Hernandia catalpifolia Britton & Harris	Hernandiaceae
Nectandra coriacea (Sw.) Griseb	Lauraceae
Micranium virgatum (Sw.) Triana	Melastomaceae
Cissus sicyoides L.	Vitaceae
Nectar Plants Introduced into the Forest Habitat	
Asclepias curassavica L.	Asclepiadaceae
Spathodea campanulata Beauv.	Bignoniaceae
Bidens pilosa L.	Compositae
Urena lobata L.	Malvaceae
Lantana camara L.	Verbenaceae
Nectar Plants present in Marginal Secondary Forest	
Asclepias curassavica L.	Asclepiadaceae
Pachystachys coccinea (Aubl.) Nees in DC	Acanthaceae
Spathodea campanulata Beauv.	Bignoniaceae
Bidens pilosa L.	Compositae
Urena lobata L.	Malvaceae
Hibiscus rosa-sinensis L.	Malvaceae
Psophocarpus palustris Desv.	Papilionaceae
Lantana camara L	Verbenaceae
Hedychium coronarium Koenig	Zingiberaceae

While it is obvious that over millennia the insect must have been able to find adequate nectar sources within the forest, the fact that this insect now visits many flowering species including small plants such as *Asclepias* and *Bidens*, not usually present within the forest, and is also prepared to fly to visit *Spathodea* and introduced flowering plants at the forest margins, suggests that making additional nectar sources available might be beneficial, allowing adults to remain closer to larval foodplants. Conversely, if there was a larger area of undisturbed forest with native flowering plants it would be less likely that adults would choose to find nectar from introduced plants along forest trails and at the forest margins. Nevertheless, adult males do show the propensity to fly away from core population areas from time to time. This behavior likely enhances chances of males finding females in more distant locations while at the same time diminishing inbreeding (T. Turner, pers. obs.) It should be noted that such flights still remain within nearly contiguous forest or shaded river courses and do not take place over large discontinuities in forest cover (Turner, 1991; Turner & Turland, 2017). Although normally obligate forest butterflies such as *Doxocopa laure* Hűbner (Nymphalidae) have been observed making flights of many kilometers between patches of forest in Jamaica, this is not the usual behavior demonstrated by Homerus Swallowtail. The swallowtail has been observed crossing openings of up to 350 meters within the forest and leaving the contiguous forest for about the same distance along forested waterways, but otherwise the species remains within or near larger areas of contiguous forest.

Egg parasitism and forest density. At lower elevations in the upper Rio Grande valley some already established *Hernandia* trees remain in the open after the forest around these has been cleared for cultivations, especially at elevations below 300 m. Here, the streams beside which *Hernandia* grows run through forest clearings and encounter a mix of abandoned fields, small-scale agriculture, and forestry plantings of Caribbean Pine. These locations are frequented by Homerus Swallowtail in the cooler, dryer months, especially between December and March (Turner, 1991; Garraway *et al*., 1993; Garraway *et al*., 2008a). Again, because this insect is reluctant to fly across open areas, adults are mostly restricted to flights up and down these narrowly wooded stream courses. As documented by Garraway the *Hernandia* plants growing here are also exposed at the edge of the forest or within cultivated fields and are readily accepted as oviposition sites by females, but perhaps these more exposed plants also facilitate detection of eggs by egg parasitoids (Garraway *et al*., 2008a). In those studies, egg parasitism, primarily from a species of *Chrysonotomyia* (Eulophidae), was as high as 75.6% in the most exposed locations falling to 47.4% where forest cover was estimated to be 70%. No egg parasitism was observed in undisturbed forest at Corn Puss Gap at an elevation of 640 m, but 30% of a small sample of eggs collected from that locality at a later date were found to be parasitized by two species of *Chrysonotomyia* (Eulophidae) (Turner, 1991; Garraway *et al*., 1993). So, not only is the species' area of occupancy between the end of September and the following March significantly decreased in effective size in response to climatic conditions, especially lower temperatures, but the forest cover available at lower elevations is mostly sparse disturbed forest, perhaps less well suited for adult occupation. Here, immature stages experience significant losses from parasitoids during the months that adults oviposit at these lower elevations (Garraway *et al*., 1993).

It has been suggested that, although there can be large losses from egg parasitoids, the *Hernandia* plants that were studied were underutilized, and that there was adequate availability of nectar sources, implying that the population existed at a level below which these resources become limiting (Garraway *et al*., 1993). Conversely, it could be argued that if the larval foodplants were growing in undisturbed primary forest there would be lower exposure to egg parasitoids found more commonly at the forest margin, perhaps leading to greater survival.

Humidity and the immature stages. During rearing of the immature stages at the University of the West Indies, Mona, between 1966 and 1970, cuttings of *Hernandia catalpifolia* obtained at Corn Puss Gap were placed in plastic bags and brought back to the insectary at the then Department of Zoology (now part of the Life Sciences Department). The cuttings, on which immature stages were placed, were inserted into jars of water inside large 30 cm x 90 cm round mesh cages covered in clear plastic bags. However, these cuttings lasted in a fresh state for no more than three days before wilting, becoming unacceptable to the larvae. This necessitated nearly a full day's trip to return to Corn Puss Gap to obtain fresh foodplant supplies. As an alternative, small saplings of *H. catalpifolia* were uprooted and placed in jars filled with a mixture of soil from the habitat and freshwater. Plants in this condition lasted in suitable condition for between seven and ten days, still requiring arduous field trips for frequent replenishment. This problem was resolved by collecting small, rooted plants of *Hernandia jamaicensis* Britton & Harris, a plant requiring less groundwater, from the Cockpit Country, potted in soil and water, and caged as before, on which larvae could be maintained for several weeks, thus also demonstrating that larvae from the Eastern Subpopulation accepted and could be raised on *H. jamaicensis.* Immature stages of Homerus Swallowtail collected from the Cockpit Country were also raised in the laboratory, marking the first time this plant was identified as Homerus Swallowtail's larval foodplant in that subpopulation (Garraway & Emmel, 1990; Turner, 1991). It was also noted that larvae drank water from leaf surfaces, especially from the third instar onwards, so it was necessary to mist leaves with water daily to mimic the water from rainfall and condensates occurring in the natural habitat (Turner, 1991; Garraway *et al*., 1993). Failure to maintain near 100% humidity within rearing cages resulted in desiccated pupae. However, plastic covers were removed from cages while immature stages were examined under magnification for descriptive purposes, allowing for periods of aeration of at least one hour daily. Specimens reared from both Eastern and Western Subpopulations never showed any indication that either subpopulation appeared to be experiencing deleterious effects from inbreeding, such as unexplained larval mortality or adult wing deformities (T. Turner, pers. obs.). Nor were any obvious signs found that might indicate that these subpopulations might be different subspecies after a separation of just 150 years, though such differences might exist but not be visibly evident (T. Turner, pers. obs.). However, samples were very small with no more than five specimens reared at any one time.

Predation and disease. Homerus Swallowtail employs a number of strategies that appear to benefit survival of the immature stages and longevity of the adult in the field, but in spite of camouflage and chemical defenses, parasitism, bacterial diseases, and unexplained losses occurred in all the life stages.

Eggs are laid singly on top of leaves, and eggs of more than one age can be found on a single leaf. Although significant parasitism of eggs has been documented in secondary forest locations, far fewer eggs were parasitized within closed primary broadleaf forest (Turner, 1991; Garraway *et al*., 1993). This is a significant consideration for any larval foodplant planting project. Occasionally, eggs were removed from leaves by the Trap Jaw ant, *Odonotomachus bauri* Emery, locally known as Kop Kop (Turner, 1991). Predation of first instar larvae by a species of Carpenter Ant (*Campanotus* sp.) was also observed on one occasion (Garraway *et al*., 2008a).

In the first two larval instars the tiny black larvae with a white saddle on terminal segments depend on deception to avoid predation, appearing similar to lizard excrement. The larger third instar larvae employ a similar pattern but with additional white markings and blue spots as well as eyespots on enlarged thoracic segments, perhaps appearing more like bird excrement. The final two instars are predominantly green but with black dorsal x-marks and well-developed spectacled eye

spots on the metathorax. While the osmeteria are only deployed with reluctance in the first three instars, they are extruded more readily when the larva is disturbed during the last two instars, disseminating a turpenoid scent (Turner, 1991). In addition, these larger larvae raise the head and anterior segments from the leaf when disturbed, perhaps an effective defense posture against diurnal anoles and nocturnal frogs (Turner & Turland, 2017).

No instances of losses of larvae from bacterial infections were recorded in the field or laboratory (Turner, 1991), but losses from three species of bacteria were noted in all stages of both wild collected and caged immature stages in the 1993 study (Garraway *et al*., 1993). Larvae "in any stage" were killed by species of *Bacillus* Cohn, *Enterobacter* Hormaeche and Edwards, and *Klebsiella* Friedländer bacteria (Garraway *et al*., 2008a). These were larvae in captivity either caged in the laboratory or sleeved on foodplants in the wild, although larval density and percentage humidity in caged conditions were not stated. Pupae also succumbed to bacterial infections (Garraway *et al*., 2008a). No instances of bacterial infections in caged or wild-found larvae or pupae were observed in other studies (Turner, 1991).

The Jamaican Elaenia, *Myiopagis cotta* (Wagler), (Tyrannidae), was observed on several occasions removing first to third instar larvae from *Hernandia* leaves. Similarly, the Jamaican Oriole, *Icterus leucopteryx* (Gosse), (Icteridae), was observed consuming fourth and fifth instar larvae from tops of leaves (Turner, 1991).

Larvae move away from the larval foodplant to pupate and pupae rely on camouflage for protection, appearing like a broken stick with small pinkish-white fungal spots commonly present on rotting twigs in this habitat. Pupae can be gray, brown, brown and green, or green, depending on whether the selected pupation site was, for example, a bare brown or gray twig or green and brown fern (Turner, 1991; Garraway *et al*., 1993; Turner & Turland, 2017). Some 13% of pupae were lost due to bacterial infection under caged conditions (Garraway *et al*., 1993; Garraway *et al*., 2008a).

Adults, when handled, release an oily secretion from the thoracic segments. The scent is similar to that of the roots of the grass *Chrysopogon zizanioides* (L.) (Poaceae), used as a perfume and locally known as Khus Khus (Turner, 1991). The essential oils found in Khus Khus include sesquiterpenoids (Chahal *et al*., 2015). Species of *Hernandia* have long been used in preparation of native medicines, especially in Asian countries, and analyses indicate that one of the several chemicals present in the leaves of some *Hernandia* are triterpenes (Primeau, 2007). Such chemicals are presumably sequestered from *Hernandia* leaves by the larvae, then during the pupal stage chemical modifications or sequestration evidently occurs resulting in the perfumed oily substance present in the adult. Such a product would not only be of benefit against nocturnal predators when the insect is resting beneath a leaf but might also be released while under aerial attack from birds during the day. Whether this scent is disseminated either defensively or during courtship flights remains to be determined.

The Jamaican Loggerhead Kingbird *Tyrannus caudifasciatus jamaicensis* Chapman, (Tyrannidae), was observed attacking adult Homerus Swallowtail on numerous occasions, either when settled, sunning on a leaf with wings outspread, or while in flight. Although no Homerus Swallowtail were observed being captured, many escaped with wing damage (T. Turner, pers. obs.). Wing damage from birds was evident on approximately one third of specimens examined in museum collections (T. Turner, pers. obs.). Wings with bluntly pointed or rounded sections removed from the same place on both wings suggested this damage was possibly caused by lizard or frog attack while at rest under a support such as a leaf with wings closed, but actual attacks have not been observed.

Poaching. Historically, there has been persistent collection of Homerus Swallowtail from the Eastern Subpopulation. Earliest reports predating the 1950s mention people in the town of Bath beside the Sulphur River, who reared specimens and sold them locally or mailed them overseas. Prior to 1988, when the insect was placed on the CITES Appendix 1 listings, collecting this insect was not illegal (Collins & Morris, 1985). It is now illegal to disturb, collect, or export specimens without a permit under both CITES and the Wildlife Protection Act 2000.

While there are few, if any, *Hernandia* trees remaining in the lower reaches of the Sulphur River, the insect is still sometimes seen along this watercourse and there are repeated reports, some verified personally as recently as 1991, of people supplied with large nets being paid to collect specimens for export, mostly to Japan. Large numbers of adults have also been documented being collected in a short space of time by visiting collectors. In one such instance a commercial collector caught thirty specimens between September and November 1983 along the trail from Portland to St. Thomas parishes, including eighteen females (R. King, pers. comm.). Seventeen specimens were sold to a single commercial dealer from Japan in 1986 (Garraway & Emmel, 1990).

While removal of adults from the habitat, especially females, has an immediate impact on the breeding population, the removal of immature stages for raising adults by local residents, especially at times when the adult population is at its lowest numbers, can, presumably, have an even greater deleterious effect since such poaching is also continuous.

In the 1970s, in the upper reaches of the Rio Grande River valley, local resident Orlando Wilson, was approached by commercial dealers from the United States and Germany to collect and export specimens at a time before the butterfly had received protected status. Payments Orlando received were between US$15 and US$50 per specimen (Garraway & Emmel, 1990). Protections for Homerus Swallowtail were initiated in 1983 as noted in The IUCN Invertebrate Red Data Book (Turner, 1983a, Turner, 1983b, Wells *et al*., 1983). In 1984 Orlando was employed as a Field Officer by Dr. Eric Garraway from the University of the West Indies, Mona to participate in Homerus Swallowtail life history studies and subsequent conservation programs (Garraway *et al*., 2017).

Prices offered to local collectors in the 1960s averaged US$25, while sales abroad increased from US$400 to US$1,500 between 1970 and 1980, with one report that a specimen sold at auction in Paris, France, for US$8,000 (B. Heineman 1967, pers. comm.). In the 1980s prices abroad were said to be as

high as US$3,000 per specimen. In 2021 a specimen was being offered for sale for $3,000 on a website in Germany (R. King, pers. comm.). Occasional offers for sale of specimens occur on websites around the world, but attempts to trace the people behind these offers are quickly blocked. As of 2019 there are persistent reports of people in the Rio Grande valley, trained by people allegedly from Japan to collect immature stages, rear these to adults and carefully kill these by injection so as to obtain perfect specimens before mailing them overseas, even though this insect is now a protected species. There is evidence that well-organized but illegal collection and export of specimens aided by local people continues to the present time (T. Turner, pers. obs.).

Loss of occupied habitat. Since 1925, and in particular in the forty years between 1940 and 1980, there has been continuing loss of suitable forest habitat around the periphery and within areas occupied by both Eastern and Western Subpopulations (Camirand & Evelyn, 2003; Turner & Turland, 2017). In the seventy-five years between 1940 and 2015 approximately 50% of the habitat occupied by each subpopulation of Homerus Swallowtail has been lost, as measured by presence or absence of mesic broadleaf forest together with documented sightings of the butterfly over time (Turner & Turland, 2017). The continuing removal and disturbance of forest is primarily responsible for the declining areas suitable for occupation by the swallowtail and is the main present threat to the survival of the species.

Records noting presence or absence of adults observed in flight over time between 1940 and 2015 indicate that in 1940 the range of flight of the Eastern Subpopulation occupied approximately 250 km^2 (25,000 ha). The present area occupied is now approximately 116 km^2 (11,600 ha), representing a loss of flight range of 54% with a known foodplant distribution of just 22 km^2 (2,200 ha) within this area, although additional surveys are needed. As stated earlier, this insect is an obligate forest dweller reluctant to cross open deforested areas. As the forest is removed the insect becomes confined to whatever forested areas remain. Loss of flight range is directly attributable to loss of contiguous forest cover (Turner & Turland, 2017). The climatic, edaphic, and biotic conditions of the Eastern and Western Subpopulations differ significantly in many respects, but they share in common the ill-effects of deforestation as a result of human activities (Craton & Walvin, 1970; Füllberg-Stolberg, 2010).

During the middle of the year, especially between June and August when flight ranges of both subpopulations of Homerus Swallowtail reach their maximum expanse, males in particular are seen at the periphery of available undisturbed forest, giving the impression that the insect occupies these peripheral locations year-round (T. Turner, pers. obs.). Although distribution of larval foodplants and understanding of adult behavior still needs refining, there is no evidence that this extended range of flight necessarily represents the area permanently occupied. In the remaining months, usually between November and March, the insect is found only in far more restricted locations, so any assumption that the population is healthy based on sightings in peripheral areas can be misleading. The remaining areas of suitable forest which Homerus Swallowtail occupies year-round are much smaller, but still need to be accurately redefined (Turner & Turland, 2017).

THE WESTERN SUBPOPULATION

Geographic and climatic factors. The terrain occupied by the Western Subpopulation (Fig. 10) differs significantly from that of the Eastern Subpopulation. The karst terrain in western Jamaica consists of numerous forested convex conical hills. Some of these hills are as high as 120 m, often arranged in close proximity with relatively little distance between. As a result, the hill's aspect results in part of each hill and the enclosed cockpit depressions, some as deep as 120 m, being almost totally shaded, while in larger depressions there may be almost total daily sun. Relatively little soil remains on the tops of the hills and the sides are sometimes vertical cliffs with little vegetation. The hills, and most cockpits between, are covered in mesic broadleaf forest, also known as lowland evergreen forest, but the vegetation on top of the hills consists of shorter, narrower stemmed plants, reflecting the conditions they experience from thinner soils and greater water stress (Proctor, 1983). Conversely, the cockpits have deeper soil and accumulations of leaf litter. This allows for more abundant moisture, which together with evapotranspiration and dispersal of volatile compounds from the vegetation from larger trees growing between the hills, promotes convectional rain. In typical years this rain falls in some parts of the Cockpit Country nearly every day between May and October (Proctor, 1986; Laurence, 2004). Noticeably less rainfall occurs between November and April, when irregular rain from cooler northwesterly winds known as Northers, adds to the total annual rainfall (Nancoo *et al*., 1963). There are very few groundwater streams, these being confined to the fringes of the Cockpit Country where they emerge from the limestone as springs before flowing to the north or south coasts as streams or rivers (Fincham, 1997). No less than six major river systems originating from this region supply the requirements of agriculture, towns and villages, and the numerous coastal hotels and guest houses which form the backbone of one of Jamaica's primary sources of income, namely tourism (Jamaica

Figure 10. Landscape view of Primary Mesic Broadleaf Forest, Cockpit Country north of Quickstep, Trelawny Parish, December 2010.

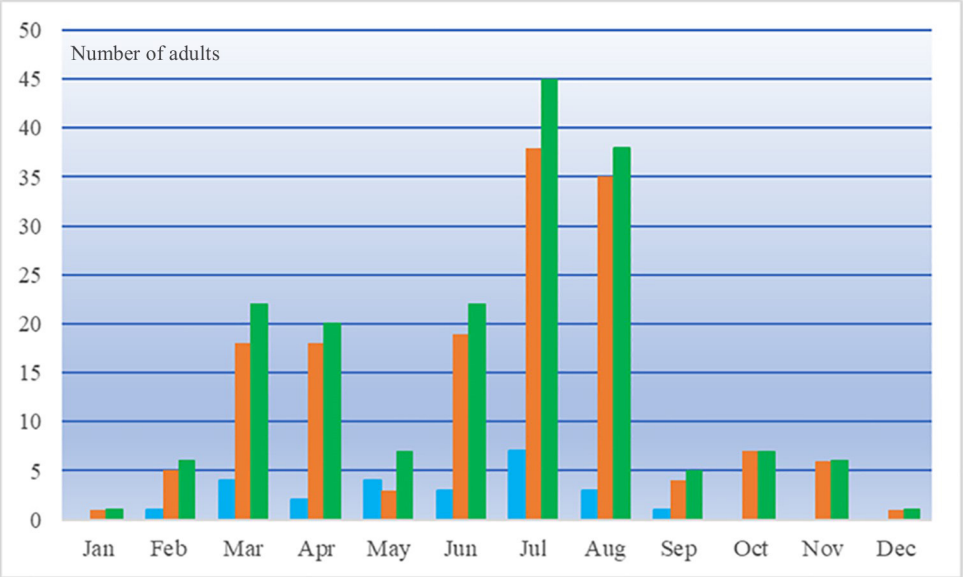


Figure 11. Monthly numbers of adults 2006-2016. Western Subpopulation near Quickstep, Trelawny [after Turland and Turner, 2017].

Information Service, 2019). Preservation of the forest canopy in the Cockpit Country, the source of these rivers, is not only necessary for Homerus Swallowtail but also for the protection of the watersheds of these rivers (Proctor, 1986).

Although difficult to document due to limited time in the field, it was also observed that in all locations there were years when Homerus Swallowtail appeared to be more abundant than others. The reasons for this have not been determined but may relate to the amount and distribution of annual rainfall. For example, in four visits to the Cockpit Country in the peak butterfly season of 2020, Turland did not observe a single specimen of Homerus Swallowtail. The forest was extremely dry, to the point where there was a noticeable near absence of the usually prolific wood mosquitos and with many lichens and mosses near desiccated.

Population studies. Monthly records for the Western Subpopulation were obtained in the Cockpit Country from sightings of adults flying in rugged terrain while walking along the only available existing trails on a weekly or monthly basis (M. Schwartz, 2013; Turner & Turland, 2017). The process used by the authors for counting Homerus Swallowtail was based on a modified Pollard Walk (Pollard, 1977). Because the terrain is both mountainous with heavily wooded slopes, and with the insect preferring to fly along water courses in the Eastern Subpopulation and soaring over and around cockpits and associated convex limestone hillsides in the Western Subpopulation, the concept of recording specimens observed in a moving five-meter box ahead of the observer as suggested by Pollard could not be strictly applied. A modified Pollard Walk which he described as “imperfect” due to the terrain was also employed for surveys overseen by Schwartz (M. Schwartz, 2013).

Counting the number of adults seen on a one-day visit, usually of four-hour duration, took place between 0900-1400 h. Visits could not always be made weekly, but over a number of years trips did include all weeks of the year. The accumulated data provided the monthly distribution of adults. Visits were conducted by walking along a trail in one direction counting Homerus Swallowtail as it crossed the path or circled a glade, then continuing on. The same trails were visited on repeated visits. Where there were trees such as *Spathodea campanulata* Beauv., or *Bauhinia divaricata* L., which attract larger numbers of the butterfly when flowering, the number of adults circling the tree were counted, care being made not to count specimens more than once, not moving on until a satisfactory count had been made. Since usually no more than eight of these butterflies were ever seen at such trees at the same time, it was not difficult to resolve the total number seen.

Whenever it was possible to determine the sex, this too was noted. Even though the sexes are similar, it is possible with practice to identify each by size and color with a high degree of reliability. This process of counting was repeated to the end of the trail, usually over a distance of about 6.5 km, before turning back. The return trip offered a different view of the terrain, and sometimes an adult spotted in a new location could be counted as a new sighting, but counting adults near locations where adults were previously seen was avoided unless, for example, the first adult seen was a male and the second a female. Specimens observed ovipositing always provided a certain identity. Sometimes it was possible to avoid counting specimens twice by observing distinctive wing damage. Upon returning to flowering trees previously seen, another count would be made. If there were larger numbers now nectaring, the difference between the first count and second would be added, or if one female had been observed during the first count and now there were two females, another female would be added to the original number. Overall, counts were made on the side of conservatism, tending to underestimate numbers seen rather than overestimating by counting every sighting as a new record. The accumulated data provided a good basis for ascertaining annual population fluctuations and provide evidence of a critical survival period that needs to be taken into consideration in any conservation plans (Turner & Turland, 2017).

The number of adults present throughout the year were determined by trail counts between 2006 and 2016, as described earlier, with monthly adult frequency surprisingly similar to those from the Eastern Subpopulation. In this instance however, the smaller area occupied by Homerus Swallowtail between October and March has not yet been fully determined.

Number of generations. Observations, together with presence or absence of immature stages, suggest that this subpopulation, like the Eastern Subpopulation, also goes through five overlapping generations in the Cockpit Country between October of the first year and the end of September in the second year; two overlapping generations between October and February, followed by three additional generations between February and late September (Fig. 11). The smaller but critical generations between October and February are at a time when nightly temperatures, like those of the Eastern Subpopulation, fall below 20ºC.

Distribution of larval foodplant. *Hernandia jamaicensis* (Fig. 12), the larval foodplant of Homerus Swallowtail in these forests, is a tall emergent forest tree up to 20 m in height, not as dependent on surface running water for growth and seed dispersal, although it does appear that *Hernandia jamaicensis* seedlings favor germinating in damp shaded locations. The seeds are most probably dispersed by birds (D. Adams, pers comm; S. Koenig, pers. comm.), although Koenig notes that one of the suggested dispersers, parrots, tend to consume rather than disperse such seeds. Fruit bats are another probable disperser. The scattered locations of these trees may also reduce the incidence of egg parasitism in this habitat. To date no parasitism has been recorded here, but the immature stages of this subpopulation have been far less studied.

There is continuing marginal deforestation including loss of *Hernandia jamaicensis* trees. Because the *Hernandia* trees are scattered, each larval foodplant or foodplant cluster removed along the forest margins may result in a significant reduction in density of available foodplants. Although the density per km^2 of this *Hernandia* species in the Cockpit Country has not yet been determined, in certain areas it has been described as “common” (Garraway *et al*., 2008b; Lehnert, 2008). Our observations indicate “locally common” would be more appropriate.

Seasonal availability of nectar sources. As in the Eastern Subpopulation, nectar sources appear to be both seasonal and limited (Schwartz, 2013). Flowering trees of *Bauhinia divaricata* L. and *Spathodea campanulata* Beauv. May attract as many as eight adults of either sex at any given moment. Nectaring has been observed between 0900 h and 1600 h, although the total number of different specimens visiting a single tree on the same day has not been determined. When certain species of *Psychotria* L. are flowering, a single plant may attract as many as two to three adults simultaneously (Turner & Turland, 2017). However, these nectar plants are both uncommon in frequency and flower seasonally.

Poaching. The terrain in and around the Cockpit Country where the insect occurs is extremely rugged and difficult to traverse and collection of data from these forests has been far more difficult than from the forests of the Eastern Subpopulation. Adult Homerus Swallowtail are distributed through favorable areas of the forest where there is high humidity. One benefit from the difficult terrain is that poaching, so far as is known, is thought to be not as high as in the Eastern Subpopulation (Turner & Turland, 2017).

Location of critical habitat. The boundary around the area occupied by adults and immature stages between October and January still needs to be defined. It is believed that this refugia is within some of the humid cockpits of the west central Cockpit Country, where average rainfall is not less than 5,080 mm per annum. Absence of adults from peripheral forest locations where the insect is usually seen between March and October suggests these locations surround the area occupied by Homerus Swallowtail the remainder of the year. In addition, the precise smaller areas occupied by Homerus Swallowtail between late September and February within the forest fragments now separated from the Cockpit Country have also not been determined.

Forest fragmentation in the Western Subpopulation. Fifty-four percent of the area occupied by the Western Subpopulation has been lost in the last 75 years (Turner & Turland, 2017). Continuing clearing and thinning of the forest are reasons for great concern, not just for Homerus Swallowtail, but also for a habitat that contains many other endemic plants and animals (Proctor, 1986; Chenoweth *et al*., 2001; Koenig, 2015; Turner & Turland, 2017; Koenig, 2019). Furthermore, the periphery of this subpopulation, especially to the southwest and southeast, is being pinched off by deforestation into even smaller isolated fragments where the butterfly can still be found for the present.

All of these forest fragments were included in a proposed boundary for preservation by the Cockpit Country Stakeholders Group (CCSG), encompassing an area of approximately 1,163 km^2 (116,300 ha) (Koenig, 2019), but in 2017 the Government of Jamaica selected a smaller area for protection approximating

Figure 12. *Hernandia jamaicensis* in Mesic Broadleaf Forest of the Cockpit Country, July 2011.

to 772 km^2 (77, 200 ha) (Lyew-Ayee, 2005; M. Schwartz, 2013; Jamaica Information Service, 2017). Included within this boundary is 36,000 ha of Forest Reserve. The area finally approved for protection is 780.24 km^2 (78, 024 ha). This recently designated Cockpit Country Protected Area (CCPA) includes many habitations and adjacent cultivated areas, especially within the more accessible valleys, while excluding forested areas where both the larval foodplant and adult butterfly are present. Despite their protection under the Wildlife Protection Act 2000, there are no provisions for how Homerus Swallowtail and other key species in these areas outside the designated CCPA will be protected. Notwithstanding, some of these small areas do include Forest Reserves or forest plantations or 'Crown Lands' managed by the Forestry Department which theoretically should provide additional protections. Unfortunately, although Homerus Swallowtail is accorded legal protection, the habitats in which it occurs are given no protection. The Forest Reserves and plantations alone appear to be too small in area to maintain a viable subpopulation of Homerus Swallowtail indefinitely. Additionally, those areas managed as forest plantations are subject to ongoing disturbance and clearance with access to logging under permit.

It should be rightfully applauded that the government has recognized the need to protect both the essential water supply emanating from the Cockpit Country (Fincham, 1997), and the unique biodiversity of a habitat within a map drawn boundary which was finally approved in March 2022.

Forest loss within the Cockpit Country Protected Area (CCPA). The Cockpit Country Protected Area (CCPA), excludes some of the peripheral forest fragments where Homerus Swallowtail still occurs. The swallowtail does not permanently occupy all of the protected area, especially to the east where the forest is dryer. If these isolated populations are excluded, along with the eastern part of the protected area, the remaining body of the Cockpit Country where Homerus Swallowtail can be found at time of optimal population size in July and August results in a range of flight covering approximately 428 km^2 (42,800 ha), but monthly observations suggest the insect occupies a core area estimated at just 200 km^2 (20,000 ha) within that area year-round. It is along the periphery of this core area that the immature stages and adults have been studied, first between 1965 and 1970, and again between 1999-2001, and between 2006 and 2016 (Turner, 1991; Garraway *et al*., 2008b; Turner & Turland, 2017).

There is incremental loss of forest within the designated protected area. The rate of removal of the forest is uneven, progress being marginal on steeper ground but progressive in the valleys between hills where yams, bananas and other smaller crops, such as hot peppers, are frequently grown (Fig. 13). The greater loss of forest occurs along any existing access road and includes licensed and unlicensed lumber extraction. While there is no great loss of canopy when removing single trees within the forest, the stated intention by the Forestry Department to replant broadleaf timber trees in areas within or adjacent to the existing forest being discussed is still largely an objective rather than a reality, specifically as it pertains to the forests within the CCPA (Camirand & Evelyn, 2003; Bijleveld & M. Schwartz, 2010; Headley, 2012). Illegal logging of valued timber trees and tree-cutting with permits occurs within the Cockpit Country forests for extraction of boards. The availability of portable sawmills is an additional threat to be recognized. The tailings from logging along with trees cleared for cultivations are used to produce charcoal in large quantities, another product widely used across the island and another major cause for forest removal.

Marginal cutting and clearing of forest proceeds at an average annual rate of approximately 0.6 km pa. along available access roads, beginning with forest thinning and underplanting with yams (Dioscoreaceae), especially Yellow Yam, *Dioscorea cayenensis* Lam., and Yampie, *D. trifida* L., Cassava, *Manihot esculenta* Crantz., Sorrel, *Hibiscus sabdariffa* L., Dasheen, *Colocasia esculenta* (L.), Schott, Pumpkin, *Cucurbita moschata* Duchesne, Coconut, *Cocos nucifera* L., and smaller vegetable crops (T. Turner, pers. obs.). Cleared land is often followed by abandonment, a return to grass and the introduction of tethered cows and free roaming goats. Some deforested hillsides have failed to return to forest even after many years of abandonment. Species which invade disturbed land and halt the regeneration of the forest, include ferns such as *Gleichenia* sp., *Dichranopteris* sp., *Nephrolepis multiflora* (sword fern), and *Thelypteris opulenta*. The red bead tree (*Adenanthera pavonina*) can become established on hills and forms monocultural stands in some places, while bamboo (*Bambusa vulgaris*) takes over abandoned cockpit bottoms. Rose-apple trees (*Syzgium jambos*), an introduced species which is native to Asia, are spreading through the Cockpit Country and may be displacing native species, although they seldom form single species stands. The development of practical ways to control invasive species, particularly ferns on hilltops denuded by cultivation and fire, could be one of the most important single contributions to conservation of the Cockpit Country (Koenig, 2016).

Small roadside shelters with zinc roofs (Fig. 13) may be built during the process as a place to gather reaped crops for transportation out of the forest as well as shelter from frequent rains, but these shelters are not permanently occupied and can be dismantled and repositioned further into the forest as needed. Trees are also cut and removed from the forest for residential construction and for fence posts, but the greatest destruction comes from the cutting of saplings by the truck load for use as yam sticks and fish pots (Turner & Turland, 2017).

Yams (Dioscoreaceae) are a very important local staple, grown in large quantities on smaller acreages across the island, including many locations around, as well as in a few clearings within, the Cockpit Country (Turner & Turland, 2017). Barker and Beckford noted that southern Trelawny and northern Manchester parishes accounted for more than 50% of Jamaica's yam production, and data collected from more than 200 farmers indicated that more than 73,000 sticks had been used, of which more than 50% were cut from the Cockpit Country (Forestry Department, Jamaica 2017b). Each yam stick, depending on the species of tree cut, lasts for only two growing seasons or two years, after which new saplings at least ten feet tall must be cut from the forest again. In 1994 it was estimated that 15 million yam sticks per year were being cut from remaining Jamaican forests (Barker, 1998; Barker & Beckford, 2003). To achieve usable height most saplings are cut at ground level, resulting

Figure 13. Some ongoing causes of loss of Jamaica's Cockpit Country Forest habitats: a. Destruction of primary forest for hardwood lumber; b. Hardwood saplings cut for yam sticks; c. Yam vines supported by hardwood sticks; d. Free roaming animals grazing; e. Charcoal ready for market made from hardwood; f. Cleared areas for cultivation now abandoned; g. Shelters in cleared areas; h. Tethered animals grazing.

in total loss of that plant. The cutting of yam sticks along with thinner pliable saplings used for making 'Antillean Z fish traps' results in the loss of plants which would have eventually replaced the loss of more mature trees. Fish pots rot, get lost or destroyed in storms and need to be replaced twice or more annually (Turner & Turland, 2017).

Status of the peripheral forest fragments

In 1940 the entire range of flight of Homerus Swallowtail in the Western Subpopulation, from reported sightings, covered approximately 1,024 km^2 (102,400 ha). By 2015 this range had been divided into four segments; with 780.24 ha finally approved as a preservation area. Three peripheral fragments which also host the butterfly are now isolated from the main Cockpit Country population and remain unprotected. (M. Schwartz & Koenig, 2016; Turner & Turland, 2017). These are referred to as The Catadupa, Nassau Mountain, and Litchfield Mountain-Matheson's Run Fragments (Fig. 4).

The Catadupa fragment (Fig. 4, 1). Along the western edge of the Cockpit Country where the swallowtail is also found is a narrow band of forest also referred to as the Catadupa Key Biodiversity Area (KBA), running approximately north to south southeast between Mount Horeb and Ipswich covering an area of approximately 112.5 km^2 (11, 250 ha). This area is separated from the main forested area of the Cockpit Country along the road from Maroon Town to Elderslie by an area of cleared forest not less than 2 km wide, now mostly abandoned or occupied by small scale cultivations. The area of occupancy is estimated to be 85 km^2 (8,500 ha).

As recently as April 2023, Homerus Swallowtail was observed to fly southwards along the wooded YS river as far south as YS Falls (V. Turland, pers. obs.). The narrowly forested Great River flows northwest along the western edge of the Fyffe and Rankin forests close to Spring Garden, near Reading, on the north coast and a male Homerus Swallowtail was observed here in both 1995 and 1997 (Rezbanyai-Reser, 1998). However, these flight records are distant from the areas where larval foodplants are to be found within the forest fragments previously mentioned, and are the only records of such longer distance flights.

The Nassau Mountain fragment (Fig. 4, 2). The most isolated forest fragment is the Nassau Mountains to the south of the Cockpit Country proper, where the insect is still present (M. Schwartz, 2013). This small mountain range with a maximum elevation of 364 m is forested but covers an area of less than 17 km^2 (1,700 ha), of which the estimated area of occupancy is 14 km^2 (1,400 ha). Sugarcane plantations of the Appleton and Siloah estates separate these mountains from the nearest habitable forest to the east, north, and west, and bauxite mining interests threaten from the south, effectively isolating this forest which as recently as 1940 was almost contiguous with the Matheson's Run/Litchfield forests to the east and the Elderslie area to the west.

The Litchfield Mountain-Matheson's Run fragment (Fig. 4, 3). To the southeast of the Cockpit Country are the towns of Troy and Wait-a-Bit, where the insect was seen up to 1940, but continued clearing of the forest between then and the present time has occurred and there are no recent records from these localities. In March 2024 a single adult was reported along the Burnt Hill Road to the north of Warsop (A. Haynes-Sutton pers. comm.). In 2013 the insect was reported, along with larval foodplants, in the Dry Harbour Mountains near Litchfield in an area known as Matheson's Run, confirming that there is another small, isolated segment of the population on the southeastern side of the Cockpit Country (M. Schwartz, 2013). The area of this forest is approximately 157.45 km^2 (157,450 ha) but the northern half of this forest is both dryer and subject to bauxite mining and the insect has not been observed here. Additional sightings of the swallowtail were made in the southern half of this forest in September 2018 (V. Turland, pers. obs.). The forest on the eastern side of this forested area has already been removed by bauxite mining, and licenses have been issued for mining to continue westwards into the eastern section of Matheson's Run district of the Cockpit Country. The present area of occupancy is estimated to be approximately 53.0 km^2 (5,300 ha).

Protection of the habitat for Homerus Swallowtail and other key species in these three fragments outside the designated boundaries of the Cockpit Country Protected Area has yet to be resolved. The most serious problem facing the Western Subpopulation is, like that of the Eastern Subpopulation, loss of mesic broadleaf forest. Since the swallowtail is a protected species, a strategy needs to be developed to protect the habitat in each forest fragment. It is expected that as the loss of forest habitat where the insect is found continues, there will come a tipping point when, as occurred in the Central Subpopulation, both the Eastern and Western Subpopulations will be too small to maintain viability.

Population density. Using mark and recapture of specimens from the Catadupa forest fragment from Mount Horeb in the north to the forest fragments of Fyffe and Rankin, Niagara, and Ipswich in the south, a combined area of approximately 112.5 km^2, (11,250 ha), it was estimated that the size of that population in July and August 2004 to be not more than fifty adults (Lehnert, 2008). Recaptured adults were nearly all males, providing an assessment that population density for males at that time was approximately one adult per 2.2 km^2. Since the sex ratio for male to female in laboratory conditions is 1:1 the density might be closer to one pair of adults per 2.2 km^2 (Garraway *et al*., 2008a), which, by extrapolation, suggests there might be twice as many adults occupying this area during the most optimal periods. Males appear to occupy larger territories than females and visit trails more frequently where they are more easily observed, with four males historically being seen for each female. During the cooler months between October and March adults are rarely seen. Accurate estimates of population densities throughout the year still remain to be determined.

External threats from mining. A major threat to the survival of the Western Subpopulation of Homerus Swallowtail comes

from loss of forest from mining and quarrying activities for bauxite and limestone immediately to the east of the designated protected area, where large scale removal of forest, reduction of humidity along remaining forest margins, and dust created during these activities results in a decrease of available habitat (Farmer, 1991). As the forest continues to be thinned the remaining fragments will no longer be of sufficient size and humid enough for Homerus Swallowtail to survive, as occurred in the central subpopulation (T. Turner, pers. obs.).

Bauxite mining is responsible for the largest loss of forest in Jamaica (Berglund & Johannsson, 2004). Mining activities have continued for more than seventy years and attention is now being paid to the quarrying of fine quality limestone, a commodity more valuable than bauxite. The Government has modified the Special Mining Lease (SML) 173 to Noranda Jamaica Bauxite Partners II to mine 83.35 km^2 (originally 177 km^2) of land on the eastern flanks of the Cockpit Country. This still means excavating valleys containing bauxite while leaving inaccessible forested hilltops. Like other mining sites, this area will experience the creation of large access roads, dynamiting through limestone hillsides, removal of bauxitic soils and all the associated dust, as well as the loss of vegetation and the accompanying decrease in humidity. The area for mining destroys and negates the vital protective buffer zone abutting the designated protected area on the northeastern edge of the Cockpit Country (Koenig, 2021). Mining activities will undoubtedly result in the lessening of humidity on the eastern side of the CCPA and may also lessen the amount of rain falling further west inside the CCPA. Mining exploration and mining for the extraction of bauxitic soils is by far the greatest threat to the entire ecosystem, including the hydrology within and around the Cockpit Country, because it entails complete destruction of the forest with the exception of small islands of natural forest that remain on inaccessible rocky prominences lacking bauxite deposits. The first phase of mining is the relocation of any existing inhabitants within areas to be mined followed by exploration, with wide swathes of forest cut down to access and prospect for bauxite deposits within intervening valleys (Koenig, 2022). Once deposits are located, wide roads are constructed to reach the deposits, destroying all existing surface vegetation. The mining site is scraped clear and topsoil, if present, is reserved for use for later restoration, actually referred to as "rehabilitation," of the mined-out site before large excavations, some as deep as 30 m are made to remove bauxite (M. Schwartz, 2013).

Immediately to the east of a Special Mining Lease issued in 2018 on the northeast boundary of the CCPA is the town of Gibraltar, St. Ann Parish. Here, one can see the biological wasteland remaining even after so-called "rehabilitation", which involves replacing a shallow 15-20 cm layer of marl fill and topsoil on the excavated hollows created during mining (Bijleveld & M. Schwartz, 2010). Some reclaimed hollows are suitable for pasture or growing certain vegetables with the application of fertilizers and irrigation. While a few rehabilitation projects have been somewhat successful in such confines, most hollowed out pits surrounded by exposed white limestone cliffs are too dry for cultivation, supporting mostly Guinea Grass, *Panicum maximum* Jacq., (Poaceae) and goats. The thin soil offers no prospect for restoration of the forest and rewilding is not evident many years later (T. Turner & V. Turland, 2015, pers. obs.).

The understory of the forest in the Cockpit Country and adjacent forests support large numbers of plants, including terrestrial and arboreal bromeliads which retain water critical for the survival of some animal species, including endemic damselflies and dragonflies, beetle larvae, crabs and frogs. More importantly, "tank" bromeliads greatly enhance the humidity of the forest. Once established, bromeliads reproduce vegetatively, but during the first two years of their existence function like other plants, obtaining all their nutrients from photosynthesis (Heitz *et al*., 2006; Corbara *et al*., 2019). Only in their third year do tank bromeliads begin to hold water while also beginning to change the way in which they metabolize. Exposure to less humid conditions as a result of forest clearing prevents growth of first stage bromeliads for a distance of some 40-60 m from the forest edge (Laurence, 2004). Bromeliads, including species of *Achmea*, *Hohenbergia*, *Pitcarnia*, *Guzmania*, and *Vriesea*, are critical contributors to the maintenance of humidity in these forests (Adams, 1972; A. Schwartz & Fowler, 1973; A. Schwartz & Henderson, 1991; Koenig, 2019; Desai, 2001). Rainfall accumulating in their leaf-storages overflows and runs down the plant stems on which they grow, providing water for spongy mosses and lichens and wetting leaf litter on the forest floor, which in turn also contributes to the maintenance of high humidity in the forest. The Cockpit Country is a biological "Hotspot" with at least 60% of the endemic species found there already considered globally threatened by the IUCN (Koenig, 2019).

The well-documented adverse effects of forest removal by mining activities are detrimental to a much larger area of forest than is generally known. Increased temperatures, decreased humidity, and increased vulnerability due to wind in newly created forest gaps negatively affected the forest fringe for a distance of 100 m (S. Koenig 2019, pers. comm.). In these dryer locations bromeliads, such as some species of *Tillandsia*, that are better adapted to dryer conditions replace the tank bromeliads (Heitz *et al*., 2006). All of these activities in and adjacent to the CCPA need to be resolved and actively managed if the CCPA forest is to be truly protected.

From the documented reduction in flight range of Homerus Swallowtail over the last 80 years, we know that the rate of removal or drastic thinning of the forest or essential peripheral areas surrounding the CCPA will be directly proportional to the rate of decline and eventual loss of Homerus Swallowtail in the Western Subpopulation. Lehnert concluded that despite all present protections "the remaining populations are critically small; a conservation plan and breeding program are needed to save this species from extinction" (Lehnert 2005; Lehnert, 2008; Lehnert *et al*., 2017). However, there would be no point in a captive breeding program if there is insufficient suitable habitat available for the release of raised adults. Emphasis must be not only in preserving existing remaining forest in and around where Homerus Swallowtail flies, but also in extending present forest cover at the margins of each subpopulation, especially in view of increasing temperatures predicted because of global warming.

As a result of a warming world climate the average monthly temperatures have been slowly rising, a trend that is expected to become increasingly apparent over the next 30-50 years. As temperatures gradually increase rainfall patterns are expected to change, with periods of drought becoming more prevalent (Stephenson *et al*., 2014; Planning Institute of Jamaica, Climate Studies Group, 2015). Average monthly rainfall amounts in eastern Jamaica have been slowly declining, partly because of removal of the coastal forest but also because large areas of the island are now devoid of forest, increasing daily temperatures and lowering humidity, each contributing to a decline in average annual rainfall. In addition, removal of the forests worldwide and adverse emissions from transportation, industrial and agricultural activities, and the concentration of paved areas in cities and towns, all contribute to the overall warming of the planet.

Against these trends there must be a concerted effort to protect Homerus Swallowtail, because protecting this species' habitat will also result in the protection of numerous other endemic and rare species that reside there. The survival of a species is dependent on the availability of suitable habitat with adequate food resources - in this instance both for larval development and requirements of the adult - with a population size large enough to maintain genetic viability. In addition, the species must be adapted to the habitat to be able to counter the adverse effects of predation, parasitoids, disease, drought, violent storms, and extremes of temperatures. A balanced interrelationship between the insect and the many occupants of its habitat, including predators, has evolved over many thousands of years. Animal communities are not able to adapt quickly in response to the sudden changes such as removal of forest.

Within the CCPA boundary are species of animals and plants that once occurred in several locations across the island but are now restricted to the undisturbed forest comprising the Cockpit Country. Several endemic species of animal have been discovered here and are unique to these forests and the underlying hydrology, including species of *Peripatus*, isopods, sesarmid crabs, more than thirty endemic snails, endemic grasshoppers, stick insects, the only member of an endemic genus of butterfly, and several other endemic species including bees, frogs, and a galliwasp, and the largest remaining population of the endemic Jamaican boa. In addition, 95% of Jamaica's endemic Black-billed Parrots live here as well as some of the last remaining Jamaican Hutia (A. Schwartz *et al*., 1973; Koenig, 2019). There are some 106 species of endemic plants, including several species of orchids, some known from the top of just one hillside (Proctor, 1986).

Between 2009 and 2016, while conducting studies of butterflies, many of which are indicator species for particular habitats, it was found that a large number of species, which are not commonly found in the Cockpit Country, were quietly resting under leaves while the habitats in which they are normally found outside of the Cockpit Country were experiencing severe drought. It became evident that these species were using the relatively cooler and more humid forest of the Cockpit Country as a refugium during adverse times (Turner & Turland, 2017). The Cockpit Country is the largest remaining reserve for much of Jamaica's fauna (Koenig, 2016; Koenig, 2019).

In summary, while essential life history information has been gathered between 1967 and the present (Garraway & Emmel, 1990; Turner, 1991; Garraway & Bailey, 1992; Garraway *et al*., 1993., Garraway *et al*., 2008a; Garraway *et al*., 2008b; Turner & Turland, 2017), time has been lost in addressing the main threat to the continuing existence of both remaining subpopulations of Homerus Swallowtail. This was, and remains, the continuing loss of primary forest habitat in terms of both forest area and forest density after selective removal of trees for lumber, home construction, charcoal making, cultivations, and the cutting of saplings of certain species for use as yams sticks and fish pots.

ASSESSMENT OF THE CURRENT CONSERVATION STATUS OF HOMERUS SWALLOWTAIL

A key natural factor determining the presence and future survival of Homerus Swallowtail is the preservation of a large enough area of contiguous mesic broadleaf forest containing larval foodplants where annual rainfall approximates to between 1,900 mm and 5,000 mm, but how large an area should this be to ensure the long-term survival of the insect? The territory occupied by Homerus Swallowtail expands and contracts during each year, with the largest numbers of adults seen between May and September over the entire flight range. Adults are less commonly seen during the cooler months between November and February, when the flight range is evidently restricted. Available records indicate this pattern has gone unchanged over the last 80 years. It must be concluded that the larger range occupied has been essential for continued survival of a large enough population to maintain apparent genetic viability in both subpopulations. How large an area is required for continuing viability of each subpopulation has not yet been determined, but the apparently isolated fragments where Homerus Swallowtail is still present in the Western Subpopulation are between 14 km^2 (1,400 ha) and 85 km^2 (8,500 ha) in size. Tentative estimates suggest that these fragments of forest combined contain an estimated 150 pairs of adults at the time of maximum population expansion, with such population fragments more vulnerable to total destruction from hurricanes (Lehnert, 2008; Lehnert *et al*., 2017; Turner & Turland, 2017). Estimates of numbers of adults during the cooler dryer months of the year where research suggests the population size is at the lowest point have yet to be determined, but may be just a few individuals along with an undetermined number of immature stages (Turner, 1991; M. Schwartz, 2013; Turner & Turland, 2017). How long these subpopulations will persist even if there is no further forest degradation is unknown, but these will eventually be lost if there is continuing deforestation, or if the few individuals present become too inbred to survive. While there is a temporary solution to mitigate the problem of genetic depression, the three fragments containing Homerus Swallowtail at present are subject to continuing loss of forest and will probably not be able to support subpopulations of the insect in the relatively near future.

The protected area of the Cockpit Country is divided into a core area with a boundary. However, the core of relatively

undisturbed forest is already edged with a disturbed transition zone up to 5 km wide in some locations, where tree removal and cultivated areas exist within the recently approved preservation boundary (T. Turner 2018, pers. obs.). The boundary, in turn, needs to be surrounded by a buffer zone, but this zone already includes permanent residences, semi-permanent cultivations, and roads, all with relatively few trees, forming an outer boundary across which Homerus Swallowtail will not fly.

To the northeast of the CCPA is a mining lease which will bring removal of most remaining forest to the edges of the CCPA boundary, thus eliminating any proposed buffer zone in that quadrant. The forest in this mining lease is undoubtedly contributing to the amount of rainfall occurring downwind to the west, which includes the wettest part of the core which Homerus Swallowtail occupies during the critical low population period between November and April. Any further reduction of rainfall and humidity during these months in particular would almost certainly adversely affect survival rates.

Both Homerus Swallowtail subpopulations have demonstrated their ability to withstand fluctuating weather conditions and the adverse effect of hurricanes over the approximately 175 years since the Eastern and Western Subpopulations were isolated.

Fragmentation and loss of undisturbed forest caused by many anthropomorphic activities, exposure of Homerus Swallowtail eggs to high levels of parasitism in thinned marginal forest bordering undisturbed forest, mining activities which threaten to reduce rainfall amounts in the preservation area of the Cockpit Country, possible limitations imposed by the availability of adequate nectar sources, and poaching, are the primary threats facing the continued existence of Homerus Swallowtail in both the Eastern and Western Subpopulations. Both subpopulations are in a state of gradual decline. To arrest this trend will require the cooperative actions of multiple agencies following a mutually agreed and coordinated plan.

A REVIEW OF THREE PROPOSALS FOR CONSERVATION OF HOMERUS SWALLOWTAIL

To address the declining Homerus Swallowtail subpopulations, there have been a number of well-intended suggestions in recent years, ostensibly to contribute to the conservation of Homerus Swallowtail. However, some of these projects are impractical or financially unfeasible because they do not account for all aspects of the habitat conditions required by the swallowtail. Obviously, it would also be best to avoid any proposals that are not cost-effective that might also divert funds from more practical solutions.

Captive breeding program. A captive breeding program has been suggested (Desai, 2001; Lehnert *et al*., 2017), which would involve caging adults with larval foodplants, rearing the eggs laid to adults, and releasing adults from one subpopulation into the other to relieve inbreeding depression or to reinvigorate individual subpopulations. This suggestion reverts to the original proposal for reciprocal exchanges of adults between subpopulations made by Thomas Emmel (Garraway & Emmel, 1990). However, that inbreeding depression exists has only been assumed, never established. This project would entail building a large flight cage; Hope Gardens, in Kingston, has been one site suggested (Desai, 2001).

Homerus Swallowtail would require a very large cage for this project to succeed and humidity would have to be maintained at more than 75%. The cost to build, plant shade trees and nectar plants, provide water, and maintain a large enough flight cage would be prohibitive and the entire project could be quickly destroyed by a hurricane or other extreme weather events.

A more viable solution would be rearing within or adjacent to existing habitats using larvae caged on small foodplants, as described earlier. Adults would be released immediately back into the habitat. While certain species of Jamaican butterflies are behaviorally suitable for display in butterfly houses, many, including Homerus Swallowtail which requires abundant space, are not. Finally, there is little point raising adults in captivity for release back into their natural habitats to strengthen numbers if the main reason for decline in the areas occupied by each subpopulation is loss of suitable habitat due to deforestation. However, there are situations where population enhancement might be of short-term value.

Planting forest corridors. Tree plantings have been proposed to link the main body of the Cockpit Country to nearby forest fragments (Emmel, 1987). While this is a technique that has been implemented successfully in certain countries, this is unlikely to be successful in Jamaica unless there is a single landowner or if, for example, the land to be planted is government owned. Where multiple landowners have already cleared land for cultivation there will be great reluctance to return any land to forest, and probably no united political will to create a legal framework to encourage or enforce this imperative. Even if there were to be a single owner or government-owned land between the Cockpit Country and one of the neighboring forest fragments, for the forest to reach the density required to be re-occupied by Homerus Swallowtail will take not less than ten continuous years of tree growth with significant maintenance and protection costs. Except in unique circumstances, building natural corridors to link the main body of the Cockpit Country to neighboring forest fragments appears to be impractical and unlikely to be successful. Creating forest corridors should not be confused with tree plantings required at the margins of existing forest, which are necessary.

Development for tourism. Taking tourists on tours of the Cockpit Country has been suggested as a possible way to raise revenue toward the protection of Homerus Swallowtail, but vehicular access into the forest is limited. Such trails are narrow and unsuitable for large groups. The terrain is rough and lacks infrastructure to support taking tourists from cruise ships or hotels for a one-day venture into this habitat.

Tourists should not be taken into the prime areas where the butterfly occurs especially with regard to keeping locations safe from the ever-present threat of poaching. Access to the forest should be limited to licensed wildlife tour operators taking small groups of observers, for example experienced bird watchers familiar with such terrain. The tour operators must be prepared to deal with situations such as heat stroke and anaphylactic

shock and the possible emergency extraction of injured persons from the forest. In summation, based on our twenty years of practical experience with ecotourism in Jamaica, any such project is unlikely to be financially viable.

STRATEGIES FOR CONSERVATION

The primary threat to the continued existence of this swallowtail is loss of suitable habitat. More recently this is being exacerbated by the uncertainties of global warming with the possibilities of more tropical storms and increasing number of droughts resulting from the projected increase in frequency of El Niño events.

Conservation requires the improvement of measures in four areas, namely, a continuation of Scientific Research, Habitat Protections in addition to those programs already initiated by the Forestry Department, a continued Awareness Campaign, and additional enforced Legal Protections.

Future scientific research

To be successful this program will require two full-time "Homerus Swallowtail" Field Officers employed over an initial five-year period, one 4WD vehicle, along with uniforms and equipment such as GPS, and cameras to conduct field surveys. The continuation of field surveys island-wide for both adults and larval foodplants are required to determine current population numbers and distribution, including those in forest fragments. During these surveys, assessments can also be made to determine areas which might be suitable for the replanting of *Hernandia* and other broadleaf forest trees for canopy restoration and nectar sources (Turner & Turland, 2017). This is the most urgent but operationally most expensive strategy needing immediate attention. Comprehensive protections can only be made after all occupied territory is identified. Field surveys required will be in areas of difficult terrain and because Homerus Swallowtail is more easily seen between May and August when the insects are most common, it is estimated that this project will need to be conducted over an initial five-year period. Most, but not all, areas for additional surveys have already been identified (Turner & Turland, 2017). It will be necessary to plot the presence or absence of adults in all months of the year with the aim to identify summer maximum and winter minimum territories occupied.

a. Construction of an insectary. A small, screened insectary is required where caged immature stages can be reared so observations can be made under natural conditions, especially to determine life history information between November and March, with release of adults back into the forest. This facility should be constructed in a location adjacent to existing Homerus Swallowtail territory. The design envisioned requires features for permitting unobstructed light to enter part of this insectary for specific life history studies and designed for protection against predators such as ants and lizards.

b. Seedling collection and propagation. The collection of seeds and propagation of seedlings for resource plantings can also be conducted within this insectary. *Hernandia catalpifolia* has been successfully propagated from seed. It will be necessary to collect seed from *H. jamaicensis* since this species will be needed for both the protected forest areas as well as forest fragments in and around the Western Subpopulation. Nectar source seedlings would also begin life in this insectary.

c. Increase larval foodplants and nectar resources within each subpopulation. It needs to be determined where additional nectar sources and plantings of *Hernandia* might be of benefit for each subpopulation. *Spathodea campanulata* would be a reliable nectar plant for the Eastern Subpopulation; *Bauhinia divaricata*, *Spathodea*, and *Psychotria* would be of benefit in the Western Subpopulation. Seeds or seedlings planted now would probably not produce flowers in meaningful quantities for at least five years. Note that although *Spathodea* is an introduced species, this tree is already present in and around the forests where Homerus Swallowtail has sometimes been observed. Care must be taken in the location of any plantings with regard to exposure to possible poaching, and there should be liaison with the Forestry Department to avoid any possible technical conflicts of interest.

d. Revitalizing Homerus Swallowtail subpopulations in forest fragments. There needs to be a program to revitalize subpopulations of Homerus Swallowtail in forest fragments around the Cockpit Country where fragmentation has occurred during the last 80 years using adults obtained from immature stages reared in the insectary. The aim is to release small numbers of adults into each forest fragment over a few years while conservation measures for forest fragments, if any, can be determined. At the same time there is a need to assess the feasibility of forest restoration to improve quality of fragments and to determine any other options for preservation.

There should be a very select planting of additional *Hernandia* trees where needed, along with suitable additional nectar sources within protected areas and forest fragments, not at forest margins. Valuable information will be gathered on population size in each forest fragment, and the minimum size of territory required for continued survival, and the ecological condition of each forest fragment, as well as determining the feasibility of linking any of these fragments to the main population centers. *Hernandia jamaicensis* is often present along forest trails and the saplings are a valuable larval foodplant resource that should be conserved rather than destroyed during trail maintenance programs.

e. Introduction of adults into a new area. Determine feasibility of introducing adults from the Eastern Subpopulation into the Spanish River watershed in Portland Parish where *Hernandia catalpifolia* already grows (Adams, 1972; Garraway *et al*., 2008a). If the introduction were to be successful this would be the first expansion of the Eastern Subpopulation.

Habitat protection

Homerus Swallowtail cannot be protected through scientific studies alone, although these studies provide guidelines as to

the best ways protective measures can be implemented. Lasting protections can only be achieved with the participation of other stakeholder agencies and private landowners.

a. Reforestation. We recommend plantings of native broadleaf tree species, beginning with the forest fringe areas of the CCPA and streams in upper Rio Grande Valley. This would include replanting of abandoned plots adjacent to existing forest within the CCPA boundary, and between streams in the upper Rio Grande valley. Such plantings are already within the stated aims of the Forestry Department (Bijleveld & Schwartz, 2010; Headley, 2012; M. Schwartz & Koenig, 2016, Forestry Department, Jamaica, 2017a) and the Spinal Forest Project 2002 (Gage & Edwards, 2003).

The Forestry Department's National Forest Management and Conservation Plan (Forestry Department, Jamaica 2017b) also outlines pilot projects for yam stick production, fuelwood plantations, and development of the bamboo industry for charcoal. However, the demand for yam sticks and charcoal at present far outpaces any replacement projects.

b. Peripheral Forest enhancement. At present there is no officially accepted buffer zone around habitats occupied by Homerus Swallowtail. However, to maintain humidity levels, there should be a forested zone of not less than 200 m wide along the periphery of the boundary of each territory occupied by Homerus Swallowtail. Any destructive activities in areas immediately outside protected Homerus Swallowtail territories will impact the adjacent interior of the protected area. A plan is required for increasing the number of trees in all buffer areas around the present Homerus Swallowtail subpopulations.

c. The Western Subpopulation buffer zone. In the Cockpit Country, portions of the preservation area include residences either just inside or just outside of the "Ring Road" which sometimes borders or dissects the designated protected area. Much of this zone has already been cleared of primary forest and remains in small-scale agriculture or fallow. Multiple landowners are undoubtedly involved and all will not be receptive toward replanting abandoned areas with native trees. However, local residents might be amenable to planting fruit trees, especially if assurances were to be provided from the makers of fruit juices, fruit flavored ice cream producers, and from local hotels that these fruits will be purchased. This project would provide a valuable source of additional income to local residents. Ideally a small collection and processing center would be established to receive produce from which purchases could be made by representatives of the industries concerned. Once the trees are in production, assurances could be turned into contracts. Growers could also be involved in processing excess fruits into preserves and shorter-term crops such as papaya and pineapple could be interplanted with fruit trees to provide more immediate income.

d. The Eastern Subpopulation buffer zone. This same fruit-growing concept has also been promoted by Eric Garraway from the University of the West Indies for areas around the Eastern Subpopulation. Garraway also noted that a fruit-processing facility is required for this concept to succeed (Symposium on the Conservation of the Homerus Swallowtail, Kingston, Oct. 2019, S. Koenig, convener).

School students and 4 H clubs, for example, could be encouraged to participate in this program, bringing fruit tree seeds from home to plant in recycled containers in compost made at the school, then watered until large enough to plant out in buffer areas. This practice can be expanded to all schools for trees to be planted across the island.

e. Additional mining rehabilitation. Rehabilitation of mined-out areas is indirectly connected to preservation of the Cockpit Country. Such areas are largely, though not exclusively, found east of the declared CCPA preservation area and include or will include areas to be mined that encroach on the buffer zone. Here, certain trees beneficial to the Jamaican economy should be planted to further restore those mined-out areas that are not in a productive state at present to provide forest cover (Horn *et al*., 2017).

While there have been notable examples of successful rehabilitation of mined-out areas, the fact remains that large areas have not been returned to any useful production, leaving partially exposed limestone cliffs and hollows with very thin topsoil sometimes covered in grass. The mining companies must play a greater part in rehabilitating the landscape after receiving permission from landowners. Despite any such programs, it must be recognized that the forests can never be restored to their original composition and value for biodiversity as evidenced by surveys in Manchester parish at Kirkvine Works (V. Turland pers. comm.)

Plants in many mined-out areas will often only receive natural rainfall, so plants that can withstand arid conditions would be best suited for the purpose. This would include trees for charcoal production such as Cashaw, *Prosopis julifera* (Sw.) DC., *Albizia lebbeck* (L.) Benth., and *Acacia macracantha* Humb. & Bonpl. Logwood, *Haematoxylum campechianum* L., would be of benefit to the Logwood honey industry, and trees such as Quickstick, *Gliricidia sepium* (Jacq.) Kunth ex Griseb., *Spathodea* or *Haematoxylum* should be planted for "living fences". Either seeds or seedlings or both could be planted at the appropriate time of year, depending upon rainfall.

Public-awareness campaigns

In 1995, a Jamaica Conservation & Development Trust (JCDT) partnership with the Rare Foundation, Eric Garraway, and local organizers, initiated a national pride campaign with school children, residents, and farmers, under the auspices of the Bowden Pen Farmers Association in the upper Rio Grande valley, to support protection of the natural environment and wildlife centered on Homerus Swallowtail (Garraway *et al*., 2017). In 2015, the Blue Mountain and John Crow Mountains National Park, established in 1993, was also recognized as a UNESCO World Heritage site. However, in spite of these protections and awareness campaigns the continued destruction of the forest, along with poaching, are still ongoing major problems.

In western Jamaica, the late Michael Schwartz, of the

Windsor Research Centre, and others championed town hall meetings in towns and villages around the Cockpit Country to create awareness to threats from bauxite prospecting licenses, which potentially threatened not only to destroy the forests, but also to displace entire communities. The attention resulted in the voluntary withdrawal of Alcoa from one Special Exclusive prospecting License and non-renewal of at least two other prospecting licenses. While failing to secure the Cockpit Country Stakeholders Group (CCSG) boundary which includes fragments of forest where Homerus Swallowtail is known to occur, the publicity generated over 10 years did finally bring to fruition a government-designated boundary for the core area of the Cockpit Country (CCPA). This area is now declared "closed to mining" and represents a major accomplishment for forest conservation in Jamaica.

The much-acclaimed success of the Public Awareness campaign initiated in 1984 by Garraway in the upper Rio Grande Valley with residents of Milbank, and expanded island-wide, should be continued. The principles involved need to be expanded to include wildlife protection of not just Homerus Swallowtail, but all Jamaican flora and fauna, again using Homerus Swallowtail as a flagship example. The best place to promote this concept is in the school curriculum using examples of Jamaican species requiring protection. Recommendations for how best to proceed are outlined by Garraway *et al*. (2017).

Legal Protections and enforcement

a. Regulating access to forests occupied by Homerus Swallowtails. There needs to be a significant reduction in anthropomorphic activities in and around protected areas, including limiting access into and out of protected forests. When drivable roads extend into primary forest areas, licensed lumber extraction, unlicensed charcoal production, the cutting of yam sticks, the introduction of livestock, tethered or untethered, the clearing of plots, erection of shelters and planting of small plots with a variety of crops, soon follow.

In the Eastern Subpopulation a large landslip destroyed the track from Barrett's Gap to Corn Puss Gap in the mid-1960s. Lumber extraction ceased, huts were abandoned, cattle were extricated and the track itself became overgrown. After 10 years seedlings reached stem diameters of 100-150 mm when measured 1 m above ground, and overall heights of 5 m (T. Turner pers. obs.). Here also, the steepness of terrain and presence of clay soils along with high rainfall has largely prevented the successful establishment of roads. For example, two attempts to build a road from St. Thomas Parish via Cuna Cuna Pass, west of Corn Puss gap, to Portland parish ended in failures when large sections of road slipped away. The absence of roads allows for natural growth of the forest, while there is no doubt that the presence of a road or even a maintained trail permits significant encroachment, even within areas of protected forest.

In the Western Subpopulation where roads are largely built on limestone, destruction of the forest proceeds on either side of those roads. As demonstrated by the landslides in the Eastern Subpopulation, when there is no vehicular access encroachment of the forest is limited to those items which can be brought out by hand or pack animal. While all Jamaican residents should have access to the forests in National Parks and preservation areas, there needs to be enhanced monitoring of activities which would be best achieved by building Forestry Department Ranger Stations on roads entering the CCPA, a solution which would of course be expensive.

Large roadside signage should mark the entrances in addition to the concrete makers being used to identify the CCPA boundary. Such signage has already been torn down when erected, but people-friendly signage could still be placed with the cooperation of local residents. All those entering and leaving the protection area should be documented. Here, illegal entry of trucks to obtain yam sticks, for example, could be blocked. The occupants of these Ranger Stations could also be responsible for supervising the propagation of forest tree seedlings for forest restoration.

Importantly, the CCPA designation does not afford any guaranteed protection from mining, since The Mining Act, 1947 takes precedence over the Forest Act, 1996. The CCPA has to be declared "Closed to Mining" by the designated minister for it to be afforded legal protection from mining.

b. Poaching. There is a need for the efficient application of existing regulations for protection of the habitats concerned in coordination with researchers and government agencies as well as addressing poaching problems persisting in the Eastern Subpopulation.

The National Environment Planning Agency (NEPA) presently acts on all reported illegal activities involving the collection of Homerus Swallowtail adults or immature stages for rearing adults for export to overseas entities. Reporting of illegal activities originates from forest rangers, researchers, and local residents and penalties are already in place for appropriate application when needed. Past efforts to thwart wildlife smuggling have been successful. The placing of occupied housing units at entry points to the forest around Homerus Swallowtail subpopulations in both eastern and western Jamaica, occupied by forest rangers or wardens also supervising tree seedling nurseries, would be the most effective way of monitoring those who enter the forest. At present there are not enough rangers in place to achieve effective monitoring. Legitimate wildlife research permit holders are already required to submit entry applications two weeks in advance of any visit and must check in at the nearest ranger station before entering the forests, but these stations are not at the entrances to the forest, and illegal operators of course bypass present checkpoints. This expansion or relocation of present Forest Ranger Stations would not stop all illicit collecting, but could certainly minimize it, along with better control of fuel-wood and yam stick cutting.

Poaching activities, along with supporting evidence of loss of territory, formed part of the initial submissions to the International Union for Conservation of Nature and Natural Resources (IUCN) requesting this species be accorded protection (Turner, 1983a; Collins & Morris, 1985). The plight of Homerus Swallowtail was subsequently documented in The IUCN Invertebrate Red Data Book, where this insect was initially listed as Vulnerable but subsequently elevated to the

Endangered after losing more than 50% of its territory (Turner, 1983a; Turner, 1983b; Wells *et al*., 1983; Turner & Turland, 2017). Since then, there has been further loss of suitable habitat and some researchers already consider the species to be Critically Endangered (Lehnert *et al*., 2017).

Homerus Swallowtail is provided protection first under Section 6 of the Wildlife Protection Act of 1945, wherein it is a criminal offense for any person to be in possession of a protected animal or any part thereof and can be liable on conviction to a fine of 100,000 Jamaican dollars. Further protection is provided by the Endangered Species Protection, Conservation and Regulation of Trade Act, 2000, with obligations under CITES. The insect has been listed under CITES Appendix 1 since October 22, 1987 (Collins & Morris, 1985; Preston, 1988). These acts are regulated by NEPA, the insect may not be collected or disturbed by law and permits have to be granted or waived by NEPA before any research with this species is conducted. In Jamaica, the Natural Resources Conservation Authority (NRCA) has the overall responsibility for the protection of species and their habitats. The Natural Resources Conservation Authority Act of 1991 provided "the legislative framework for the establishment and management of a System of National Protected Areas" (Forestry Department, Jamaica, Forest Resources Information, Nov. 2017a). The Blue and John Crow Mountains National Park was established as Jamaica's first national park with management delegated to the Jamaica Conservation and Development Trust (JCDT). The Blue Mountain and John Crow Mountains National Park covers an area of 495.3 km^2 of lower montane forest and includes all the known territory currently occupied by the Eastern Subpopulation of Homerus Swallowtail, although it should be noted that Homerus Swallowtail occupies only a small area within the park approximating to 116 km^2. A part of the habitat occupied by Homerus Swallowtail in the Cockpit Country was, at this time, also designated Priority 1 under the System of Natural Protected Areas for protection and a "Jamaican Giant Swallowtail Recovery Plan" was prepared by the National Resources Conservation Act (NRCA) in 2001 to address the plight of both Homerus Swallowtail subpopulations (Forestry Department, Jamaica, Forest Resources Information, Nov. 2017a).

REASSESSMENT OF CONSERVATION STATUS [AS DETERMINED BY APPLICATION OF IUCN RED LIST CRITERIA (2023)]

Here we apply the current IUCN (2012) Red List Criteria to determine the current conservation status of Homerus Swallowtail.

A. Population size reduction.

All populations have suffered loss of suitable forest habitat, unlikely to be reversed (A2(c)). **Eastern Subpopulation**: Estimated additional loss of 54% of occupied territory in the last 80 years. **Central Subpopulation:** Extirpated circa 1925. **Western Subpopulation**: Estimated additional loss of 57% of occupied territory in the last 80 years.

Assessment: Based on population size reduction, Homerus Swallowtail meets IUCN thresholds for **Endangered** (A2c, loss of habitat >50% and <80%).

B. Geographic range.

The Western Subpopulation has an AOO of 200 km^2 and is divided into four fragments (B2a). The Eastern Subpopulation has an AOO of 116 km^2. Both subpopulations are experiencing continuing decline in area of suitable habitat (B2a,b).

Assessment: Based on geographic range, Homerus Swallowtail meets IUCN thresholds for **Endangered** (B2a,b, AOO <500 km^2 and > 10km^2, range severely fragmented (B2a) and continuing to decline (B2b)).

C. Population size and decline.

The number of adults in both remaining subpopulations is estimated to be less than 650 during the summer expansion, and no more than 150 during the winter contraction. At present rates of decline the Eastern Subpopulation could be extinct within the next 75 years. Only the largest of the four small populations in the Western Subpopulation will probably still be extant within the next 40 years. The species shows extreme fluctuations in the number of mature individuals (C2b).

Assessment: Based on population size, Homerus Swallowtail meets IUCN thresholds for **Critically Endangered** (C2b, number of mature individuals during winter < 250, extreme fluctuations in number of mature individuals).

D. Very small or restricted population.

As stated above under C, number of adults in both remaining subpopulations is estimated to be at its minimum no more than 150 during the winter contraction.

Assessment: Based on restricted population size, Homerus Swallowtail meets IUCN thresholds for **Endangered** (D, number of mature individuals during winter < 250 and > 50).

E. Quantitative analysis. Due to difficulties in obtaining data a quantitative analysis has not been possible. However, if current rates of decline continue the Eastern Subpopulation could be lost within the next 75 years. In the Western Subpopulation, the species could be extirpated from the three smaller forest fragments within the next 30 years, leaving only a small population of questionable viability in the Cockpit Country Preservation Area.

Overall Assessment. Homerus Swallowtail, *Pterourus homerus*, an obligate forest species, was first IUCN Red Listed as Vulnerable in 1983 (Wells *et al.,* 1983), but in 1985 this status was upgraded to Endangered (Collins & Morris, 1985), which is also the status listed with the IUCN by Giminez Dixon in 1996. Here, we revise the status of the species to **Critically Endangered** (C2b).

CLOSING CONSIDERATIONS

Over the years between 1960 and the present time much information has been gathered on the life and behaviors of Homerus Swallowtail, a species found nowhere else in the world. Resolving the problems that threaten this species'

continued existence, and in particular providing the protection and, where necessary, the restoration of the habitats where the insect occurs, has the added benefit of protecting numerous unique plant and animal species. But the broader impact will be internationally, demonstrating an environmentally conscious and progressive nation acting expeditiously during times of global climate change for the benefit of all Jamaicans as well as visitors to the island.

Unfortunately, if such programs as suggested above are not implemented immediately and destruction of mesic broadleaf forest continues unchecked, then Homerus Swallowtail will gradually disappear, beginning with the smallest forest fragment. Likewise, if marginal degradation of the forest within the CCPA is not checked, then the existence of this swallowtail in the Western Subpopulation will be increasingly threatened, and the same will occur in the Eastern Subpopulation as the forests there continue to be cleared or thinned.

Tree planting in the spirit of Trees for Tomorrow and Jamaica's Spinal Forest project, beginning with locations in the seven parishes surrounding the two Homerus Swallowtail subpopulations, would help to maintain high relative humidity and rainfall and provide watershed protection, but any such plans need to be accelerated. Efforts implemented to assist Homerus Swallowtail should be considered just a beginning. Tree planting needs to be expanded island-wide with careful selection of suitable species. Trees planted now will only become large enough to begin to make a tangible difference to the environment after five to ten years. By then our world will be significantly warmer. Time is of the essence.

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The life cycle of the endemic Blue Kite Swallowtail *Protographium marcellinus* (Doubleday, 1845) (Papilionidae: Leptocircini, Papilioninae) in Jamaica, West Indies, and the urgent need for additional conservation measures

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Abstract: The life cycle of the endemic Jamaican Swallowtail *Protographium marcellinus* Doubleday is described in detail for the first time, including an account of the migratory behavior of the adult. Four small breeding sites are documented along with present threats to destruction of the only known larval food plant at each of these sites. Evidence supporting the need for additional protection for this insect is provided. The IUCN Red Data Book status is reviewed.

Key Words: Black Lancewood, breeding sites, Leptocircini, migration, pupal diapause.

INTRODUCTION

Turner (cited in Collins & Morris, 1985) proposed that Jamaica's endemic Blue Kite Swallowtail *Eurytides* (*Protesilaus*) *marcellinus* (Papilionidae), now referred to as *Protographium* (*Neographium*) *marcellinus* (Doubleday, 1845) (Fig. 1, 2), be considered for protection in the IUCN Red Data Book in view of the single small breeding site known at that time, along with difficulties in obtaining data because of the unusually short flight periods of the adults. Consequently, this insect was listed as Vulnerable by Collins & Morris (1985). This insect, referred to in Jamaica as the Blue Swallowtail, was known for seasonally appearing suddenly, often in large east to west migrations through Kingston, the capital of Jamaica, and then disappearing again after being present for just three weeks. Turner initiated a search for the origins of these migrations in late 1962, continuing for the next six years. Because the insect was seen infrequently and then only for very short periods of time in any given year, it was not until October 1967 that a single larva was found by Turner on a leaf of the larval foodplant, *Oxandra lanceolata* (Sw.) Baill. (Annonaceae) (Adams, 1972).

Farr (1982), and Turner (cited in Collins & Morris, 1985) provided incomplete descriptions of the egg and larva, and Garraway *et al.* (1993) indicated the eggs were "unsculptured

Figure 1. Male *P. marcellinus* at Portland Ridge, Clarendon Parish in May 2009.

Figure 2. Male *P. marcellinus* at Crownlands, Trelawny Parish, April 2015.

except for a pattern of numerous, incised small circles". This 1993 publication also provided brief descriptions of the final stage larvae and the pupa with a short series of color photographs, noting that, "Further studies on the biology and ecology of the species are necessary".

In this paper, the 1966 migration from Rozelle is described and laboratory and field studies of the immature stages made between 1967 and 1971 are reported for the first time. We also discuss the subsequent population trend for this species and its present status, including its current legal protection, and conclude that *Protographium marcellinus* meets the IUCN criteria for listing as Critically Endangered.

MATERIALS AND METHODS

Field surveys and rearing methods. From 1967 to 1971 a total of eighty-eight visits were made to the site where the larva was first recorded, inland from Rozelle Falls, St. Thomas Parish, between 0600 h and 1800 h, with most visits between 1000 h and 1500 h. One to six additional visits were made each year from 1971 to 1979, with five additional visits between 1992 and 1995, and one visit each in 2009 and 2010 to examine the habitat and presence or absence of the insect.

Immature stages were collected in 1967 and 1968 at the breeding site and were taken to the Entomology building of the Zoology Department, University of the West Indies, Mona (now part of the Life Sciences Department) for detailed study. Eggs and first and second instar larvae were placed in small, cylindrical plastic containers (5 x 3 cm); larger larvae were placed in larger plastic containers (25 x 10 cm). Moisture was provided by placing damp tissue paper inside the container lids. Larvae were fed with leaves of the food plant obtained as fresh cuttings from Rozelle, and containers were cleaned daily. Before pupation, larvae were transferred to cylindrical, screened cages (18 x 60 cm) with branches of food plant in jars of water. Leaf litter from beneath the larval food plant trees at Rozelle was also placed in the bottom of these containers. Plastic bags were placed over the cages to maintain high humidity but were left open at the bottom for ventilation. After pupation in the leaf litter, pupae in their leaf shelters were collected and transferred to individual plastic containers (15 x 10 cm). A small piece of tissue paper was placed on the bottom of these containers and moistened with water every third day. All stages were kept in a shaded insectary at 25-30° C. Day length varied between 13.00 h and 13.05 h in June and between 12.20 h and 12.25 h in October.

Measurements were made with calipers or metric ruler and samples of each stage were preserved in Dietrich's Solution. Thirty eggs, fifty larvae, and twenty-six pupae were studied in the insectary. The nomenclature of the immature stage morphology largely follows Peterson (1962). Voucher specimens of all stages were deposited in the collection of the Allyn Museum, Sarasota, now housed within the Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida.

Flight speeds of adults were measured by driving alongside individuals or groups of adults flying parallel to the road and recording the speed. Flight speeds fell into two main categories: local directional flights away from Rozelle usually while searching for nectar plants, or rapid flight of large numbers of insects in headlong migrations. All plant identifications follow Adams (1972). Adult insects were photographed using Nikon D800 and subsequently a Nikon D850 camera with a Micro Nikkor AF-S 105 mm lens.

Study area. The study area was approximately 0.8 km due north of Rozelle Falls in St. Thomas Parish, in southeastern Jamaica and covered an area of approximately 1.3 km^2. The terrain in 1967 consisted of loam and clay with an almost continuous covering of loose limestone rocks and boulders interspersed with fixed limestone outcrops at elevations between 60 m and 200 m above sea level. Saplings of *Oxandra lanceolata* (locally known as Black Lancewood for its straight growth habit) up to 5 m in height were the dominant plants, with shorter trees of *Prosopis julifera* (Sw.) Dc., and *Acacia tortuosa* (L.) Willd. (Mimosaceae), and *Cassia emarginata* L. (Caesalpiniaceae), also present in significant numbers.

The location was generally dry with rainfall distributed in discrete seasons with arid periods between. Rozelle receives between 1,150 mm and 1,650 mm rain per year and lies between the relatively humid area of Morant Bay to the east, which receives more than 2,000 mm of annual rainfall, and the rain shadow area of Yallahs to the west, which receives less than 1,000 mm of rain each year (Nancoo *et al.,* 1963). Little or no rain falls at Rozelle between December and late May in most years; little rain falls in July, and between mid-August to the end of September it is usually very dry. During wet months from late May to early July, and again in October and November, short heavy downpours occur with periods of bright sunshine in between. On rare occasions there were three consecutive days of overcast conditions.

In addition to the intermittent rainfall there were, at the time, significant quantities of underground water which surfaced as springs just south of the study site. These became waterfalls that cascaded over a 2 m high limestone bluff beside the main coast road before flowing into the sea on the south side of the road. Old illustrations from the early 1900s show that a large volume of water flowed over an almost continuous waterfall approximately 120 m wide. By 1965 this flow had been reduced to three small streams, and by 1995 only one stream remained. In 2015 the flow ceased completely for a period of ten months because of reduced rainfall. There has been extensive deforestation from sea level to the top of Yallahs Mountain (elev. 730 m) north of the study area, which undoubtedly has contributed to the loss of groundwater. However, it is this groundwater that is believed to contribute to the rich diversity of plants in the study area and to their survival in this otherwise often arid habitat.

At the time of this study daily temperature ranged between 24° C and 30° C, moderated by onshore winds from the southeast. During dry months relative humidity remained close to 20%, although readings of up to 10% higher were recorded under 5 cm of leaf litter beneath the *Oxandra* trees. Between tropical downpours in wetter months the humidity was usually greater than 85%.

RESULTS AND DISCUSSION

Larval food plant. The only recorded larval food plant is *Oxandra lanceolata* (Sw.) Baill. (Annonaceae) (Fig. 3) (Collins & Morris, 1985; Garraway *et al.* 1993; Turner & Turland 2017). This fine-grained wood was favored for making furniture in the 17th and 18th centuries, a period when many larger trees were cut and exported to Europe (Long, 1774). Although this tree species grows to a height of at least 10 m, saplings are now more frequently encountered than mature trees. The species is widely distributed in drier limestone habitats from 7 m above sea level to an altitude of 1,500 m, often as individual plants, in the parishes of St. Thomas, St. Catherine, Clarendon, Westmoreland, St. James, Trelawny, and St. Ann. Small stands of a few hectares where *Oxandra* is the dominant tree are still found in St. Thomas, St. Catherine, and Clarendon parishes, and large stands were formerly recorded in Westmoreland Parish (Adams, 1972). Breeding sites have only been found where this tree occurs in dense stands.

At the study area inland from Rozelle Falls, *Oxandra* puts out flushes of new growth within seven days of receiving between 75-100 mm rainfall within a 1 to 4-day period following dry periods with virtually no rainfall for up to 6 months in drier years, or 3 months in wetter years (Turner & Turland, 2017). This amount of rain following drier periods occurs at Rozelle in two well documented seasons referred to in Jamaica as "the May rains" and the "October rains", although these seasons may start a few weeks early or late in any given year (Nancoo *et al*., 1963).

Emergence of *Protographium marcellinus* in numbers from pupae present under leaf litter below the Lancewood trees also follows such rainfall, although a few adults may be seen at Rozelle following smaller amounts of rainfall both before and after these main emergence events.

Description of the immature stages

Egg. Spherical, 0.73-0.78 (0.75) mm in height; 0.78-0.86 (0.82) mm in diameter (n=30); base approximately 0.5 mm in diameter flattened where attached to larval food plant; chorion patterned with many minute, polygonal markings of equal size; apical micropyle with smaller irregular-shaped markings. Pale green during first 12 hours after oviposition, gradually becoming pale blue-green, then losing this color to become off-white tinged with brown. After 36 hours chorion heavily speckled with brown spots concentrated in a circumferential ring; apical region becomes reddish-brown and then black as larval development progresses, becoming dark gray to black with larval setae becoming visible before larval emergence; larval emergence occurs 48-52 hours after oviposition.

Figure 3. Larval food plant of *P. marcellinus*. Sapling of *Oxandra lanceolata* (Sw.) Baill., locally known as Black Lancewood at Fyffe and Rankin Forest Reserve, St. James Parish, August 2009.

In the field the chorion is usually eaten except for the basal disc. In the laboratory where young leaflets were available in close proximity to the newly emerged larva, only 38% of the larvae ate the chorion (n= 30).

First instar. Head black with five very short, black simple setae around stemmata; five longer, black, forward-curving, simple setae of differing length on each epicranial hemisphere, longest seta at Pd1. Two short straight setae on frons; a few short simple setae associated with mouthparts; all setae with small basal tubercles. Thoracic and abdominal segments dark gray to black except for pale whitish-gray dorsolateral patches on abdominal segments A3 to A7; thoracic and anterior abdominal segments enlarged, tapering toward posterior; A9 and A10 larger than preceding segments but not as prominent as anterior segments. Segment T1 with a mid-dorsal osmeterial pit between head and prothoracic shield; osmeterium pale greenish-gray in color; rarely used; prothoracic shield heavily sclerotized extending across dorsum, terminating dorsolaterally on each side; each side of mid-dorsum with a pair of simple setae of unequal length, with a short seta anterior of a longer seta. Laterodorsally, two additional setae; anterior seta short and simple, posterior seta, long, forward-curved with flattened spatulate tip. Dorsolaterally, a cluster of six forward curved setae comprising two shorter simple setae and four longer (0.3 mm) setae with enlarged basal tubercles and spatulate tips. Above spiracles a group of three simple setae sharing a common basal tubercle with median setae three times as long as other two. Two, very short, simple sub-spiracular setae of equal lengths. Segments T2 and T3 similar with long, curved seta with spatulate tip and tuberculate base on either side of mid-dorsum; a similar seta with two short simple setae on a common tuberculate base laterodorsally; laterally, a roughly circular sclerotized plate bearing two long, forward curved spatulate setae, with two short simple setae posterior of spatulate setae. Supra-spiracular and sub-spiracular setae arranged like those of T1. Segments A1 and A2 display similar setation: each with a compound dorsal tubercle on second annulation of segment bearing one very long and one shorter spatulate setae; shorter seta anterior of longer seta. Laterally on fourth segmental annulation a single tubercle bearing a long, curved, spatulate seta. Tubercle present on third annulation above spiracle bearing a long simple seta, and two short simple setae with small tubercles below spiracle. Simple, short, pedal setae. On segments A3-A7, short anterior seta of dorsal group, usually absent, or if present, simple; only occasionally spatulate; lateral setae always present but shorter; setae above and below spiracle similar to those found on A1 and

A2. Setae on segments A9-A10 longer than those of preceding segments. A9 with a single, simple, mid-dorsal seta with a tuberculate base; a similar dorsolateral seta on a saddle-shaped caudal shield. Laterally, a single tubercle with a long spatulate seta and a short simple basal seta. Two simple, sub-spiracular setae. A10 with single mid-dorsal seta with tuberculate base. Laterally, a large compound tubercle with a cluster of five long simple setae of varying lengths. True legs, prolegs and claspers with several short, simple pale gray setae; laterally on claspers, a sclerotized plate bearing cluster of nine simple setae. Crotchets of prolegs arranged in a uniserial, uniordinal, mesal penellipse.

First instar larvae are approximately 2 mm in length at time of emergence from the egg, becoming approximately 5.5 mm in length at end of this stadium which is completed in 48-50 hours. Initially gray-black, becoming gray or gray-brown toward end of instar; lighter lateral abdominal markings become more conspicuous, as does a darker black lateral stripe above spiracles which extends along entire length of larva.

Second instar. Head capsule dark gray with the simple setae like those of first instar; black and of equal length. T1 with osmeterial pits outlined in black; laterodorsally, a wedge-shaped white marking which terminates on T2. After 24 hours a vertically elliptical white eye-spot appears laterodorsally on posterior margin of T3. All abdominal setae lost but short setae retained on A10 forming a dorsolateral cluster of simple setae on each side of the midline. Simple gray pedal setae, most conspicuous on claspers. Osmeterium located within T1, pale green but rarely everted. Larval shape similar to first instar with a relatively small head, enlarged thoracic region, tapered abdominal segments and enlarged caudal prominence. Larvae initially dark gray dorsally, orange-brown ventrally. After 24 hours head becomes pale orange; thoracic segments dark gray. Pale whitish-gray dorsolateral patches on A3-A7 of first instar now become a dashed white stripe extending from A2-A9. A dull white lateral line also develops and extends from A1-A9. All dark pigmented areas above the lateral line are dotted with microscopic tubercles, each bearing a minute short simple seta, which impart a velvety texture to larva.

Larvae initially 5 mm in length becoming approximately 9 mm long at end of this stadium which is completed in 48 to 52 hours.

Third instar. Head pale orange, with short forward projecting darker simple setae. Osmeterial pits on T1 edged with black; osmeteria gray-green when extended; area behind head above lateral line, orange. White laterodorsal markings on T1-T2 and faint, vertically elliptical eye-spot of third thoracic segment retained. Microscopic setae on the dark pigmented area of dorsum are also retained but each seta is now surrounded by a microscopic white ringlet which becomes visible around each basal tubercle. Short groups of setae retained on A10 but no longer prominent. Simple gray setae with small basal tubercles ventrally. Similar setae pedally, especially on T1. When at rest, head tucked under greatly enlarged thoracic segments. Thoracic and abdominal segments dark gray dorsally; gray ventrally, with orange-brown markings. A prominent white laterodorsal stripe extending from A2 to A9. A light yellowish-green longitudinal stripe above spiracles separated by a thin gray stripe from a dark yellow spiracular stripe which includes discontinuous patches of white. Abdominal segments tapered; caudal segments now smaller than preceding segments.

Larvae increase from approximately 9 mm to 16 mm in length during this stadium which is completed in 48 to 52 hours.

Fourth instar. Head pale orange with a few very short, simple, black setae; conspicuous eye-spot. Laterodorsal and lateral markings of third instar retained. Thorax and abdomen, initially dark gray dorsally and light gray ventrally with white laterodorsal and lateral markings; setation as in previous instar. A discontinuous white line develops along base of legs, especially conspicuous at base of each proleg. First thoracic segment with osmeterial pit edged internally with white, externally with black. Between T3 and A1 a small vertically elliptical eye-spot of previous instars becomes conspicuous consisting of a roughly circular black marking within which, on T3, lies a vertically elliptical white marking. Anterior of black marking but separated from it, a vertical yellow crescent; posterior of black marking on A1 is a vertical white crescent, also separated from it. These crescents bracket black marking and enhance false eye-spot; this entire feature located between laterodorsal and lateral white stripes. Two slightly enlarged orange caudal processes bearing short setae. After approximately 36 hours, larvae differentiate into one of three color forms in approximately equal numbers; one third remaining predominantly black with a faint darker mid-dorsal line most conspicuous on terminal segments. Posterior abdominal segments may also exhibit a purplish bloom. A third become predominantly gray and remaining third become light

Figure 4. Final instar larvae of *P. marcellinus* from Rozelle, St. Thomas Parish, May 1968: top, black form; bottom, green form.

Figure 5. Pupa of *P. marcellinus*, June 1968: top, dorsal aspect; bottom, ventral aspect.

green with olive green ventrum. Pedal areas are gray in all color forms.

Larvae reach a length of approximately 26 mm during this instar which is completed in 48 to 52 hours.

Fifth instar (Fig. 4). Head, yellowish-orange, small in relation to enlarged anterior segments. Larval setation and color patterns of fourth instar retained. Lateral eye-spot becomes more prominent, especially size of white "pupil" within circular black spot. Clusters of caudal setae are lost. Crotchets of prolegs arranged in a biordinal mesoseries. After 48 hours larvae become blue-green with yellowish head and legs and a light gray ventrum. After approximately 72 hours when larvae have reached a length of about 35 mm, larvae become light brown or pale green with white stripes retained and descend larval food plant to pupate in leaf litter.

A few overlapping dead leaves are sewn together with a few strands of silk to form a shelter. Head and pedal regions yellowish; segments constricted, prominently rounded. A loose girdle of black or white silk is spun which barely suspends larva. A few strands are spun to form a pad for the strongly hooked cremaster. Pupation occurs after 36-48 hours.

Pupa. Pupae (Fig. 5) are between 15 and 20 mm in length (n=26), and approximately 7-9 mm wide at widest point on abdomen just behind wing-cases, and are short, stout, and roughly spherical in cross-section. Head with two pairs of small dark ventral spots located between small black markings over eyes; thoracic segments dark and light brown flecked or brownish-green; abdomen with dorsum darker than ventrum, dark brown with light brown or gray, broad, dorsolateral, lateral, and subspiracular stripes, only slightly differentiated from ground color or not visible in darker pupae. There is a small projection in front of each eye and a small depression behind eyes near each wing-base; base of wing slightly pronounced. Thoracic segments roughly cylindrical, lacking a dorsal prominence. Central wing area only moderately narrowed, becoming slightly flared distally. Abdominal segments compressed, quickly tapering to a short, curved cremaster. Color dull green immediately after pupation and may remain brownish-green with lighter abdomen and dark mid-dorsal line for up to 9 days

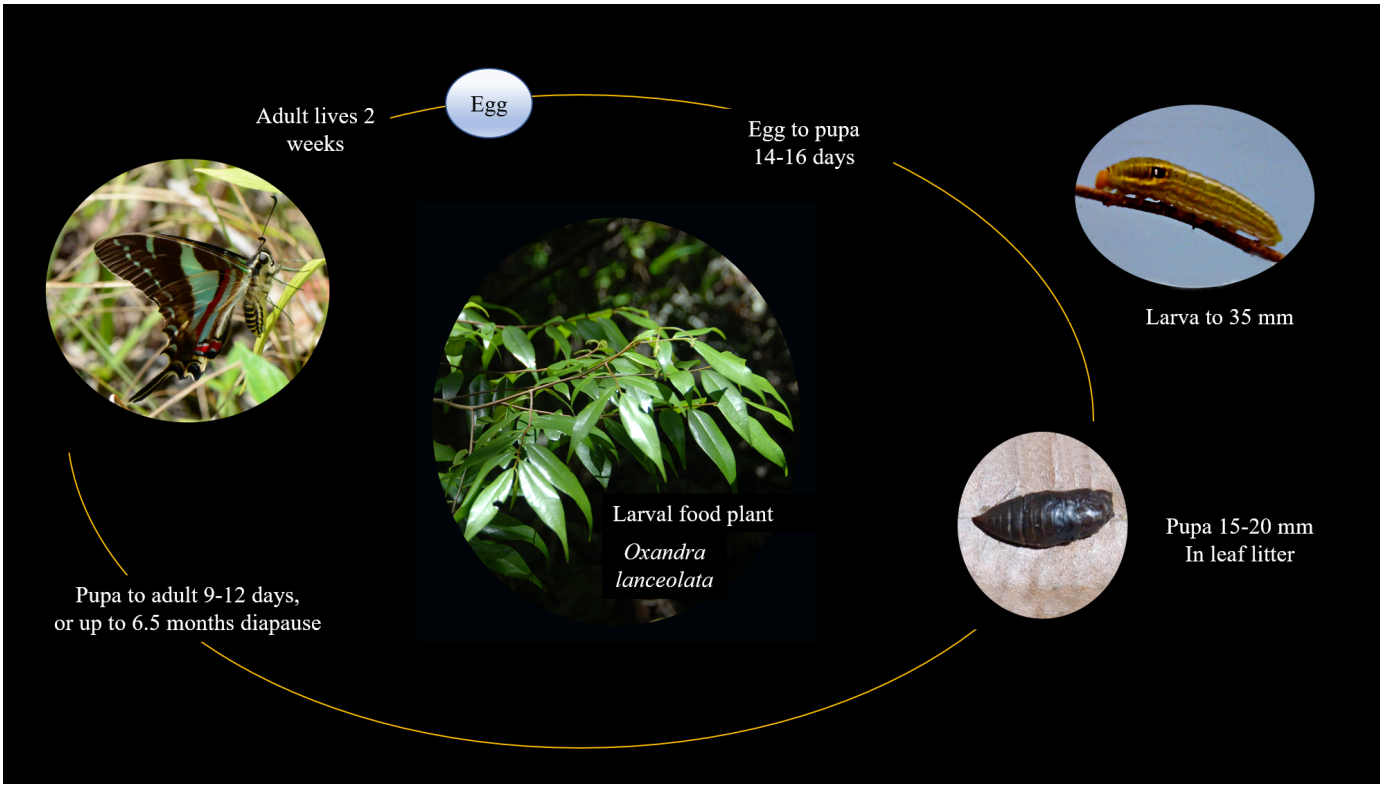

Figure 6. Life cycle of *P. marcellinus*.

before becoming darker brown 3-4 days before eclosion, or pupae brown, with darker brown ventral countershading and with near black, small lateral chevrons. Adult wing pattern and some blue-green color become faintly visible before emergence which occurs between 0600 h and 1000 h. Males emerge as early as 9 days after pupation and females after 12 days.

In captivity the entire life cycle (Fig. 6) from egg to pupa occurred within 14-16 days. This corresponds closely with field observations between May and June 1968, when the period from first egg observed to first pupa obtained was 20 days, with adults emerging from non-diapausing pupae after an additional 9 to 12 days. Other adults emerged between 14 to 21 days, or 29 to 31 days after pupation, but these emergences represented just 3% of the total sampled. The majority of pupae (82%) entered a state of diapause lasting as long as six months with eclosion recorded at intervals of 182, 187, and 191 days. In the insectary, 15% of the pupae became desiccated and failed to emerge.

Adult. Males and females are similar in size and color. Male forewing length 30.0-34.0 (32.7) mm; n=30. Female forewing length 30.0-35.0 (32.7) mm; n=30. The sexes are indistinguishable in flight.

These fast-flying black and bright blue insects with long (10 mm) narrow tails are easily recognized in the field. Newly emerged adults display brilliant green pigmented scales along the veins of the ventral wing-base but this color fades rapidly after death. No seasonal variations in color, wing patterns or size occur. Stored specimens lose their bright blue color after a few months and fade to pale blue-green even if kept in darkened containers. After exposure to light for several years the blue-green color fades to whitish gray and the surrounding black dorsal color becomes somewhat brown, though not as light as the brown ventral markings. Only the red anal spot on the dorsal hind wing and the brown and red ventral markings remain relatively unchanged after prolonged storage.

There are two broods each year, the largest usually between late May and early June but sometimes as early as February depending on rainfall patterns. The second much smaller brood occurs between September and November, but usually in October.

Field observations of adults and immature stages

Adult behavior. Adults rest singly at night on top of leaves of low growing shrubs and vines near the site of emergence with the body angled upwards, the head usually facing the stem of the selected plant and wings held closed above the head. Those adults on plants exposed to the morning sun open their wings, beginning about two hours after first light. Those in shaded locations make a short flight to a sunlit location. Wings are exposed to the sun for 20-30 minutes before active flight begins. Active flight continues as late as 1600 h.

Mating of five pairs of adults was observed in May 1970. There was no courtship. Between 1000 h and 1200 h, males approached the fast-flying females and grappled with them in mid-air about 3 m above the ground in clearings between the *Oxandra* trees. Both insects then tumbled to the ground and after fluttering briefly in short grass or low shrubbery the pairs became quiescent. Mating pairs were very reluctant to fly if disturbed but flew short distances of less than 2 m with difficulty if forced to. In other Jamaican genera, such as *Danaus* (Nymphalidae), *Phoebis* (Pieridae) and *Dryas* (Nymphalidae), such disturbance often results in much longer relocation flights. Four couplings continued for approximately two hours, but one coupling lasted for four and a half hours.

Oviposition was observed between 0800 h and 1200 h. Adults emerged from the pupae in large numbers following seasonal rains. Leaf buds on terminal and lateral branches of *Oxandra* trees which were dormant in the preceding drier months began to enlarge, and females selected terminal shoots bearing these expanding buds for egg laying. These buds subsequently open into small leafy shoots within the 2.5 days it takes the larva to emerge from the egg. Oviposition, however, was not usually on the leaf buds. After hovering over the selected shoot tips and briefly making tarsal contact with the plant, the female descended 15-20 cm below the top of the shoot and selected an older leaf, usually free of other eggs, on which to oviposit. The female clung to the leaf tip, curved the abdomen beneath the leaf and placed the egg at the margin approximately two-thirds of the distance between leaf tip and petiole. The wings fluttered during oviposition or could become momentarily motionless as the egg was laid. Selected *Oxandra* leaves were between 2.5-5.5 cm in length (n=117) and of 68 eggs examined in the field in June 1968, 79% were found within 1 cm, and a further 16% were within 2 cm of the petiole, with the remaining 5% deposited nearer the leaf tip. The weight of the female occasionally (3% of observations) caused the leaf to twist over resulting in the egg being deposited on the upper leaf margin, but 97% of eggs were laid beneath the leaves. Although many females competed for oviposition sites, from a sample of 100 egg-bearing leaves 91% of eggs were laid singly on older leaves below an expanding terminal shoot. Two eggs were laid on the remaining 9%. Five days after the leaf buds opened a few eggs were laid on the newly expanding shoots. Eleven females that were observed laid between one and five eggs on a single plant in less than a minute. During three years of field observations only four eggs in the laboratory failed to develop and appeared to be infertile. No egg parasitoids were recorded.

In late May 1969, the "May rains" were intermittent. Adults emerged and commenced oviposition, but no further rain fell and the new terminal leaves withered. No surviving eggs or larvae were found but adults were present in small numbers throughout the summer. The "October rains" were also of brief duration and adults were never seen in large numbers that year, suggesting that the life cycle was influenced by the occurrence of reliable and adequate seasonal rainfall.

No predation of the fast-flying adults by birds was recorded, but between 1967 and 1969 five adults were observed caught in spiders' webs and one was observed being eaten by a species of praying mantis.

Adults of both sexes were observed nectaring on *Lantana camara* L. and *Stachytarpheta jamaicensis* (L.) Vahl. (Verbenaceae), *Cordia brownei* (Friesen) I. M. Johnston, *Cordia globosa* var. *humilis* (Jacq.) I. M. Johnston (Boraginaceae) and *Morinda royoc* L. (Rosaceae) at Rozelle. *Capparis flexuosa* (L.) L. (Capparaceae) and *Guaiacum officinale* (Zygophyllaceae)

were nectar sources west of Rozelle in St. Thomas Parish and *Bauhinia divaricata* L. (Caesalpiniaceae) was an additional nectar source in St. Andrew Parish. Farr (1986) noted species of *Fagara* flowers as a nectar source.

Protographium marcellinus is an opportunistic feeder, selecting nectar from a wide range of available plants, usually those with short tubular flowers. At Rozelle, when adults were numerous or if nectar sources were scarce, adults commonly fed on wet sand beside the roadside waterfall, at puddles created by rain, and on pebbles and pieces of red seaweed wet with salt spray on the beach south of the breeding area. Eighty-four adults captured and released at wet roadside sand or on the beach at Rozelle were all males. King (1984, pers. comm.) noted small numbers of adults attracted to bovine wastes just east of Rozelle.

Larval behavior. Larvae emerging from eggs in the field usually consumed the chorion (88.5%), as opposed to only 38% in captivity where leaf shoots were available in close proximity to the egg. In the field, newly emerged larvae from eggs laid on older leaves walked to the petiole and then up the stems to reach the newly expanding pink terminal leaves to commence feeding. Larvae then returned to a shaded location on top of an older leaf during the day and fed mostly at night. In all instars, larvae usually rested with heads facing the leaf tip and could raise the head, thorax, and anterior segments of the abdomen above the leaf surface. This behavior was observed mostly between late morning and mid-afternoon and may assist with thermoregulation during the hottest part of the day.

Larvae generally became more active from the third instar onward. If disturbed, larvae either remained motionless, or rocked from side to side or from back to front, perhaps to better display the developing anterior eye-spot and contrasting longitudinal stripes. When branches bearing larvae were tapped, the larvae remained motionless or walked backward briefly before becoming motionless. This behavior was observed to occur naturally during rainfall and may be a response to this phenomenon, thereby placing the larva in a more protected location near the plant stem during adverse weather. In the fourth and fifth instars, usually after color differentiation occurred into either green, gray, or black morphs, most larvae continued to rest exposed on top of older leaves during the day. However, if overlapping foliage was available, larvae sometimes stitched two or three leaves together with a few strands of colorless silk to form a shelter in which to rest during the day. Leaves of these shelters were not consumed. Larvae moved out to feed on terminal shoots, mostly at night, before returning to the shelter after feeding. From a sample of 139 larvae in captivity, only 13% constructed shelters. Occupied and abandoned shelters were found in the field only occasionally.

Diseases, parasitism, and predators of the immature stages. No diseases or parasitoids of any immature stage were recorded in the field during these studies. A large number of immature stages were collected and raised in captivity and a few of these larvae (12.5%) developed symptoms of bacterial infection when kept crowded in hot humid conditions, but this was not observed in the field. The absence of parasitoids was surprising because egg, larval, and pupal parasitoids were found on other species of Lepidoptera in the same habitat during these studies, including egg parasitoids of species of *Phyciodes* (Nymphalidae), tachinid parasitoids of larvae and pupae of species of *Danaus* and *Anaea* (Nymphalidae), chalcid wasp parasitism of pupae of species of *Heliconius* and *Mestra* (Nymphalidae), and braconid wasp parasitism of sphingid larvae. Also, while several species of ants, ladybird adults and larvae, syrphid larvae and *Polistes crinitus* Felton wasps were predators of both eggs and larvae of these genera in the field, no loss of *P. marcellinus* eggs or larvae from these predators was ever observed.

In May 1968, during the night, an unidentified species of spider interlaced the terminal shoots of all the *Oxandra* trees in the study area with dense silk webbing. A search of these shoots revealed characteristic notched leaf damage typical of *P. marcellinus* larval feeding, but larvae were no longer present. This association of spiders' webs and the overnight disappearance of early-stage larvae was also observed in June 1970. During those years when spiders' webs were present very few adults were subsequently seen.

Larvae rarely displayed the osmeterium even when tapped sharply. Second to fifth instar larvae released a pungent apple-like scent if disturbed while at rest, without everting the osmeterium. The conspicuous disposition of larvae on top of leaves and bright coloration suggests that they might be distasteful to potential predators, and there was no observation of removal of larvae by birds, lizards or frogs. However, susceptibility to predation was not tested in the insectary under controlled conditions.

Pupae remained totally immobilized even after stimulation, which together with dull color and their partially surrounding leaf shelters, may assist in minimizing detection by several species of ground-foraging birds, such as thrushes, which were observed searching the leaf litter.

Migration. *Protographium marcellinus* is strongly migratory within the island and undoubtedly capable of reaching other Caribbean territories. In August 1960, Turner observed three specimens of what were presumed to be *Protographium zonaria* (Butler) at sea, 13 km off the west coast of Haiti flying west northwest toward Cuba. Minno and Emmel (1993) documented the possible occurrence of *P. celadon* (Lucas) from Cuba in the Florida Keys. However, so far there are no confirmed records of *P. marcellinus* occurring outside of Jamaica.

Conspicuous migrations have been observed in Kingston, approximately 32 km west northwest of Rozelle (Walker, 1942; Lewis, 1947, 1951, 1953, 1954). Between 1918 and 1966, six large migrations involving many thousands of adults, and an additional twenty large migrations involving many hundreds of individuals, were recorded, along with smaller numbers of migrants in intervening years, as summarized in Turner & Turland (2017). One of these large migrations occurred in the month of April, six between late May and early June, and one in July. Another large migration was documented in September, three in October, and one in November, these occurrences coinciding with the two broods the insect produces during each year. The commencement of a large migration from the Rozelle site was documented in May 1966.

Twice-monthly visits were made to Rozelle between 1962 and 1966 while attempting to find the immature stages. Between December 1965 and April 1966 no adults were seen, no significant rain fell, and the habitat remained very dry with many plants in a state of temporary wilt. On 2nd May 1966 torrential rain fell all day at Rozelle, and on 3rd May adults began emerging in large numbers. On 4th May many adults were observed at 0800 h visiting puddles on the side of the coast road. Just north of the waterfalls, adults were observed flying presumably in search of flowers, but these were in short supply because of the preceding drought. At 0900 h a few adults were observed flying west northwest from the emergence area at approximately 1 m above the ground at a speed of 9-14 km per hour. They were either single or in small groups of 2-9 adults flying toward Yallahs, 13 km west of Rozelle, with larger flights observed further north through Easington and Cambridge Hill.

After quickly returning to Kingston, ahead of the migrants, an observation post was set up at the University of the West Indies consisting of a 3.5 m base-line marked across the expected flight path determined from smaller flights in previous years. A solitary insect was observed at 1130 h but no other adults were seen until 1210 h, when large numbers of individuals appeared flying west northwest about 1 m above the ground at a measured speed of approximately 22.5 km per hour. When solid objects such as buildings were met the insects turned upwards just before striking them. They then flew up and over these and descended on the other side to continue the flight, again at approximately 1 m above the ground. The migrating adults, as confirmed with the reports from other observers, extended over a front 4.8 km wide, from Up Park Camp in the south to Papine in the north and continued until 1515 h. While it was not possible to confirm numbers along this entire front, an average of 49 insects per minute crossed the measured base-line for three hours. It is conservatively estimated that at least 150,000 adults crossed the 4.8 km front during this period. Of interest was that, during brief overcast conditions, flight direction became somewhat scattered, with a few individuals flying between southwest and north. After the clouds dispersed, flights became strongly directed to the west northwest once again, suggesting that the direction of the migrating insects was influenced by the position of the sun.

This migration continued on 5th May and 6th May but with significantly reduced numbers. A few individuals were observed daily between 7th-10th May, all flying west northwest between 0900 h and 1500 h, after which no more were observed. However, B. L. Williams, in Walker (1954), recorded migrations in Kingston taking place until 1600 h and noted that in June 1945 flights continued as late as 1800 h following afternoon rainfall.

No attempts were made at this time to follow the migrants further west, but distributional data suggests the flight breaks up over the central mountains, northwest of Kingston. No return flights to Rozelle have been documented.

In recent years, the habitat at Rozelle has been greatly compromised by human activities and the once dependable Rozelle Falls which flowed year-round is now reduced to a single source which now flows intermittently. *Protographium marcellinus* still occurs here but in significantly smaller numbers and no other large-scale migration has been documented from this habitat since 1966 (Garraway, 2008, pers. comm).

Breeding sites and their present status

Although at one time thousands of *Protographium marcellinus* dispersed across the island in greater or lesser numbers each year from Rozelle, some recorded sightings of this short-lived insect did not always coincide with the periods of large flights observed in Kingston, suggesting there were other sites where the insect might be breeding. Island-wide surveys were begun in 1968, and between then and the present time an additional three small breeding sites were identified. Three of the four known breeding sites are found in dry limestone forest habitats characterized by long periods without rain, interrupted by short periods of heavy rain (Fig. 6).

The second breeding site was found in 1968 at Crownlands on the southern side of the Cockpit Country in Trelawny Parish. Reports of occasionally large migrations of the insect across Portland Bight led to the subsequent discovery of another breeding site at Lancewood Valley in the arid Hellshire Hills, St. Catherine Parish (Woodley, 1970, pers. obs.), Large numbers of sightings were also made to the west of this site at Portland Bight and at Round Hill in dry limestone forest habitat along the south coast in Clarendon Parish. However, these are not proven breeding sites. Finally, small but frequent annual sightings of the insect led to confirmation of a breeding site in 1991 near Rio Bueno on the north coast in St. Ann Parish. No other breeding sites are known at present. However, in June 2022, as a key component of a European Union funded project, an initial workshop led by Turland was held by Caribbean Coastal Area Management Foundation (C-CAM) to commence the assessment of the status of the Blue Kite Swallowtail in the Portland Bight Protected Area. As of March 2024, only one adult had been reported since commencement of the project.

All breeding sites are subject to several years when very few adults appear (Walker, 1943), followed by the occasional year in which thousands of insects emerge and participate in large migrations. The periods of emergence are less well defined at the Crownlands site, which is located in mesic broadleaf forest in contrast to the dry limestone forest sites that are subject to extended periods of drought.

Although monitoring since 1918 has been irregular, older data suggest that there may have been a six to seven-year cycle for larger migrations prior to more recent habitat destruction. Large migrations in recent years are very infrequent now only originating from the least disturbed sites at Lancewood Valley and Crownlands (Turner & Turland, 2017).

Rozelle. This breeding site was the first to be discovered, in 1967. Larval food plants of *Oxandra lanceolata* were then approximately 5 m in height, spaced approximately 3 m apart, with lower branches of adjoining trees meeting. In addition, there were a small number of older, taller, emergent *Oxandra* trees approximately 9 m in height. Subsequent explorations of the site determined that the total breeding area covered approximately 5.2 km^2.

In 1992, another small stand of *Oxandra* trees was

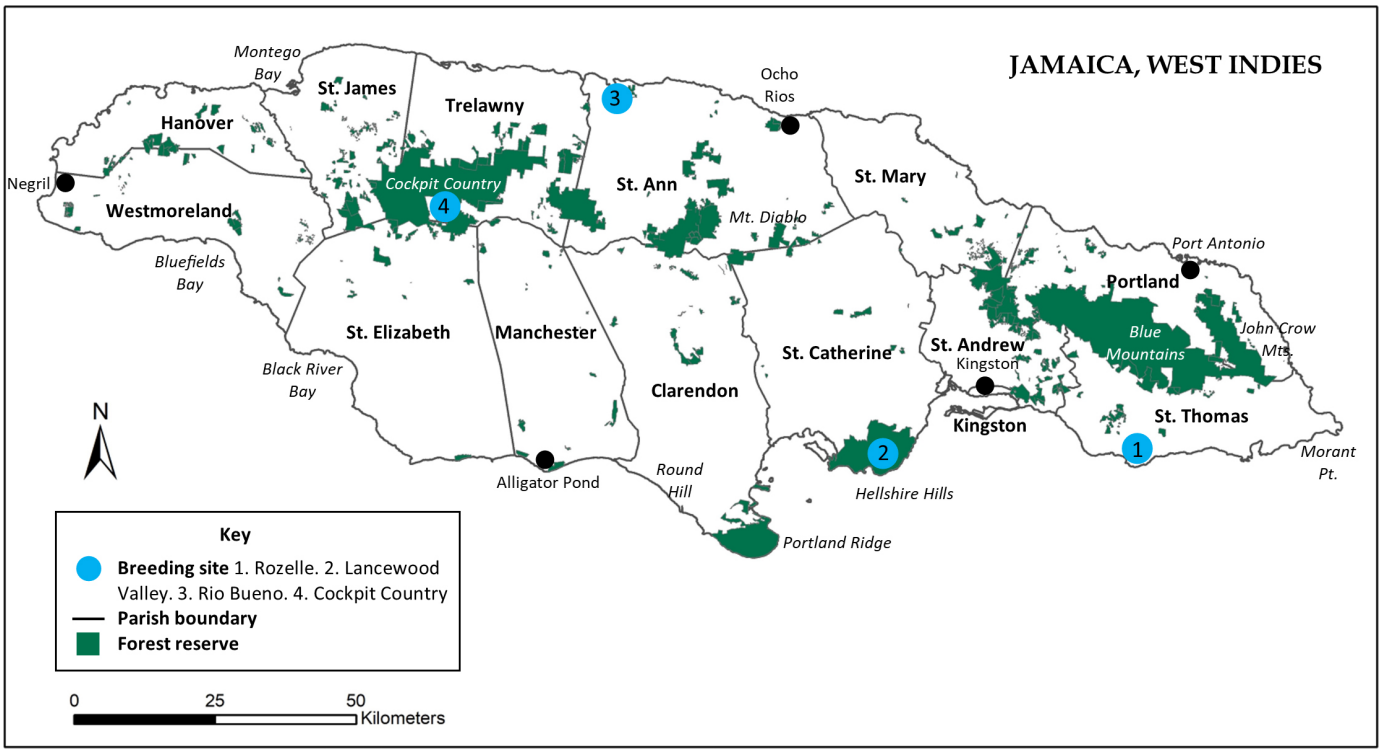

Figure 7. Known breeding sites of *P. marcellinus.*

discovered in a valley 3.2 km northeast of the original breeding site. This additional area was approximately 1.3 km^2. *Protographium marcellinus* immatures were present, increasing the known breeding area to 6.5 km^2. However, even at time of discovery, this new area was already being destroyed by charcoal-making, and some of the *Oxandra* trees had their lower branches removed and were acting as living poles for yams (Dioscoreaceae) planted at the base of each tree. When both authors revisited Rozelle in 2010, nothing of this segment of the site remained except grassland; no charcoal or yams or any other crops or livestock were observed.

The fate of the original 5.2 km^2 site has been no less turbulent. The property was originally owned by a single landowner who took interest in the butterfly and granted permission for field studies. However, the Land Development and Utilization Act of 1967 was introduced by the government to encourage farmers to place underutilized acreages in excess of ten acres into production or risk having the lands confiscated for others to farm. Whether such an order was served to this landowner is not known, but part of the breeding site was bulldozed in 1971 and converted into pasture for cattle and land for the cultivation of plantains. The property was subsequently sold, the cattle removed and the plantains abandoned. Part of the site is now a land settlement area with houses immediately to the east of what remains of the breeding site. As of 2010, some of the emergent *Oxandra* trees are still present along with an unknown number of younger *Oxandra* and the butterfly still occurs here but in far fewer numbers. This site was once the largest known sub-population of this swallowtail, but no large-scale migrations from Rozelle have been documented since 1966.

In the forty-three years between 1967 and 2010, 135 visits were made to monitor this site (Fig. 8). As of 2010, a total of 80% of the breeding site at Rozelle has been lost with the known breeding site now reduced to approximately 1 km^2 in area.

Lancewood Valley. This site is located within the weathered honeycomb and much faulted and fissured dry limestone terrain of the Hellshire Hills, an area of 114 km^2 with the highest of four mountain ridges, the Central Ridge, reaching an elevation of just 240 m (Fig. 10). The area receives less than 1,270 mm of annual rainfall, with no more than 125 mm per month in all months except October, when approximately 250 mm of rain occurs. Additional rainfall may occur at infrequent intervals from passing low pressure systems such as hurricanes.

Temperatures vary between 21° C between December and February and 35° C between June and September. The University of the West Indies Climate Studies Group (2015)

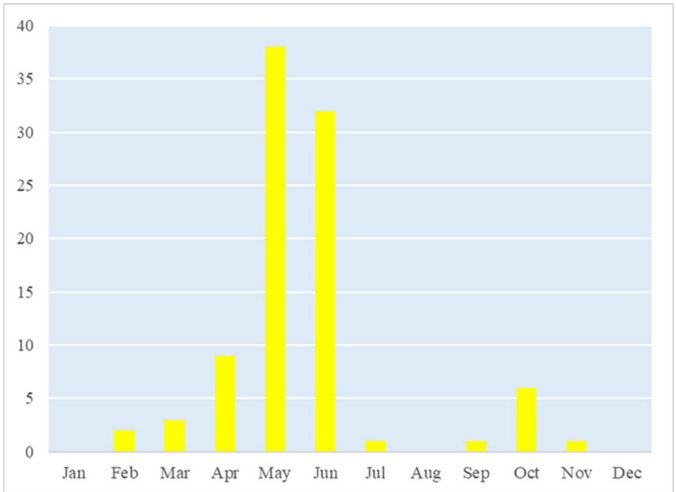

Figure 8. Frequency of sightings of adult of *P. marcellinus* by month at Rozelle, St. Thomas Parish, 1918-2009.

project predicted slowly increasing temperature and increasing droughts during the next fifty years. These trends are already becoming evident (Stephenson *et al.,* 2014; Planning Institute of Jamaica, 2017).

Several trails cross the study site region, which are used by hog hunters with dogs, by sportsmen while shooting pigeons, by wild goats, and by charcoal-makers. Clear-cutting of trees for charcoal for both local use and for export to Haiti has also occurred in these forests, even though the area is a Forest Reserve and the last natural refuge of the endemic Jamaican Iguana, one of the two most endangered iguana populations in the world (Grant & Pasachnik, 2021). As stated in the Hellshire Hill Scientific Survey 1970, "Weathering of the limestone produces a coarse reddish soil which is easily transported into hollows and crevices. Large areas of bare rock are generally visible. Many of the trees, rooted in crevices, seem to grow out of solid limestone. Because of the high permeability of the substrate, rainwater quickly soaks down from the surface and may be out of reach of the vegetation unless their roots are long or the water table is high. This means that the drought conditions are effectively more severe for the plants than might be supposed from the rainfall figures" (Woodley, 1971).

Lancewood valley is located approximately 0.8 km south of the south end of Salt Island Lagoon and comprises a relatively level site sheltered by a steep hill to the northeast. In 1970, the woodland was described (Woodley, 1971) as "relatively undisturbed" with a "more or less continuous uniform canopy" with trees growing in a "moderate accumulation of bauxitic soil and some leaf litter and humus over the limestone" noting, "The outstanding features of this vegetation are the extremely concentrated presence of Lancewood trees *Oxandra lanceolata*…". The dense occurrence of *Oxandra* trees together with an accumulation of leaf litter and humus appear to be prerequisites for a successful breeding site, yet overall, in the Hellshire Hills, other than at Lancewood Valley, *Oxandra* is rare (Adams & Duquesnay, 1971). This site is estimated to occupy an area of approximately 0.25 km^2 and is threatened by thinning of the forest for charcoal-making. From surveys in 2023, removal of trees for charcoal has now significantly declined and trails are becoming overgrown through less use (A. Haynes-Sutton, 2024, pers. comm.). However, the last large migration of *P. marcellinus* that is believed to have originated from this location was documented in 2009.

Figure 9. Typical Dry Limestone Forest of the south coast, March 2022.

The peninsula at Portland Bight is approximately 16 km southwest of Lancewood Valley. Round Hill (352 m) lies a further 16 km to the west northwest of Portland Bight. While *P. marcellinus* has been observed on occasion in large numbers at both locations, these are perhaps adults migrating from Lancewood Valley. No evidence has so far been found of *P. marcellinus* breeding at these locations, but surveys are continuing. *Oxandra* is present at both locations but there are no reports of dense stands of this plant (Kapos, 1983). There are recent reports of forest clearing, cultivations and charcoal-making at the Round Hill location (A. Haynes-Sutton, 2022, pers. comm.).

Rio Bueno. This confirmed dry limestone forest breeding site has undergone significant disturbance. The site is located primarily at the foot of the 60 m high cliffs positioned at the landward side of the wave-cut platform along the north coast of the island east of the town of Rio Bueno. Here, most of the shorter Lancewood trees have been harvested, leaving mostly older emergent trees which support only a small but persistent population of this butterfly. No large migrations have been observed from this site, but emerging adults appear to fly along the coast and for a short distance inland both to the east and west of this site (Garraway *et al.*, 1993; Turner & Turland 2017) (Fig. 10).

A number of *Oxandra* trees were included in part of the forest that was removed during road widening in the 1970s, and currently there is a fine-dust-producing limestone quarry and limestone processing mill at the west end of this site. A determination needs to be made as to whether or not this dust is adversely affecting this sub-population (Farmer, 1993). Forest has been thinned or entirely removed over the entire breeding site with the insect now dependent on scattered, larger *Oxandra* trees. In 2017, it was estimated that just 20% of the original site remains.

Crownlands. This site was discovered at the end of a road extension from Crownlands into the Cockpit Country in 1968. Completion of this project, to link some of the existing trails from the south to north side of the Cockpit Country, was halted by the cost of continuing this road through difficult karst terrain. At the end of this trail is a dense patch of *Oxandra* trees, though most of these trees are no longer growing straight, but bent and intertwined, possibly a reflection of the mesic broadleaf forest (Fig. 11) which is shaded by other species of larger emergent trees where the *Oxandra* grows. As a result of this growth habit and difficulty of extraction, these *Oxandra* trees are unsuitable for harvesting for yam sticks and support a thriving subpopulation of *P. marcellinus*. However, annual appearances (Fig. 12) are still subject to the population fluctuations observed in the dry limestone subpopulations on the south coast. In some years, migrations are not seen, with just a few adults emerging which remain near the breeding site. In other years many adults are seen, usually migrating individually, for example to

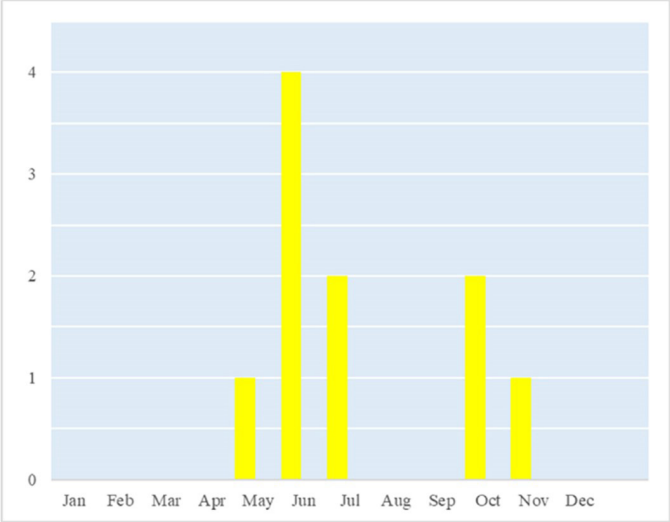

Figure 10. Frequency of sightings of adult of *P. marcellinus* by month at Rio Bueno, St Ann Parish, 1979-1992.

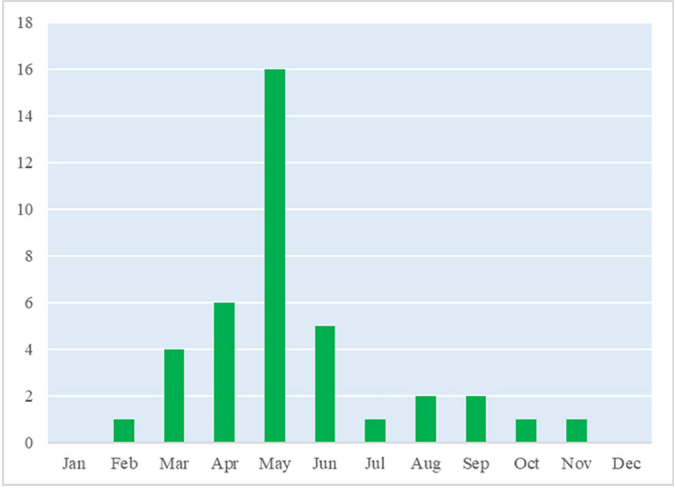

Figure 12. Frequency of sightings of adult of *P. marcellinus* by month at Crownlands, Trelawny Parish, 1968-2013.

Figure 11. Typical Mesic Broadleaf Forest, Fyffe and Rankin Forest Reserve, St. James Parish, February 2014.

the Windsor Research Centre some 9 km to the north (Koenig 2019, pers. comm.), and along the north coast as far as Negril at the western end of Jamaica. However, the number of adults seen here even after a relatively large emergence, as compared with the Rozelle site in 1965, suggests that this breeding site is less than 1 km^2 in area.

Records over time reveal that adults have been seen in more months of the year in this mesic habitat, suggesting periods of diapause might be terminated more frequently than those of pupae in diapause located in dry limestone habitats where there are long droughts between periodic rainy seasons (Turner & Turland, 2017). Observations at Crownlands nevertheless still indicate the continuous breeding throughout the year does not occur.

Main threats to survival

Saplings of the only known larval food plant are still in high demand locally, cut in the thousands each year for use as sticks for yam cultivation. Barker and Beckford (2003) obtained data from 216 farmers who were estimated to be producing half of Jamaica's yam cultivations at that time, noting that a total of 732,115 yam sticks were cut during the study period and that these lasted no more than two years before they had to be replaced. Half of the yam sticks in this study were said to be from the Cockpit Country. This practice is a major contributor to deforestation in Jamaica (Turner & Turland, 2017). Additional, smaller Lancewood saplings are used in the construction of Antillean Z fish pots, which are lost or damaged in storms and frequently have to be replaced (Turner & Turland, 2017).

A high density of Lancewood trees appears to be a prerequisite for the breeding sites of *P. marcellinus* as noted at Rozelle, St. Thomas Parish, Crownlands in the Cockpit Country, Trelawny Parish, and at Lancewood Valley, St. Catherine Parish. Any thinning of *Oxandra* at any of the breeding sites would be detrimental, resulting in lower humidity within the leaf litter in which the pupae diapause. Deforestation is also continuing at each of the known breeding sites as a result of licensed and illegal logging, the tailings being used along with other trees harvested to make charcoal, which is a large, unregulated industry in Jamaica (Turner & Turland, 2017).

The Rozelle, Lancewood Valley, and Braco breeding sites have already been adversely affected by the cutting of *Oxandra* trees for use as yam sticks and fish pots, and by clearing of forest for making charcoal or for small cultivations (Figs. 14, 15). It takes approximately five years of regrowth for any surviving *Oxandra* stumps to reach a height of about 1.5 m, when such plants become tall enough to be of interest to ovipositing *P. marcellinus* females at a breeding site, but most trees do not survive such drastic cutting, often failing to regrow (Turner & Turland, 2017).

Quarrying for limestone, once not of major concern, has become more prolific with the refined product now more valuable than bauxite. There is a well-established processing facility near Braco. It also needs to be determined if the expanding limestone quarrying operations in the Hellshire Hills north of Lancewood Valley are negatively affecting that breeding site (Farmer, 1993).

Figure 13. Ongoing causes of loss of Jamaica's forest habitats: a. Cutting of hardwood saplings for yam sticks; b. Antillean Z fish pots; c. Kiln for making charcoal from hardwood species; d. Limestone quarrying destroys habitat and creates dust, coating larval food plants. Photo courtesy of Wendy Lee.

Current protection

Protographium marcellinus is protected under the Jamaican Wild Life Protection Act (1945). Fines up to J$100,000 per specimen or one year in prison can be levied for possessing any life stage of this insect. Before conducting any scientific studies, a permit must first be obtained from the Jamaican National Environment Planning Agency (NEPA). The Endangered Species Protection Act 2000 is "an act to provide for the prosecution, conservation and management of endangered species of wild fauna and flora and for the regulation of trade in such species and for connected matters". However, in spite of both NEPA regulations and the present IUCN Vulnerable designation, the adults are occasionally offered for sale on overseas websites, with female *P. marcellinus* advertised for sale from one commercial source in 2006 for US$ 150.00. It should be noted that adults are rarely collected; the insect only reproduces in very few locations and flies for short periods. The flight is very fast, and, in some years, adults may not be seen, so opportunities to collect the adult butterfly are limited. Therefore, even if a few specimens were to be caught illegally this would pose little harm to this species.

The primary conservation need for this species is the protection of breeding sites. On 17th March 2022, the Most Honorable Andrew Holness, Prime Minister of Jamaica, announced that definition of the boundary of an area proposed for protection of 78,024 hectares of Jamaica's Cockpit Country had been finalized and this area is now protected by law. Except for the Crownlands site in the Cockpit Country Protected Area (CCPA), and the Hellshire Hills site which is within the Portland Bight Protected Area, the other breeding sites are presently unprotected. However, even at the Crownlands site, encroachment from nearby neighborhoods has steadily degraded the forest along the access track into the Cockpit Country, removing trees for construction and creating grassland for goats and cattle, now approximately 1.5 km away from one of the most environmentally important forest sites. For example, the Crownlands site is the type locality for several endemic species of moths (Todd, 1982), the type locality for the genus *Troyus* and where the immature stages of *Troyus turneri* (Hesperiidae), were also discovered and described (Turland *et al*., 2012); this is a breeding site for the Homerus Swallowtail and one of the prime sites to continue studying a subpopulation of the endemic *Atlantea pantoni* (Nymphalidae), whose immature stages are still unknown (Turner & Turland, 2017).

So far there have been no effective measures taken to stop this creeping destruction of the habitat, which continues at an average rate of 0.6 km per year along access roads into the

Cockpit Country (T. Turner, pers. obs.). While the designated protected area (CCPA) was formally recognized in March 2022, mining leases were subsequently issued with mining permitted right up to the CCPA boundary without provisions for a buffer zone. Legal appeals were made by residents and environmental organizations opposing the dislocations of property owners and the environmental damage that would result from this mining, and mining operations were paused. As of April 2024, court cases continue regarding mining licenses granted in areas adjacent to the CCPA.

Since 1985, *P. marcellinus* has been listed in the International Union for Conservation of Nature and Natural Resources (IUCN) Red Data Book as Vulnerable: "taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating" (Collins & Morris, 1985). The species is listed for protection by the IUCN but has not yet been accorded protection under CITES.

In 2004, a request was submitted to the United States Fish and Wildlife Service (USFWS) suggesting the species be considered for further protection under the US Endangered Species Act of 1973. A review of the status determined that no further actions were necessary at that time, but noted that USFWS was open to receiving any new information on this matter. Although there have been periodic reviews since that time, the present USFWS "Listing Priority Assignment Form" based on information dated July 2022 acknowledges that "The magnitude of threats to Jamaican kite swallowtail is high" but asks "Is Emergency Listing Warranted?" The form concludes "No; There is currently no emergency posing a significant risk to the conservation of the Jamaican kite swallowtail" (pers. comm., M. Williams, Director, U. S. Fish and Wildlife Service, June 20, 2023). Evidence presented here unequivocally supports the need for a reassessment of the conservation status of this species, given the loss of habitat which has placed the four known, critically small, breeding sites in imminent danger of extirpation.

Reassessment of conservation status of *P. marcellinus*

Here we apply the IUCN Red List Criteria (2023) to determine the current conservation status of *P. marcellinus*.

Population reduction. There are just four confirmed breeding sites, which in 1965 occupied a collective area of just 8.75 km^2, but now occupy a total area of approximately 2.5 km^2, an overall loss of 70%, with the Rozelle and Rio Bueno sites each having lost 80% of permanently occupied areas. The sites at Rozelle and Braco are severely compromised by thinning of the forest and loss of *Oxandra*. The northern boundary of the Crownlands site still needs definition, but based on observations of the numbers of adults emerging, it is clear that this site is also very small, approximately 1 km^2. A person with a chain saw can quickly harvest large numbers of *Oxandra* in a few hours. The density of this tree at a breeding site acts as an incentive for tree fellers to select that location for cutting, as has already happened at the Rozelle and Braco sites. Thinning of the forest creates unsuitable conditions for survival of diapausing pupae and increases the probability of the site becoming unsuitable for continued occupation. **Assessment: Critically Endangered (A2, A2(c)).**

Geographic range. *Protographium marcellinus* is a Jamaican endemic species, which, from records accumulated over 100 years, disperses island-wide (an area of 10,992 km^2) in the short flight season. However, any such occurrence is for just a few days in some years or for a few weeks in other years. Because the insect is periodically seen in large numbers this creates the false impression that the insect requires little protection. However, the total area of permanent occupancy is now approximately 2.5 km^2, located in four very small sites where pupae remain in a state of diapause through most of each year. **Assessment: Critically Endangered (B2(a)(b)(c)).**

Population size and decline. Many thousands of insects could be seen migrating in large numbers over a period of several days from the Rozelle site in favorable years, up until 1966. One documented migration is estimated to have consisted of some 750,000 individuals over a seven-day period (Turner, pers. obs.). Following large scale destruction of the Rozelle habitat, numbers have been reduced to just a few individuals migrating in subsequent years. Fair numbers are seen in occasional years from the Lancewood Valley and Crownlands sites, but while adults may be abundant for a few days, no large-scale migrations like those from the original Rozelle site have been observed. Now, only a few hundred individuals are seen in a favorable year, but more commonly, less than one hundred individuals may be seen from all four sites combined. In some years no adults are seen. When the subpopulations are at critically small numbers, they are far more vulnerable to any adverse habitat incursions such as removal of larval food plants for use as yam sticks or brush fires. **Assessment: Critically Endangered (C2(b)).**

Very small or restricted subpopulations. The breeding sites are limited in number and area, and emerging females mate and lay eggs only at the site of their emergence. Even though *Oxandra* occurs at other locations, especially across the western half of the island, the trees are scattered, not meeting the required density essential for oviposition. There is an unidentified nocturnal spider that is a major predator of larvae at Rozelle. It is not yet known if such predation also affects other sites but the number of adults emerging each year at each of the sites fluctuates greatly. In some years, no adults or very few adults are observed. The reasons for these dramatic population fluctuations still need to be determined but evidently must include years when larvae fail to pupate, or when diapausing pupae fail to emerge, whether from predation, natural causes such as desiccation, or because of human activities. As stated above, the combined permanent area of occupation for all four breeding sites is now reduced to approximately 2.5 km^2. **Assessment: Critically Endangered (D2).**

Quantitative analysis. A quantitative analysis has not been possible due to the irregular appearance of the adult and resultant difficulty in obtaining meaningful data. However, a single forest fire, harvesting of trees for fish pots and yam sticks,

government-licensed mining, or clearance for development, could destroy any one of the four breeding sites in a few hours. The Rozelle, Lancewood Valley, and Rio Bueno sites are most at risk from these activities, which are ongoing. These sites will probably be lost in the relatively near future. This could occur in any given year, but almost certainly within the next 25 years. The Crownlands site now lies within the declared Cockpit Country Protected Area, but continuing destruction within this forest, if unchecked, is expected to reach this site within 5 years. **Assessment: Critically Endangered (E).**

Overall Assessment. Based on all the evidence at hand, *Protographium marcellinus* is considered to be **Critically Endangered**.

SUMMARY

The four confirmed breeding sites, on which the survival of the species depends, now occupy no more than 0.3 km^2-1.5 km^2 each in area, or approximately 2.5 km^2 in total. Three of the four sites are threatened with almost certain habitat destruction within the next 25 years. Although the larval food plant grows across much of Jamaica, it is not in sufficiently dense stands to maintain conditions essential for a breeding colony. The breeding sites are extremely limited. Adults emerge simultaneously and mate; the female lays eggs at the emergence site only; larvae pupate under *Oxandra* trees, most entering a state of diapause lasting up to six months.

Successful conservation of this butterfly species therefore requires not only the protection of existing sites, but also enhancing of these sites by planting additional *Oxandra* to restore or improve density of the larval food plant. These trees should later be topped after reaching a height of 2.5 meters to make them unsuitable for harvesting for yam sticks. The breeding sites are experiencing rapid habitat destruction, making this insect close to becoming extinct. Changing the present IUCN category from Vulnerable to Critically Endangered does little to protect this species unless positive steps are taken on the ground by the Government of Jamaica to protect and enhance the existing breeding sites.

In June 2022, the Caribbean Coastal Area Management Foundation (C-CAM) held an initial workshop at the Portland Bight Discovery Centre in Salt River to focus on the status of the Blue Kite Swallowtail in the Portland Bight Protected Area. This is an important component of the European Union-funded project "Enhancing the capacity for dry forests in the Portland Bight Protected Area, Jamaica". The protected area includes the Lancewood Valley breeding site as well as other areas, such as Portland Ridge, where the species has previously been observed in numbers and where the larval food plant is present. The project has established a training and observation program for the butterfly using mostly community members. The data collected, using smart devices, will enable a more detailed knowledge of the current status of the species in the protected area. Meteorological data for the project's duration will also be analyzed and this will further facilitate a better understanding of weather conditions and other events that may affect the seasonal emergence of adults and their numbers. Mapping of the larval food plant locations in Hellshire, the Brazilletto Mountains and Portland Ridge, has progressed and reports will be published.

On completion of the present project, any data collected will be used as a basis to develop a conservation program specific to the Portland Bight Protected area that could also be applied to the other very small sites in Jamaica where the butterfly is known to breed. It is of significance that only one adult was reported during the period September to November 2022 to March 2024 from Portland Bight Protected Area. There were reports of small numbers of adults, usually less than ten in a day, during April and May 2023 from the Windsor Research Centre in northern Trelawny Parish. No adults were reported from locations along the north coast from Discovery Bay and Rio Bueno areas during 2023. Previous studies of the subpopulation at Rozelle also concluded that emergencies in the September to November were often small and confined to the breeding site, usually without conspicuous migrations.

ACKNOWLEDGMENTS

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