

Male-Male Interactions in the Endangered *Homerus Swallowtail*, *Papilio homerus* (Lepidoptera: Papilionidae), in Jamaica

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ABSTRACT.—The *Homerus Swallowtail*, *Papilio (Pterourus) homerus*, is an endangered butterfly endemic to Jamaica. We report conspecific male interactions observed in the Cockpit Country. Field observations of the patrolling behavior and the conspecific male circular flights suggest that males are territorial. Unlike most previous reports of male butterfly territoriality, physical contact occurs in the male circular flights, evidenced by the sound of the wings hitting each other, which may contribute to wing damage. We were able to quantify the extensive wing damage accumulated on a single territorial male with photographs; this male lost more than 90 percent of an individual wing, and still patrolled an area. In addition, we discuss the possible variables that might determine the outcome of territorial disputes, the habitat associated with territory establishment, and lekking in this species.

KEYWORDS.—Cockpit Country; *Papilio (Pterourus) homerus*; territorial behavior; wing damage; butterfly territoriality

INTRODUCTION

The *Homerus Swallowtail*, *Papilio (Pterourus) homerus* Fabricius (Lepidoptera: Papilionidae), is endemic to Jamaica (Garraway et al. 2008) and is the largest butterfly in the Western Hemisphere, with a forewing length greater than 80 mm (Emmel and Garraway 1990, 1994; Lehnert 2008), although some females exceed 90 mm (Bailey 2003; Vane-Wright and Hughes 2004). Likely due to anthropogenic factors, its range has dwindled from seven of Jamaica's 14 parishes to two isolated populations: an eastern population at the merger of the John Crow and Blue Mountain Ranges and a western population in the remote Cockpit Country (Brown and Heineman 1972; Garraway et al. 1993; Emmel 1995). The butterfly is one of four species listed in the IUCN Red Data Book, *Threatened Swallowtail Butterflies of the World* (Collins and Morris 1985) and is protected by the Jamaican Wildlife Act of 1988 and by CITES as an Appendix I species.

The population size of *P. homerus* was estimated previously in the Cockpit Country (Lehnert 2008). During field observations, males of *P. homerus* performed conspecific circular flights. Our objectives were to investigate male-male interactions and quantify the wing damage of a single male frequently encountered in the study region.

MATERIALS AND METHODS

Study site

The study took place near Niagara at the merger of the St. Elizabeth and St. James Parishes in the Cockpit Country, Jamaica, from 11 July to 14 August 2004. The Cockpit Country is a 644 km² region of unique terrain characterized by steep rolling mountains interspersed by deep valleys (Fig. 1). In Niagara, a path led west into tropical rainforest and turned south along a mountainside. After 373 m, the path abruptly turned west and continued along



FIG. 1. Photograph of the Cockpit Country terrain in Jamaica.

a different mountainside; this right angle of the path received more sunlight than any other area of the path, and is referred to hereafter as Area 1 (Fig. 2). Area 1 was 482 m above sea level (asl) and had a treeless diameter of 9 m and a 30 m circumference that was sporadically lined with nectar sources such as *Lantana camara* L. (Verbeniaceae) and *Tabernaetha montana* Urb (Apocynaceae) that *P. homerus* and other Lepidoptera were observed to utilize (Lehnert 2008). In addition, the sole known host plant for the western population, *Hernandia jamaicensis* Britton and Harris (Hernandiaceae) (Emmel and Garraway 1990), was common in the forest. At the bottom of the two adjoining mountains was a sinkhole. The overall presentation of the study area was an amphitheatre-like landscape covered in lush tropical rainforest; ideal habitat for *P. homerus* (Avinoff and Shoumatoff 1940; Emmel and Garraway 1990).

Field sampling

Males were captured with an aerial net and identified with a number marked on

the ventral side of the hindwing in the discal cell by a metallic-colored Sharpie® marker (Lehnert 2008). Forewing length was measured, and each butterfly was photographed with a Nikon® Coolpix 8700 digital camera before release. The entire handling process took less than three minutes. The net was checked for evidence of wing or body damage after each capture. Con-specific male interactions were timed using a stopwatch.

Wing damage analysis

Sequential photographs of a single male (ID# 002) were analyzed to determine percent wing damage using Adobe Photoshop 6.0® (Adobe Systems Inc, San Jose, CA) and Scion Image® (Scion Corp., Frederick, MD), as outlined by Lehnert (2010), but a brief overview is given here. Each photograph (JPEG) was initially opened in Adobe Photoshop 6.0®. All four wings were lassoed and moved into new folders. The erase tool was selected and used to clean each image so only the presumed shape of an undamaged wing remained,

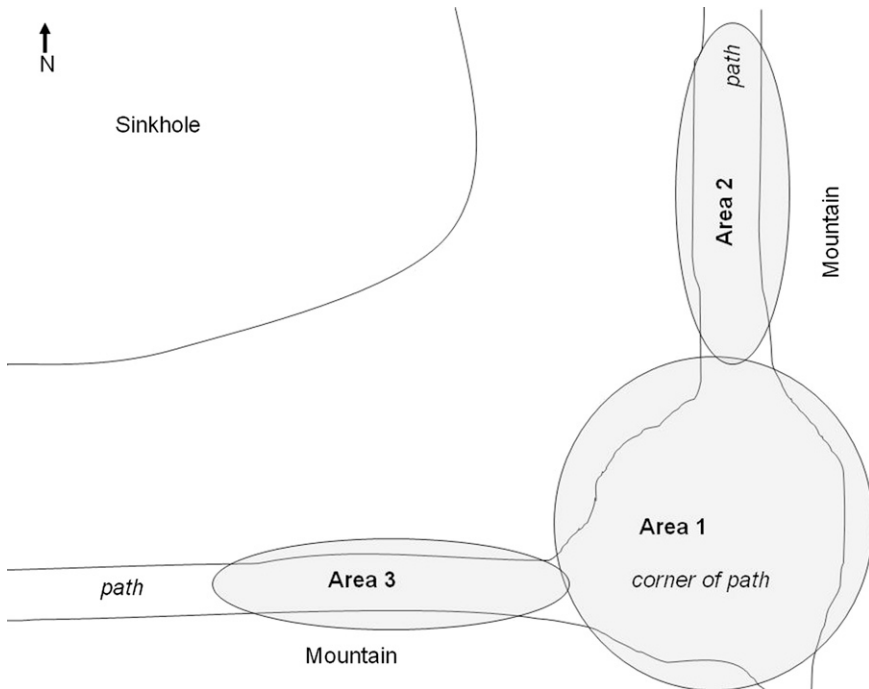
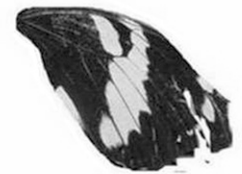


FIG. 2. A map illustrating the three areas patrolled by *P. homerus* males along the sampling transect. Area 1 was the most active region and is where conspecific male interactions ($n = 18$) were observed. Map is altered from Lehnert (2008).



Undamaged wing



Damaged wing

FIG. 3. Method used to determine percent wing damage. This specific example estimated 8.7% wing damage of the right forewing (146651 pixels damaged wing / 160698 pixels undamaged wing = 91.3% wing area; $100 - 91.3 = 8.7\%$ wing damage). The details of these methods are described by Lehnert (2010).

which was then greyscaled and saved as a TIFF file. The same process was used to clean and save images representing the actual damaged wing. The photographs (TIFF) were then opened in Scion Image® to receive a pixel count to determine the percent wing damage (Fig. 3):

$$WA = (DW/UW) \times 100$$

$$WD = 100 - WA,$$

where WA is the percent wing area, DW is the number of pixels of a damaged wing, UW is the number of pixels of the undamaged wing, and WD is the percent wing damage.

RESULTS

Description of conspecific male interactions

All conspecific male interactions ($n = 18$) occurred in Area 1. Only one male was

observed to fly a circle around the perimeter of Area 1 at a time, usually at a similar height as the canopy (4 – 8 m) from 0900 h when sunlight first penetrated the area until 1200 h. Males flew around the perimeter in approximately 15 minute intervals, interspersed by 3 to 4 minutes of basking on leaves of the surrounding trees. Of the 18 male-male interactions, 16 occurred between 1000 h and 1200 h, and none were witnessed after 1200 h.

There were two smaller areas on the path that neighbored Area 1 and were patrolled by males in a similar manner (Area 2 and 3, Fig. 2), but male occupation of these areas was less common, and only occurred when a sole male was already circling Area 1. All three areas were sporadically lined with nectar sources, but these nectar sources were more abundant in Area 1; however, males only rarely utilized the nectar sources. All three areas, particularly



FIG. 4. Two males of *P. homerus* engaged in a circular flight.

Area 1, shared the common characteristic of open space.

A male flying around the perimeter of Area 1 reacted when another male flew into the area; both males flew at each other and collided, producing a loud sound, which was followed by both males flying circles around each other (approximately 0.33 m in diameter) (Fig. 4). Wing contact was audible throughout the circular flight, but never as loud as the initial impact. The circular flight transitioned into one male pursuing the other male outside the area, and returned an average of 3.30 ± 0.93 min later (mean \pm SE, $n = 16$). The length of these interactions averaged 20.36 ± 1.78 sec ($n = 11$, Table 1). The average forewing length of the male that returned to the area after the pursuit was 72.3 ± 0.67 mm ($n = 2$), whereas the average forewing length of the male pursued out of the area was 73.3 ± 0.33 mm ($n = 3$). Of the observed 18 battles, 78% resulted with the resident male maintaining occupancy (Table 1). Male ID# 002 was the original occupant of Area 1 in 14 of the 15 male interactions that included this butterfly, and maintained residency after 79 % of them. Although male ID# 002 was chased out of the area at least temporarily in three

interactions, he returned and chased away the new occupant immediately after one of these interactions.

Despite extensive searches, females were rarely seen and only observed in Area 1. Females flew out of the forest on one side of the area, passed through the area, and exited on the other side. No intersexual interactions were witnessed, and the mating behavior of these rare butterflies is still unknown.

Wing damage analysis

One male (ID# 002) was observed in Area 1 for 19 days from 18 July to 5 August 2004, and interacted with other males ($n = 15$) (Table 1). Male ID# 002 had a forewing length of 73 mm; the average forewing length of males collected at the study site was 72.7 ± 0.53 mm ($n = 13$). Subsequent captures of this male revealed an accumulation of wing damage (Fig. 5). As much as 93% of the left hindwing was lost, and the other wings suffered 40, 18, and 29 % of wing loss from the right hindwing, left hindwing, and right forewing, respectively, yet this male was still capable of flight (Fig. 6).

TABLE 1. Raw data and outcome of conspecific male interactions of *P. homerus*.

Battle #	Date (2004)	Time (h)	Length of interaction (sec)	Outcome (winner)
1	19 July	1101	20	Resident*
2	19 July	1103	25	Resident*
3	19 July	1114	Unknown	Resident*
4	19 July	1118	Unknown	Intruder*
5	19 July	1150	>30**	Resident*
6	23 July	1027	Unknown	Resident*
7	23 July	1138	20	Resident*
8	26 July	1040	23	Intruder
9	26 July	1046	Unknown	Intruder*
10	27 July	1105	Unknown	Resident*
11	28 July	951	18	Resident*
12	28 July	1030	25	Resident*
13	28 July	1110	25	Resident*
14	28 July	1111	7	Resident*
15	28 July	1114	Unknown	Intruder*
16	29 July	941	18	Resident*
17	30 July	1047	15	Resident
18	3 August	1045	28	Resident

*conspecific male interactions involving male ID# 002

**conspecific male interaction was not included in average length of interactions

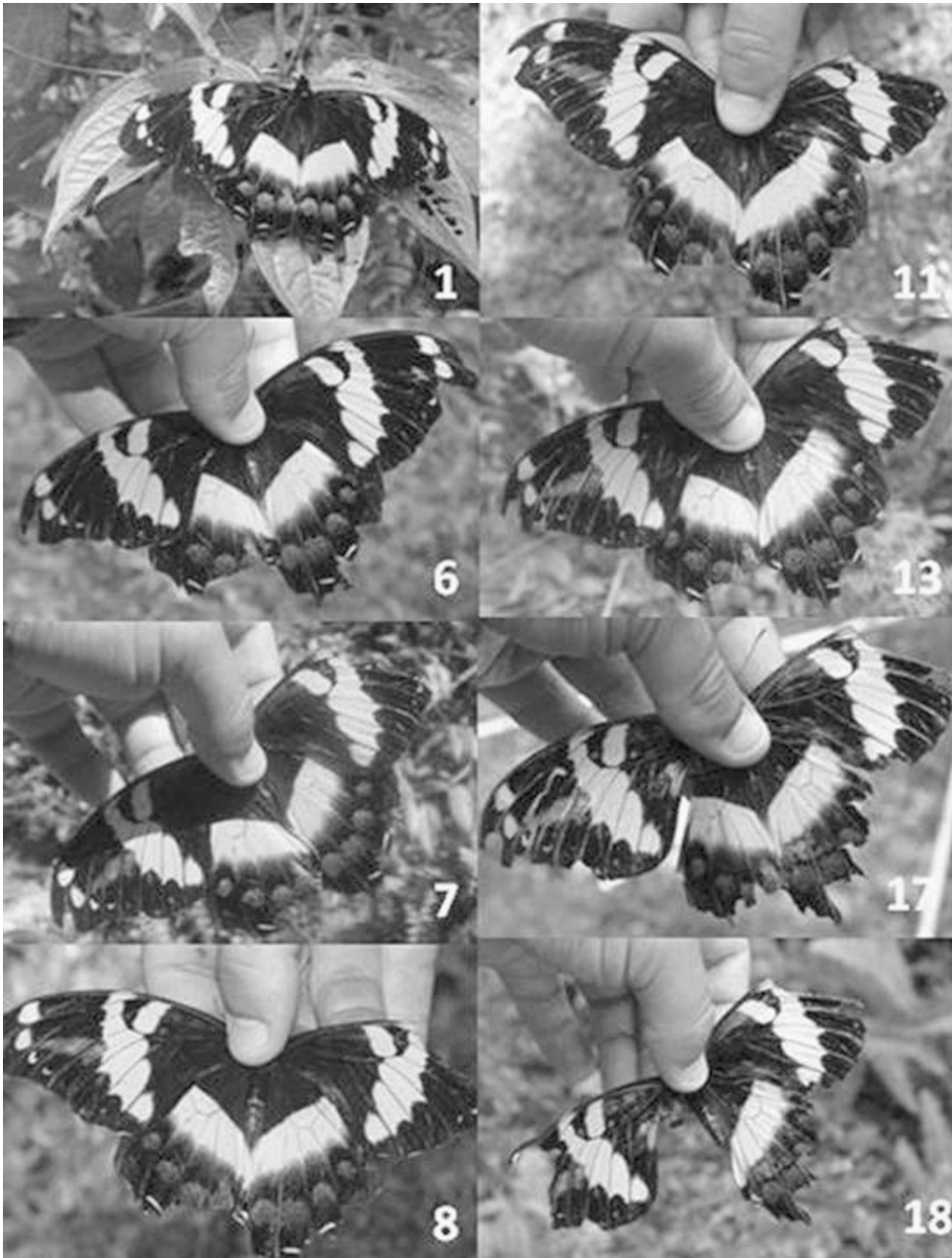


FIG. 5. Sequential photographs of male ID# 002 measured for wing damage analysis. Number shown in each image refers to the number of days that passed between initial capture (day 1) and subsequent captures (day 6, 7, 8, 11, 13, 17, 18). Image from day 18 was originally displayed by Lehnert (2008).

DISCUSSION

The patrolling behavior in a topographically unique area (Frietas et al. 1997), the occupation by a single male in a defined area

for a prolonged period of time, and the conspecific male flights of *P. homerus* correspond with territorial behavior of other Lepidoptera (Rutowski 1991; Kemp and Wiklund 2004; Takeuchi and Honda 2009),

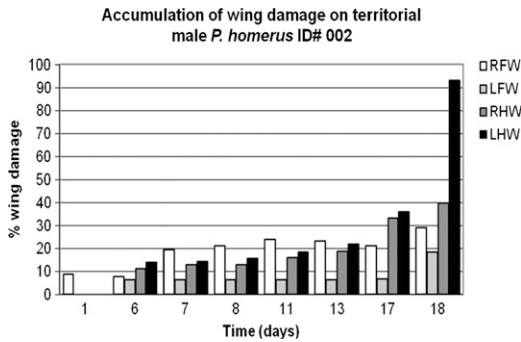


FIG. 6. Quantified accumulation of wing damage on male ID# 002. As seen above, the right forewing (RFW), left forewing (LFW), right hindwing (RHW), and the left hindwing (LHW) accumulated damage.

suggesting males of *P. homerus* are territorial. Wickman and Wiklund (1983) described the aerial flights of territorial Lepidoptera as the spinning-wheel flight, the horizontal flight-pursuit, and the horizontal-spiraling flight-pursuit. Males of *P. homerus* displayed all three flight strategies, but the horizontal-spiraling flight-pursuit, defined as two males flying circles around each other until one male is chased out of the territory by the other, was the most common form witnessed.

Territorial behavior is the act of excluding intruders from an area by threat, advertisement, attack, presence, or a combination of these (Brown 1975; Baker 1983). Outcomes of male conspecific territorial encounters in the Lepidoptera are based on differential body temperature (Stutt and Willmer 1998; Geister and Fischer 2007), residency (Davies 1978; Rosenberg and Enquist 1991; Bergman et al. 2007), age and experience (Lederhouse 1982; Kemp 2002; Takeuchi and Honda 2009), size (Kemp 2000), and motivation due to increased interactions with females (Bergman et al. 2010). Residency appears to be an important component determining the outcome of male-male interactions of *P. homerus*; why a resident male usually maintained occupancy is unknown.

The majority of literature states that territorial aerial encounters of Lepidoptera are a non-physical, weaponless act to determine male dominance (Kemp and Wiklund 2001; Kemp and Alcock 2003; Bergman et al. 2010),

but there are some exceptions, including *P. homerus*. Wickman and Wiklund (1983) filmed males of *Pararge aegeria* L. (Satyridae) diving into the other during spinning-wheel flights. Males of the rare *Papilio indra minori* Cross (Papilionidae) in Western Colorado, U.S.A., are reported to cause wing damage during territorial encounters, and Eff (1962) stated this behavior as a possible reason why there are few captured male specimens with intact wings in collections. Rather than a physical aerial contest, males of *Charis cadytis* Hewit (Riodinidae) partake in "sumo" matches where one male tries to push another male off of a leaf; the loser either starts another contest or leaves the core area in the territory (Chaves et al. 2006).

We suggest that the territorial behavior of the resident male in this study contributed to the wing damage; the initial impacts and circular flights were physical. Additionally, the winner of the interaction pursued the other butterfly outside the area while flying between branches and circling around tree trunks. Other factors may have contributed to wing damage, such as mate-seeking, weather, predation, catching and releasing the butterfly, and brushing against leaves while flying through the rainforest. The contribution of territorial behavior to wing damage is supported by the observation that other nonresident males of *P. homerus* had less wing damage, and that females in the area had little or no wing damage.

Davies (1978) states that resident dominance may have evolved as an evolutionary stable strategy (ESS) to settle territorial disputes quickly in order to prevent wing damage and costly energy expenditure (Maynard Smith and Parker 1976). In Davies' study with *P. aegeria*, residents displayed relatively long-term perching behavior in sunspots whereas intruders flew intermittently and briefly into the territory; this difference in behavior between resident and intruder may serve as a visual cue establishing which butterfly had territorial rights to the area, preventing a long costly battle. Differences in territorial behavior of *P. aegeria* and *P. homerus* prevent the application of the ESS in this context: both resident and intruder males

of *P. homerus* are in flight when one takes notice of the other; therefore, there was no clear observable distinction in flight behavior between intruder and resident. Perhaps the extremity of *P. homerus* territorial disputes has to do with a lack of an obvious visual cue distinguishing the intruder from the resident; a lack of an obvious ESS. Removal experiments with other territorial Lepidoptera confirm that the ESS can be confused if two males are manipulated into believing they are the sole resident of a territory, resulting in an escalated contest rather than the dispute being settled quickly (Maynard Smith and Parker 1976; Davies 1978). The resident male *P. homerus* still almost always maintained residency after these interactions, suggesting that there is another variable that contributes to ESS theory in this species. Future investigations are needed to exactly describe this seemingly complex system.

The wing damage accumulated by the resident male in this study could possibly impact the butterfly's ability to seek mates or evade a predator's attack. It is unknown if wing damage of this magnitude is a common occurrence in other resident *P. homerus* males, as the rarity of the species prevented additional measurements. No adults were seen on a subsequent trip to the study area during the winter months of 2004-2005 (Lehnert 2008), but a follow-up visit to the site on May 16-17 2009 by Emmel and other observers witnessed two fresh males patrolling two areas daily (one area being Area 1, and a second area at an open ravine site about 300 m south) between 0900 and 1200 h, suggesting that Area 1 may serve as a desirable territory for male occupancy. During this study, male ID# 002 was observed on one occasion to utilize *T. montana* near the sinkhole (433 m asl) at approximately 1400 h, 2.5 h after it was last seen in Area 1, and was observed occupying Area 1 the following day, suggesting that this male traveled throughout a home range larger than Area 1 daily, but only occupied Area 1 during peak *P. homerus* activity for reasons other than nectar availability.

Previous reports of butterfly territoriality associated with lekking state that topo-

graphically significant areas, such as hill-tops or emergent trees above the forest canopy stratum, are defended (Alcock 1983; Rutowski et al. 1989; Turner 1990). In this case, Area 1 was unique in that it offered a clearing that admitted a large area of direct sunlight not found within the immediate vicinity of the mountainsides. Garraway et al. (2008) suggested males of *P. homerus* associate open space with territory establishment. Sunlight for basking and warming thoracic wing musculature may be an important ecological attribute of a chosen territorial site (Emmel unpubl. data).

Another important component of lekking is that a territory usually represents an area with high female visitation, thus increasing the chances for resident males to encounter a female. Although no male-female interactions were witnessed, all females observed in this study flew through Area 1. Lehnert (2008) estimated the size of this subpopulation of *P. homerus* to be small, less than 50 adults, which could possibly explain the lack of observed intersexual interactions. In addition, the long and probably continuous breeding season of *P. homerus* coupled with the skewed sex ratio (Lehnert 2008) are common characteristics of other lek species (Emlen and Oring 1977; Alcock 1981; Lederhouse 1982), suggesting that *P. homerus* also displays lek behavior.

Increasing the sample size and sampling period of future studies of the rare Homerus Swallowtail is necessary to add supplementary data to further understand the mating system. However, the local extinction and recolonization of this subpopulation suggests complex metapopulation dynamics (Garraway et al. 2008) that complicate studies of this butterfly. Understanding the reproductive potential could play a critical role towards understanding the rarity of *P. homerus* and contribute to future breeding programs needed to help replenish wild numbers.

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