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Biogeography of a disjunct population of *Hemileuca peigleri* (Lepidoptera: Saturniidae) in the coastal bend of Texas

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Abstract
DNA barcoding and genitalia morphology are used to confirm the identity of an isolated population of *Hemileuca* in Calhoun County, Texas. Evidence from mitochondrial DNA, genitalia dissection, and morphological evidence supports a species determination of *Hemileuca peigleri* Lemaire, 1981 despite isolation of the population by host plant and apparent geographic distance from the only other known populations on the Edwards plateau of Texas.

Keywords: *Hemileuca peigleri*, buck moths, Saturniidae, Hemileucinae, Calhoun County, Texas

Introduction

Moths in the genus *Hemileuca* are members of the family Saturniidae, first described by Walker in 1855. “The genus Hemileuca, contains more than 35 species ranging from Canada to Southern Mexico” (Steele & Peigler, 2015) [1]. Sometimes referred to as “buck moths”, these day flying moths are associated with a wide variety of host plants, among them *Quercus*, *Artemisia*, *Eriogonum* and *Mimosa* (Stone, 1991) [2]. *Hemileuca* caterpillars typically progress through six (6) instars and are gregarious in early instars but typically disperse and become more solitary in their last several instars. *Hemileuca* caterpillars have several rows of urticating spines and can cause minor “stings” to people due to their habit of curling up and dropping from trees when disturbed.

Hemileuca peigleri was first described in 1981 by Claude Lemaire as a subspecies of *maia* (Lemaire, 1981) [3]. It was elevated to full species status in 1989 by Peigler and Stone (Peigler & Stone, 1989) [4]. In 2002, Claude Lemaire concurred and treated it as a full species (Lemaire, 2002) [5].

Evidence supporting the species-level determination of the *Hemileuca* from Calhoun County, Texas includes studying of male genitalia, comparative adult and larval morphology, and through mitochondrial DNA sequencing from Cytochrome Oxidase 1 gene. *Hemileuca peigleri* is now known to occur on the coastal sand beach and barrier island complex of Calhoun County, which dates from the Sangamonian interglacial period and is geologically known as the Ingleside Formation (Davis, 2011) [6]. In December 2003, Brush Freeman posted to the Tex LEPS list-serve hosted by The University of Houston (TexLEPS, December 2003), to announce sightings of buck moths in Port O'Connor, Texas. This post drew the attention of the authors because moth flight activity was not expected for several months due to sub 60°F (15.5 °C) temperatures. The authors contacted Freeman for more information about the sighting. Freeman indicated that he had first seen buck moths on December 20, 2003 in the town of Port O’Connor. The authors, accompanied by David Kent, visited the locality in December 2005.

Biogeographical Information: The Texas Coast is dominated by a string of sandy barrier islands and peninsulas visible on any highway map. These include Bolivar, Galveston, Matagorda, St. Joseph, Mustang and Padre. Less well recognized are the inland remnants of their predecessors which are visible today on any map of the coast as a string of peninsulas jutting out into the coastal bays. Only as late as 1939 (Price, 1939) [7], was this inland chain of barrier islands named the Ingleside Formation (Fig. 1) and differentiated from the broad aeolian sands of South Texas. It was recognized as being of Pleistocene age and more akin to the clay-rich Beaumont Formation. Prior to that, it was considered to be of recent and currently forming aeolian origins. Deussen (1924) [8] lumped the south Texas dunefields and aeolian sheets as one with these ancient barrier islands. Interestingly, he did differentiate the areas of Calhoun County in discussion. He noted that they were different color sand and suggested that they may be derived from the underlying Beaumont Formation. The Ingleside formation remains islandic in nature despite being no-longer surrounded by water. The chain of ancient barrier islands sit atop the clay-rich Beaumont Formation, just inland of the bays and lagoons. It is bordered on the inland side by prairies on the dense clays of the Beaumont Formation. Current geological thought places the origin of these sandy antecedents of Padre Island approximately 125,000 years ago, during the penultimate interglacial period when sea levels were ten to twenty feet (3 to 6 meters) higher than present (Davis, 2011) [6]. So the current concept of these Ingleside peninsulas pushes their origins back in time through the most recent spell of ice-ages to the time before that, known as the Sangamonian interglacial. Given this age and affinity with similar formations that stretch north to the cheniers of Louisiana and even on to the Pleistocene barriers of Georgia and Florida, the flora and fauna of Calhoun County may be expected to have eastern affiliations competing with the Tamaulipan and even some degree of endemism.

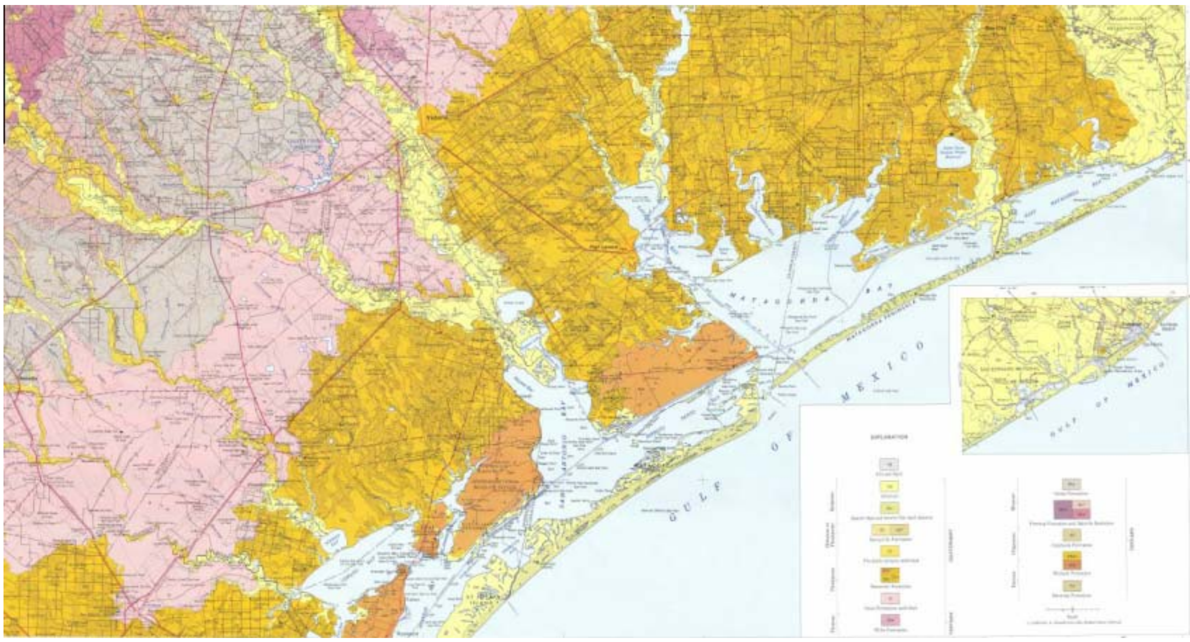

Fig 1: The Geologic Atlas of Texas, Beeville Sheet shows the Ingleside Formation in brown. The coastal edge of Calhoun County and several counties to the South are characterized as Ingleside Formation.

Fig 2: *Hemileuca peigleri* female ovipositing on *Quercus minima* (Sarg.) Small

Oaks of the locality are difficult to identify. Oviposition (Fig. 2) has only been observed by the authors on *Q. minima*. Texas Parks and Wildlife Department, in its draft descriptions of vegetation types, classifies the sandy areas of Calhoun County within the "Texas Coastal Fringe Forest and Woodland" Elliott *et al*., (2010) [9]. NatureServe (2009) [10] identifies this ecological community as "Central and South Texas Coastal Fringe Forest and Woodland" (CES203.464). Both of these references list *Quercus fusiformis* Small and *Quercus hemisphaerica* Bartram ex Willd. but not *Q. minima*. Jones (1982) [11] reported *Q. minima* from the Ingleside of Aransas County and it has been reported from northern Padre Island (Negreet *et al*., 1999) [12]. Regardless, all three oaks have eastern affinities. Their genetic influence from the Mexican live oak relative, *Quercus oleoides* Schltdl. & Cham., is rarely mentioned. The sister-species relationship between *Q. hemisphaerica* and *Quercus laurifolia* Michx., is worth noting based purely on morphological similarity.

Geography: The shortest distance from the only other known populations of *H. peigleri* is about 130 miles (209 kilometers) to populations in the Edwards Plateau. Prior to this publication, *H. peigleri* has been characterized as endemic to the Edwards Plateau (Lemaire, 1981) [3] (Peigler & Stone, 1989) [4]. In relation to the Edwards Plateau population, the Calhoun County population of *H. peigleri* is lower in elevation with sandier, more acidic soil than in the EPA Level IV Ecoregion 34h - mid-coast barrier islands (Griffith *et al*., 2004) [13]. Three other level IV ecoregions separate the two populations. Climate differences provide key evidence supporting the reproductive isolation of this coastal colony. Wind patterns in November and December for central Texas tend to blow any dispersing moths from the two populations away from each other, rather than together. In November, when *H. peigleri* is flying in the vicinity of Austin, Texas, South winds prevail. In December, at the peak time of the Calhoun County *H. peigleri* flight, North winds prevail and tend to blow moths toward the Gulf of Mexico. Many are blown out to sea and washed-up on beaches. Beach windrows of insects blown out to sea are a common occurrence on Texas beaches as noted by Burke (1991) [14]. The authors have observed that a majority of the *H. peigleri* adults in flight in Port O'Connor are traveling with the prevailing wind, North to South, during the flight period. Freeman reports that the majority fly South, borne by the prevailing winds; (personal communication, Freeman, December, 2009).

Freeman states on December 19, 2009 "They were flying anywhere from 6 to 35 ft. (1.8 to 10.6 meters) high and all directly South." (TexLEPS, December 19, 2009). This and the short time-span of reproductive lifetimes support the hypothesis that the distance between the coastal population and the Edwards Plateau population is not likely to be easily passable by the adult moth – thus suggesting the potential for reproductive isolation between the two populations that might be documented with more thorough genetic testing.

Flight Period: Observations by the authors and other publicly reported observations, indicate that most Texas species of *Hemileuca* fly in October and November, with the exception of coastal populations of *H. peigleri*. In Calhoun County, *H. peigleri* flies in mid to late December, later than observed flights of any other Texas congeneric species. Based on the reported emergences of adults by Freeman and Hockey, coastal *H. peigleri* is the latest emerging population of *Hemileuca* known in Texas. Freeman and Hockey, state that *H. peigleri* has never been seen to fly earlier than December. A temporal reproductive dyssynchrony between the two populations is suggestive of reproductive isolation in the Calhoun County *Hemileuca* population. Based on conversations with Dr. Richard S. Peigler, we hypothesize that the observed difference in flight times is more likely explained by microclimate factors influenced by latitude and coastal weather effects than any other factor.

Fig 3: A shot of the typical Q. minima mottes bordering CR1289 and Highway 85 in Calhoun County. It is in these areas of Calhoun County where the host plant is abundant that the adults can be found during the flight period in December.

Habitat and Host Plant: The low, spreading oak mottes of Calhoun County sands (Fig. 3) are often mistaken for live oaks belonging to the taxonomically contentious group containing *Quercus virginiana* Mill., *Quercus fusiformis* Small and *Quercus oleoides* Schltdl. & Cham. However, the host plant on which adults have been observed to oviposit, is a different species of shrubby oak along the roadsides on CR 1298 and Hwy 185 in Calhoun County. This oak species has been identified as *Quercus minima* (Sarg.) Small (personal communication, Singhurst, March 2015). In Calhoun County, *Q. minima* is typically less than 5 feet (1.52 meters) high in dense, irregular mottes (Fig. 1). These mottes remain a distinctive feature of the sandy barrier islands and their predecessors, the inland Pleistocene barrier islands of the Matagorda country (Matagorda Island and Peninsula).

Most theories of the origin of the name "Matagorda" center on the Spanish roots "mata", for bushes or shrubs and "gorda", for fat, dense or thick (Hyde, *et al*. 2001) [15]. The word "motte or mott" is a Texas word centered on the coastal bend of Texas (Jordan *et al*. 1984) [16]. Jordan makes a compelling argument for a Spanish origin of the name "motte" from the Spanish "mata" of Mata…gorda. Hyde *et al*. state that the main interpretation of the word "mata" in Matagorda Island relates to the presence of dense canebrakes along the lower Colorado River. To the best of our knowledge, the authors are the first to suggest that the distinctive mottes or matas of *Q. minima* that dominate the Ingleside Formation, (Fig. 2) and that provide habitat for *Hemileuca*, are the root cause for the mysterious origins of one of the oldest geographical names in Texas.

Fig 4: Ova rings deposited by *H. peigleri* on *Q. minima*. These ova rings are usually located on branches typically near the top of the plant.

Hemileuca peigleri larvae on the Edwards Plateau feed on a diverse range of oaks: Texas live oak (*Q. fusiformis*), Havard oak (*Quercus havardii* Rydb.), Shumard oak (*Quercus shumardii* Buckley), and Nuttall oak (*Quercus texana* Buckley) (Stone, 1991) [14]. *Hemileuca peigleri* larvae feed primarily on *Q. minima* and *Q. fusiformis* in Calhoun County but there is evidence that they prefer *Q. minima*. Females of the species oviposit on *Q. minima*, and to date, no ova rings (Fig. 4) have been located on any other species of oak in Calhoun County. The authors have observed post-dispersal, late instar caterpillars on both *Q. minima* and *Q. fusiformis* in Calhoun County. *Quercus minima* has a highly restricted range in Texas, occurring in just a few counties. It does not occur within the range of *H. peigleri* on the Edwards Plateau.

Materials and Methods

Isolation of DNA for Comparative CO1 Barcoding Analysis

DNA barcoding Methods and Materials: During the December 2013 adult emergence of *Hemileuca* in Calhoun County Texas, seven male specimens were placed into individual containers of 100% ethanol upon capture and kept frozen until DNA extraction, amplification and purification could be completed. DNA processing was completed in the biology laboratory at Jarvis Christian College by Dr. Shakhawat Bhuiyan using a Carolina Biological Supply DNA barcoding product.

To amplify DNA, the laboratory protocols followed the Carolina Biological DNA Barcoding product guidelines. For both, 10 mg. of each sample were used. Insect primers were provided by Carolina Biological Supply and PCR products were sequenced by Genewiz using Genewiz Primer M13F(-21) on unpurified PCR.

The samples were packed in ice and sent to Genewiz for DNA sequencing. In total, seven DNA extractions were processed resulting in 14 sequences, both forward and reverse. In two of the 14 samples, the primer did not work and they were unusable. These were removed from the data set. Of the remaining 12 sequences, six forward sequences proved to be suitable for analysis. All comparisons were run against the possible *Hemileuca* species in Texas for which sequences are publicly available.

Genitalia Dissection Methods and Materials: Three male *H. peigleri* (December 2013 flight) from Calhoun County were shipped to Dr. Stefan Naumann, in Germany, for mounting and photography of genitalia. Naumann performed the dissections and placed the anatomical structures in alcohol for preliminary photography. After these photographs were taken, the organs were further treated and suspended in Euparal during the process of slide mounting. The slides and the original specimens are deposited in the collection of the author's (Nuelle). Naumann provided photographs of comparably prepared *H. peigleri* (Edwards Plateau) and *H. maia maia* genitalia structures from previous dissections for comparison.

Observations and Results

DNA Analysis: The gene-sequencing analysis suite of applications collectively known as DNA Subway were used to process, trim, create consensus samples and compare sequences to other known congeners from the region (University of Arizona iPlant Collaborative, NSF-funded project). The DNA Subway function, "Determine Sequence Relationships Workbench" was used to compare sequence similarity. Records from the Moth Photographers Group website indicate six other species of *Hemileuca* are known to occur in Texas: *Hemileuca maia maia* (Drury, 1773), *H. peigleri*, *Hemileuca chinatiensis* (Tinkham, 1943), *Hemileuca slosseri* Peigler & Stone, 1989, *Hemileuca grotei* Grote & Robinson, 1868 and *Hemileuca oliviae* T.D.A. Cockerell, 1898. Sequences of *H. peigleri* resulting from this study were compared with these above with the exception of *H. slosseri*.

Hemileuca sequences from GenBank were all imported by entering their accession numbers and stored within the DNA Subway project file. The sole sequence for *H. peigleri* was obtained from the public records within BOLD.

The program "Sequence Viewer" (a DNA Subway application) was used to review all sequences. Next the automated sequence trimmer function was used to trim unidentified terminal sequences. A series of comparisons of sequence similarity were made within six DNA sequences (WG1–F through WG6–F). The program "Muscle" (a DNA Subway application) was used to compare all sequences (Table 1).

Table 1: Intraspecific comparisons across all six CO1 sequences within the coastal *Hemileuca*. Core similarities (excluding sample WG1-F) are indicated in red.

		Sample Number					
Sample Number		1	2	3	4	5	6
Sample WG1-F	1	100.00					
Sample WG2-F	2	97.95	100.00				
Sample WG6-F	3	97.31	99.2	100.00			
Sample WG4-F	4	96.71	99.36	100.00	100.00		
Sample WG5-F	5	92.15	99.36	100.00	100.00	100.00	
Sample WG3-F	6	97.31	99.2	99.84	99.84	99.84	100.00

Among the Calhoun County specimens of *H. peigleri*, raw sequence differences ranged from identical to 7.85% difference. Sequence WG1-F accounts for most of this infrasample variation. The mean value for sequence comparisons was 98.50 with a standard deviation of 2.06. Based on these results, sequences WG2-F, WG3–F, WG4–F, WG5–F and WG6–F form a core of sequences with similarity within the range of the standard deviation.

Table 2: Coastal *Hemileuca* compared individually against other regional species. The high similarities between *H. peigleri* (Coastal) and *H. peigleri* (Edwards Plateau) are highlighted in light green and bolded.

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	47.64	44.66	47.93	48.92
Hemileuca oliviae	2	94.10	100.00	48.69	45.61	49.25	49.59
Hemileuca peigleiri (Edwards)	3	47.64	48.69	100.00	**93.96**	54.23	54.85
Hemileuca (Coastal) Sample WG1-F	4	44.66	45.61	**93.96**	100.00	54.77	54.97
Hemileuca grotei	5	47.93	49.25	54.23	54.77	100.00	89.26
Hemileuca maia maia	6	48.92	49.59	54.85	54.97	89.26	100.00

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	46.51	46.00	47.19	46.53
Hemileuca oliviae	2	94.10	100.00	46.51	46.00	47.19	47.03
Hemileuca peigleiri (Edwards)	3	46.51	46.51	100.00	**98.48**	55.29	54.31
Hemileuca (Coastal) Sample WG4-F	4	46.00	46.00	**98.48**	100.00	55.11	54.11
Hemileuca grotei	5	47.19	47.19	55.29	55.11	100.00	89.26
Hemileuca maia maia	6	46.53	47.03	54.31	54.11	89.26	100.00

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	48.62	46.21	47.55	48.57
Hemileuca oliviae	2	94.10	100.00	49.36	46.68	48.40	48.74
Hemileuca peigleiri (Edwards)	3	48.62	49.36	100.00	**97.25**	59.34	58.17
Hemileuca (Coastal) Sample WG2-F	4	46.21	46.68	**97.25**	100.00	58.43	56.90
Hemileuca grotei	5	47.55	48.40	59.34	58.43	100.00	89.26
Hemileuca maia maia	6	48.57	48.74	58.17	56.90	89.26	100.00

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	46.51	46.00	47.19	46.53
Hemileuca oliviae	2	94.10	100.00	46.51	46.00	47.19	47.03
Hemileuca peigleiri (Edwards)	3	46.51	46.51	100.00	**98.48**	55.29	54.31
Hemileuca (Coastal) Sample WG5-F	4	46.00	46.00	**98.48**	100.00	55.11	54.11
Hemileuca grotei	5	47.19	47.19	55.29	55.11	100.00	89.26
Hemileuca maia maia	6	46.53	47.03	54.31	54.11	89.26	100.00

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	49.04	47.88	47.75	46.91
Hemileuca oliviae	2	94.10	100.00	48.34	47.38	47.75	47.41
Hemileuca peigleiri (Edwards)	3	49.04	48.34	100.00	**98.30**	54.49	52.73
Hemileuca (Coastal) Sample WG3-F	4	47.88	47.38	**98.30**	100.00	54.21	52.45
Hemileuca grotei	5	47.75	47.75	54.49	54.21	100.00	89.26
Hemileuca maia maia	6	46.91	47.41	52.73	52.45	89.26	100.00

		1	2	3	4	5	6
Hemileuca chinatiensis	1	100.00	94.10	43.90	43.77	48.07	48.24
Hemileuca oliviae	2	94.10	100.00	44.84	44.64	47.39	47.90
Hemileuca peigleiri (Edwards)	3	43.90	44.84	100.00	**97.88**	56.80	55.58
Hemileuca (Coastal) Sample WG6-F	4	43.77	44.64	**97.88**	100.00	57.69	56.35
Hemileuca grotei	5	48.07	47.39	56.80	57.69	100.00	89.26
Hemileuca maia maia	6	48.24	47.90	55.58	56.35	89.26	100.00

A subsequent comparison was run for all six coastal *H. peigleri* DNA sequences against the available congeneric sequences (Table 2). The results refute the hypothesis that the coastal populations of *Hemileuca* being investigated are conspecific with or sister species to *H. maia maia*. These results support the hypothesis that the subject population is most closely related to other *H. peigleri* populations in the Edwards Plateau of Texas.

Discussion

Adult Morphology: Initially, subtle differences in the s-shaped white marking of the forewing discal cell were thought to represent a discrete difference separating the coastal populations, but this character failed to hold-up under examination of long series of individuals (over 100). No discrete morphological differences were found to support the hypothesis that the coastal population is distinct. Wing coloration in both the coastal population and other inland populations of *H. peigleri* are more transparent than *H. maia maia* (Fig. 5).

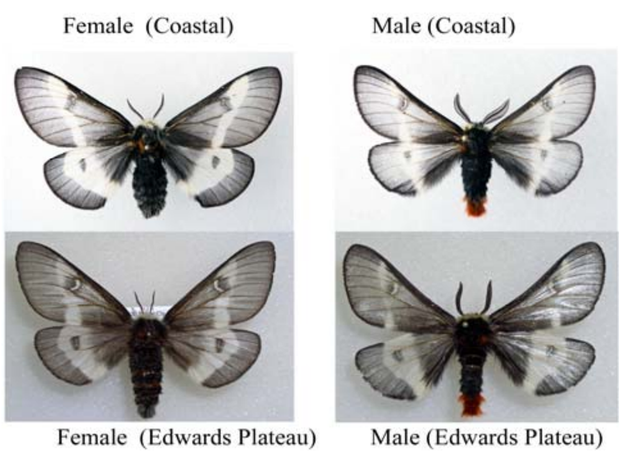

Fig 5: *Hemileuca peigleri* male and female from the 2 populations.

Genitalia Morphology: Male genitalia were compared against both *H. peigleri* (Edwards Plateau) and *H. maia maia* and although slight differences were detected between the structures, no diagnostic differences were found. This analysis was initially conducted by Dr. Richard Peigler and Dr. Stefan Naumann and later confirmed by the authors. Subtle differences were attributed to differences in orientation and distortion of specimens from the dissection and preparation process (Fig. 6). The author's inability to find discrete genitalia differences further supports the hypothesis that the population in Calhoun County is conspecific with *H. peigleri*.

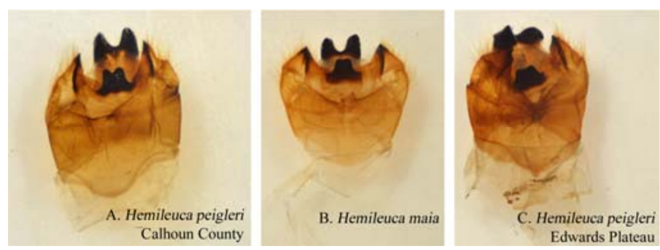

Fig 6: Male genitalia preparations from two specimens of *H. peigleiri* and one specimen of *H. maia maia*

Larval Morphology: In December, 2013 the authors collected 27 ova rings on *Q. minima* in Calhoun County. These ova were allowed to hatch and the resulting caterpillars were reared to adult. Ova were divided between the authors and Dr. Richard S. Peigler to increase the chances of complete development. The authors' cohort was fed *Quercus nigra* L., while Peigler's cohort was fed *Q. shumardii*. All caterpillars followed the normal six-instar life cycle and Peigler was able to compare the coastal specimens to *H. peigleri* larvae obtained from the Edwards Plateau.

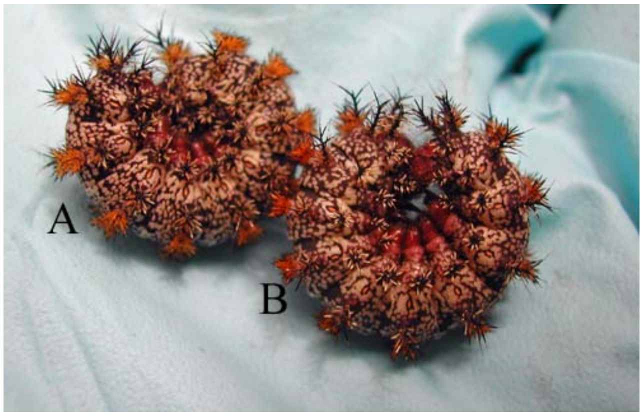

Fig 7: Two mature caterpillars of *H. peigleiri*. The leftmost larva (A) is from the coastal population in Calhoun County and the other (B) is from Concho County on the Edwards Plateau.

Larva from the coastal egg rings were indistinguishable from *H. peigleri* from the Edwards Plateau in appearance and ontogeny. Progressive changes in coloration from first to sixth instar were not noticeably different between the coastal population and larvae from the Edwards Plateau. Peigler's detailed notes compared the cohort in his care with other larvae from the Edwards Plateau; "Attached also is another image (Fig. 7) showing mature larvae side-by-side of Calhoun County and *H. peigleri* from Concho County. Some from Concho County were lighter, but a couple like this one were darker….The darker *peigleri* ones are IDENTICAL to Calhoun County ones….Calhoun County ones showed no variation in color." (personal communication, Peigler, May, 2014).

Conservation Concerns: While the authors have studied this coastal population of *Hemileuca* for ten years, from 2005 to 2015, mid-December flights of adult moths have remained consistently abundant. At times during the December emergences, the adult moths are visible flying continuously during daylight hours for 2-3 weeks. In April 2015, caterpillars in the coastal oak mottes of Powderhorn Ranch Conservation Area were estimated at over 1,000 per acre.

This biomass represents a considerable food source for overwintering migratory birds or late fall neotropical migrants. Eastern Phoebe, *Sayornis phoebe* (Latham) have been observed preying on adult buck moths on the wing at the Powderhorn Ranch Conservation Area (personal communication, Bownds, December, 2015). Gregory (1998) [17] reported the solitary vireo, *Vireo solitarius* (Wilson) feeding on flying *Hemileuca* in New York and speculated that the moth there was an important food item for fall migrants.

Meanwhile, 130 miles (209 kilometers) northward across 11 counties of the Edwards Plateau of Texas, populations of *Hemileuca* appear to have been in decline over the last decade and are rarely observed at the type locality in San Antonio, Texas (personal communication, Peigler, Dec. 2015).

In the absence of the coastal population of *H. peigleri*, the species is at greater risk of being considered of conservation concern. If the coastal buck moths are the strongest remaining populations of *H. peigleri*, with those of the Edwards Plateau in decline, then habitat management changes to the area supporting the coastal populations may place the entire species at risk. Populations of *H. slosseri* in the panhandle of Texas were nearly eliminated by oak abatement practices including burning and herbicide treatment (Slosser, 2001) [18]. This possibility should be considered when land managers contemplate elimination of oak mottes in Calhoun County.

Conclusion: Despite subtle difference in biology (flight period, host plant) and apparent geographic isolation, the coastal population of *Hemileuca* in Calhoun County, Texas exhibits no observed morphological or genetic characters supporting its recognition as a separate species but may represent the strongest population of the species remaining.

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