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Cover illustration: Fifth instar larvae of *Calyptra canadensis* (Bethune) on host plant, photo taken by J. L. Snyder See article on page 253.

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DISTRIBUTION, PHENOLOGY, AND NOTES ON THE LIFE HISTORY OF *CALYPTRA CANADENSIS* (BETHUNE) (EREBIDAE: CALPINAE)

JULIA L. SNYDER, GARETH S. POWELL, ROBERT S. BEHRING, ADAM M. ALFORD, MEGAN E. MCCARTY AND JENNIFER M. ZASPEL

Department of Entomology, Purdue University, 901 West State Street, West Lafayette, IN 47907, USA
Corresponding author email: snyder65@purdue.edu

ABSTRACT. The genus *Calyptra* Ochsenheimer is known for its atypical behavior of exhibiting both obligate fruit piercing and facultative blood feeding as adults. The genus has been reported piercing a vast array of fruits including citrus, figs, grapes, and raspberries. One species, *Calyptra canadensis* (Bethune), more commonly known as the Meadow Rue Owlet moth, is the only member of the genus known to occur in the New World. The extent of this species' range, along with its adult host breadth, remains unknown. Museum specimens of *C. canadensis* from 20 institutions and private collections were examined and georeferenced to generate the most comprehensive distribution map for the species to date. Locality data was analyzed to explore the phenology of *C. canadensis*, recovering an adult activity period from May to October. Larval rearing experiments were also undertaken, documenting the presence of five larval instar stages and a development time ranging from 6 to 8 weeks. Overall this study expands what is currently known about the biology of *C. canadensis*, specifically its larval development, adult distribution, and activity period.

Additional key words: Meadow Rue Owlet, *Thalictrum*, development, rearing, collection records

Erebidae (Lepidoptera: Noctuoidea) is a diverse lineage composed of approximately 1,760 genera including around 24,600 species (van Nieukerken et al. 2011). Members of this family exhibit a vast array of feeding behaviors including lachryphagy (tear feeding), hematophagy (blood feeding), and frugivory (fruit eating) (Büttiker et al. 1996, Bänziger 2007, Zaspel et al. 2011). Within the subfamily Calpinae, obligate fruit piercing and facultative blood feeding behaviors have been documented. These feeding strategies have been observed in *Calyptra* Ochsenheimer; the vampire moth genus, both experimentally and in the laboratory (Bänziger 1982, 1986, 2007; Zaspel et al. 2007).

The genus *Calyptra* can be found on most continents, however only one species is known from the New World. This species, *Calyptra canadensis* (Bethune), commonly known as the Canadian Owlet or Meadow Rue Owlet moth, is distributed throughout northeastern and central North America, occurring in open habitats including fields, wet meadows, and woodland edges (Wagner 2005, Wagner et al. 2011). The larval host plant, Meadow Rue (*Thalictrum* spp. L.), is also known to occur in these types of habitats (Wagner 2005).

Like other members of the subfamily Calpinae (Kitching and Rawlins 1998), *C. canadensis* caterpillars, are heterochromatic, and exhibit a change in color as they progress from early to late instars. The early instars of *C. canadensis* tend to be "waxy yellow-green with or without dark subdorsal spots," present the length of the body. During later instars, the dorsal coloration changes to white; yellow and black maculations develop laterally, and the ventral surface darkens to a uniform black (Fig. 1c) (Wagner et al. 2011).

Although the general larval habits of *C. canadensis* have been previously summarized, the complete life history of the species remains largely uncharacterized. Thus, the objective of this study was to observe, document, and illustrate the life stages of *C. canadensis* and investigate the extent of its geographic range. An additional aim was to determine the degree to which flight period is linked with geographic location. This relationship has been recovered in Lepidoptera in previous studies using Satyrinae as a model (e.g., Brakefield 1987, Pollard 1991), similar methods were employed to test this potential trend. Within this study, summarization of development times for each larval instar, estimation of the number of instars required to reach pupation, and development of a specimen-level locality database of *C. canadensis* were completed. These data were used to generate a comprehensive distribution map for the species and to characterize adult phenology across its range. Here, for the first time, a detailed life history dataset for this species and a discussion of phenological patterns in the context of geographical distribution are provided.

MATERIALS AND METHODS

Rearing. Larvae of *C. canadensis* were collected from Marlborough, New Hampshire during the summer of 2015 and obtained as freshly emerged 1st and 2nd instars (Fig. 1a–b). Individual larvae were isolated in small plastic cups with damp filter paper and fed leaves of *Thalictrum dasycarpum* Fisch. and Avé-Lall. Larvae were placed in a controlled rearing room (24ºC) with a photoperiod of 16 hours. Due to a high desiccation rate within the first 24hrs, methods of

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rearing were modified: half of the persisting larvae remained in the rearing cups and were moved to a cooler location to prevent further desiccation. The other larvae were placed in a rearing cage on a potted *Thalictrum polygamum* Muhl. and left within the rearing room. These individuals were allowed to move freely about the plant and were not disturbed until their final instar. The change in host plant was solely due to availability of plant material.

Upon reaching the final instar, larvae were placed into a plastic rectangular container (2295 cm^3) with 5 cm of soil on the bottom and covered with a mesh lid. The soil was used in an attempt to provide the necessary resources for pupation based on the behaviors of related species and earlier observations of individuals surrounding themselves with dead leaf tissue, creating an outer casing of dry plant material. Future final instars were given ample plant material to facilitate this behavior and leaves that were not used in the pupation process were removed. Once pupation occurred, the pupae were moved to the plastic containers to give emerging moths adequate space to complete development.

Measurements and Images. To quantify larval instars, head capsules were measured periodically throughout the rearing process. Measurements were grouped based on similar widths and compared to an individual that was tracked across its complete development. Resulting head capsule widths were averaged within each group to define typical sizes for each larval instar of *C. canadensis* (Table 1). In some cases, high mortality of larvae during rearing resulted in inconsistent replicates of head capsule measurements.

High-resolution images of the larval head capsules were taken using a Leica DFC450 camera mounted onto a M165C stereomicroscope and measured using the Leica Application Suite version 4.2.0 (Leica Microsystems, USA). Larval head capsules were measured at the widest point from a dorsal perspective to investigate and document the changes in growth during development. Adult specimens were imaged with a Canon EOS Rebel T3i DSLR camera, Canon MP-E 65mm f/2.8 1-5X macro lens, controlled by Zerene Stacker automontage software.

TABLE 1. Larval head capsule measurements with estimated corresponding instar and Dyar's Law estimates calculated using an average ratio of 1.71.

Instar	Number of Individuals	Average Width (mm)	Dyar's Law
1	11	0.30	–
2	19	0.62	0.51
3	1	0.96	0.88
4	2	1.84	1.50
5	3	2.40	2.56

Adult Specimens Examined. A total of 264 adult specimens were examined, and 220 records were obtained from 20 collections; the Moth Photographers Group provided an additional 105 records. Institutions and private individuals that contributed locality data without the study of physical specimens by the authors are denoted with a "*" after the full collection name.

AMNH American Museum of Natural History (New York, NY)
ARC Albert J. Cook Arthropod Research Collection (East Lansing, MI)
CNC Canadian National Collection (Ottawa, ON, CAN)*
CUIC Cornell University Insect Collection (Ithaca, NY)*
FMNH Field Museum of Natural History (Chicago, IL)
FLMNH Florida Museum of Natural History (Gainesville, FL)
SEMC Snow Entomological Museum Collection (Lawrence, KS)*
LACM Los Angeles County Museum (Los Angeles, CA)
LAFC Les Ferge Private Collection (Middleton, WI)*
MCZ Museum of Comparative Zoology (Cambridge, MA)
MEM Mississippi Entomological Museum (Starkville, MS)*
NHM The Natural History Museum (London, UK)
NCSU North Carolina State University (Raleigh, NC)*
OSUC Charles A. Triplehorn Insect Collection (Columbus, OH)*
PERC Purdue Entomological Research Collection (West Lafayette, IN)
UCBC University of Connecticut Biodiversity Research Collections (Storrs, CT)*
UMSP University of Minnesota Collection (St. Paul, MN)
UNSM University of Nebraska State Museum (Lincoln, NE)*
USNMNH U.S. National Museum of Natural History (Washington, D.C.)
WIRC Wisconsin Insect Research Collection (Madison, WI)

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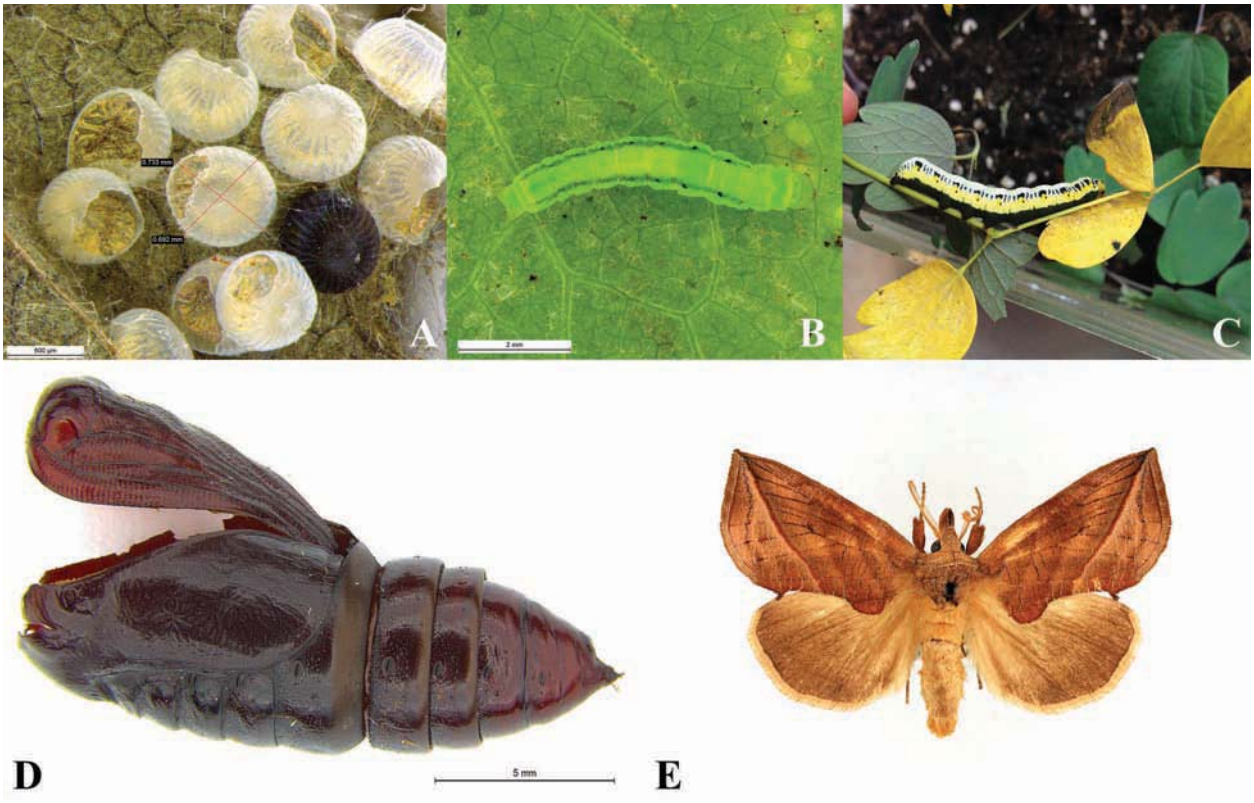


FIG. 1. *Calyptra canadensis* (Bethune) life stages **A**. eggs, **B**. 2nd instar larva, **C**. 5th instar larva, **D**. pupal case, **E**. adult moth.

Distribution Mapping. To develop a comprehensive distribution map for *C. canadensis*, locality data were transcribed and georeferenced for 474 specimens from 20 institutions, private collections, and the Moth Photographers Group. Databased records were georeferenced in Google Maps with the Lat-Long Crosshairs (Canadensys) plug-in, resulting in GPS points in decimal degrees following the methods of Wieczorek et al. (2012). The georeferenced coordinates were then mapped using QGIS v2.12.1 Lyon (Quantum GIS Development Team 2009).

Phenology. To estimate the adult activity period of *C. canadensis* museum records were aggregated representing almost 150 years of collection efforts. Specimen data were first summarized by month, and then adult frequencies were compiled. The original collection dates were transformed from the various formats on specimen labels to numeric ordinal date. This is a date format where each day of the year is numbered sequentially 1–365 (or 1–366 on leap years). The georeferenced dataset was then used to compare adult collection date with latitude of collection locality. A simple linear regression was performed in RStudio v.0.99.879 (RStudio Team 2016) to demonstrate the relationship between latitude as a predictor of adult activity period. Prior to the linear regression, ordinal dates were binned by two degrees latitude and a standard deviation (SD) was calculated for each bin. Calculating the SD of ordinal date allowed for the summarization of total variation of adult activity within its representative bin. In this manner, a larger SD corresponds to a longer adult active period than that of a smaller SD. All graphs were created with the package ggplot2 (Wickham 2009) in RStudio v.0.99.879 (RStudio Team 2016).

RESULTS AND DISCUSSION

Larval Morphology. Throughout the rearing process, morphological changes were observed and recorded. Eggs were spherical with longitudinal ridges radiating from the micropylar region (Fig. 1a). First instar larvae were uniformly bright green and developed dark, lateral spots in the second instar (Fig. 1b). Two dark bands running the length of the body were present in the second instar but were secondarily lost in the third; lateral spots were more prominent during the third instar. The head capsule transformed from a very light, almost translucent green, to an opaque darker

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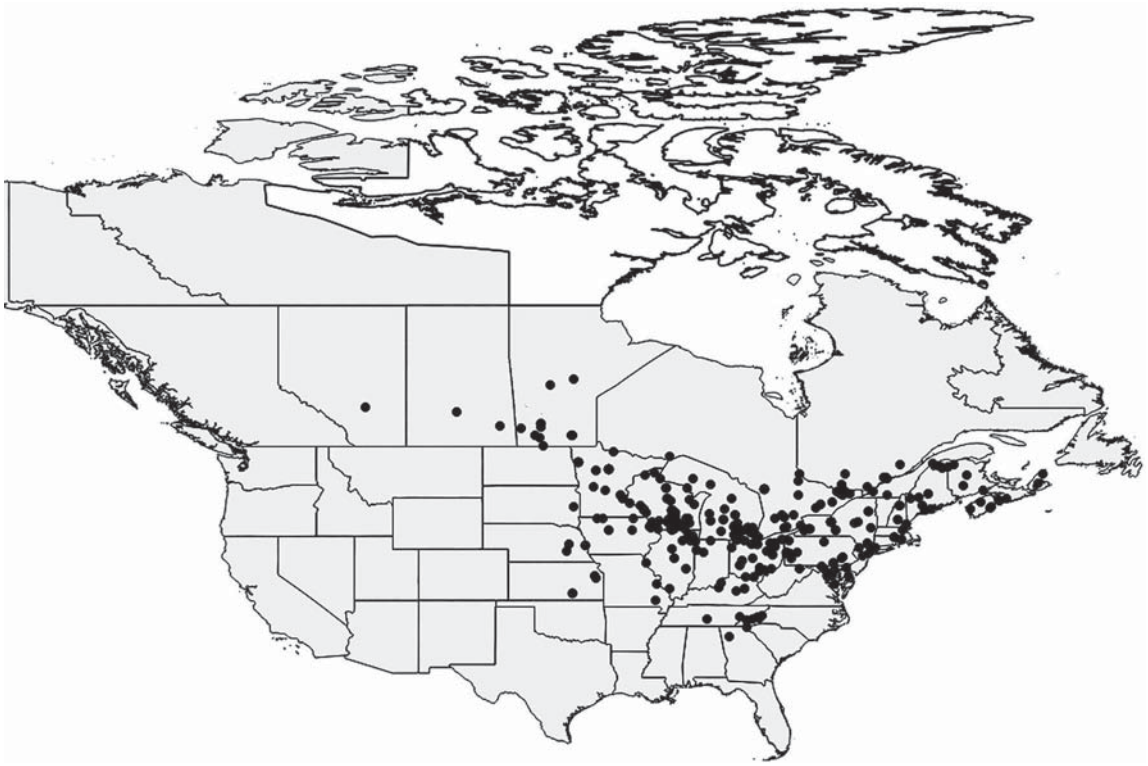


FIG. 2. Complete distribution map for *Calyptra canadensis* (Bethune), with larval host plant (*Thalictrum* spp.) range shaded in dark grey.

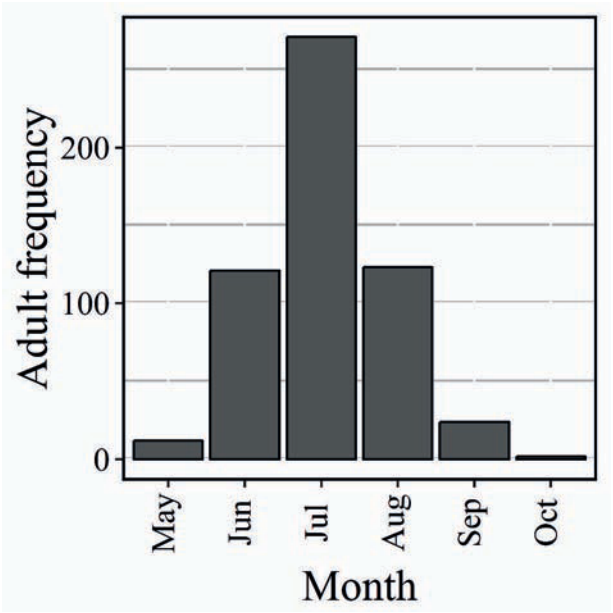


FIG. 3. *Calyptra canadensis* (Bethune) adult museum records grouped by month collected.

green, and then finally yellowing with the addition of some black maculations. During the 4th and 5th instars, the body coloration became more complex. The ventral surface darkened significantly and a clear division between that and the dorsal surface was apparent. Lateral spots remained clear on a generally uniform yellow background. The dorsum was green in coloration and developed intricate black and yellow markings that persisted the full length of the larva (Fig. 1c).

The analysis of larval instars provided evidence for a total of five instar stages for *C. canadensis*. Head capsule width increased by an average ratio of 1.71 for each successive instar. The reported head capsule widths are in general agreement with predicted widths using Dyar's method (Dyar 1890). Deviations from the predicted head capsule widths in the last two instars are likely due to a small sample size and it is unlikely an instar was missed. Development times varied under the rearing conditions, yet most individuals on the plant reached pupation at approximately 4–5 weeks. The individuals kept in rearing cups had an average development time of 5–6 weeks. Pupation in all individuals spanned an average of 2 weeks before emerging as adult moths.

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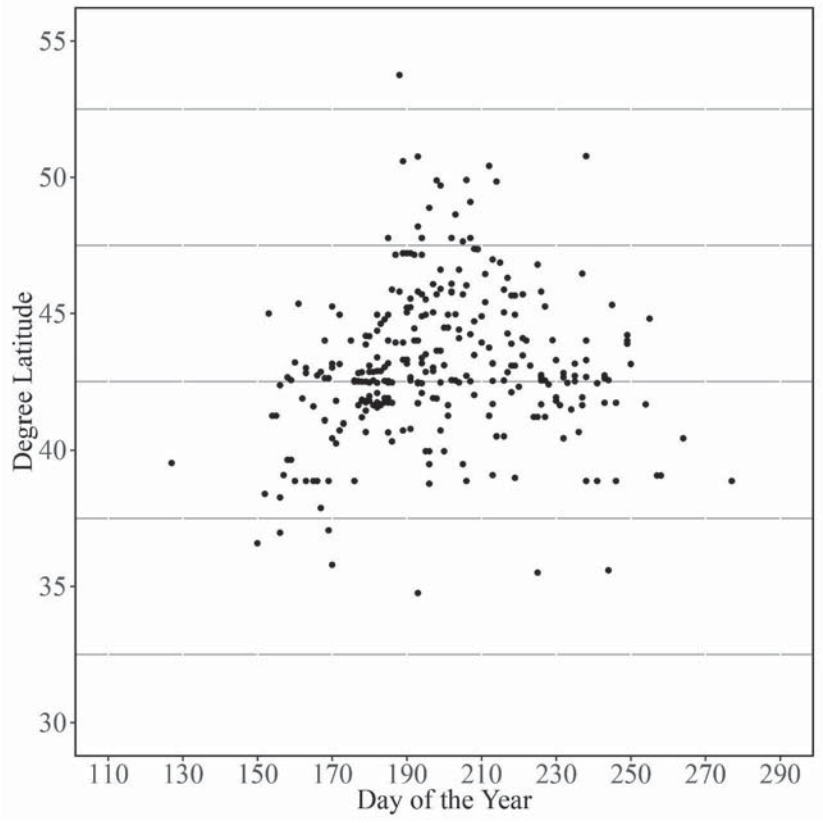


FIG. 4. Collection data for *Calyptra canadensis* (Bethune) graphed across latitude gradient of locality. Date of specimen collection transformed to ordinal numbering scheme to visualize breadth of adult activity period.

Distribution. Locality data collected as part of the study resulted in a comprehensive range map for *C. canadensis* (Fig. 2). Black points represent adult specimen records and the range for the host plant, *Thalictrum* spp., is illustrated with grey shading. The breadth of the species' range begins in the Canadian province of Alberta and extends east to the province of Nova Scotia persisting as far south as Georgia and continues west across the Midwest to Kansas. For the northern extent of *C. canadensis*' range, the distribution and habitat data largely agree with Wagner (2005) and Wagner et al. (2011). Specifically, records documenting collection events in bogs, fens, prairies, and other fragile habitats were observed across southern Canada and the northern Midwest, while specimens from the east coast and across the southern extreme of the range were more commonly collected in woodland habitats.

From the resulting dataset, complete overlap between *C. canadensis* and its host plant was observed, although the range for *Thalictrum* spp. is much broader. This discrepancy could be driven, in part by the vast diversity of the genus *Thalictrum* or unknown host limits for *C. canadensis*. The expansive distribution of the larval host, but relatively restricted range of the adult moth, suggests other factors could be influencing or driving distribution in this species. The adult feeding behaviors and host preferences of *C. canadensis* are also vastly uncharacterized, but it is likely an obligate fruit piercer like most other species within the genus. Recent laboratory experiments resulted in the first video observations of adult *C. canadensis* piercing fruit for 15 minutes (Zaspel et al. unpublished). Thus, the availability of adult fruit hosts could be another factor shaping the range of *C. canadensis*.

Phenology. Museum records were used to estimate the adult phenology of *C. canadensis* throughout its distribution. The results from this study confirm the adult activity period for *C. canadensis* is from May to October (Fig. 3). The majority of adult specimen records (49%) were recorded from July; 22% of *C. canadensis* records were recorded from both June and August, respectively. These three months account for 515 out of the 553 total records that were included. The adult activity period was then visualized using a scatterplot (Fig. 4). Our dataset shows a wider range of

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collection dates for *C. canadensis* associated with lower latitude with the range narrowing as latitude increases. Above the 47th parallel, the flight period of *C. canadensis* was limited to approximately 60 days; below the 40th parallel the flight period range roughly doubled. A linear regression comparing the variation of dates (y) collected across the latitude gradient (x) showed a significant trend (y = -4.65x + 46.09; $F_{1,6}$=55.46; p-value <0.001; R^2=0.8861) of decreasing variation, and therefore a reduction in adult activity period with increasing latitude. This could mean that individuals of *C. canadensis* are reproductively active for longer periods of time the further south in the range they are found. In general, our findings support the hypothesis that *C. canadensis*' activity period tends to be longer in warmer temperatures, and gives valuable information on the times of the year that it could be collected.

This study provides a comprehensive characterization of the life history and distribution of the Meadow Rue Owlet Moth, *C. canadensis*. This species completes development through five larval instar stages and takes approximately eight weeks to reach adulthood. An analysis of distribution and activity period for *C. canadensis* was documented across a latitude gradient, providing necessary temporal data that could be used in targeted collection of this species. A thorough understanding of *C. canadensis*' life history, distribution, and phenology will ensure the establishment of laboratory colonies for future physiological and behavioral experiments. Prior to this work, controlled studies on a vampire moth species were not possible. This contribution will allow researchers to unravel the molecular and environmental underpinnings of the enigmatic adult feeding behaviors in vampire moths and their fruit-piercing relatives.

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PACIFIC NORTHWEST POPULATION OF *LOPHOCAMPA MACULATA* HARRIS 1841: EVIDENCE OF A POSSIBLE HYBRID ORIGIN

KENNETH G. STROTHKAMP
Department of Chemistry, Portland State University, Portland, OR 97201, Email: kstrot2@pdx.edu

ABSTRACT. The different geographic populations of *Lophocampa maculata* Harris 1841 are characterized by a variety of phenotypic differences, of which larval color is the most obvious. Individuals of the Pacific Northwest (PNW) populations display significant variation in late instar coloration, arising from variation in setae pigmentation. Such variation is not found in other populations of *Lophocampa maculata*, including the western Interior population (WI) and California Coastal population (CAC). Analysis of the pattern of pigmentation of the PNW population suggests it represents a combination of features of the CAC and WI populations. A simple scheme that accounts for all of the color variations seen in the different geographic populations of *L. maculata* is presented. A laboratory mating experiment involving WI and CAC individuals resulted in viable offspring displaying the range of larval coloration seen in the wild PNW populations. The F1 hybrids were fertile and produced an F2 generation also exhibiting the PNW larval color patterns. Taken together, these results suggest that the PNW populations arose via hybridization between the adjacent WI and CAC populations. Evidence from laboratory-raised broods of wild-caught females suggests there can be significant individual variation in pigmentation even within a single brood. The present day PNW populations demonstrate features of a hybrid swarm resulting from relatively recent hybridization. A model for this process since the last glacial maximum is presented.

Additional key words: setae pigmentation, hybrid swarm, mosaicism, rare allele phenomenon, ecological speciation

The Spotted Tussock Moth, *Lophocampa maculata* Harris 1841, (Erebidae, Arctiinae (Lafontaine 2010)) is found across a wide expanse of North America, where it exists as several distinct populations defined primarily by last instar coloration (Strothkamp 2015). Each of these populations is characterized by one, or at most two, last instar color patterns, which are constant over a large geographic range. The one exception is the Pacific Northwest (PNW) population. This population extends from roughly the California/Oregon border to southwestern British Columbia, Canada and from the Pacific coast to the west slope of the Cascade Mountains (Strothkamp 2015). Within this region, last instar coloration is extremely variable in several respects.

The PNW population is bordered on the south along the Pacific coast by the California Coastal (CAC) population and on the east by the Western Interior (WI) population (Strothkamp 2015). These adjacent populations are characterized by a number of phenotypic distinctions from the PNW population, with larval coloration being the most obvious. Adults of the CAC and WI populations differ somewhat in wing patterns, as previously described (Strothkamp 2015). At present, the CAC and WI populations in California are kept isolated by the central valley of California.

This paper details both fieldwork defining the PNW population and a laboratory hybridization study. Together, these suggest the PNW population is derived from hybridization of WI and CAC individuals. A model for this process, in the context of the northward migration of both the CAC and WI varieties shortly after the last glacial maximum (LGM) is presented.

MATERIALS AND METHODS

Field data were collected with the aid of many individuals, who provided observations, photographs and specimens. Without their assistance this work could not have been carried out and they are listed alphabetically in the Acknowledgements section. Their efforts are a wonderful example of citizen science in action.

Detailed study of the offspring from wild females forms a major part of this work. Eggs and larvae were kept at 18–24° C and a light: dark cycle of 16:8 hours in glass petri dishes or, as they grew larger, in polyethylene plastic boxes covered with fine nylon mesh. Mating experiments on moths were conducted in nylon mesh cages under ambient summer conditions. Females were allowed to deposit eggs on the mesh walls. Newly hatched larvae were then transferred to leaves kept in petri dishes. Larvae were fed either pacific willow (*Salix lasiandra*) or vine maple (*Acer circinatum*). Previous work had shown that choice of food plant did not alter larval appearance (Strothkamp 2015). The CAC population showed a strong preference for willow as a food source, while PNW and WI larvae did well on either tree species.

Hybridization of WI and CA Individuals

Moths were obtained from pupa raised the previous year. The CAC pupae were from a larval brood of the black/yellow/black last instar color variety (see Strothkamp 2015) from Aptos, CA. This brood consisted of all black/yellow/black individuals as 5th instars. Two males were used in the hybridization

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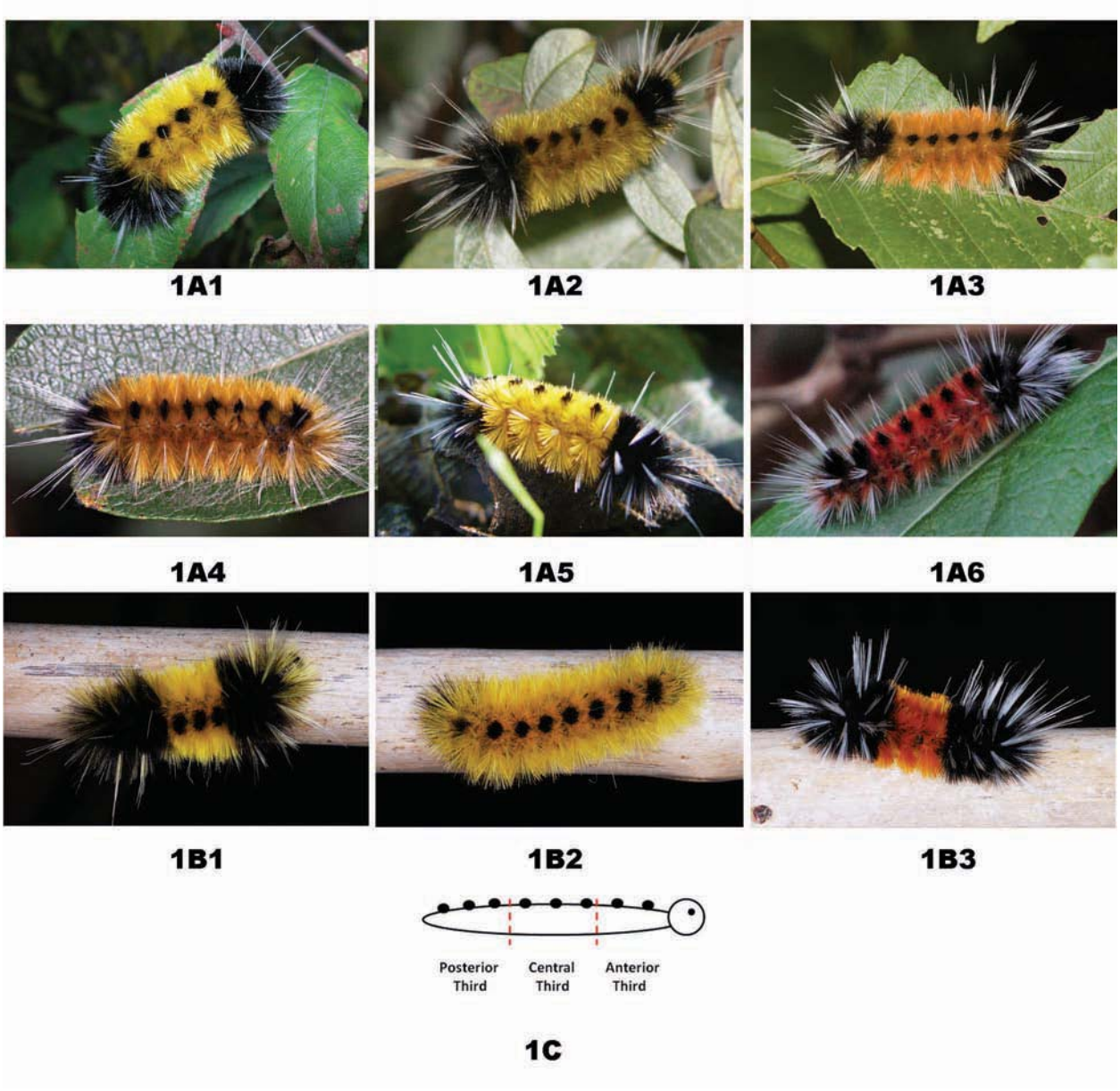


FIG. 1. Patterns of coloration in 5th instar *Lophocampa maculata*. All have long white setae clustered at both ends of the body. The shorter setae are pigmented. The Pacific Northwest (PNW) population is characterized by great variability in coloration (**A 1-6**). The Eastern and California Coastal (CAC) populations consist of two color phenotypes (**B 1,2**), while the Western Interior (WI) populations have only one (**B 3**). The color patterns of all 5th instar *Lophocampa maculata* can be explained by the diagram in (**C**). The red dashed lines divide the body into anterior, central and posterior regions. See text for the details of the pigmentation scheme.

experiment. The WI pupae were from a typical black/orange brood from the Sierra Nevada Mountains near Bishop, California. Three females from this brood were used in the hybridization experiment. Pupae were kept in individual containers prior to eclosure, insuring that mating did not occur prior to placement of the moths in the same cage for the experiment.

All five moths were placed in a mesh cage and maintained outdoors under ambient late summer conditions. They were provided with a dilute maple syrup solution on a banana slice. Oviposting began on the third night and continued for an additional two nights. Eggs were laid in clusters on the mesh top and upper sides of the cage, as is typical for this species when bred in captivity. Eggs were misted lightly with water to prevent desiccation. The eggs hatched over a one-week period and the newly hatched larvae were transferred to leaves of pacific willow (*Salix lasiandra*)

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in glass petri dishes. They ate avidly and development throughout the larval stage was typical for this species. Cocoon formation and pupation occurred in late summer/early autumn.

Pupae of the hybrids were kept together in a mesh cage. They eclosed the following year and mated, producing fertile eggs. These F2 hybrid larvae were reared to the last instar as previously described.

RESULTS

Data on the larvae of the PNW population were obtained from Oregon, Washington and southwest British Columbia. Data on last instars are the most readily available because of their size, bright coloration and activity. Figure 1A shows examples of the great variety of last instar color patterns found throughout the Pacific Northwest. Figure 1B shows the two color varieties of the CAC population and the single color pattern that is found in the WI population.

The pattern of coloration in all *Lophocampa maculata*, is dependent on the spatial arrangement of the variously pigmented setae, which densely cover the body of 5th instar larvae. A hallmark of the species is the long setae at both ends of the body. These are invariably lacking in any pigment and thus white in color. All the shorter setae contain an exogenous xanthophyll pigment, which gives them a bright yellow color. In some cases, they contain black or orange pigment in addition (Strothkamp 2015). In the latter cases, the color of the setae is determined by the black or orange pigment. The diagram in Figure 1C accounts for the observed patterns of coloration of the Eastern, CAC and WI populations of *L. maculata*. The body is divided into three regions, anterior, posterior and central regions, each comprising about 1/3 of the body length. There is a uniform yellow coloration of all the short setae and, in addition, a row of eight black dorsal tufts in all populations except the WI. In all WI, the central region is overlaid with orange pigment, which obscures the yellow color. In addition, the anterior and posterior regions have black pigment, which also obscures the yellow. The Eastern and CAC populations can be simply all yellow with black dorsal tufts or can have black pigment on the setae of the anterior and posterior thirds of the body. The extent of these black colored regions is variable, which results in variation in the number of observable black dorsal tufts. The greater the extent of the anterior and posterior black regions, the fewer the number of visible black dorsal tufts. The PNW populations have variable amounts of orange and, perhaps, traces of black pigment overlying the yellow background color. This produces a wide range of background coloration, which can vary from bright yellow to golden yellow to orange to red-orange. PNW populations also have variable extents of anterior and posterior black pigmentation, which can range from none to roughly the anterior and posterior thirds of the body. The PNW populations always have the black dorsal tufts, which can vary in number as described above. The combination of orange central region and black dorsal tufts is a feature unique to the PNW population

The realization that the great variety of last instar coloration in the PNW population could be understood as an admixture of CAC and WI color determinants, along with the geographic proximity of the WI and CAC populations to the PNW population, suggested that the PNW varieties could be explained by hybridization of CAC and WI individuals. As a way to explore this possibility, a mating experiment utilizing CAC males and WI females was attempted. The two CAC males came from a brood raised in captivity from a wild gravid female caught in Aptos, CA. This brood was entirely the B/Y/B color variety as last instars and adults had the low contrast wing pattern (Strothkamp 2015). The three WI females were from the Sierra Nevada mountains (Bishop, CA) and had the standard WI color pattern as last instars. As moths they had the high contrast wing pattern.

The F1 larvae were uniform in appearance for the first three instars but beginning with the 4th instar, considerable individual variation was observed, which was even more pronounced in the final instar (Fig. 2A). Because the matings were done under communal conditions, the assignment of color varieties to broods produced by specific parents was not possible. However, the range of color patterns found in the hybrids matches well with the variety found in wild PNW individuals (compare Figs. 1A and 2A).

As adults, the hybrids showed the high contrast wing pattern (Strothkamp 2015), characteristic of the WI population. The adults resulting from this hybridization experiment were allowed to breed and produced a second generation of hybrid larvae. These larvae, as last instars, showed the same variety of color patterns as their parents (Fig. 2B). The F2 hybrids are evidence of several important points. First, the 1st generation hybrids were obviously fertile. Second, the variability of last instar coloration was passed on from 1st to 2nd generation larvae.

An interesting feature of the laboratory hybrids were two individuals, one a 5th instar, and the other a 4th, which had small regions of the body with a mixture of yellow and orange setae, found on the same pinaculum (Fig. 2C 1,3 (dorsal view)). I have never observed this in CAC or WI individuals, either raised in captivity or

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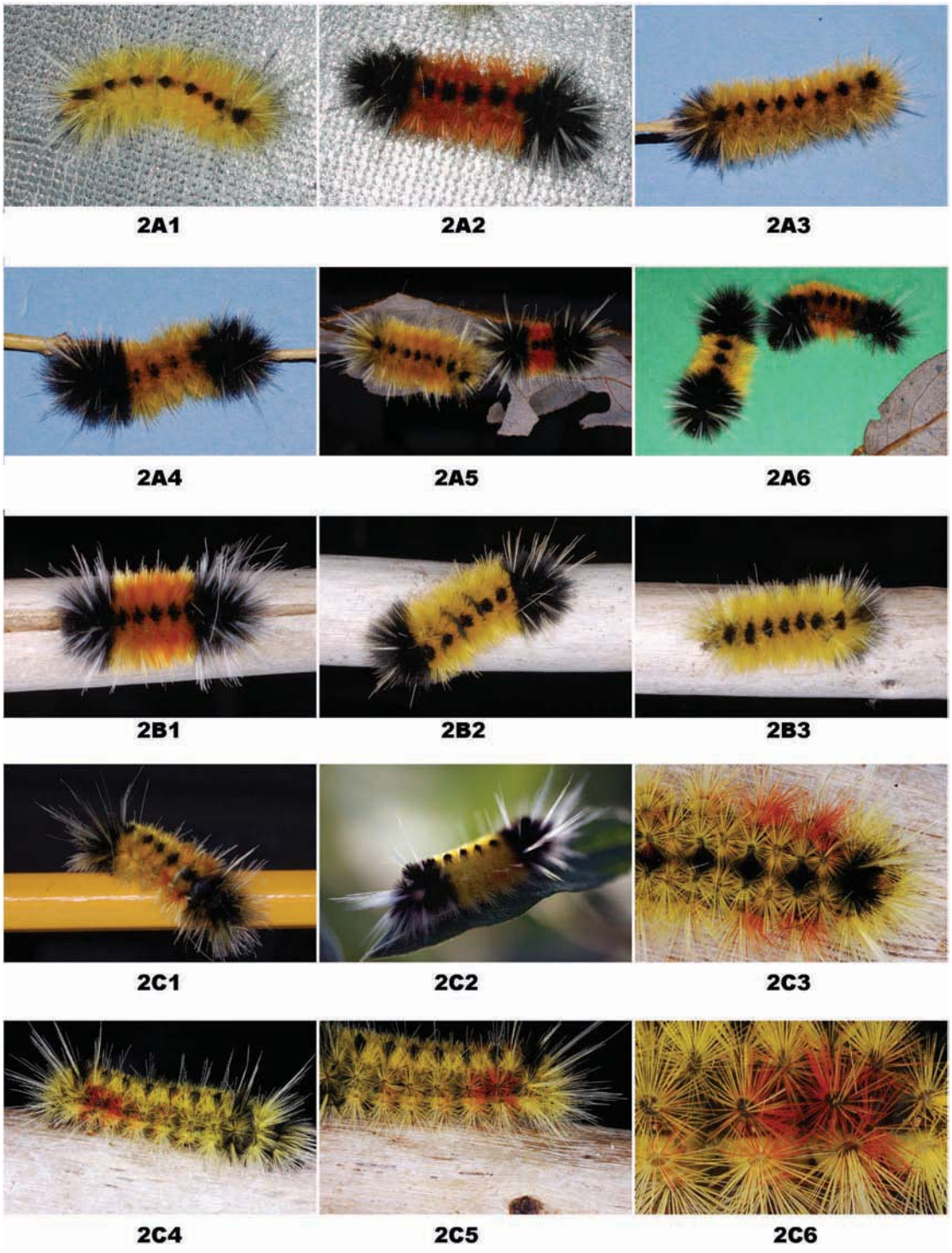


FIG. 2. Coloration in 5th instar laboratory hybrids resulting from mating of CAC and WI individuals. The F1 generation is shown in (**A**), and is characterized by a wide range of coloration (compare with wild PNW individuals (Figure 1A). The F2 generation (**B**) shows a similar variety of color patterns. Individuals showing a mosaic pattern of small orange regions on a yellow background are shown in (**C**). Figure **C 1** shows an F1 5th instar laboratory hybrid. Note the symmetrical location of the orange setae. Figure **C 2** shows a wild PNW 5th instar from Vancouver Island, British Columbia, Canada, which also show a mosaic pattern (photo courtesy of David Droppers). Figure **C 3, 4, 5** show the symmetrical location of orange pigment regions in an F2 4th instar laboratory hybrid from a dorsal view (C3) and lateral views from the right (**C4**) and left (**C5**) sides.. Figure **C6** show a close-up of an orange region. Note that within a pinaculum there are both yellow and orange setae.

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found in the wild. However, a wild PNW individual, as a 5th instar, had a similar pattern (Fig. 2C 2). This appears to be a form of mosaicism. Figure 2C 4–5 show right side lateral and left side lateral views of the 4th instar individual. Figure 2C 6 is a close-up of the 4th instar individual. Note in Figure 2C 1,3,4,5 the symmetrical location of the orange regions. Within a pinaculum there are both yellow and orange colored setae, most clearly seen in Figure 2C 6, with the two most posterior pinacula on either side having the greatest number of orange setae. The number of orange setae in a pinaculum decreases as you move anteriorly or above or below the lateral row of pinacula.

Because all matings were carried out under communal conditions, and larvae were raised together from multiple egg masses, it is not possible to know whether a single brood of the hybrids, resulting from a mating between a female and a single male, would produce uniform coloration of larvae within the brood or a random mixture of coloration among individuals of the same brood. A small egg cluster obtained from Port Alberni, British Columbia, Canada, which consisted of five eggs, all produced by the same female, provides a partial answer to this question. The five individuals, as forth and fifth (final) instars, show marked variation in coloration (Fig. 3). Other broods from single females, also from Port Alberni, were highly variable in coloration as 4th instars but uniformly colored as 5th instars. Thus, while PNW populations can show considerable intrabrood heterogeneity in instar coloration, that is not always the case and variability in one instar does not predict variability in a subsequent instar.

Discussion

Lophocampa maculata consists of several populations characterized by a number of phenotypic distinctions, of which last instar larval coloration is the most obvious (Strothkamp 2015). Within each geographic region, except for the Pacific Northwest populations, there is uniformity of last instar coloration, with a single phenotype in the WI populations and two phenotypes in the Eastern and CAC populations. The diversity of the Pacific Northwest populations was discovered based on random observations of individuals from across the region. The methods by which this variation was discovered raised the question of whether it resulted from intrabrood variability or interbrood variation, with, in the latter case, all individuals of a single brood being uniform in coloration. The data from captive rearing of egg clusters from wild-caught females (Fig. 3) indicate that a single brood can exhibit great variability in ultimate or penultimate instar coloration, although that does not necessarily have to be the case. Thus, the accumulated data on PNW color variation indicate it is the result of both intra and interbrood variability, both of which exhibit a much greater range than in other *L. maculata* populations.

The resulting limited color variations, found in all populations of *L. maculata*, could be accounted for by a small number of "patterning genes," which control expression of pigmentation in the different regions of setae. The color variation found in the central region of the PNW populations is in contrast to the uniform orange or yellow pigmentation of the WI, Eastern and CAC populations respectively. This may reflect variation in the amount of black and orange pigment, which overlies the yellow color. Similar striking patterns of coloration are found in the fur pigmentation of many mammals, such as many of the large felines. The main difference is the addition of black or orange to the yellow base color of the setae, as opposed to the white base color of unpigmented mammalian fur.

The data presented in this paper suggest that the PNW population of *L. maculata* shares characteristics of both the WI and CAC populations. In particular, larval coloration appears to be a mixture of features characteristic of the WI and CAC populations. All of this suggests that the PNW population resulted from hybridization between the WI and CAC populations. The laboratory hybridization experiment, which produced viable F1 and F2 generations, both having larval coloration similar in variety to wild PNW individuals, is consistent with that interpretation. The different populations of *L. maculata* suggest an evolutionary history in which the organism has recently experienced both divergent evolution into several distinct populations, as the result of range expansion since the last glacial maximum (LGM), and hybridization between the distinct CAC and WI populations giving rise to the PNW population.

The hybridization experiment leads to several conclusions. First the successful mating of CAC and WI individuals supports the argument that all *Lophocampa maculata* populations should, at least based on ability to reproduce successfully, be considered the same species, although clearly significant diversification has occurred in the different geographic regions. Hybrids produced from the CAC and WI populations were fertile and produced a second generation of individuals exhibiting similar variation in last instar coloration. The color variability of the hybrids thus appears to be stably transmitted from one generation to another. In addition, these varieties of coloration match well with those seen in

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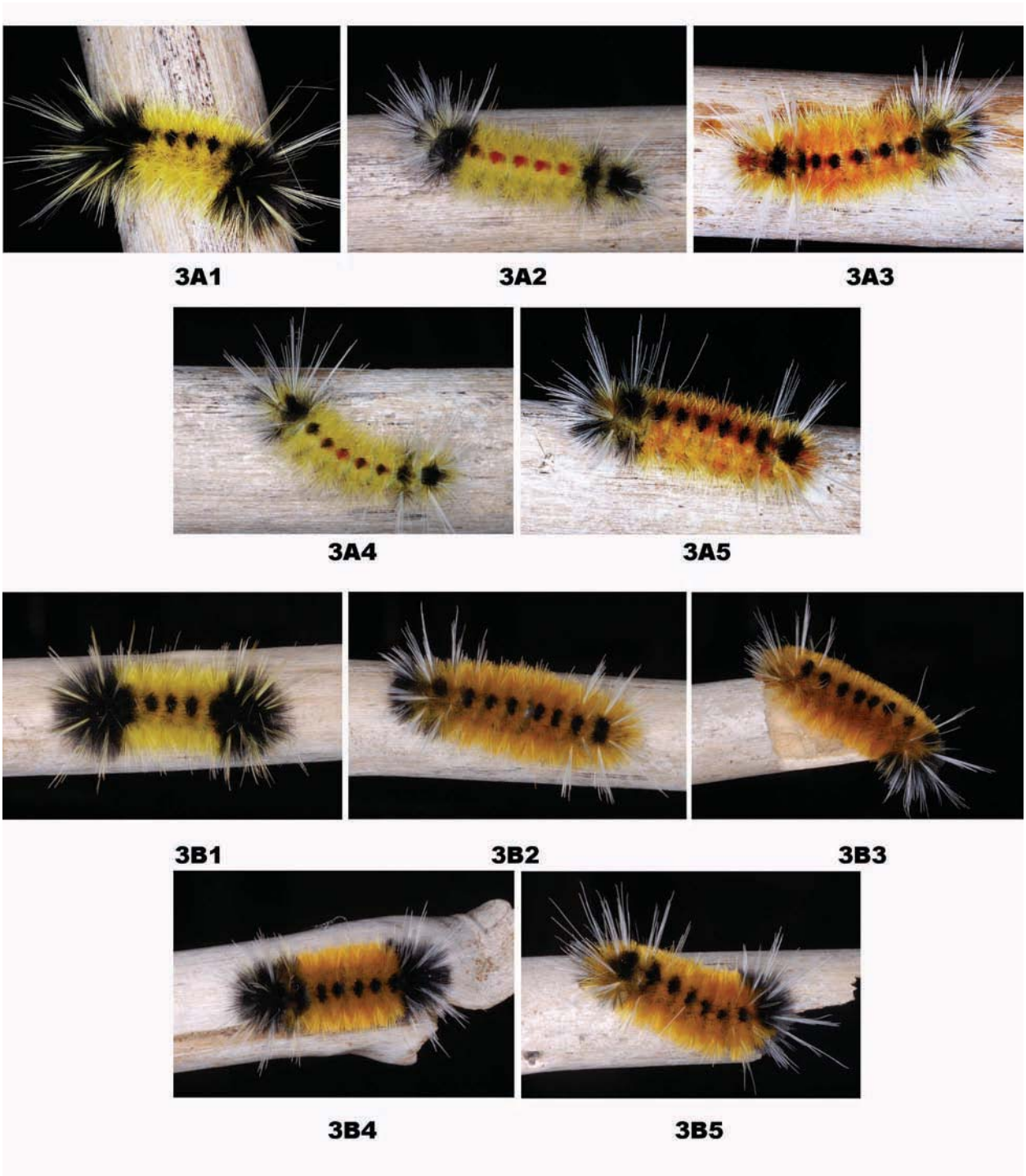


FIG. 3. The five individuals shown in this figure were obtained from a small egg cluster from a single wild-caught female. The individuals, numbered 1–5, which differ dramatically in coloration, are shown as 4th instars (**A**) and 5th instars (**B**).

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PNW wild individuals (Figs. 1A and 2A). Thus, a reasonable scenario is that the present PNW populations resulted from hybridization of CAC and WI individuals.

Hybridization has been historically considered to be unimportant in evolution. However, more recently it has been recognized as a factor contributing to the origin of species (Arnold 1997; Mallet 2007), and several well-documented examples of homoploid hybridization between animal species have been discovered (Dowling 1997, Buerkle 2000, Abbott 2013), including Lepidoptera (Mavarez 2006, Gompert 2006). The entire *L. maculata* complex, consisting of several clearly defined populations, may be an example of speciation in progress, involving both divergent and hybridization speciation.

Geographic isolation of the present Eastern, WI and CAC populations is maintained by regions of unsuitable habitat: the Great Plains separate the Eastern and WI populations and the Central Valley of California separates the WI and CAC populations. *L. maculata* is not found in the Central Valley now (Strothkamp 2015) and paleoclimate data based on pollen records (Adam 1981, 1983; Davis 1988), sedimentary charcoal deposits (Brunelle 2003), geochemical data (Street 2012) and hydrologic data (Goman 2000, Malamud-Roam 2006) suggest it has been unfavorable habitat since LGM because of both climate and lack of suitable plant species for larval development. These three allopatric populations have diverged enough to have distinct phenotypes (Strothkamp 2015).

The Siskiyou Mountains, which form a high elevation, forested bridge between the Sierra Nevada/Cascade Mountains and the Pacific coast created a region of sympatry between the WI and CAC populations, allowing them to hybridize. Movement of the hybrids north into the Pacific Northwest climate zone, west of the Cascade Mountains, may have provided the reproductive isolation necessary for the hybrids to become established (Gross 2005). A similar hybridization involving hybrids occupying an "extreme" habitat not suited to either parental species has been proposed for Lycaeides butterflies (Gompert 2006, Gompert 2014).

The present day CAC population is bivoltine, while the WI and Eastern populations are univoltine. The PNW population appears to be universally univoltine. This raises the question of whether the timing of the adult stage would have allowed for mating between the CAC and WI populations. It is possible that the differences in voltinism between the WI and CAC populations result in phenological isolation. Phenological isolation has been reported for elevation-based differences in flight period for *Euphilotes enoptes* (Peterson 1995). Study of present day WI and CAC populations indicates that there would be overlap of the flight period of the WI populations with the spring CAC flight period and an even greater overlap with the late summer flight (compare Figure 6 a & c of Strothkamp 2015), thus allowing for hybridization to occur even if the CAC population was already bivoltine when the WI and CAC populations met.

Among the often-observed characteristics of a hybrid population are (1) considerable individual genetic variation, a "hybrid swarm," often detected by allozyme analysis (Seehausen 2004) and (2) an increased frequency of rare alleles that are found in the parental populations (Bradley 1993, Hoffman 1995, Schilthuizen 1999, Schilthuizen 2004). The *L. maculata* of the PNW appear to show both characteristics. The great variation in larval coloration may be a visual indication of a "hybrid swarm." This variation is found both in wild individuals, captive reared broods obtained from wild females and the laboratory hybridization experiment. All populations of *L. maculata* experience a rare phenomenon referred to as partial depigmentation (Strothkamp 2011, 2015), where an individual looses some, but not all, of its typical setae pigmentation as a third or forth instar but returns to normal coloration as a fifth instar and adult. This is thought to result from a rare allele or combination of alleles affecting the patterning genes, which control pigmentation of setae. While the specific coloration of these "white" individuals seems to be population specific, it occurs in all the geographic populations of *L. maculata*. It is impossible to quantify the frequency with which this form occurs in wild populations for a variety of reasons. However, over a five-year period of collecting reports on this variation, it appears to occur much more frequently in the PNW populations, especially on Vancouver Island, British Columbia, Canada. This appears to be an example of the "rare allele" effect in a hybrid population.

Another very rare feature of the wild PNW populations and the laboratory hybrids, is a mosaic pattern of coloration in which regions of yellow setae have small areas of setae with orange pigmentation (Fig 2C). Mosaics are individuals that consist of two genetically different cell types. There are many types of mosaics and they can arise in a variety of ways. In many cases the mosaic cells may be difficult to distinguish. However, if the mosaic cells are involved in the pigmentation of skin, fur or setae, obvious visible differences can occur. Variation in fur pigmentation in mammals (Robinson 1957), particularly the mouse

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(Mus musculus) (Gruneberg 1966, Panthier 1990, Favor 1994), has been well documented.

The mosaic individuals seen in *Lophocampa maculata* have only been observed in the Pacific Northwest populations, and may be a consequence of their hybrid origin. The F1 generation of the hybrids has, of necessity, a genome in which the pairs of homologous chromosomes are derived from parents from the two different populations and are thus likely to differ at many loci, including those responsible for setae pigmentation. The same will be true of many individuals from succeeding generations. Thus, somatic cell mitotic crossing over could explain the observed color mosaics in *L. maculata* (Bateman 1967, Koopman 1999).

In summary, the phenotypic characteristics of the PNW populations of *Lophocampa maculata* suggest this population has evolved from a hybridization of the CAC and WI populations. Investigation of the molecular genetic characteristics of the population will undoubtedly shed more light on this possibility.

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PITCHER PLANT MOTHS (EXYRA) FLY FROM PITCHERS IN RESPONSE TO SMOKE

JAKE LEE, JACOB BRUMLEY, MEGHAN RYCKELEY, CARTER SMITH, JANIS LEMASTER,
CHRISTINE RICCI, ALBERT J. MEIER

Department of Biology, Western Kentucky University, 1906 College Heights Blvd., #11080 Bowling Green, KY 42101-1080,
E-mail: jacob.lee851@topper.wku.edu

AND

BARRY MCPHAIL

Bayside Academy, 303 Dryer Ave, Daphne, AL 36526

ABSTRACT. Pine savannas in the Southeastern United States are subject to an historical regime of periodic fire, with many and varied ecological consequences. Insectivorous plants of the genus *Sarracenia* (L.) (Sarraceniaceae) often entirely lose their above-ground leaves to these periodic fires. During the growing season, these tubular leaves, which act as pitfall traps for insects, are host to pitcher plant moths, *Exyra* (Grote) (Noctuidae), which live their entire life cycle within the plant. This study tested the effect of smoke on a small sample of *Exyra semicrocea* in pitchers, and demonstrated that they respond quickly by flight.

Additional key words: *Exyra, Sarracenia*, Fire

Pine savannas of the Southeastern United States are dominated by the large southern yellow pines, which include *Pinus palustris* (Mill.), *Pinus taeda* (L.), and *Pinus elliottii* (Engelm.). These forests do not have a dense canopy, which allows for the growth of a rich understory (Harrington et al. 2013), including in scattered suitable microenvironments pitcher plant savannas (Wells 1928, Walker & Peet 1983). Hydric pine savannas have wet, sandy soil that is nutrient poor, and contain several species of carnivorous plants, including several species of pitcher plant (Folkerts & Folkerts 1993). Such savannas and bogs, the pitcher plants they contain, and a rich associated biota are of high conservation concern because of the biological diversity of the areas and their greatly reduced modern extent (Stephens et al. 2011).

Longleaf pine forests are subject to frequent fire (Komarek 1974, Platt et al. 1991) and contain plant and animal species that are fire adapted, and which are the subject of a rich literature reviewed by Van Lear et al. (2005). Historically, fires in pine savannas of the coastal plain occurred at intervals of one to ten years (Komarek 1974, Platt et al. 1991), and the US Forest Service manages such sites with controlled burns every 3 years (USDA National Forest Service 2002). The insectivorous pitcher plants, *Sarracenia flava* (L.) and *Sarracenia leucophylla* (Raf.) are adapted to these frequent fires (Brewer 1999). The plants have subterranean rhizomes, which allow them to quickly replace their above-ground parts and avoid competition with other plants (Barker et al. 1988).

Pitcher plants have no less than 17 arthropod symbionts, given relatively little study compared to the pitcher plants themselves (Stephens et al. 2011), among which are pitcher plant moths, *Exyra* (Grote) (Noctuidae) (Stephens & Folkerts 2012). Two of the three species of *Exyra*, the pitcher plant mining moth, *E. semicrocea* (Guenée) and Riding's pitcherplant looper moth, *E. ridingsii* (Riley) are prevalent in the pitcher plant savannas of the Southeast where they inhabit the pitcher plant savannas (Stephens & Folkerts 2012). The moths live out the majority of their life inside pitcher plants (Jones 1921), only emerging at night (Stephens & Folkerts 2012). The adults lay one egg in a plant. The larvae pupate after five larval instars and the adults shelter in the plants, only flying out at night.

Given that these savannas burn frequently, and that pitcher plant moths are found in pitchers that have grown since recent fires (Ricci 2015), we would expect pitcher plant moths to be adapted to frequent fires. Prior to this study, it was unknown if the adult moths flee fires and survive, or if they fail to avoid fire and risk death. We hypothesized that the moths would leave the pitchers when fire approached, despite our experience that *Exyra* strongly resist physical efforts to force them to leave pitchers during the day. Furthermore, our experience was that when physically forced to depart pitchers, we rarely observed them to fly more than 20 meters during the daytime (McPhail and Meier pers. obs.). This distance is unlikely to be sufficient to avoid fires.

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METHODS

Fire Experiment 1. On October 17, 2015, between 0700 hours and 0800 hours, at 30º 41.138'N, 88º 3.879'W within Mobile, Alabama, we placed two *Sarracenia leucophylla* pitchers in separate jars full of dry pine needles and grass. One pitcher at a time, we then set the pine needles and grass ablaze. We recorded the number of moths that left their pitcher as well as the time in which it took them to leave. No moths were killed while conducting this experiment.

Fire Experiment 2. On October 18, 2015, in the Sumatra Pine Savanna within the Apalachicola National Forest between 1300 hours and 1400 hours, we found six Pitcher Plant Mining Moths in five tubular leaves of *S. flava*. Their coordinates were 30º 2.407'N, 84º 57.684'W.

The first treatment was to observe the moths in the pitchers for two minutes to determine if they would leave the pitcher without disturbance. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. In the second treatment, a group member exposed the moths to two minutes of gently blowing air with a bee smoker that had not been ignited at ca. 10cm from the opening of the pitcher. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. In the third and final treatment for this second experiment, a group member flicked, squeezed, and shook the pitchers to provoke the moth into leaving. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. For the experimental trial, we exposed each of these moths to smoke from burning dry pine needles and grass within the smoker. A group member subjected each plant to smoking while holding the bee smoker 10cm away from the pitcher. It was intended that smoking of the pitcher should continue for up to two minutes if the moths remained in the pitchers. We recorded the number of moths that left their pitcher plants as well as the time which it took them to leave. Once the moths left their pitchers, we attempted to follow two of the moths to determine the distance that they would fly. No moths were killed while conducting this experiment.

Temperature of the Smoke. A bee smoker was filled with pine needles and lit. We held the smoker at 10cm from the opening into the pitcher and applied smoke to three pitchers from *S. leucophylla* in a fashion similar to that used by us in the field. We used a Fluke Hydra Series II thermocouple, set on channel 1, to read in degrees C., in the J temperature range. We took six sequential readings from each pitcher at 5 second intervals at 10 cm deep inside the pitcher, this being the minimum depth in the pitcher where moths were located. We took two readings before wafting smoke towards the pitcher, and four after the pitchers began receiving smoke.

Statistical Analysis. We used the VasserStats Online Program to perform a Chi-Square independence test comparing the frequency of departure within two minutes for each of the trials.

RESULTS

Fire Experiment 1. When we started the fire underneath two of the pitcher plants, both moths emerged. The first flew out 13 seconds after the pine needles were lit, and the other flew out 17 seconds after the needles were lit. It is interesting to note that the needles began smoking profusely a short period of time after being lit. If the time that they began to smoke is set as the reference point, then it took the first moth 4 seconds to leave the pitcher, and the second moth 7 seconds to leave the pitcher.

Fire Experiment 2. The three control trials caused no moths to leave their plants. None of the moths even moved when left alone or blown on. When the pitchers were vigorously shaken and flicked with our fingers, the moths moved around the inside of their pitchers and ultimately moved deeper into them. When smoked, every moth almost immediately left its plant (n = 6; mean = 6.5 seconds; s = 2.7). A chi-square test comparing experimental and control was highly significant ($\chi^2 = 12$, df = 2, $p = 0.0025$).

A group member followed two of the moths after they fled their pitcher plant. Both moths flew over 200 meters before entering another pitcher plant.

Influence of the smoke on temperature. Wafting smoke past the openings of *S. leucophylla* in a fashion similar to that used on the moths in the field yielded a maximum temperature change of 0.1 degrees C among all 3 pitchers tested.

DISCUSSION

We hypothesized that the moths would leave their pitchers and take flight in the presence of smoke as a means of escape before being consumed by fire. This hypothesis suggests that existing populations of pitcher plant moths can emigrate to survive fires; thus inviting comparisons to the shifting mosaics and metapopulation dynamics described by Harrison et al. (1988), Hanski et al. (1994), and Hanski et al. (1995) for butterflies. Given past personal experiences with the moths' reluctance to leave pitchers during the daytime, we were not certain that they would do so under the influence of smoke (Pers. Obs. McPhail and Meier). Fire might severely

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reduce a local population of pitcher plant moths if they fail to respond, and assuming that they do not employ a life cycle approach to survival (for example, pupating underground). In order to successfully employ a metapopulation strategy, *Exyra* moths must be able to successfully recolonized areas that are burned. Until recently there was no research on this subject. Ricci (2015) suggested that Riding's pitcherplant looper moths may employ a metapopulation strategy despite showing low mobility. We found in a small sample of six pitcher plant mining moth that even a few seconds exposure to smoke caused moths to leave the pitchers and fly. The results of this study support the additional hypothesis that smoke, not temperature is the stimulus that triggers the emigration of the moth from one habitat to another. Temperature differences inside the pitchers were minimal, 0.1 C, when the moths were exposed to smoke.

Despite our previous observations of daytime movements limited to 20 meters, when confronted with smoke, the moths were observed traveling much longer distances (200 meters). This ability to flee longer distances increases the opportunities for pitcher plant moths to survive fires, and relocate if necessary.

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IMMATURE STAGES AND NATURAL HISTORY OF THE NEOTROPICAL SATYRINE *PAREUPTYCHIA OCIRRHOE INTERJECTA* (NYMPHALIDAE: EUPTYCHIINA)

ANDRÉ V. L. FREITAS[1,2*], EDUARDO PROENÇA BARBOSA[1] AND MARIO ALEJANDRO MARÍN[1]

[1] Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
[2] Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
* Corresponding author

ABSTRACT. The present paper describes the immature stages of the common Neotropical satyrine butterfly *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952). The solitary eggs are white and round, turning black 4 to 6 hours after oviposition. The four solitary larval instars are predominantly green and feed on grasses (Poaceae), including *Setaria* in nature and several other native and introduced species in captivity. The pupa is short and smooth and entirely green. Except for the black eggs, the immature stages are similar to those of other forest species of Euptychiina. The most remarkable and unique characteristic of *P. ocirrhoe interjecta* is the shiny black eggs, a possible synapomorphy for *Pareuptychia* not known in any other Euptychiina.

Additional key words: Atlantic Forest, *Cepheuptychia, Godartiana, Taydebis, Zischkaia*

The Euptychiina (Nymphalidae: Satyrinae) is one of the largest and most diverse butterfly subtribes, contributing a significant portion of Neotropical butterfly diversity (Peña et al. 2010, Marín et al. 2011). With over 400 recognized species (Lamas, 2004), Euptychiina butterflies occur in virtually all habitats and vegetation types from sea level to over 3500 m (DeVries 1987, Marín et al. 2011). However, despite this large species richness, immature stages have been described for a very few species and genera of Euptychiina (DeVries 1987, Murray 2001, Freitas et al. 2016). For the genus *Pareuptychia*, for example, immature stages have never been described in detail, and available information includes only textual descriptions in DeVries (1987) and pictures of larvae and pupae in Janzen and Hallwachs (2015).

Species of *Pareuptychia* are associated with forested habitats across the Neotropics (DeVries 1987), and they may be abundant. The genus is very homogeneous, and its eight described species (Nakahara et al. 2016) are very similar in wing pattern and morphology, suggesting that this is a monophyletic group (except maybe for *Pareuptychia lydia* (Cramer, 1777)). However, because of similarity in wing patterns, species limits and identities are not well established and the genus needs to be studied from both morphological and molecular perspectives (Marín et al. in prep.). In addition, knowledge about the immature stages of *Pareuptychia* could be of help in understanding the taxonomy of this group.

In this context, the present paper offers a detailed description of the immature stages of *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952) and compares them with those of other neotropical Euptychiina butterflies.

MATERIALS AND METHODS

Study sites. Adults and immatures of *P. ocirrhoe interjecta* were studied in four different localities in São Paulo State, Southeastern Brazil: 1) Reserva Biológica Municipal da Serra do Japi, Jundiaí (900–1100 m; 23º13'S, 46º57'W); 2) ARIE Mata de Santa Genebra, Campinas (600–620 m; 22º49'S, 47º6'W); 3) Fazenda Santa Elisa, IAC, Campinas (630-650 m; 22º51'S, 47º5'W); 4) Parque Estadual Xixová-Japuí, São Vicente (20–200 m; 23º59'S, 46º23'W).

Sampling and rearing of immature stages. Fertile eggs were obtained from wild-captured females confined in plastic bags warmed by a 40W bulb and provided with leaves of several species of native and introduced grasses. Larvae of *P. ocirrhoe interjecta* and of the additional species mentioned in the discussion section were reared in plastic containers cleaned daily, with fresh plant material provided every two or three days (following Freitas 2007). Data were recorded on behavior and development time for all stages. Dry head capsules and pupal cases were retained in glass vials. Immature stages were fixed in Kahle-Dietrich solution (Triplehorn & Johnson 2005) when the number of specimens was sufficient. Voucher specimens of the immature stages were deposited in the Museu de Zoologia "Adão José Cardoso" (ZUEC-AVLF), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Morphology. Measurements were taken and general aspects of morphology were observed using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Scanning electron microscopy (SEM) was conducted using a JEOL® JSM-5800 microscope (JEOL Ltd., Japan), and samples were critical-point dried in a Bal-tec® – CPD030 (Leica Microsystems, Germany), attached with double-sided

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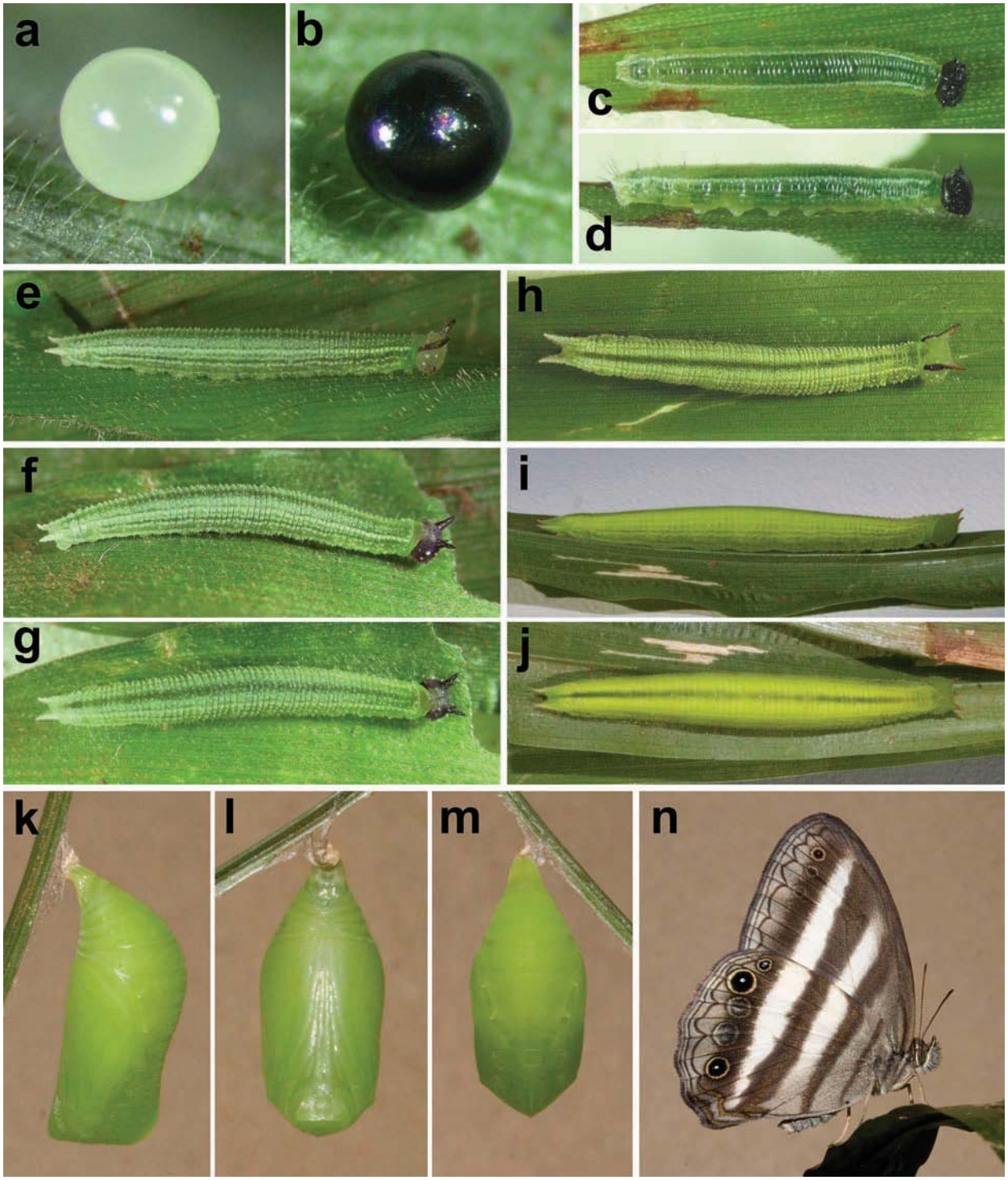


FIG. 1. Immature stages and adult of *Pareuptychia ocirrhoe interjecta*. **a, b.** egg, white and black; **c, d.** first instar, dorsal and lateral; **e.** light head capsule second instar, lateral; **f, g.** dark head capsule second instar, dorsal and lateral; **h.** third instar, dorsal; **i, j.** fourth (last) instar, lateral and dorsal; **k, l, m**. Pupa, lateral, ventral and dorsal; **n.** Adult male.

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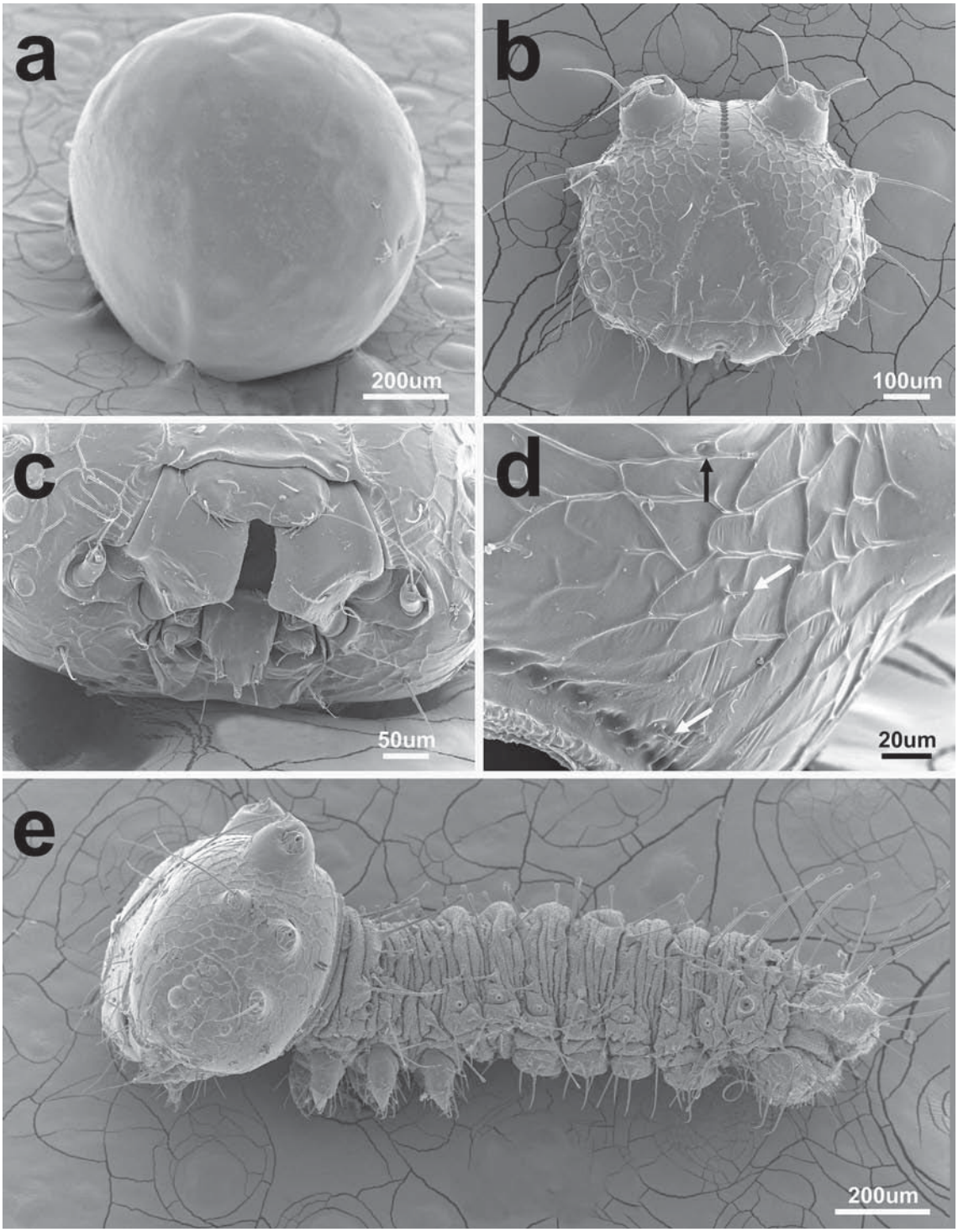


FIG. 2. Egg and first instar of *Pareuptychia ocirrhoe interjecta*. **a.** egg; **b.** Head capsule, general frontal view; **c.** Detail of frontal region; **d**. Detail of posterior region: white setae show microsetae and black seta show a pore; **e.** Early first instar, general lateral view.

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tape to aluminum stubs, and coated with gold/palladium with a Bal-tec® – SCD050 sputter coater (Leica Microsystems, Germany). Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas 2007). Terminology for early stages descriptions followed García-Barros & Martín (1995) for eggs and Stehr (1987) for larvae and pupae.

RESULTS

Description of immature stages. The following descriptions and measurements are based on material reared from one female from Serra do Japi, Jundiaí, São Paulo (material reared from three other localities gave similar results).

Egg (Figs. 1a,b – 2a). White, round, turning black 4 to 6 hours after oviposition. Height and diameter 0.94 – 0.96 mm; duration 5 – 6 days (n = 8).

First instar (Figs. 1c,d – 2b-e). Head capsule width 0.64 – 0.70 mm (mean = 0.66 mm; SD = 0.026 mm; n = 5); head scoli 0.08 – 0.10 mm (mean = 0.09 mm; SD = 0.008 mm; n = 5). Head black, with enlarged chalazae, bearing a pair of short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body light green, with white longitudinal stripes, turning dark green after first meal; caudal filaments very short. Legs and prolegs light green. Setae light green from T1 to A7, black from A8 to A10, all dorsal and subdorsal clubbed at tip (Fig. 2e). Maximum length 5 mm. Duration 6 – 7 days (n = 8).

Second instar (Figs. 1e,f,g). Head capsule width 0.90 – 1.00 mm (mean = 0.94 mm; SD = 0.052 mm; n = 5); head scoli 0.40 – 0.46 mm (mean = 0.43 mm; SD = 0.022 mm; n = 5). Head green with two short dark brown scoli on vertex (Fig. 1e,g); in some individuals head is mostly dark brown (Figs. 1f,g). Body green, striped longitudinally with white; caudal filaments short. Legs and prolegs light green. Maximum length 9 mm. Duration 4 – 8 days (n = 8).

Third instar (Fig. 1h). Head capsule width 1.38 – 1.46 mm (mean = 1.45 mm; SD = 0.056 mm; n = 5); head scoli 0.60 – 0.66 mm (mean = 0.62 mm; SD = 0.024 mm; n = 5). Head green, with two diverging very short scoli on vertex; these are reddish with a posterior dark brown line extending to head capsule. Body light green with a conspicuous dark green dorsal stripe and several additional longitudinal markings; caudal filaments short. Legs and prolegs light green. Maximum length 15 mm. Duration 7 – 9 days (n = 6).

Fourth (last) instar (Figs. 1i,j). Head capsule width 2.18 – 2.20 mm (mean = 2.20 mm; SD = 0.016 mm; n = 4); head scoli 0.74 – 0.82 mm (mean = 0.78 mm; SD = 0.034 mm; n = 4). Head green, with two diverging short scoli with reddish apex on vertex. Body light green with a conspicuous dark green dorsal stripe and several fine longitudinal stripes; caudal filaments short and reddish on apex. Legs and prolegs green. Maximum length 25 mm. Duration 7 – 10 days (n = 6).

Pupa (Figs. 1k,l,m). Short and smooth; entirely green; short rounded ocular caps; cremaster light green; dorsal abdomen smooth without projections. Total length 10.0 – 10.5 mm (n = 5). Duration 9 – 14 days (n = 4).

Behavior and natural history. *P. ocirrhoe interjecta* (Fig. 1n) is common in several environments in the Atlantic Forest from sea level to 1000 m altitude. Oviposition behavior was not observed in the field, but two solitary eggs, two larvae and one pupa were collected in the field in an unidentified native species of *Setaria* (Poaceae) in a shaded narrow trail inside the forest. Eggs were laid singly in the laboratory and larvae easily accepted the same hostplant mentioned above. Larvae were solitary in all instars and did not exhibit cannibalistic behavior (several larvae of different instars were reared together in small pots). Adults were easily observed along forest edges and in clearings flying low in the understory, rarely rising above 2 m above the ground. Flight was erratic and fast and, when disturbed, butterflies performed unpredictable aerial maneuvers with alternating flashes of white and dark, which makes them difficult to capture in flight. Adults feed on fermenting fallen fruits, feces and several other decaying substances, being never observed visiting flowers. However, there are reports of adults feeding on extrafloral nectar (Barbosa 2013; AVLF pers. obs.).

DISCUSSION

The immature stages of *P. ocirrhoe interjecta* are quite morphologically simple and similar to those of several other species of Neotropical Euptychiina: larvae lack body scoli, present short head horns and caudal filaments and pupae are short and smooth. The entirely green last instar, although not rare in Euptychiina, is apparently uncommon; most known last instars of small forest Euptychiina are predominantly brown or have color tones that make them cryptic on the background of dead leaves and stems (Singer et al. 1983, DeVries 1987, Murray 2001, Kaminski & Freitas 2008, Janzen & Hallwachs 2015). Species with similar green last instars and/or pupae includes other species of *Pareuptychia* (AVLF unpublished; Janzen & Hallwachs 2015), *Cepheuptychia cephus* (Fabricius, 1775), *Taydebis peculiaris* (A. Butler, 1874), *Zischkaia pacarus* (Godart, [1824]), *Godartiana muscosa* (A. Butler, 1870) (Figure 3) and *Forsterinaria pronophila* (Freitas & Peña 2006). Although *Cepheuptychia* and *Taydebis* are genera related to *Pareuptychia* in part of the "*Pareuptychia* clade" (Peña et al. 2010), the similarity in color pattern is not related to phylogenetic relationships. For example, other forest species belonging to the "*Pareuptychia* clade" present predominantly non-green last instars, including *Chloreuptychia arnaca* (Fabricius, 1776), *Megeuptychia antonoe* (Cramer, 1775) (Janzen & Hallwachs 2015), *Splendeuptychia furina* (Hewitson, 1862) and *Splendeuptychia doxes* (Godart, [1824]) (Freitas, unpublished). The greenish last instars of *Satyrotaygetis satyrina* (H. Bates, 1865) are quite distinct from those of *Pareuptychia*, especially in the longer, strongly diverging head horns.

The most remarkable and unique characteristic of the immature stages of *P. ocirrhoe interjecta* is the shiny black eggs. This trait, present also in other species of *Pareuptychia* (DeVries 1987, AVLF unpublished), is unique among all known Euptychiina (however, color

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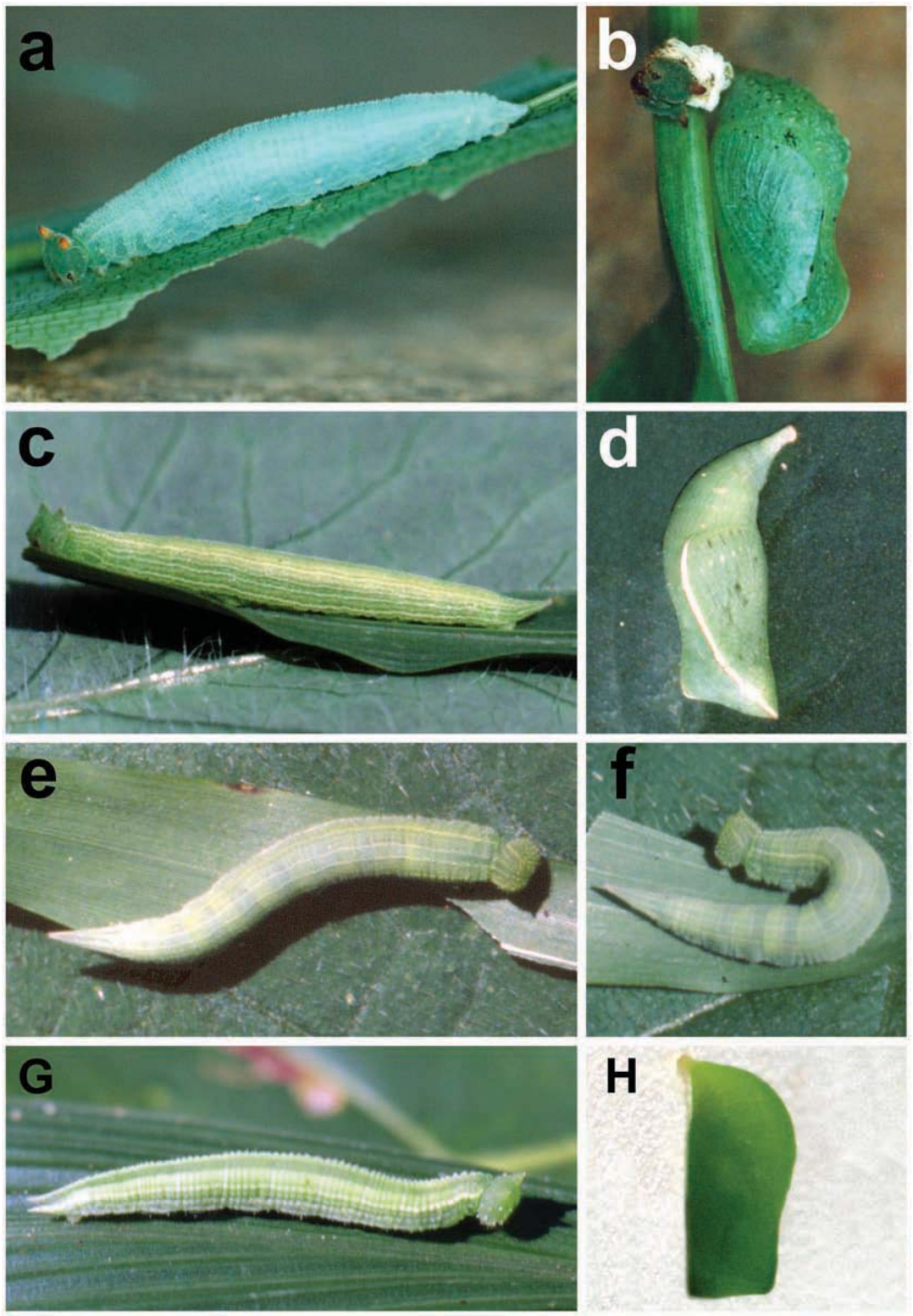


FIG. 3. Immature stages of Euptychiina (all from Brazil). **a, b.** *Cepheuptychia cephus*, fourth (last) instar and pupa (both lateral), Upper Juruá River, Marechal Thaumaturgo, Acre; **c, d.** *Taydebis peculiaris*, fourth (last) instar and pupa (both lateral), Santa Virgínia, São Luis do Paraitinga, São Paulo; **e, f.** *Zischkaia pacarus*, third instar, dorsal and lateral, Morro Grande, Cotia, São Paulo; **g, h.** *Godartiana muscosa*, fourth (last) instar and pupa (both lateral), Serra do Japi, Jundiaí, SP.

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IMMATURE STAGES AND NATURAL HISTORY OF THE NEOTROPICAL SATYRINE *PAREUPTYCHIA OCIRRHOE INTERJECTA* (NYMPHALIDAE: EUPTYCHIINA)

ANDRÉ V. L. FREITAS[1,2*], EDUARDO PROENÇA BARBOSA[1] AND MARIO ALEJANDRO MARÍN[1]

[1] Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
[2] Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
* Corresponding author

ABSTRACT. The present paper describes the immature stages of the common Neotropical satyrine butterfly *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952). The solitary eggs are white and round, turning black 4 to 6 hours after oviposition. The four solitary larval instars are predominantly green and feed on grasses (Poaceae), including *Setaria* in nature and several other native and introduced species in captivity. The pupa is short and smooth and entirely green. Except for the black eggs, the immature stages are similar to those of other forest species of Euptychiina. The most remarkable and unique characteristic of *P. ocirrhoe interjecta* is the shiny black eggs, a possible synapomorphy for *Pareuptychia* not known in any other Euptychiina.

Additional key words: Atlantic Forest, *Cepheuptychia, Godartiana, Taydebis, Zischkaia*

The Euptychiina (Nymphalidae: Satyrinae) is one of the largest and most diverse butterfly subtribes, contributing a significant portion of Neotropical butterfly diversity (Peña et al. 2010, Marín et al. 2011). With over 400 recognized species (Lamas, 2004), Euptychiina butterflies occur in virtually all habitats and vegetation types from sea level to over 3500 m (DeVries 1987, Marín et al. 2011). However, despite this large species richness, immature stages have been described for a very few species and genera of Euptychiina (DeVries 1987, Murray 2001, Freitas et al. 2016). For the genus *Pareuptychia*, for example, immature stages have never been described in detail, and available information includes only textual descriptions in DeVries (1987) and pictures of larvae and pupae in Janzen and Hallwachs (2015).

Species of *Pareuptychia* are associated with forested habitats across the Neotropics (DeVries 1987), and they may be abundant. The genus is very homogeneous, and its eight described species (Nakahara et al. 2016) are very similar in wing pattern and morphology, suggesting that this is a monophyletic group (except maybe for *Pareuptychia lydia* (Cramer, 1777)). However, because of similarity in wing patterns, species limits and identities are not well established and the genus needs to be studied from both morphological and molecular perspectives (Marín et al. in prep.). In addition, knowledge about the immature stages of *Pareuptychia* could be of help in understanding the taxonomy of this group.

In this context, the present paper offers a detailed description of the immature stages of *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952) and compares them with those of other neotropical Euptychiina butterflies.

MATERIALS AND METHODS

Study sites. Adults and immatures of *P. ocirrhoe interjecta* were studied in four different localities in São Paulo State, Southeastern Brazil: 1) Reserva Biológica Municipal da Serra do Japi, Jundiaí (900–1100 m; 23º13'S, 46º57'W); 2) ARIE Mata de Santa Genebra, Campinas (600–620 m; 22º49'S, 47º6'W); 3) Fazenda Santa Elisa, IAC, Campinas (630-650 m; 22º51'S, 47º5'W); 4) Parque Estadual Xixová-Japuí, São Vicente (20–200 m; 23º59'S, 46º23'W).

Sampling and rearing of immature stages. Fertile eggs were obtained from wild-captured females confined in plastic bags warmed by a 40W bulb and provided with leaves of several species of native and introduced grasses. Larvae of *P. ocirrhoe interjecta* and of the additional species mentioned in the discussion section were reared in plastic containers cleaned daily, with fresh plant material provided every two or three days (following Freitas 2007). Data were recorded on behavior and development time for all stages. Dry head capsules and pupal cases were retained in glass vials. Immature stages were fixed in Kahle-Dietrich solution (Triplehorn & Johnson 2005) when the number of specimens was sufficient. Voucher specimens of the immature stages were deposited in the Museu de Zoologia "Adão José Cardoso" (ZUEC-AVLF), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Morphology. Measurements were taken and general aspects of morphology were observed using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Scanning electron microscopy (SEM) was conducted using a JEOL® JSM-5800 microscope (JEOL Ltd., Japan), and samples were critical-point dried in a Bal-tec® – CPD030 (Leica Microsystems, Germany), attached with double-sided

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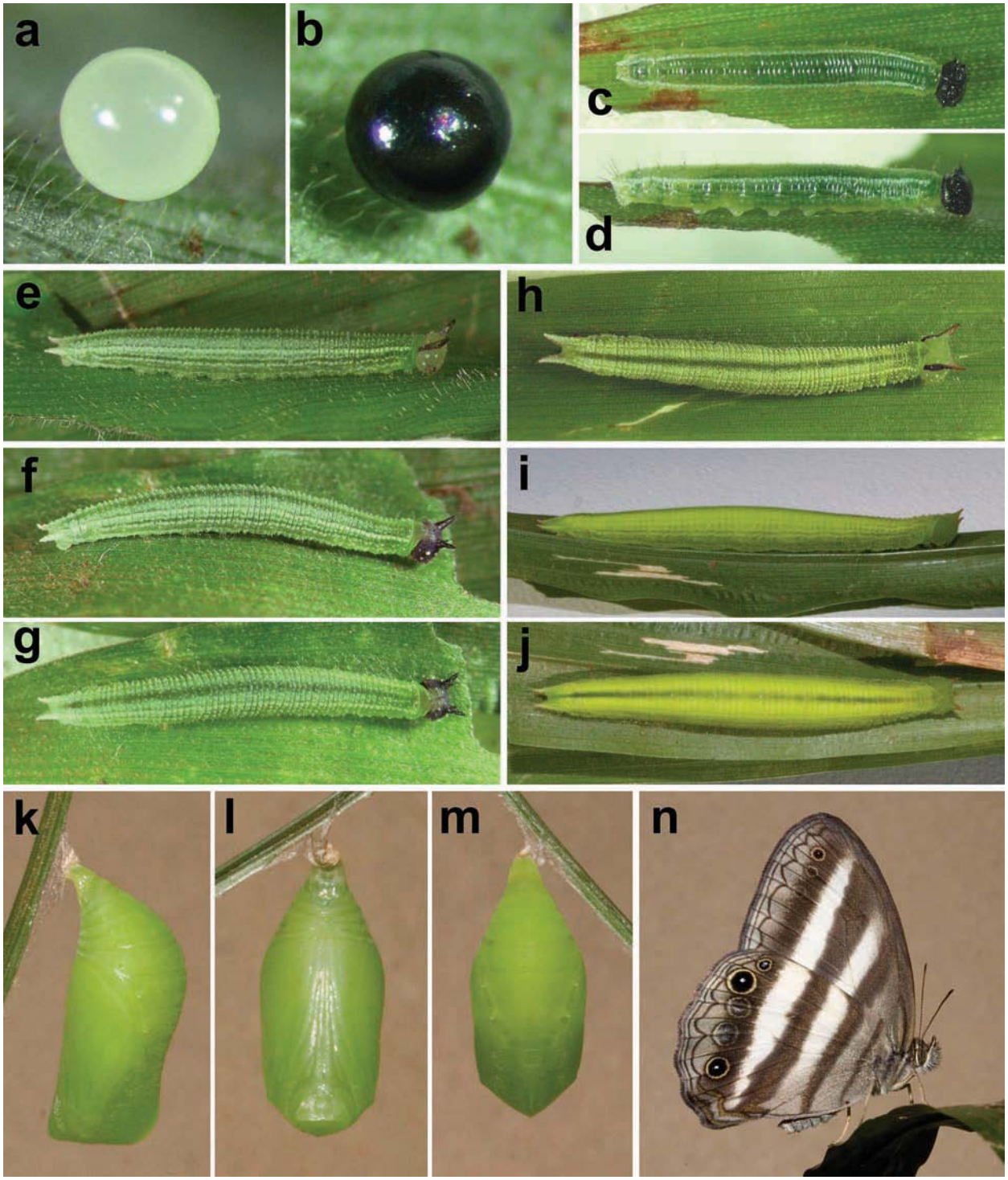


FIG. 1. Immature stages and adult of *Pareuptychia ocirrhoe interjecta*. **a, b.** egg, white and black; **c, d.** first instar, dorsal and lateral; **e.** light head capsule second instar, lateral; **f, g.** dark head capsule second instar, dorsal and lateral; **h.** third instar, dorsal; **i, j.** fourth (last) instar, lateral and dorsal; **k, l, m**. Pupa, lateral, ventral and dorsal; **n.** Adult male.

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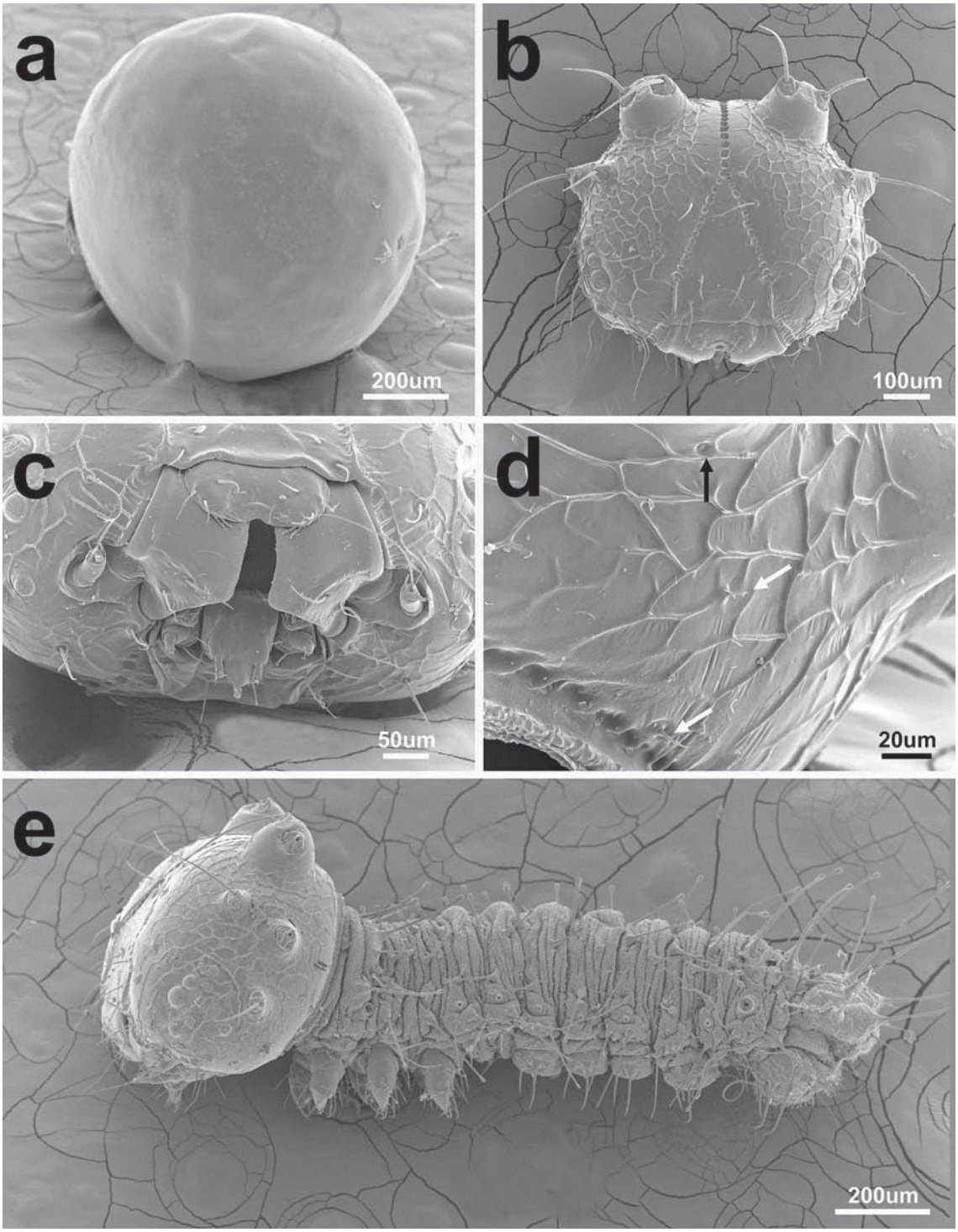


FIG. 2. Egg and first instar of *Pareuptychia ocirrhoe interjecta*. **a.** egg; **b.** Head capsule, general frontal view; **c.** Detail of frontal region; **d**. Detail of posterior region: white setae show microsetae and black seta show a pore; **e.** Early first instar, general lateral view.

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tape to aluminum stubs, and coated with gold/palladium with a Bal-tec® – SCD050 sputter coater (Leica Microsystems, Germany). Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas 2007). Terminology for early stages descriptions followed García-Barros & Martín (1995) for eggs and Stehr (1987) for larvae and pupae.

RESULTS

Description of immature stages. The following descriptions and measurements are based on material reared from one female from Serra do Japi, Jundiaí, São Paulo (material reared from three other localities gave similar results).

Egg (Figs. 1a,b – 2a). White, round, turning black 4 to 6 hours after oviposition. Height and diameter 0.94 – 0.96 mm; duration 5 – 6 days (n = 8).

First instar (Figs. 1c,d – 2b-e). Head capsule width 0.64 – 0.70 mm (mean = 0.66 mm; SD = 0.026 mm; n = 5); head scoli 0.08 – 0.10 mm (mean = 0.09 mm; SD = 0.008 mm; n = 5). Head black, with enlarged chalazae, bearing a pair of short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body light green, with white longitudinal stripes, turning dark green after first meal; caudal filaments very short. Legs and prolegs light green. Setae light green from T1 to A7, black from A8 to A10, all dorsal and subdorsal clubbed at tip (Fig. 2e). Maximum length 5 mm. Duration 6 – 7 days (n = 8).

Second instar (Figs. 1e,f,g). Head capsule width 0.90 – 1.00 mm (mean = 0.94 mm; SD = 0.052 mm; n = 5); head scoli 0.40 – 0.46 mm (mean = 0.43 mm; SD = 0.022 mm; n = 5). Head green with two short dark brown scoli on vertex (Fig. 1e,g); in some individuals head is mostly dark brown (Figs. 1f,g). Body green, striped longitudinally with white; caudal filaments short. Legs and prolegs light green. Maximum length 9 mm. Duration 4 – 8 days (n = 8).

Third instar (Fig. 1h). Head capsule width 1.38 – 1.46 mm (mean = 1.45 mm; SD = 0.056 mm; n = 5); head scoli 0.60 – 0.66 mm (mean = 0.62 mm; SD = 0.024 mm; n = 5). Head green, with two diverging very short scoli on vertex; these are reddish with a posterior dark brown line extending to head capsule. Body light green with a conspicuous dark green dorsal stripe and several additional longitudinal markings; caudal filaments short. Legs and prolegs light green. Maximum length 15 mm. Duration 7 – 9 days (n = 6).

Fourth (last) instar (Figs. 1i,j). Head capsule width 2.18 – 2.20 mm (mean = 2.20 mm; SD = 0.016 mm; n = 4); head scoli 0.74 – 0.82 mm (mean = 0.78 mm; SD = 0.034 mm; n = 4). Head green, with two diverging short scoli with reddish apex on vertex. Body light green with a conspicuous dark green dorsal stripe and several fine longitudinal stripes; caudal filaments short and reddish on apex. Legs and prolegs green. Maximum length 25 mm. Duration 7 – 10 days (n = 6).

Pupa (Figs. 1k,l,m). Short and smooth; entirely green; short rounded ocular caps; cremaster light green; dorsal abdomen smooth without projections. Total length 10.0 – 10.5 mm (n = 5). Duration 9 – 14 days (n = 4).

Behavior and natural history. *P. ocirrhoe interjecta* (Fig. 1n) is common in several environments in the Atlantic Forest from sea level to 1000 m altitude. Oviposition behavior was not observed in the field, but two solitary eggs, two larvae and one pupa were collected in the field in an unidentified native species of *Setaria* (Poaceae) in a shaded narrow trail inside the forest. Eggs were laid singly in the laboratory and larvae easily accepted the same hostplant mentioned above. Larvae were solitary in all instars and did not exhibit cannibalistic behavior (several larvae of different instars were reared together in small pots). Adults were easily observed along forest edges and in clearings flying low in the understory, rarely rising above 2 m above the ground. Flight was erratic and fast and, when disturbed, butterflies performed unpredictable aerial maneuvers with alternating flashes of white and dark, which makes them difficult to capture in flight. Adults feed on fermenting fallen fruits, feces and several other decaying substances, being never observed visiting flowers. However, there are reports of adults feeding on extrafloral nectar (Barbosa 2013; AVLF pers. obs.).

DISCUSSION

The immature stages of *P. ocirrhoe interjecta* are quite morphologically simple and similar to those of several other species of Neotropical Euptychiina: larvae lack body scoli, present short head horns and caudal filaments and pupae are short and smooth. The entirely green last instar, although not rare in Euptychiina, is apparently uncommon; most known last instars of small forest Euptychiina are predominantly brown or have color tones that make them cryptic on the background of dead leaves and stems (Singer et al. 1983, DeVries 1987, Murray 2001, Kaminski & Freitas 2008, Janzen & Hallwachs 2015). Species with similar green last instars and/or pupae includes other species of *Pareuptychia* (AVLF unpublished; Janzen & Hallwachs 2015), *Cepheuptychia cephus* (Fabricius, 1775), *Taydebis peculiaris* (A. Butler, 1874), *Zischkaia pacarus* (Godart, [1824]), *Godartiana muscosa* (A. Butler, 1870) (Figure 3) and *Forsterinaria pronophila* (Freitas & Peña 2006). Although *Cepheuptychia* and *Taydebis* are genera related to *Pareuptychia* in part of the "*Pareuptychia* clade" (Peña et al. 2010), the similarity in color pattern is not related to phylogenetic relationships. For example, other forest species belonging to the "*Pareuptychia* clade" present predominantly non-green last instars, including *Chloreuptychia arnaca* (Fabricius, 1776), *Megeuptychia antonoe* (Cramer, 1775) (Janzen & Hallwachs 2015), *Splendeuptychia furina* (Hewitson, 1862) and *Splendeuptychia doxes* (Godart, [1824]) (Freitas, unpublished). The greenish last instars of *Satyrotaygetis satyrina* (H. Bates, 1865) are quite distinct from those of *Pareuptychia*, especially in the longer, strongly diverging head horns.

The most remarkable and unique characteristic of the immature stages of *P. ocirrhoe interjecta* is the shiny black eggs. This trait, present also in other species of *Pareuptychia* (DeVries 1987, AVLF unpublished), is unique among all known Euptychiina (however, color

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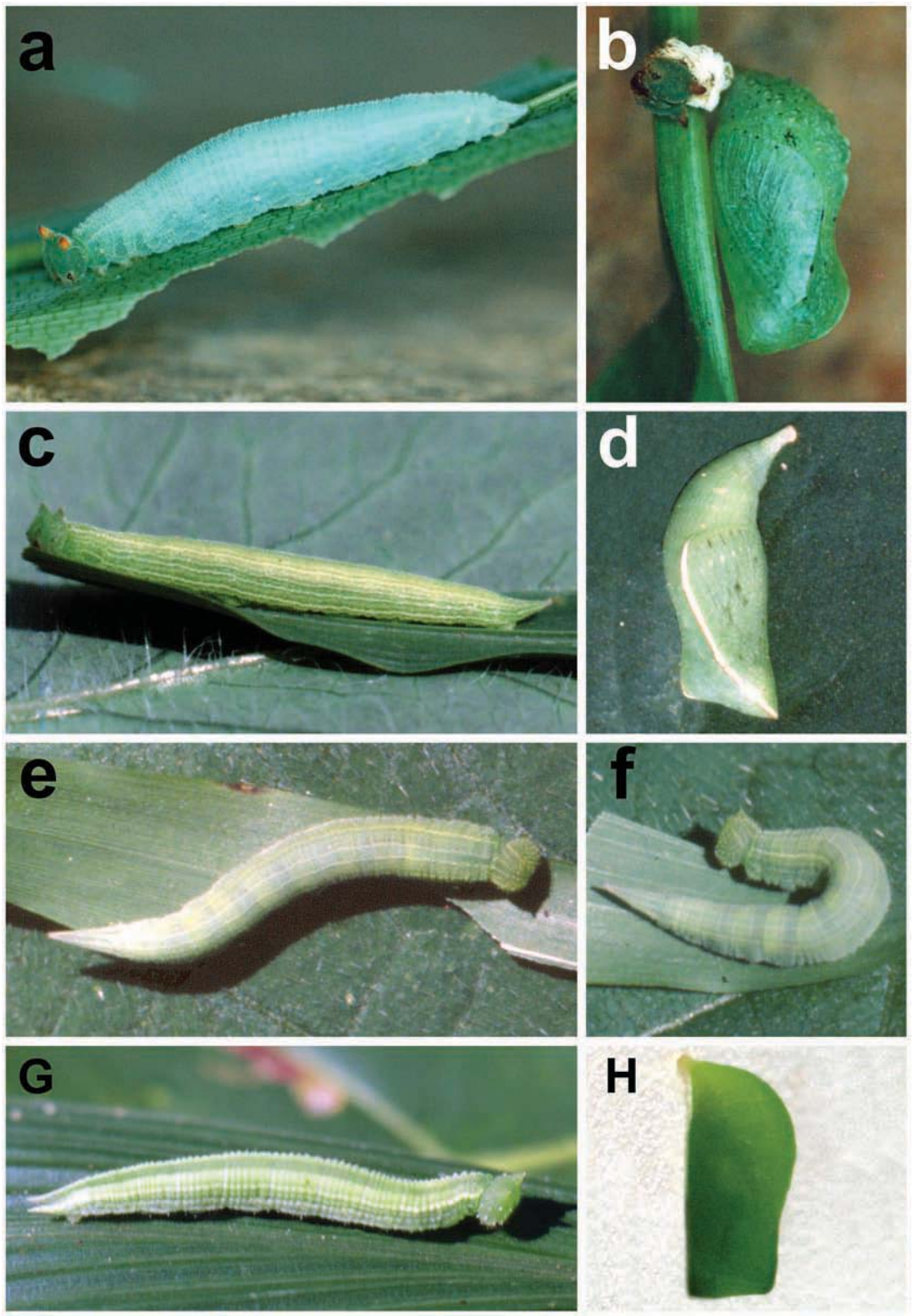


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PERFORMANCE OF WESTERN TENT CATERPILLAR (*MALACOSOMA CALIFORNICUM*) ON TWO COMMON HOST PLANTS, INCLUDING A NEW HOST PLANT RECORD

ELIZABETH E. BARNES*, SARAH GOSNELL§, CLAUDIA HALLAGAN§, KEELIA E. OTTEN§, LAINEY SLAYTER§, AND SHANNON M. MURPHY

Department of Biological Sciences, University of Denver, F. W. Olin Hall, Room 102, 2190 E. Iliff Ave., Denver, CO 80208

*Corresponding Author Email: elizabeth.barnes@du.edu
§Authors contributed equally to this research and are listed in alphabetical order

ABSTRACT. Tent caterpillars are generalists across their full host range, but display local host plant preferences. We present evidence for a new host plant record, wax currant (*Ribes cereum*), for western tent caterpillars (*Malacosoma californicum*) along the Colorado Front Range. We tested the suitability of wax currant as a host plant for western tent caterpillars as compared to chokecherry (*Prunus virginiana*), an abundant and commonly used host plant. We measured the density of tent caterpillar tents in areas where both host plants occur to assess host plant use. We reared tent caterpillar larvae on both host plants and measured fitness effects due to host plant quality (survival, pupal mass) and natural enemies (parasitism). We did not find a relationship between host plant abundance and use by tent caterpillars and found no evidence for a preference for either host plant. We found that western tent caterpillars do not differ in pupal mass when reared on chokecherry and on wax currant in a laboratory setting, but did vary in survival with greater survival on wax currant. We found no difference in parasitism rate for larvae collected from chokecherry or wax currant. Our results suggest that wax currant is a suitable yet previously unrecorded host plant for tent caterpillar larvae.

Additional key words: novel host record, host plant use, host plant preference, *Ribes cereum*, *Prunus virginiana*

The host plants that an adult female insect selects for oviposition can determine the fitness and even survival of her offspring (Thompson 1988, Renwick 1989, Jaenike 1990). Although generalist insects have a wider range of potential host plant choices available to them than specialist insects, larval fitness for generalists is still impacted by bottom-up (e.g. host plant secondary compounds, nutrient content) and top-down (e.g. predators, parasitoids) selective pressures (e.g. Greenblatt and Barbosa 1981, Shiojiri et al. 2002, Agrawal 2005). Some generalist female insects are still choosy in their host plant selection and may even act as specialists at a local level (Fox and Morrow 1981, Thompson 2005). Female insects that lay their eggs in batches and/or have larvae with limited mobility early in development are predicted to be under strong selection to be choosy in host plant selection. For species with larvae that are restricted to the plant where their mother laid them, poor host plant choice could lead to the loss of all of an individual's progeny (Knolhoff and Heckel 2014).

Western tent caterpillars, *Malacosoma californicum* Packard (Lasiocampidae), are generalists when considered across their full geographic range, but frequently show strong host plant preferences at a local level (Powell and Opler 2009). In midsummer, tent caterpillar adult females oviposit all of their eggs in one group on a tree branch (Fitzgerald 1995). The eggs overwinter on the branch and hatch in the early spring. Although it has not been verified, it is believed that the larvae primarily stay on the host plant that their mother selects (Fitzgerald 1995). It is therefore important that she select a plant that will allow her offspring to thrive. Tent caterpillars feed gregariously as larvae through their penultimate instar before dispersing. Larvae construct silk tents that last through the summer and, occasionally, into the next year. While tent caterpillars can have large-scale impacts on tree health, they rarely kill their host plants (Cooke et al. 2012).

Western tent caterpillars are commonly found on *Prunus* spp. (Fitzgerald 1995, Powell and Opler 2009) and are frequently found feeding on chokecherry (*Prunus virginiana* L. (Rosaceae)) on the eastern slope of the Rocky Mountains of Colorado (personal observation). Here we report on an additional common, but previously unrecorded, tent caterpillar host plant: wax currant, *Ribes cereum* Dougl. (Grossulariaceae). Whether wax currant is as commonly used as chokecherry or a high quality host plant has not been previously tested. Host plant preference may be revealed in the relationship between the relative abundance of a host plant in an area and the proportion of that host plant used by the herbivore (Fig. 1).

We had three research objectives. First, we assessed the frequency of host plant use by tent caterpillars for both chokecherry and wax currant by establishing transects and recording all plants with tent caterpillar tents. In addition, we counted the number of tents per plant and used these data in association with host plant abundance to assess host plant preference. Second, we

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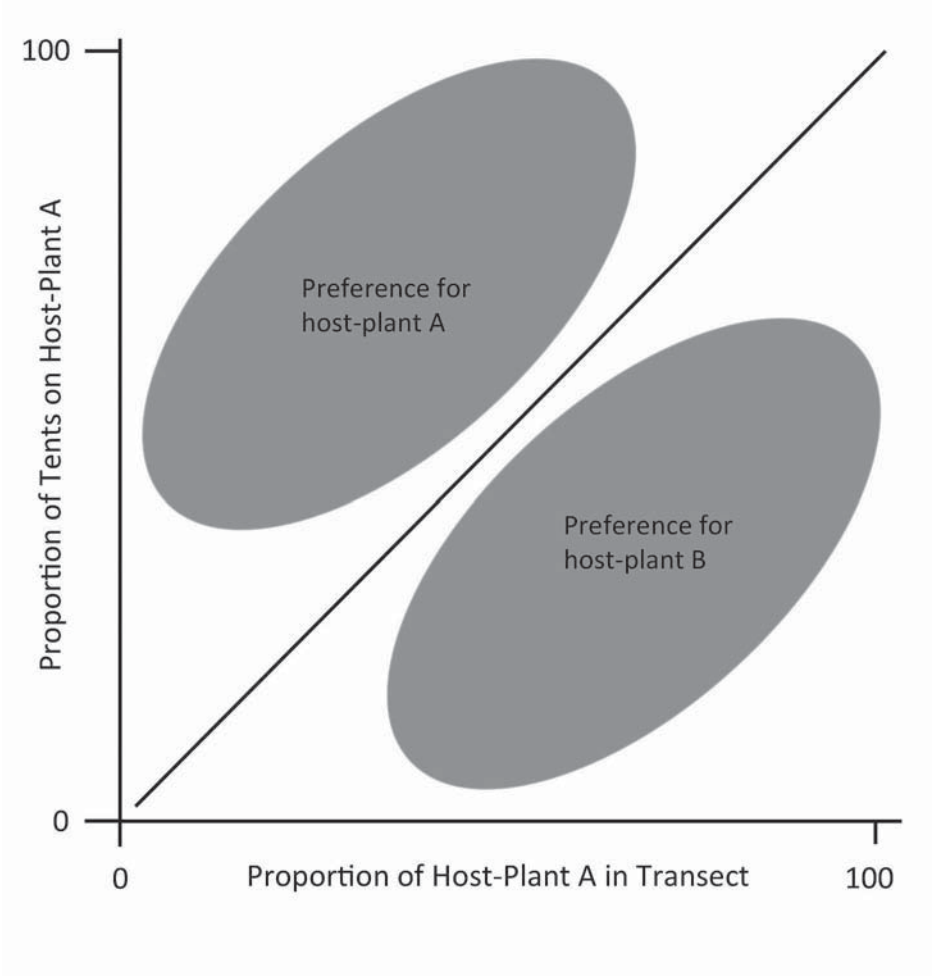


FIG. 1. Potential outcomes of host plant surveys testing host plant preference of tent caterpillars. We predicted that host plant preference would be reflected by the proportion of a species of host plant available in a transect (number of individuals of a focal plant species in a transect divided by the total number of potential host plant individuals in that transect) compared to the proportion of larvae that use that host plant (number of tent caterpillar tents on the focal host plant species divided by the total number of tent caterpillar tents in a transect). For example, if there is a low proportion of host plant A (wax currant) available compared to host plant B (chokecherry) and a high proportion of tent caterpillar tents found on host plant A, then a preference is demonstrated for host plant A because it is selected even when it is uncommon. However, if there is a high proportion of host plant A available and a low proportion of tent caterpillar tents found on host plant A, then this result suggests that host plant B is preferred. If there is no preference and tent caterpillars use plants in relation to their relative abundance, then we expect all data points to fall on the line (slope = 1). If female tent caterpillars express variation in host plant preference, then we would expect a random distribution of data with some individuals/populations preferring host plant A and others preferring host plant B.

measured tent caterpillar larval fitness on wax currant to test the quality of this newly-recorded host plant compared to a known tent caterpillar host plant, chokecherry. Third, we measured parasitism rate for tent caterpillars on the two host plants by recording the number and kind of parasitoids that emerged from larvae collected from each plant. Together this information allows us to determine whether wax currant is a superior-, inferior-, or equal-quality host plant for tent caterpillar larvae compared to the previously recorded host plant, chokecherry.

METHODS

We surveyed riparian areas in the foothills of the eastern slope of the Colorado Rocky Mountains. We conducted our experiments at four sites in Colorado: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Red Rocks (N39°39'56", W105°12'21"), and Centennial Cone Park (N39°45'42.3", W105°20'32.6"). At each site, chokecherry and wax currant bushes are dispersed throughout a mix of wooded areas and meadows. We selected these sites because they contain both focal

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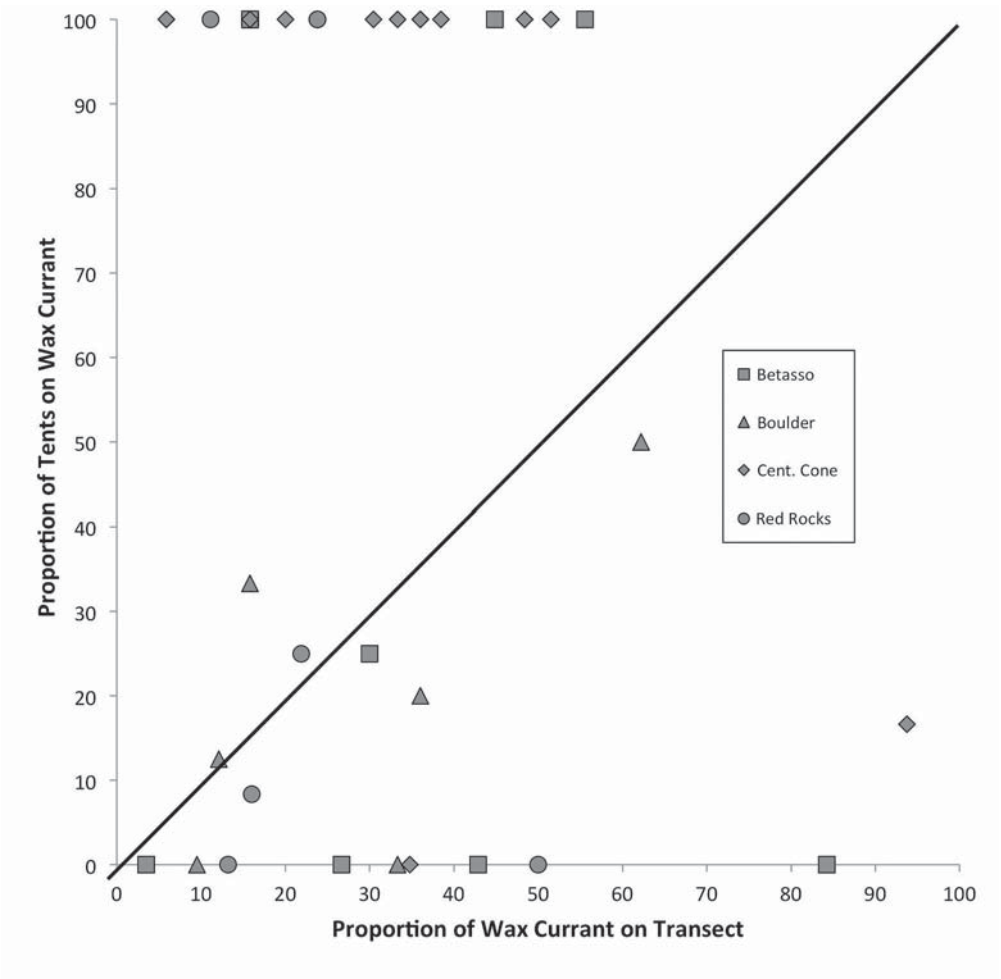


FIG. 2. Relationship between the proportion of wax currant available and the proportion tent caterpillar tents found on wax currant (χ^2 = 1.4, *df* = 1, N = 35, P = 0.23). Site are represented with the following symbols: Betasso Preserve: square, Boulder Canyon: triangle, Centennial Cone Park: diamond, and Red Rocks: circle.

plant species and numerous western tent caterpillar tents. We surveyed all sites from April to May 2015 after tent caterpillar larvae had constructed their tents.

Objective 1: Survey of Host Plant Use. To measure the abundance of chokecherry and wax currant at each site and the frequency that tent caterpillar larvae use each plant species as a host, we conducted plant surveys in the summer of 2015. Our transects were 20 m by 2 m and were centered at a focal chokecherry or wax currant plant with at least one tent caterpillar tent. We surveyed 18 transects with chokecherry as the focal species (Red Rocks: n=6, Centennial Cone: n=2, Boulder Canyon: n=7, Betasso Preserve: n=3), and 23 transects with wax currant as the focal species (Red Rocks: n=3, Centennial Cone: n=12, Boulder Canyon: n=3, Betasso Preserve: n=5) for a total of 41 transects. No transects overlapped and were at least 20m apart. For all chokecherry and wax currant plants within the transect area, we recorded the species, distance from focal tree, and the presence or absence of tent caterpillar tents; if tents were present on a plant, we also counted the number of tents.

Objective 2: Effects of Host Plant Quality on Tent Caterpillar Fitness. To test the effect of host plant quality on tent caterpillar fitness, we reared larvae on chokecherry and wax currant. In April, we collected 5–10 larvae in their second or third instar from 27 tents for a total of 235 larvae (Red Rocks: n= 71 larvae, Boulder Canyon: n=122 larvae, Betasso Preserve: n=42 larvae). We collected larvae from 16 chokecherry tents and 11 wax currant tents. We divided each tent into two groups; we reared half of the larvae from each tent on chokecherry, and half on wax currant. Thus, from each tent, half of the larvae were reared on their natal host

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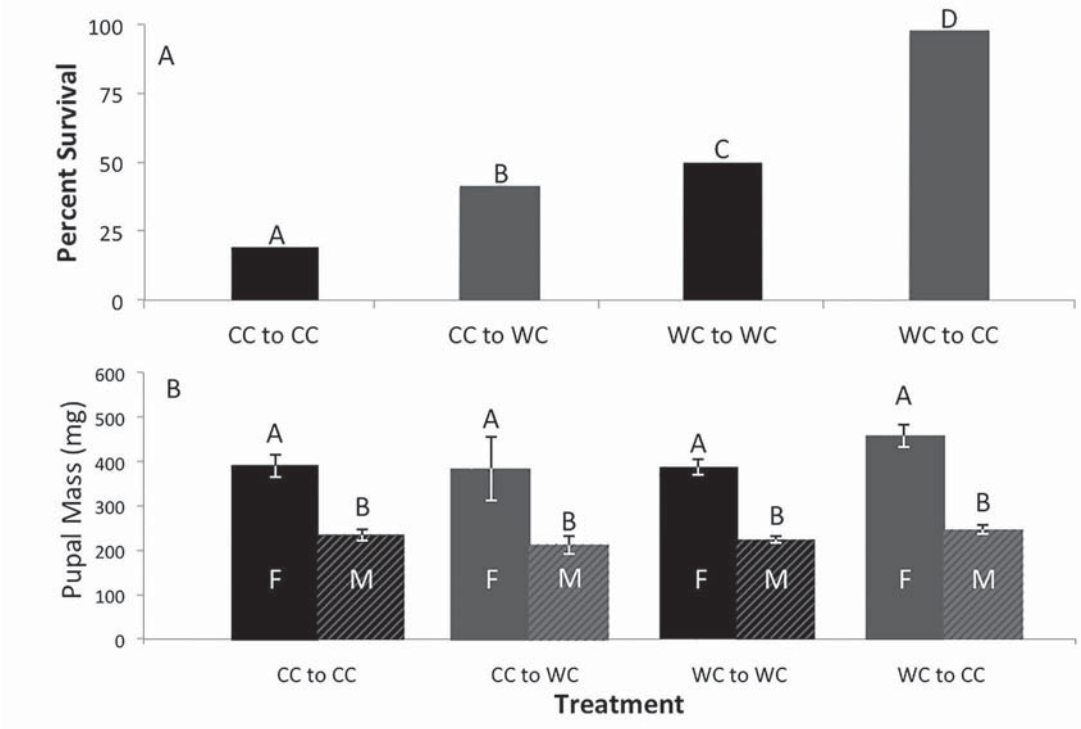


FIG. 3. Larval performance of tent caterpillar larvae reared on the four host plant treatments (chokecherry remaining on chokecherry (CC to CC), chokecherry switched to wax currant (CC to WC), wax currant remaining on wax currant (WC to WC), and wax currant switched to chokecherry (WC to CC) measured by A) larval survival (χ^2 = 66.29, *df* = 3, N = 235, P < 0.0001), B) mean female pupal mass (ANOVA: $F_{3,33}$ =1.75, P = 0.18) and mean male pupal mass (ANOVA: $F_{3,59}$ =2.01, P = 0.12). Female pupal mass is indicated with solid bars and the letter F. Male pupal mass is indicated with stripes and the letter M. Black bars indicate host plant treatments in which larvae remained on their natal host for the duration of the experiment and gray bars indicate host plant treatments in which larvae switched host plants mid-development. Error bars show ±1 standard error. Letters indicate the treatments that are significantly different.

plant while the other half were reared on the alternate host plant for a total of four treatments (chokecherry remaining on chokecherry, chokecherry switched to wax currant, wax currant remaining on wax currant, and wax currant switched to chokecherry); if we had only reared larvae on their natal host plant, any differences in larval performance between host plants could have been attributed to maternal effects since maternal lines would have been confounded with host plant. We reared larvae in deli containers in ambient conditions according to the methods outlined in Loewy et al. (2013). Larvae were reared in groups of 5–10 per container. We fed all of the larvae every three days or as needed with host plant that we collected from Betasso Preserve and Boulder Canyon Trail. All larvae were fed leaves from both field sites to control for variation in host-plants between sites.

We measured two proximate measures of fitness: pupal mass and survival. Pupal mass is a measure of fitness for Lepidoptera as heavier female pupae produce more eggs (including for *Malacosoma* spp.; Parry et al. 2001, Loewy et al. 2013). Survival is an important component of fitness because larvae that do not reach pupation are unable to reproduce. We measured pupal mass to the nearest 0.01 mg eight days after pupation using a using a Mettler-Toledo XP6 microbalance (Mettler-Toledo, Columbus, OH). We monitored all larvae daily for emergence. We used these fitness measurements to test the relative quality of each host plant type for tent caterpillars.

Objective 3: Tent Caterpillar Mortality from Parasitoids. To measure tent caterpillar mortality from parasitoids, we monitored the tent caterpillar larvae and pupae in Objective 2 for parasitoid emergence in the laboratory. We collected all parasitoids that emerged and have preserved them for future identification. We allowed parasitoids six months to emerge before the pupa was recorded as dead by other causes. We categorized parasitoids as either Diptera or Hymenoptera.

Data Analysis

For Objective 1, we analyzed results from the host plant survey by comparing the proportion of wax currant in each transect (number of wax currant plants in a

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transect divided by the total number of potential host plants in that transect) to the proportion of wax currant used by tent caterpillar larvae (number of tents on wax currant in a transect divided by the total number of tents in that transect). We plotted the results according to our prediction graph (Fig. 1) and counted the number of points that fell above and below the one-to-one line and performed a chi square test to determine if there was a preference for one host plant. We did not include any transects that only contained wax currant or chokecherry in this analysis as we were only interested in transects where the female moths had a choice between species of host plant. For Objective 2, we analyzed larval survival using a chi square test with host plant treatment as the independent variable and survival (yes/no) as the dependent variable. We analyzed the results from the lab fitness trial using an ANOVA with host plant treatment as the independent variable, and pupal mass was the dependent variable. The pupal mass data were normally distributed for both male and female pupae. For Objective 3, we collected too few parasitized larvae to analyze statistically and so report descriptive statistics. All data was analyzed using JMP Pro 11.0.0.

RESULTS

Objective 1: Survey of Host Plant Use. We found no significant relationship between relative host plant use and abundance for either wax currant ($R^2 = 0.083$, N= 27, P = 0.14) or chokecherry ($R^2 = 0.056$, N = 21, P = 0.29). We found no significant relationship between the proportion of wax currant in each transect and the proportion of wax currant used by tent caterpillar larvae (Fig. 2; $\chi^2 = 1.4$, *df* = 1, N = 35, P = 0.23). Compared to our prediction graph (Fig. 1), we found that our data points were dispersed randomly.

Objective 2: Effects of Host Plant Quality on Tent Caterpillar Fitness. We found a significant difference in larval survival between the four host plant treatments with larval survival in the wax current to chokecherry treatment 5 times greater than larval survival in the chokecherry to chockcherry treatment (Fig. 3 A; $\chi^2 = 66.29$, *df* = 3, N = 235, P < 0.0001). We found no significant difference in the mean pupal mass between the four host plant treatments for females (Fig. 3B; ANOVA: $F_{3,33} = 1.75$, P = 0.18) or for males (Fig. 3B; ANOVA: $F_{3,59} = 2.01$, P = 0.12).

Objective 3: Tent Caterpillar Mortality from Parasitoids. We recorded 6 parasitoid emergences from the 235 larvae that we collected: 3 Diptera (1 collected and reared from a larva on chokecherry; 2 collected and reared from larvae on wax currant) and 3 Hymenoptera (all collected from chokecherry; 2 reared from larvae on chokecherry and 1 reared from a larva on wax currant). The two flies recorded from wax currant both emerged from a single larva. Thus, while our sample size is too small to analyze statistically, we found 1 parasitized larva on wax currant (of the 125 that we collected; parasitism rate = 0.8%) and 4 parasitized larvae on chokecherry (of the 110 that we collected; parasitism rate = 3.6%).

DISCUSSION

Our results demonstrate that tent caterpillars neither preferentially use wax currant or chokecherry overall, nor use host plants in relation to their abundance. Instead, our results suggest that females vary in their host plant preference, with some individuals preferring chokecherry and some wax currant. We found no pattern in the relationship between the proportion of wax currant in each transect and the proportion of wax currant on which tent caterpillars tents were found. It is possible that because we counted established tents and not egg masses, we may have missed some early season mortality due to top-down (e.g. predation or parasitism) or bottom-up (e.g. host plant quality or host-larval asynchrony) factors. At our field sites, however, chokecherry and wax currant produce leaves at approximately the same time in the spring, limiting the possible influence of asynchrony between larvae hatching and bud burst (Barnes, personal observations). If the presence of tent caterpillar tents accurately reflects adult females oviposition, our findings suggest that females may select their host plant based on host plant traits or environmental effects not included in this study and that are currently unknown. For instance, perhaps intra-host variation in foliar quality for tent caterpillars is larger than inter-host variation. Furthermore, we currently know very little about the natural enemy communities associated with either of these host plants and how predators and parasitoids may affect tent establishment. Future research may help us to understand if tent caterpillar females have any preferences within or among their host plants, but our results currently suggest that they use wax currant and chokecherry equally.

Our larval fitness results demonstrate that adult tent caterpillar females do select wax currant for oviposition, and also that tent caterpillar larvae can thrive on wax currant even though it has never previously been recorded as a host plant. We found survival differences between chokecherry and wax currant, with wax currant being a higher quality host plant for tent caterpillars. Out of the four treatment groups, larvae reared on chokecherry had the lowest survival which was unexpected as it suggests that chokecherry is an inferior

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host plant despite chokecherry being well-known as a tent caterpillar host (Fitzgerald 1995, Powell and Opler 2009). Notably, we found that more larvae survived to pupation in the host plant treatments where we switched their host plants mid-development (wax currant switched to chokecherry and chokecherry switched to wax currant) than in the host plant treatments where we reared larvae on their natal host (chokecherry remaining on chokecherry and wax currant remaining on wax currant). This finding is interesting because switching hosts mid-development typically lowers or has a neutral effect on larval fitness in Lepidoptera (Bernays et al. 1994), with a few exceptions such as larvae that switch hosts for self-medication (e.g. Singer et al. 2009). Finally, we found no difference in pupal mass between host plants, which suggests that females from either host plant will be able to produce similar numbers of eggs.

Although we did not directly measure top-down fitness in our study, we found that 3.6% of the larvae collected on chokecherry were parasitized compared to only 0.8% of the larvae collected from wax currant. Although the sample size of these results is too small to form any concrete conclusions, this finding suggests that there may be differences in larval mortality from natural enemies between the two host plants. Further field trials to test top-down pressures will be required to determine if this pattern in differential mortality is broadly observed.

Our results suggest that wax currant is an adequate and frequently used host plant for tent caterpillars and our host-plant survey results do not show a clear preference between wax currant and chokecherry. Despite *Prunus* spp. being a well established tent caterpillar host plant (Fitzgerald 1995, Powell and Opler 2009), we found no evidence that chokecherry is a more suitable host plant in terms of larval fitness due to bottom-up (leaf quality) or top-down (parasitism rate) factors. Additional work should assess the fitness of larvae on both host plants in the field and test whether mortality from natural enemies such as predators varies between the hosts. Our results establish wax currant as a suitable host-plant for western tent caterpillars.

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NOTES ON THE BEHAVIOR AND DISTRIBUTION OF THE DAY-FLYING MOTH, *HETERUSIA ATALANTATA* (GUENÉE, [1858]) (LEPIDOPTERA, GEOMETRIDAE, LARENTIINAE), WITH SPECIAL REFERENCE TO MEXICO.

FERNANDO HERNÁNDEZ-BAZ

Facultad de Biología-Xalapa, Universidad Veracruzana, Zona Universitaria, Circuito Gonzalo Aguirre Beltrán, s/n, C.P. 91000, Xalapa, Veracruz, México; e-mail: fhernandez@uv.mx; ferhbmx@yahoo.com.mx

JORGE M. GONZÁLEZ

California State University, Fresno, Department of Plant Sciences, Fresno, CA 93740-8033 (Research Associate, McGuire Center for Lepidoptera & Biodiversity), USA, e-mail: gonzalez.jorge.m@gmail.com.

AND

CHARLES V. COVELL JR.

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, P. O. Box 112710, Gainesville, Florida 32611-2710, USA. e-mail: ccovell@flmnh.ufl.edu

ABSTRACT. Collecting and observation of the diurnal geometrid, *Heterusia atalantata* (Guenée, [1858]), in Natura Park, Veracruz by the first coauthor led to an interest in the distribution and behavior of this species in Mexico. Records from the literature and several Mexican collections as well as the McGuire Center for Lepidoptera and Biodiversity in Florida have resulted in these notes on the distribution, altitudinal occurrences and behavior of this species.

Additional key words: inchworm, diurnal, neotropics

Moths of the family Geometridae are cosmopolitan; however, a large majority of them are found in the neotropics (Heppner 1991, Scoble 1995). Even though most species are nocturnal and attracted to lights, some are day-flying and active during the morning mainly inside the canopy of humid forests or in open areas when conditions are misty and cloudy (Powell & Opler 2009). Very rarely are they seen in sunny open spots or in the afternoon along open spaces (Hernández-Baz unpublished)

The richness of Geometridae is substantial. More than 20,000 species have been described worldwide, and some 1,400 species are from America north of Mexico (Munroe 1982, Powell & Opler 2009). Even though there is no checklist for Mexican species, Heppner (2002) has estimated that there should be between 2,500–3,000 Geometridae in the country. Hernández-Baz & Iglesias (2001) reported 350 species in the state of Veracruz.

The genus *Heterusia* Hübner 1831 was originally described with *Heterusia conduplicaria* Hübner 1831, as type species. The syntypes were collected in Rio de Janeiro, Brazil. The genus is exclusive to the Americas (Druce 1898; Parsons et al. 1999) and includes 87 species (Scoble, 1999), with only three species previously recorded from Mexico: *Heterusia atalantata* (Guenée, [1858]); *Heterusia discordata* (Guenée, [1858]); and *Heterusia substriata* Dyar, 1910, according to the information gathered in the database "Polilla" attached to the base collection Semarnat/Cites/CP-0026-Ver/05 (CPFHB) (Hernández-Baz 2012).

Besides being a day-flying moth, not much is known about the life history, behavior, natural enemies, or trophic relationships of *H. atalantata* (BAMONA 2015). Its known overall distribution is based on isolated visual records and a small number of specimens deposited in insect collections. As part of the larger project "Inventory of the lepidopterans of the state of Veracruz, Mexico" we have focused on a detailed study of the moths found in protected areas of Mexico. One such protected area is Parque Natura, located in the central mountains of the state of Veracruz, in the Xalapa municipality (96°53'39.82 N 19°30'42.26 W) with an altitude between 1289 and 1331 m. The predominant vegetation of this protected area is a secondary forest arisen in abandoned lands that were used once in agriculture (*Acahual maduro*) with scattered coffee plantations and some native mature trees of Mountain Cloud Forests (GDV 2001, Sánchez & Gándara 2011). This park is the site of the first author's observations on the behavior of *Heterusia atalantata*.

Most day-flying moths are not well understood, and this is particularly true for most Mexican Lepidoptera. Even though a large amount of the information is based

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on published articles and books, as well as information on specimen labels held in insect collections, detailed notes about these dayflying creatures are uncommon. Works like that of Beebe & Fleming (1951) who studied migration of dayflying moths in Portachuelo Pass located in the Henri Pittier National Park, Venezuela, are rare (Sandoval et al. 2008). Thus, the main objective of this work is to provide information about the dayflying *Heterusia atalantata* (Guenée), including details on its geographic distribution and natural history.

Materials and Methods

The information presented herein comes from four main sources:

a) Specimens collected by the first author (FHB) in Parque Natura, Veracruz, Mexico. They were collected from 08:00 to 17:00 hrs using a traditional butterfly net from 21 to 25 May, 2015. Once collected, the specimens were killed inside a tightly closed glass jar charged with Ethyl Acetate ($C_4H_8O_2$) to minimize scale loss. Once in Xalapa, the specimens were pinned, spread and dried with techniques described by Steyskal et al. (1986). In addition, photographs were taken of each specimen collected, both in the field and also in the laboratory after being pinned and mounted. The camera used was a Sony Cyber Shot (10 megapixels). The identification of the specimens was first done by use of the keys in Triplehorn and Johnson (2005) and later compared with identified specimens at the Museum of Natural History (Museo de Historia Natural) in the City of México (MHNCM). The specimens were later deposited in the Lepidoptera collection in the School of Biology, Universidad Veracruzana, Xalapa, Veracruz. They were registered as DF-CC-276-13 by the Secretary for Environment and Natural Resources (Secretaría de Medio Ambiente y Recursos Naturales - SEMARNAT) of Mexico. All information from the collected specimens was included in the database "Polilla" (Hernández-Baz 2012). Specimens were collected under the permit for scientific collecting, license FAUT-0194. (SEMARNAT).

b) Records from specimens in the following insect collections: Natural History Museum of the City of Mexico (MHNCM); National Collection of Insects, Biology Institute of the National University of Mexico (CNIIBUNAM); Lepidoptera Collection of the Biology School of Universidad Veracruzana (UV-FBX-CL); Entomology Collection of the Tropical Biology Station Los Tuxtlas, of Universidad Nacional Autónoma de México (EBTLT-CE); a private Lepidoptera Collection (SEMARNAT / CITES/CP-0026-VER/05) in Xalapa, Veracruz, México (CPFHB); and the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida (MGCL).

c) Literature and online sources. Pertinent literature was reviewed in the libraries of the Biology Institute and Tropical Biology Station Los Tuxtlas, from the National Autonomous University of Mexico; Biology School, Universidad Veracruzana; Madden Library, Fresno State; and Natural History Museum of the City of Mexico. The obtained data were corroborated and searched in numerous scientific information systems such as BioOne, Wiley Interscience; Blackwell Publishing, Ebscohost, Isi-Thompson Scientific, Latin Index; and Biodiversity Library.

d) Map Generation: All records (data from bibliography and collections) were georeferenced by means of the Mexican National Institute of Statistics, Geography and Computer Science catalogue of names and the 1:250000 topographic map of Mexico 1:250 (INEGI 2012). For the Americas data, we used information obtained in http://www.google.com/earth/ The information taken from the "Polilla" database was converted into sexagesimal data for inclusion in a geographical information system for the Arc View 2.0 program (Esri 1998).

Results and Discussion

Label data from Mexican specimens examined:

DISTRITO FEDERAL: May, MHNCM, code number 10616, 2 specimens, Col. Roberto Müller (Díaz 2004). GUERRERO: Cacahuamilpa, 20 July 1956, Kent Wilson leg. NUEVO LEÓN: Linares, Porfirio Díaz, -99.58252 N. La. / 24.82906 W. Long., Cat. 494701, ID 917412, recorded 4-i-2014, Juan Cruzado Cortes (GBIF 2015); Monterrey, -99.58274 N. Lat. / 24.82839 W. Long., Cat. 581730, ID 1024418, recorded 19-iii-2014, Juan Cruzado Cortes (GBIF 2015); Monterrey, -99-90912 N. La. / 24.92953 W. Long., Cat. 624857, ID 1024180606, recorded 13-iv-2014, Juan Cruzado Cortes (GBIF 2015); Linares, -99.58291 N. La. / 24.82885 W. Long., Cat. 612914, ID 1024180527, recorded 3-iv-2014, Juan Cruzado Cortes (GBIF 2015); Monterrey, -100.26295 N. La. / 25.55762 W. Long., Cat 280714, ID 456182, recorded 13-ix-2006, Carlos Velazco; Santa Rosa Canyon, Km 28, route 5 S of Linares, 17 July 1988, C. L. Smith leg.; 4 km. NE of Santiago, Predela Cueva, 14 July 1974, Kate Bozy & E.C. Olson leg.; Cola de Caballo, 610 M elev., moist forest, 3 Sept. 1973, Station 1973-64, Lee D. & Jacqueline Y. Miller leg.; ditto, in malaise trap, 18-20 June 1975, H. V. Weems leg.; Highway 60, 9 miles E of Iturbide, 15 Aug. 1967, J. Scott leg. PUEBLA: 10 Km. South of Petlaloingo (4 Km. S Chita), 3-6 July 1992, Hans Muhle leg. QUERETARO: Cadereyta de Montes, -99.80419 N. La. / 20.68639 W. Long., Cat. 798815, ID 1434649,

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recorded 23-vii-2014, José Belem Hernández Díaz (GBIF 2015); SAN LUIS POTOSI: Cd. Valles, 14 Oct. 1976, leg. E. C. Knudson. TAMAULIPAS: Ciudad Victoria, -99.17161 N. La. / 23.05056 W. Long., Cat. 605370, ID 1061812, recorded 29-iii-2014, Juan Cruzado Cortes (GBIF 2015); San Fernando, -98.14546 N. La. / 24.84622 W. Long., Cat. 1064804, ID 1088895865, recorded 2-xi-2014, Jumtal (GBIF 2015): Miquihuana Road la Meca, -99.60275 N. La. / 23.59958 W Long., Cat 1256240, ID 2337534, recorded 4-viii-2008 Diana Terry Hibbitts (GBIF 2015). 0.8 miles NW Gomez Farias, 280 – 700 M elev., moist forest, 20 Feb. 1969, Station 40, Acc. 1969-4, L.D. & J.Y. Miller leg.; 26 Km. South of Cd. Victoria, highway 85, 16 Oct. 1984, leg. H. D. Baggett. VERACRUZ: Xalapa: Parque Natura, 96°53'39.82 N. Lat; 19°30'42.26 W. Long, 1290 m collecting time: 08:00- 10:00 hrs. 2015-v-21 day-flying, 4 ♂,1 ♀, F. Hernández-Baz (UV-FBX-CL); Coatepec, 3 km al Sur Palacio Municipal. 1180 m, 2015-v-22, 19º 26' 54"W / 96º 57' 25"N. Collecting time: 09:00 hrs. Day-flying. 1 ♂, F. Hernández-Baz. (UV-FBX-CL); Xico: 1 km al norte cascada Texolo. 1300 m. 2015-v-23, 19º 25' 12"W / 97º 00 30"N. Cloud forest, collecting time: 10:00 hrs. Day-flying, 2 ♂ F. Hernández-Baz. (UV-FBX-CL); Teocelo: km 1, road Teocelo-Xico. 1138 m. 2015-v-24, N 19º 23' 39" W. / 96º 58 44" N. Cloud forest. Collecting time: 10:00 hrs. Day-flying. 1 ♂, F. Hernández-Baz. (UV-FBX-CL). Presidio, 1 July 1955 and 1 July 1965, leg. H. L. King.

Species Distribution

Heterusia atalantata (Guenée) (Geometridae: Larentiinae) (Fig. 1a-d) was originally described[as *Scordylia atalantata* (Guenée, 1857) based on five specimens (2 ♂♂, 3 ♀♀) from Brazil. Its general recognized distribution extends from the southern Rio Grande Valley of Texas, U.S.A., through Mexico, Central America and South America to Southern Brazil (Guenée [1858]; Druce 1891-1900; Beebe & Fleming 1951; Knudson & Bordelon 2008) (Fig. 2).

Druce (1891–1900) mentioned the species from: México [Tamaulipas State (Ciudad Victoria), Veracruz State (Atoyac, Orizaba), Guerrero State (Venta de Zopilote)]; Guatemala [San Gerónimo]; Panama [Vera Paz State]; Costa Rica; Colombia [Bogota]; Venezuela; and Brazil. Díaz (2005) adds the Mexican locality of Distrito Federal (D. F.) based on two specimens deposited in the Roberto Müller Collection (MHNCM). There are five specimens deposited in the National Collection of Insects of the Institute of Biology, UNAM (CNIIBUNAM). These specimens came from three different localities within the city of Mexico, Distrito Federal (D.F.): Botanical Gardens of the UNAM, Xochimilco, and el Ajusco. The latter is located above 3000 meters and should be considered the highest recorded altitude for *H. atalantata*. Records of the species were known within the states of Nuevo Leon, Tamaulipas and Queretaro (GBIF 2015).

In the Lepidoptera Collection of the Biology School of Universidad Veracruzana in Xalapa (UV-FBX-CL) there are nine specimens of *H. atalantata*. Five of them were collected at Parque Natura, Xalapa, Veracruz; one male from Coatepec; two males from Xico; and one male from Teocelo. These localities are found along the Mountainous Cloud Forest of the State of Veracruz, México except for the Parque Natura which was in the acahual and coffee plantations previously described.

A total of 35 specimens have been located and found from Mexico, while seven have been reported from other countries in the Americas. Nine of the Mexican specimens are held in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida (MGCL). Five of them were collected in Nuevo León State, two from Tamaulipas, and one each from the states of Guerrero, Puebla and Veracruz.

As our obtained data indicate, *H. atalantata* populations have a preference for mountain cloud forests and all collecting sites coincide with mountainous regions of Mexico. The collecting sites of the species we have studied are in the plateaus of the states of Nuevo Leon and Queratoro and continue to Tamaulipas and Veracruz within the Eastern Sierra Madre mountains and extend from there to the transversal volcanic belt that goes from Orizaba, Veracruz, to Puebla (Fig. 2). Specimens collected from Central and South American countries come also from sites located in wet and cloud forests.

A geographical distribution similar to *H. atalantata* was found for the species *Apeplopoda mecrida* (Druce) (Erebidae: Euchromiina) in Mexico (Hernández-Baz et al. 2012). It appeared that both species are using the mountainous regions of Mexico as a biological corridor *sensu* Halffter (1964, 1987) and their populations are found South East by the Southern Sierra Madre entering Guatemala through the Chucumanes Sierra (Hernández-Baz et al. 2012) and then into the localities of San Geronimo and Vera Paz [as reported by Druce (1891-1900)]. Altitudinally, the range of distribution of the species extends from 2,000 to 3,000 m.

In the Henri Pittier National Park, located along the North Central region of the Northern Cordillera of Venezuela, 126 species of day-flying moths, including 8 Geometridae were collected (Beebe & Fleming 1951; Sandoval et al. 2008). Among those, specimens of *H. atalantata* were found flying through Portachuelo Pass (1,100 m) from May to July, a reduced time frame

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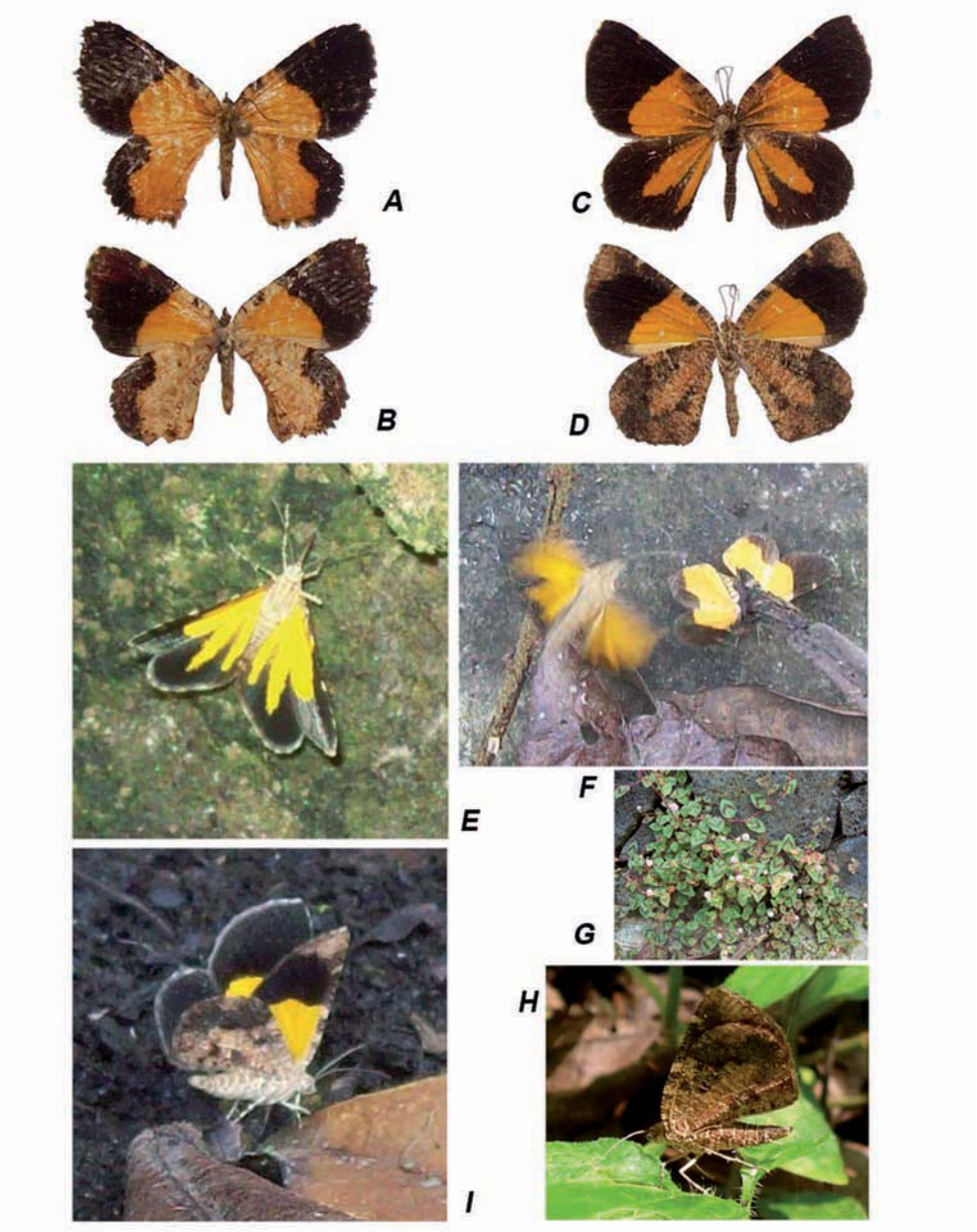


FIG. 1. **A**) *Heterusia atalantata* ♂ dorsal view; **B**) *H. atalantata* ♂ ventral view; **C**) *H. atalantata* ♀ dorsal view; **D**) *H. atalantata* ♀ ventral view. (Both ♂ and ♀ specimens were deposited in the Lepidoptera Collection of the Biology School, Universidad Veracruzana, México) (UV-FBX-CL); **E**) *H. atalantata* ♂ perched on wet rock (notice the extended proboscis); **F**) *H. atalanta* ♂ fluttering around and above a ♀; **G**) *Polygonum capitatum* (Polygonaceae) plant; **H**) Imago of *H. atalanta* perched on a low plant along the undergrowth of Parque Natura, Veracruz, Mexico; **I**) *H. atalanta* ♂ sipping salts from the ground.

contrasted to the flight season in Mexico, which is longer and extends from March to August (Beebe & Fleming 1951).

Biology and Behavior

The life history of *H. atalantata* is basically unknown (BAMONA 2015). Unfortunately, labels from collected specimens held in insect collections surveyed provided us with little information. Besides, published sources referring to this species do not include many biological details. In relation to the flying behavior of the species, it has been reported that it flies only after 07:30 hrs, in Portachuelo Pass, Rancho Grande, Venezuela (Beebe & Fleming 1951). In Parque Natura, Veracruz, Mexico, some individuals were found flying as early as 08:00 hrs, above a stone wall bordering the ecotone of oak trees (Fagaceae) and grasses (Poaceae). Adults were active

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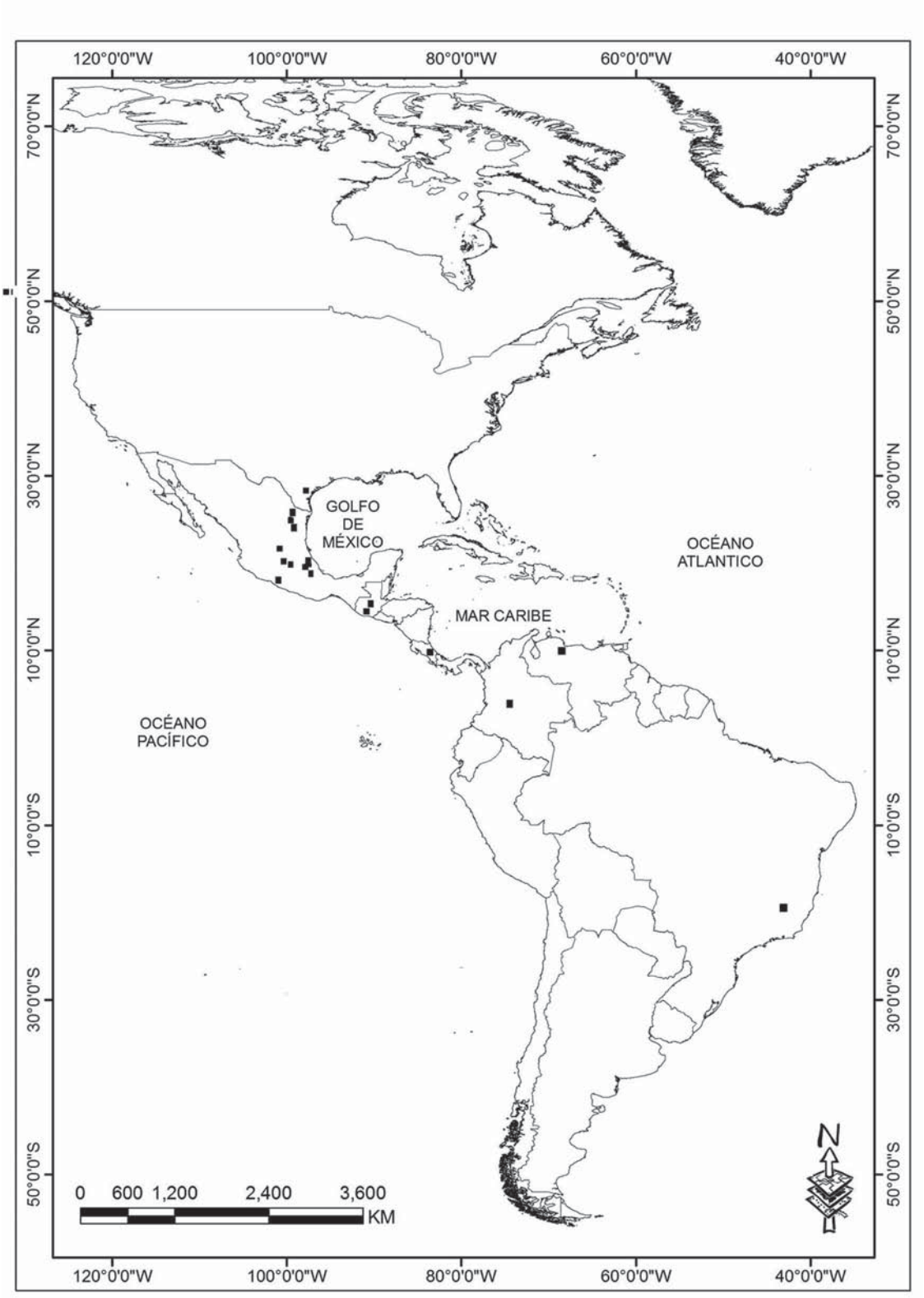


FIG. 2. Distribution of *Heterusia atalantata* in the Americas, with special reference to Mexico. These data come from specimens reported and collected from 1889-2008. Source: Data Base "Polilla".

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from 08:00 to 11:20 hrs. Females settled on rocks and lifted their abdomens while males approached closer and fluttered above and around them. No copulation was observed. Most of the time, males settled on wet rocks or on the ground to sip water. Most males also settled on inflorescences of *Polygonum capitatum* Buch.-Ham. Ex D. Don (Polygonaceae) from 10:00 to 11:00 hrs (Figs. 1e-i).

When the sun was at its highest around noon (~12:00 hrs), males and females abandoned the ecotone and flew into the forest, perhaps looking for a more humid environment, where they perched on the reverse of leaves until 17:00 hrs. Then they fluttered along open areas, avoiding direct light exposure. In the Barranca de Teocelo (Veracruz, México), isolated individuals of *H. atalantata* have been observed flying in the humid and shadowy areas from 09:00 to 17:00 hrs. We could deduce then that *H. atalantata* is strongly associated with the high humidity levels provided by the cloud forests found between 1,100 and 2,800 m altitude ranges in the Americas where the species lives.

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IMMATURE STAGES OF *ARCHONIAS BRASSOLIS TEREAS* (GODART) (PIERIDAE: PIERINI), WITH NOTES ON INTERSPECIFIC INTERACTIONS BETWEEN MISTLETOE BUTTERFLIES

LUÍSA L. MOTA, ANA K. SILVA, ANDRÉ V. L. FREITAS

Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, Campinas, São Paulo, 13083-970, Brazil; email: lulismota@yahoo.com.br, email: akristinas@gmail.com, email: baku@unicamp.br

AND

LUCAS A. KAMINSKI

Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Porto Alegre, RS, 91501-970, Brazil; email: lucaskaminski@yahoo.com.br

ABSTRACT. The immature stages of the Neotropical mistletoe butterfly *Archonias brassolis tereas* (Godart) (Pieridae: Pierini) are described and illustrated for the first time from the Atlantic Forest of Southeast Brazil. Eggs are laid in clusters on leaves of the mistletoe *Phoradendron* sp. (Viscaceae). Larvae are gregarious and underwent five instars. Mature caterpillars present yellow aposematic color pattern; pupae are yellow with black dorsal projections. Morphology, host plant use and behavior of immature stages are similar to species in the *Catasticta* group. An additional species of mistletoe butterfly, *Brangas* sp. (Lycaenidae), with gregarious and aposematic yellow caterpillars was found in sympatry on the same leaves of the host plant. These findings suggest that both interspecific competition and larval mimicry are important traits in the ecology and evolution of mistletoe butterflies.

Additional key words: Aporiina, *Brangas*, coexistence, defensive behavior, Eumaeini, Lycaenidae, Müllerian mimicry

The Pieridae butterflies are particularly diverse in the Neotropical region, but information on their natural history and morphology of immature stages are relatively scarce or incomplete (DeVries 1987, Braby et al. 2007). Recently, contributions on the natural history of pierid species that utilize mistletoes (aerial-stem hemiparasitic plants on the order Santalales) as host plants have been richly described and illustrated (e.g., Braby & Nishida 2007, 2010, Kaminski et al. 2012, Volkmann & Núñez Bustos 2015). The New World mistletoe feeding pierids belong to two independent lineages: 1) the *Hesperocharis* group (Anthocharidini), and 2) the *Catasticta* group (Pierini), which include six genera: *Melete* Swainson, *Pereute* Herrich-Schäffer, *Leodonta* A. Butler, *Catasticta* A. Butler, *Charonias* Röber, and *Archonias* Hübner (Braby & Nishida 2010).

The genus *Archonias* is composed of a single polytypic species, *Archonias brassolis* (Fabricius), which is found from southern Mexico to northern Argentina (Lamas 2004, Braby et al. 2007). This species is found in tropical forests from sea level to 1200 m (DeVries 1987, Le Crom & Llorente-Bousquets 2004, Braby & Nishida 2011, AVLF & LAK, pers. obs.). Adults of all 12 described subspecies are involved in mimetic rings with aposematic butterflies in the genus *Parides* Hübner (Papilionidae) and *Heliconius* Kluk (Nymphalidae) (DeVries 1987).

The phylogeny of the Aporiina indicates that *Archonias* and *Charonias* are sister genera (Braby et al. 2007, Wahlberg et al. 2014), and this is precisely the only lineage for which early stages have not been described. The present work aims to provide morphological and behavioral descriptions of the immature stages of *A. brassolis tereas* (Godart). In addition, we discuss the possibility of larval mimicry and interspecific competition among mistletoe butterflies.

MATERIAL AND METHODS

In May 24, 2011, an egg cluster with 26 eggs of *Archonias brassolis tereas* was collected on a leaf of the mistletoe *Phoradendron* sp. (DC.) Naudin. (Viscaceae), which was parasitizing a *Dodonaea viscosa* Jacq. (Sapindaceae) tree, in the "Reserva Municipal Biológica da Serra do Japi" (~1,100 m a.s.l.) (23°14'S, 46°56'W). This area consists of semideciduous, mesophytic forest located in the municipalities of Jundiai and Cabreúva, in the state of São Paulo, Southeastern Brazil. The area includes nearly 28,000 ha of a mosaic of primary and, mainly, secondary forests in diverse stages of succession, in altitudes that varies from 700 m to 1,300 m a.s.l. A complete and detailed description of the area can be found in Morellato (1992).

Eggs were found in a completely grazed leaf, covered by feces of an undescribed species of *Brangas* Hübner (Lycaenidae). These eggs were collected and maintained in the laboratory. As soon as *Archonias* larvae hatched, they were separated from *Brangas* caterpillars and placed in plastic pots, where they were reared with host plant leaves offered ad libitum. Pots were cleaned daily, and data on behavior and development times were taken for all stages. Some eggs and larvae of the first and last instars were separated,

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fixed in Dietrich's solution and used for morphological analysis. Shed head capsules of all stages were stored for measurements. Voucher material of the immature stages and adults were deposited at Museu de Zoologia "Adão José Cardoso" (ZUEC), Universidade Estadual de Campinas (UNICAMP), Campinas, São Paulo, Brazil.

Measurements and general morphological observations were made with a Leica® EZ4 stereomicroscope equipped with a micrometric scale. Head capsule width of larvae was measured as the distance between the most external stemmata (following Kaminski et al. 2012); maximum total length for both larvae at the end of the instar and pupae corresponded to the distance from head to posterior margin of the tenth abdominal segment in dorsal view. Terminology for early stage descriptions follows Braby & Nishida (2007, 2010).

RESULTS

Description of immature stages

Egg (Fig. 1). 1.2 mm high, 0.6 mm diameter (n = 2); white, bottle-shaped, with flattened basis and apex much narrower than the middle width. Chorion with numerous longitudinal ribs and thinner weakly marked horizontal ribs. Apical rim with 5 to 7 prominent pale nodules. Micropylar area smooth. Duration ≥ 3 days (n = 5).

First instar (Fig. 2). Maximum length 2.6 mm; head capsule width 0.43–0.47 mm (n = 4). Head black, with long translucent setae. Rectangular prothoracic shield, with longer side transversal to the body, bearing three pairs of translucent setae. Body pale yellow, pinkish in the last abdominal segments. Primary setae long and translucent, the dorsal group with a fluid-droplet on its tips. Anal shield light grey. Duration 7 days (n = 5).

Second instar (Fig. 3). Maximum length 4.5 mm; head capsule width 0.70–0.71 mm (n = 3). Head and prothoracic shield black with white setae; body greenish-yellow, more vivid than first instar, meso and metathorax reddish. Numerous pale spots and white setae inserted in white paniculum through the body. Anal shield light grey. Duration 9–10 days (n = 5).

Third instar (Fig. 4). Maximum length 7.5 mm; head capsule width 1.16 mm (n = 1). Head and prothoracic shield black with white setae; body greenish-yellow, reddish in the meso and metathorax with pale spots through the body; setae inserted in white paniculum. Anal shield pale grey. Duration 5–6 days (n = 4).

Fourth instar (Fig. 5). Maximum length 14.0 mm, head capsule width 1.79–1.84 mm (n = 3). Head black with cream panicula bearing white setae; prothoracic shield black with white setae; body greenish-yellow, meso and metathorax reddish, with purer yellow in the last abdominal segments. Paler spots and white setae inserted in white paniculum through the body. Anal plate grey. Duration 7 days (n = 4).

Fifth (last) instar (Figs. 6–7). Maximum length 27.0 mm, head capsule width 2.37–2.71 mm. (n = 3). Head black with yellowish panicula bearing white setae. Prothoracic shield black with white setae. Pro and mesothorax reddish, greenish-yellow but greener in the back and yellower in the last abdominal segments. Longer white setae are projected laterally. Paler spots and white panicula bearing white setae through the body. Anal shield black. Duration 6 days (n = 3).

Pupa (Figs. 8–9). Length 26.0 mm (n = 2); bright yellow with black spots scattered through the body. Two lines of dorsolateral spots on abdomen and smaller pale spots present in all segments. Head with a long anterior projection with bifurcated tip. Prothorax and metathorax with a yellow longitudinal ridge forming a pronounced orange bump on mesothorax. A short rounded lateral protuberance is present at the base of the forewing. Abdominal segments A2–A8 with middorsal black spine-like projections, short on A2 and long on A3–A4. Abdominal segments A2–A4 with pairs of supraspiracular black spine-like projections above the wings. Cremaster bright yellow. Duration 11 days (n = 3).

Natural history of *Archonias brassolis tereas*

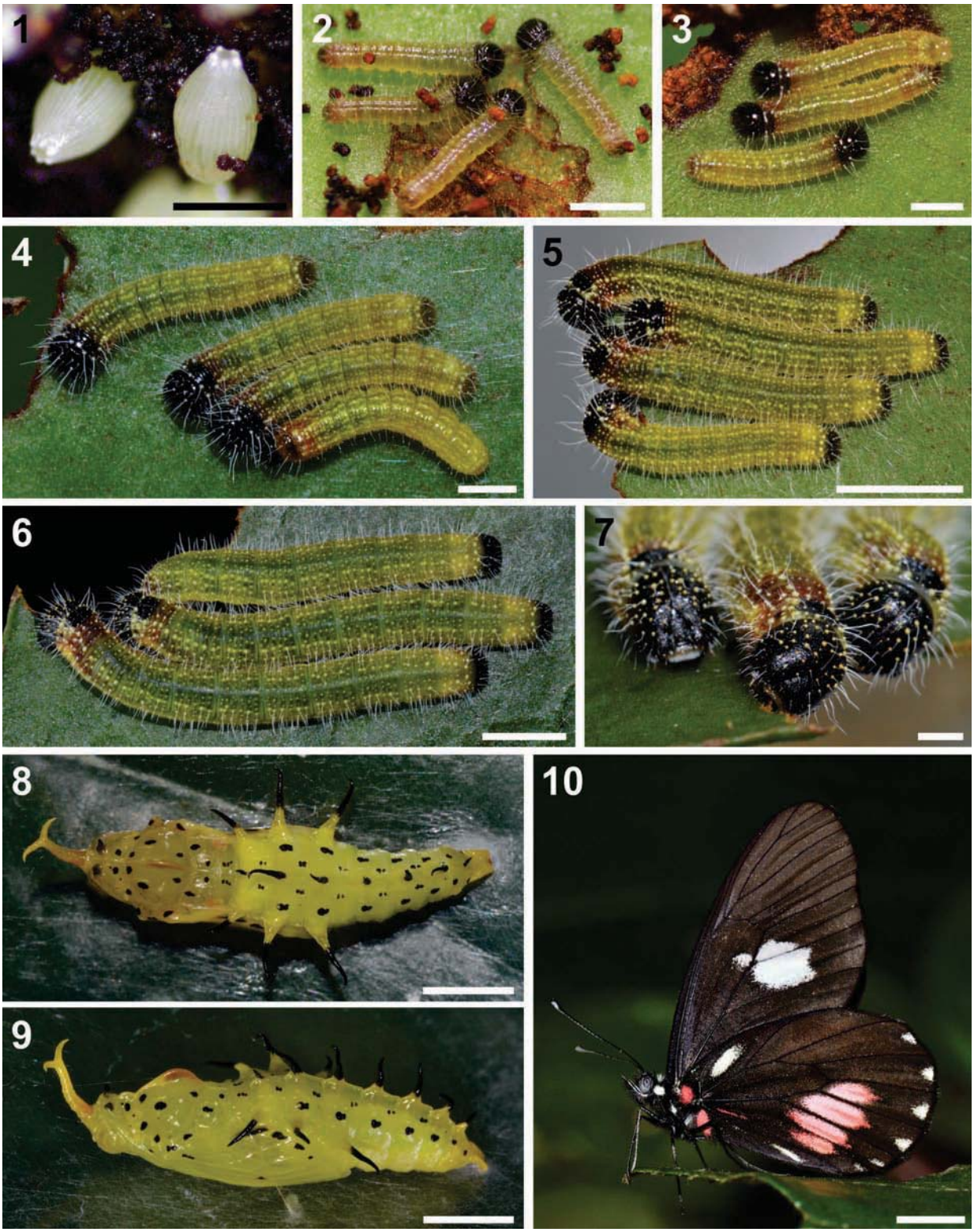
Adults (Fig. 10) have been observed in several different habitats in the Atlantic Forest, including pristine and secondary forest and coastal sand forests. The territorial males are more easily spotted in forest edges and clearings where they perch and were observed chasing other conspecific males for short periods from 9:00 to 12:00. Both sexes were observed visiting flowers of several species of Asteraceae. In the study site, the only putative mimic of *A. brassolis tereas* is the swallowtail *Parides anchises nephalion* (Godart) (Papilionidae: Troidini) (Brown 1992).

Eggs were laid in clusters with 26 eggs per cluster (n = 1 oviposition) on the upperside leaf of the food plant. The oviposition of *Archonias* shared the same leaf with empty eggs and larvae of an undescribed species of *Brangas* (Lycaenidae). These larvae had completely eaten the leaf epidermis and left the *Archonias* eggs surrounded and covered by its feces (Fig. 11). Although the effects that this could have in the *Archonias* eggs are unpredictable, food availability for caterpillars would be severely shortened since most of the mistletoe leaves would have been previously eaten by *Brangas* caterpillars and there were no additional mistletoes in the host tree. In laboratory, newly eclosed larvae devoured most of the exochorion, before proceeding to graze the leaf surface. First instar caterpillars eat by scraping the upper side of the leaf, and usually are covered by their pellets of excrements trapped in the fluid droplets present on the dorsal setae. Second instar still scrapes the leaf surface occasionally making holes at the leaf blade. From the third instar on, the whole leaf thickness is consumed at each bite. Caterpillars are gregarious since hatching, and stay most of the time leaning against each other, in parallel position. Their lateral setae are longer and usually contact setae and bodies of neighbor larvae. They all rest and eat at the same time. When molested, the caterpillar responded by regurgitating fluid from the mouth. The pupae have a conspicuous yellow color and when molested twitch with sudden jerky movements.

DISCUSSION

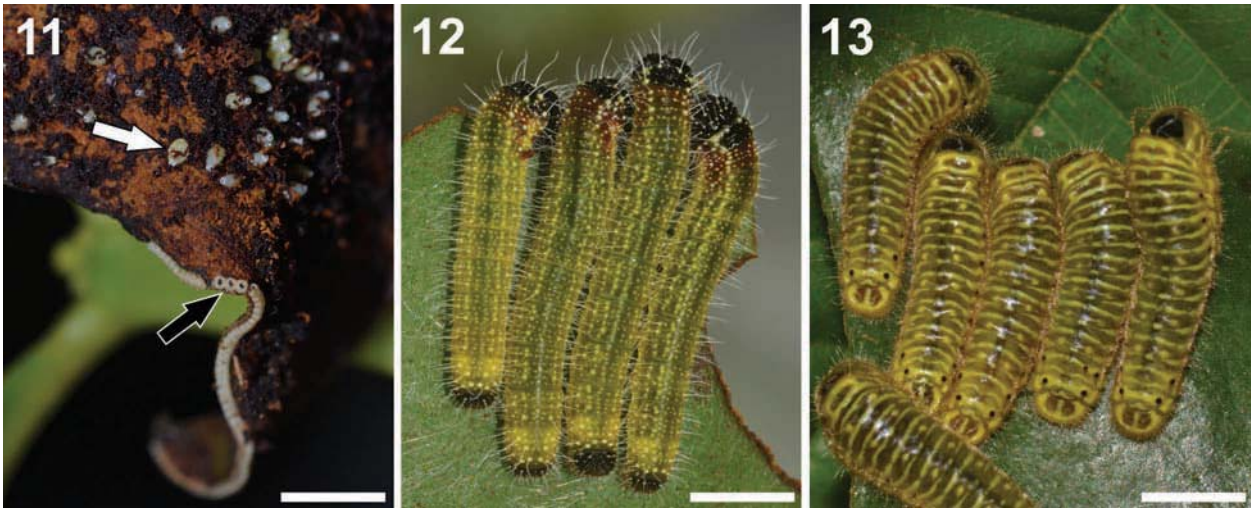
Both morphology and natural history of the immature stages of *Archonias brassolis tereas* are very similar to those of other species in the *Catasticta* group, especially *Catasticta* species (see Braby & Nishida 2010). Eggs have the typical bottle-like shape, with inconspicuous vertical lines, and larvae are slender and covered by

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FIGS. 1–10. Life stages of *Archonias brassolis tereas* on *Phoradendron* sp., from Jundiai, São Paulo, Southeast Brazil. **1**, eggs, note that feces of *Brangas* sp. are partially covering the eggs. **2**, first instar, note the graze damage and accumulation of feces. **3**, second instar. **4**, group of third instar, the rightmost caterpillar is still at the second instar. **5**, fourth instar. **6**, fifth (last) instar. **7**, fifth instar in frontal view showing details of the heads. **8**, pupa in dorsal view. **9**, pupa in lateral view. **10**, freshly emerged adult. Scales = 0.5 mm (1–4, 7), and 0.5 cm (5–6, 8–10).

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Figs. 11–13. Interspecific interaction between mistletoe butterflies on *Phoradendron* sp., from Jundiai, São Paulo, Southeast Brazil. **11**, egg clusters of *Archonias brassolis tereas* (white arrow) and *Brangas* sp. (black arrow) on the same leaf; note the feces of *Brangas* sp. partially covering the eggs. **12**, fourth instar larvae of *Archonias brassolis tereas*. **13**, last instar larvae of an undescribed *Brangas*. Scales = 0.4 cm.

short setae, inserted in panicula. The pupae are similar to those of some *Catasticta* species, such as *Catasticta ctemene* (Hewitson), *Catasticta flisa* (Herrich-Schäffer), *Catasticta hegemon* Godman & Salvin, *Catasticta sisamnus* (Fabricius), with a long anterior bifurcated projection, spine-like projections in the body, and black markings over a bright colored background. In contrast, the pupa of *Archonias* differ from *Catasticta cerberus* Godman & Salvin and *Catasticta teutila* (Doubleday), which have short projections and bird dropping aspect. Morphological and behavioral evidence from the immature stages described herein supports the close phylogenetic relationship between *Catasticta* and *Archonias* previously suggested based on molecular data (Braby et al. 2006, Wahlberg et al. 2014). The nomenclatural history and classification of *Catasticta*, however, is complex, and the genus is probably paraphyletic (see Lamas & Bollino 2004, Braby & Nishida 2010). In this way, the new data on *Archonias* immature stages can be of help in the understanding of character evolution and in the systematics of the group.

The mistletoe use has a key role in the evolution of life history attributes in Aporiina, including the colonization of new host plant families in *Eucheira* Westwood and *Neophasia* Behr (Braby & Trueman 2006). New data of *Archonias* on *Catasticta* confirm previous information indicating mistletoes as hosts (see Biezanko 1958, P. J. DeVries, pers. comm. *apud*, Braby & Nishida 2010). According to Braby & Nishida (2010), the use of mistletoes is related with the evolution of gregariousness in Aporiina, and highlights two factors: 1) selection of mistletoe host with toxic alkaloids by an aposematic ancestor; and, 2) patchy distribution of mistletoe food plant as selective force leading to the evolution of egg clustering and larval gregariousness. These same factors must have been important for the evolution of gregariousness in other mistletoe feeding species, such as species in the *Hesperocharis* group (Pieridae) and *Brangas* (Lycaenidae). Consequently, the Neotropical region present a rich community of mistletoe butterflies competing for a patchily distributed resource. In this situation, the occurrence of interspecific competition and resource partitioning among mistletoes feeding species is expected, and present results provide strong evidence in this direction. Because *Brangas* females lay large egg clusters (100–200 eggs) and larvae develop quickly feeding day and night (Kaminski et al., in prep.), *Archonias* larvae sharing the same plant would be unable to complete their cycle due to critical food shortage.

In the conceptual model proposed for the evolution of gregariousness by Braby & Nishida (2010), interspecific competition operates in the opposite direction, i.e., as a selective force limiting the clutch size and gregariousness. In addition, the competition may be important in promoting secondary host shifts events from mistletoes to the host trees parasitized by mistletoes. In Braby & Nishida (2010), there are some reports from species that co-occur on the same mistletoe clump but at least one example of a species pair that are never found together on the same mistletoe clump (*C. teutila* and *C. cerberus*). In

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summary, mistletoe butterflies are an excellent system to study the role of interspecific interactions in the evolution of life history attributes in herbivorous insects.

Although adults in the *Catasticta* group are frequently warning colored and involved in complex mimicry rings with other butterflies (DeVries 1987, Braby & Nishida 2010), larvae are usually inconspicuous and possibly non-warningly colored (Braby & Nishida 2010). Moreover, early instars of several species in *Catasticta* group are conspicuously bright yellow becoming inconspicuous in late instars suggesting a strong selection for crypsis (Braby & Nishida 2010). Two different syndromes have been described: 1) nocturnal feeding larvae of *Pereute* and *Leodonta* become dark brown (and cryptic when resting on tree trunks during the day), and 2) diurnal feeding larvae of several *Catasticta* become greenish (and cryptic when feeding on leaves). In the present study, a third different syndrome is reported: larvae of *Archonias* keep the conspicuous yellowish pattern in later instars and pupa. Moreover, present results suggest that *Archonias* larvae may also be involved in a mimicry ring with *Brangas* sp., with which caterpillars shown remarkable similarities on overall color pattern (Figs. 12–13). Although larval mimicry has been seldom reported in literature, recent studies suggest that this is a plausible scenario especially in species using the same host plants (Willmott et al. 2011). In this scenario, it is possible that other larval mimicry rings can be reported in mistletoe butterfly larvae, since there are several potential aposematic models such as *Brangas neora* (Hewitson) (Lycaenidae) and *Hesperocharis crocea* Bates (Pieridae) (see Braby & Nishida 2007, Janzen & Hallwachs 2016).

This study is another contribution to a better understanding of the natural history of mistletoe butterflies (see also Kaminski et al. 2012, 2014). Next steps includes rearing additional species of *Catasticta*, the largest genus of Neotropical Pieridae (immature stages are known to a small sample of the ca. 90 described species) and the discovery of the immature stages of *Charonias*, a genus that includes an endangered species in southeast Brazil (Freitas et al. 2011). Finally, the present publication would serve as motivation to Neotropical lepidopterists to search and publish more data on early stages of mistletoe butterflies.

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A NEW SUBSPECIES OF *OLERIA GUNILLA* (NYMPHALIDAE: DANAINAE) FROM NORTH MATO GROSSO, BRAZIL

ANDRÉ V. L. FREITAS* AND LUIZA M. MAGALDI

Departamento de Biologia Animal and Museu de Zoologia, Instituto de Biologia, Caixa Postal 6109, Universidade Estadual de Campinas, Campinas, 13083-970 São Paulo, Brazil; e-mails: baku@unicamp.br; luiza.magaldi@gmail.com
*Corresponding author

AND

KEITH R. WILLMOTT

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; e-mail: kwillmott@flmnh.ufl.edu

ABSTRACT. A new subspecies of ithomiine butterfly, *Oleria gunilla lourdes* **n. ssp.**, is described from northern Mato Grosso in central Brazil. The new taxon is confidently assigned to *Oleria gunilla* on the basis of both morphological and molecular evidence. Its wing pattern, with a broad expanse of orange on the dorsal forewing, is typical of the mimetic color patterns found in Ithomiini in the upper Amazon and Andean foothills of Peru, Colombia and Ecuador, very far from the type locality in northern Mato Grosso, where this taxon has no known co-mimics. Future studies are needed to investigate the mimetic relationships of this taxon with other sympatric butterflies.

Additional key words: Amazon, Clearwings, Ithomiini, Mimicry, Oleriina

The genus *Oleria* (Hübner, 1816) is the most species-rich within the tribe Ithomiini, with 49 known species distributed from Mexico to northern Argentina (De-Silva et al. 2016). The genus reaches its highest species richness in the eastern Andes and upper Amazon (Chazot et al. 2016), engages in several different mimicry rings (e.g., Beccaloni 1997) and individual species can present quite different color patterns across their geographic range (De-Silva et al. 2010, Warren et al. 2015). The Amazonian species *Oleria gunilla* (Hewitson, 1858) is a good example; its eight described subspecies are quite different in color pattern, representing at least six different mimicry rings (Chazot et al. 2016; see also Warren et al. 2015).

About a decade ago, the first author received some specimens of butterflies collected in the southwestern Amazon, along the Mureru River, northern Mato Grosso State, central Brazil, including a large sample of ithomiines. Among them were four specimens of an unknown 'orange-tip' *Oleria* taxon. In the present paper, we describe this taxon as a new subspecies of *Oleria gunilla*, based on morphological and molecular characters, and discuss its mimetic relationships.

MATERIAL AND METHODS

Specimens of *Oleria* were studied in several field locations in the Neotropics (KRW and AVLF) and examined in major public and private collections in Europe, North and South America, including types of all *Oleria gunilla* taxa and names. Distribution data for examined specimens were compiled in a database to permit study of related taxa and mimicry patterns. In addition, we also examined the Lamas collection of neotropical butterfly type specimen photographs at the MUSM (also available online in Warren et al. 2015), representing all relevant names of *Oleria* (see Lamas, 2004). Morphology was studied using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10–15 minutes, dissected and subsequently stored in glycerin. The following collection acronyms are used in the text: **ZUEC**, Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil; **ZUEC-AVLF**, André V. L. Freitas Collection, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Total genomic DNA was isolated from four individuals of the putative new subspecies of *Oleria gunilla* using Invisorb® Spin Tissue Mini Kit (STRATEC Molecular, Germany). The barcode region proposed by Hebert et al. (2003), which is the 5' portion of the mitochondrial DNA (mtDNA) gene cytochrome oxidase subunit I (COI, 658 bp), was sequenced according to published protocols (Wahlberg & Wheat 2008). Sequences were aligned with those of other *Oleria* from the "*amalda*" group (sensu De-Silva et al. 2010) obtained from GenBank (Table 1). The final matrix comprised 50 individuals of the six species of *Oleria* from the "*amalda*" group and one individual of *Oleria vicina* as outgroup. Bayesian analyses (BI) were carried out using the program MrBayes 3.2 (Ronquist &

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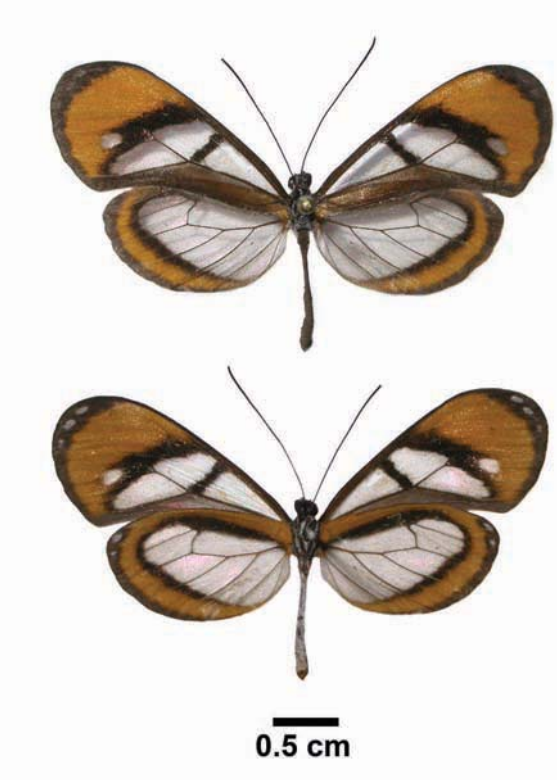


FIG. 1. *Oleria gunilla lourdes* – holotype male. Dorsal above, ventral below.

Huelsenbeck 2003) on the CIPRES portal (Miller et al. 2010). The model-jumping feature of the program was utilized, thereby sampling all possible GTR submodels according to their posterior probability (Ronquist et al. 2012). The gamma parameter was also included to allow site rate variation. Four simultaneous chains were run for 10×106 generations for two runs, sampling trees every 1,000 cycles. The first 2,500 trees were discarded as "burn in" based on when the runs had converged and reached equilibrium. The convergence of the likelihood traces of the independent runs was assessed with TRACER v1.5, and the ESS (effective sample size) values were verified to be above 300 for all parameters, which indicates that they were sufficiently sampled to estimate their posterior distributions (Drummond et al. 2006).

Oleria gunilla lourdes Freitas, **new subspecies**
(Figs. 1, 2)

Description and diagnosis. Male. Antennae entirely black, three quarters length of forewing, with 36–37 antennomeres; club with 10 antennomeres, not conspicuously developed. Thorax black with a thin white dorsal line. Patagium black; Forewing length 19.5–20.0 mm; hind wing length 14.0–14.5 mm (n = 4). Wings transparent with pattern virtually identical on dorsal and ventral surfaces, except by presence of 2–3 small white marginal dots ventrally in apical region of both wings; background transparent; both wings bordered with a marginal black stripe. Forewing with a broad submarginal transverse orange band from costa to vein 2A, this internally bordered with a broad black stripe with a conspicuous transparent patch in CuA_1–CuA_2; a narrow black stripe crossing the discal cell at middle; anal margin rust-brown dorsally, grayish ventrally. Hind wing bordered by a broad orange submarginal band from Rs to 3A dorsally and from humeral region to 3A ventraly, this internally and externally bordered by a black stripe. Male genitalia with saccus as long as tegumen + uncus; uncus somewhat curved, ending in a narrow point; valva with a single point. In dorsal view genitalia asymmetrical, with uncus slightly twisted to right. Tuba analis present and weakly sclerotized. Aedeagus long and straight, with conspicuous cornuti grouped in a single patch of small teeth. Female unknown.

The taxon is distinguished from the most similar subspecies, *Oleria gunilla lubilerda* (Haensch, 1905), from eastern Colombia, by the much broader, and slightly darker, orange borders on both wings, especially on the forewing.

Type material: Holotype male (Fig. 1) from Parque Estadual Igarapés do Juruena, Colniza, Mato Grosso, Brazil, deposited in the Museu de Zoologia da Unicamp (ZUEC), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, with the following labels (four labels separated by transverse bars): / HOLOTYPUS / Parque Estadual Igarapés do Juruena, Colniza, M[A]T[O GROSSO], BR[ASIL], 8°55'28"S 59°7'52"W, Rio Mureru, X-XI.2007, Acaccio, G. M. [leg.], DNA Voucher BLU 764 / ZUEC LEP 9780 / Holotypus – *Oleria gunilla lourdes* Freitas det. 2016 /

Paratypes. Two males, same data as holotype (DNA vouchers BLU 764, BLU 765), ZUEC LEP 9781, ZUEC LEP 9782; ZUEC. 1 male, same data as holotype (DNA voucher BAKU-34 and BLU 636); ZUEC-AVLF.

Etymology. This species is dedicated to Maria de Lourdes Retz Lucci (born - 21.II.1923, deceased - 16.XII.2015), grandmother of the first author, who always gave encouragement to his biological endeavors. The name is treated as a feminine noun in apposition.

Taxonomy and variation. All four individuals are very similar, and the only noticeable variation observed was in the size of the transparent patch in CuA_1–CuA_2 on the forewing.

Range and habitat. All four known individuals were collected in the same spot, near the banks of the Mureru River in northern Mato Grosso, central Brazil, in dense Amazonian forest.

Phylogenetic relationships. Based on DNA sequences, the four individuals of *Oleria gunilla lourdes* group together with other *Oleria gunilla* individuals from the western Amazon (Fig. 3), validating the description of this taxon as a subspecies of *O. gunilla*.

DISCUSSION

The wing pattern of *O. gunilla lourdes*, with such a broad expanse of orange, resembles the AURELIANA mimicry pattern (Willmott & Mallet 2004), which is typical of the upper Amazon and Andean foothills of Peru, Colombia and Ecuador (Fig. 4). Thus, this taxon appear to be misplaced in terms of its mimicry ring - the type locality in Northern Mato Grosso is more than 600 km distant from any other locality where similarly patterned ithomiines are found (Fig. 4). In addition, in a large sample of more than 25 Ithomiini species from

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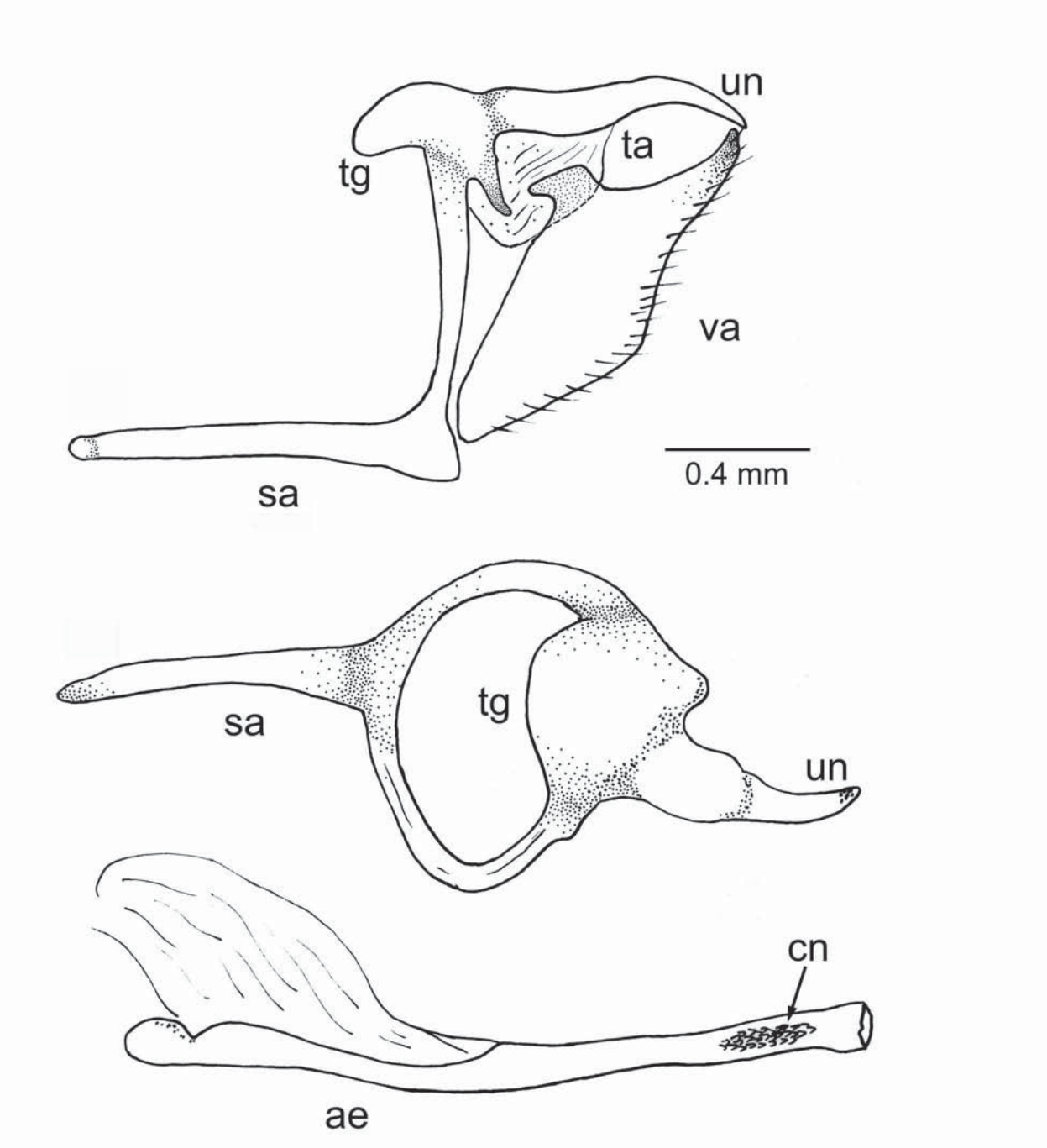


FIG. 2. *Oleria gunilla lourdes* – male genitalia. Lateral on top, dorsal at middle, aedeagus at bottom. Abbreviations: **ae** - aedeagus; **cn** - cornutus; **sa** - saccus; **ta** - tuba analis; **tg** - tegumen; **un** - uncus; **va** – valva.

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TABLE 1 - Species of *Oleria* with code, sampling sites data, and GenBank accession numbers for sequenced genes.

Code	Genus	Species	Subspecies	Country	Locality	Coordinates	Genbank code
-	*Oleria*	*vicina*		Costa Rica	Área de Conservación Guanacaste, Guanacaste	-	JQ529731
BLU636	*Oleria*	*gunilla*	*lourdes*	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258471
BLU763	*Oleria*	*gunilla*	*lourdes*	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258472
BLU764	*Oleria*	*gunilla*	*lourdes*	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258473
BLU765	*Oleria*	*gunilla*	*lourdes*	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258474
20209	*Oleria*	*gunilla*	*lota*	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068916
20641	*Oleria*	*gunilla*	*lota*	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068917
20699	*Oleria*	*gunilla*	*lota*	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068918
20249	*Oleria*	*gunilla*	*lota*	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU069096
LS02-125	*Oleria*	*gunilla*	*lota*	Ecuador	Garza Cocha, Sucumbíos	0°29'52"S 76°22'27"W	EU069097
2-289	*Oleria*	*gunilla*	*lota*	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051706
2-1304	*Oleria*	*gunilla*	*lota*	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051707
2-1979	*Oleria*	*gunilla*	*lota*	Peru	Km 35 Tarapoto-Yurimaguas, San Martín	6°25'29"S 76°15'02"W	HM051708
2-2118	*Oleria*	*gunilla*	*lota*	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051709
4-346	*Oleria*	*gunilla*	*lota*	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051710
2-194	*Oleria*	*gunilla*	*serdolis*	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051711
2-196	*Oleria*	*gunilla*	*serdolis*	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051712
2-1477	*Oleria*	*gunilla*	*serdolis*	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051713
2-1981	*Oleria*	*gunilla*	*serdolis*	Peru	Km 35 Tarapoto-Yurimaguas, San Martín	6°25'29"S 76°15'02"W	HM051714
4-508	*Oleria*	*gunilla*	*serdolis*	Peru	Km 22, Nuevo Lima - La Perla del Ponacillo, San Martín	7°10'04"S 76°20'42"W	HM051715
4-509	*Oleria*	*gunilla*	*serdolis*	Peru	Km 22, Nuevo Lima - La Perla del Ponacillo, San Martín	7°10'04"S 76°20'42"W	HM051716
5-436	*Oleria*	*gunilla*	*serdolis*	Peru	Cerro Mira Culo, Loreto	7°27'12"S 75°50'16"W	HM051717
5-870	*Oleria*	*gunilla*	*serdolis*	Peru	Caño Negro, Río Biabo, PNCAZ	7°45'10"S 76°20'03"W	HM051718
5-922	*Oleria*	*gunilla*	*serdolis*	Peru	Quebrada Machaco, Cachatigre, Río Biabo, PNCAZ, San Martín	7°43'05"S 76°20'51"W	HM051719
5-923	*Oleria*	*gunilla*	*serdolis*	Peru	Quebrada Machaco, Cachatigre, Río Biabo, PNCAZ, San Martín	7°43'05"S 76°20'51"W	HM051720
4-470	*Oleria*	*gunilla*	*serdolis*	Peru	Km 22, Nuevo Lima, Selva Andina, San Martín	7°11'36"S 76°20'06"W	EU069098

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TABLE 1 - Continued.

Code	Genus	Species	Subspecies	Country	Locality	Coordinates	Genbank code
8369	*Oleria*	*rubescens*		Panamá	Quebrada Hornito, Chiriquí	8°69'28"N 82°22'45"W	DQ085460
8404	*Oleria*	*rubescens*		Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646327
CJ8093	*Oleria*	*rubescens*		Panamá	Quebrada Alemán, Fortuna, Chiriquí	8°76'70"N 82°23'26"W	FN646328
CJ8094	*Oleria*	*zelica*	*pagasa*	Panamá	Quebrada Alemán, Fortuna, Chiriquí	8°76'70"N 82°23'26"W	FN646344
8396	*Oleria*	*zelica*	*pagasa*	Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646345
CJ8398	*Oleria*	*zelica*	*pagasa*	Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646346
CJ8433	*Oleria*	*zelica*	*pagasa*	Panamá	Quebrada Hornito trail, Fortuna, Chiriquí	8°69'28"N 82°22'45"W	FN646347
CJ8473	*Oleria*	*zelica*	*pagasa*	Panamá	Cerro Campana, Panamá	8°68'74"N 79°91'97"W	FN646348
F17-7	*Oleria*	*zelica*	*zelica*	Ecuador	Lita, Carchi	-	FN646349
EC94	*Oleria*	*amalda*	*modesta*	Ecuador	Km 106.5 from Mindo, Pichincha	-	FN646262
EC135	*Oleria*	*amalda*	*modesta*	Ecuador	near Hotel Tinalandia, Alluriquín, Pichincha	-	FN646263
KW10	*Oleria*	*amalda*	*faunula*	Ecuador	Río Chuchuví, Km 12.5 Lita-San Lorenzo rd., Esmeraldas	0°52'85"N 78°30'90"W	FN651609
8474	*Oleria*	*paula*		Panamá	Cerro Campana, Panamá	08°68'74"N 79°91'97"W	FN646319
CJ8824	*Oleria*	*paula*		Panamá	Cana, near runway, Darién	07°75'68"N 77°68'41"W	FN646320
CJ8089	*Oleria*	*paula*		Panamá	Bocas del Toro, 9.5 Km Chiriquí Grande-Almirante, Chiriquí	08°98'10"N 82°24'00"W	FN646321
CJ9026	*Oleria*	*paula*		Panamá	Río Pi-as Campsite, Darién	07°63'62"N 78°18'97"W	FN646322
MAL-04156	*Oleria*	*paula*		México	Res. de la Biosfera de Calakmul, Zona K, Dos Naciones, Campeche	17°58'19"N 89°21'28"W	GU658907
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste, Sector Cacao, Estacion Cacao, Guanacaste	10°55'36"N 85°28'5"W	JN807066
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste,Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ542174
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste,Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ542175
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste, Rincon Rainforest, Montanya Figueres, Guanacaste	10°53'2"N 85°17'27"W	JQ543493
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Coneja, Guanacaste	11°0'54"N 85°23'52"W	JQ548213
-	*Oleria*	*paula*		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ548220
4-400	*Oleria*	*estella*	*estella*	Peru	La Antena, Km 16 Tarapoto - Yurimaguas, San Martín	06°27'18"S 76°17'54"W	FN646295
2-406	*Oleria*	*estella*	*estella*	Peru	La Antena, Km 16 Tarapoto – Yurimaguas, San Martín	06°27'18"S 76°17'54"W	FN646296

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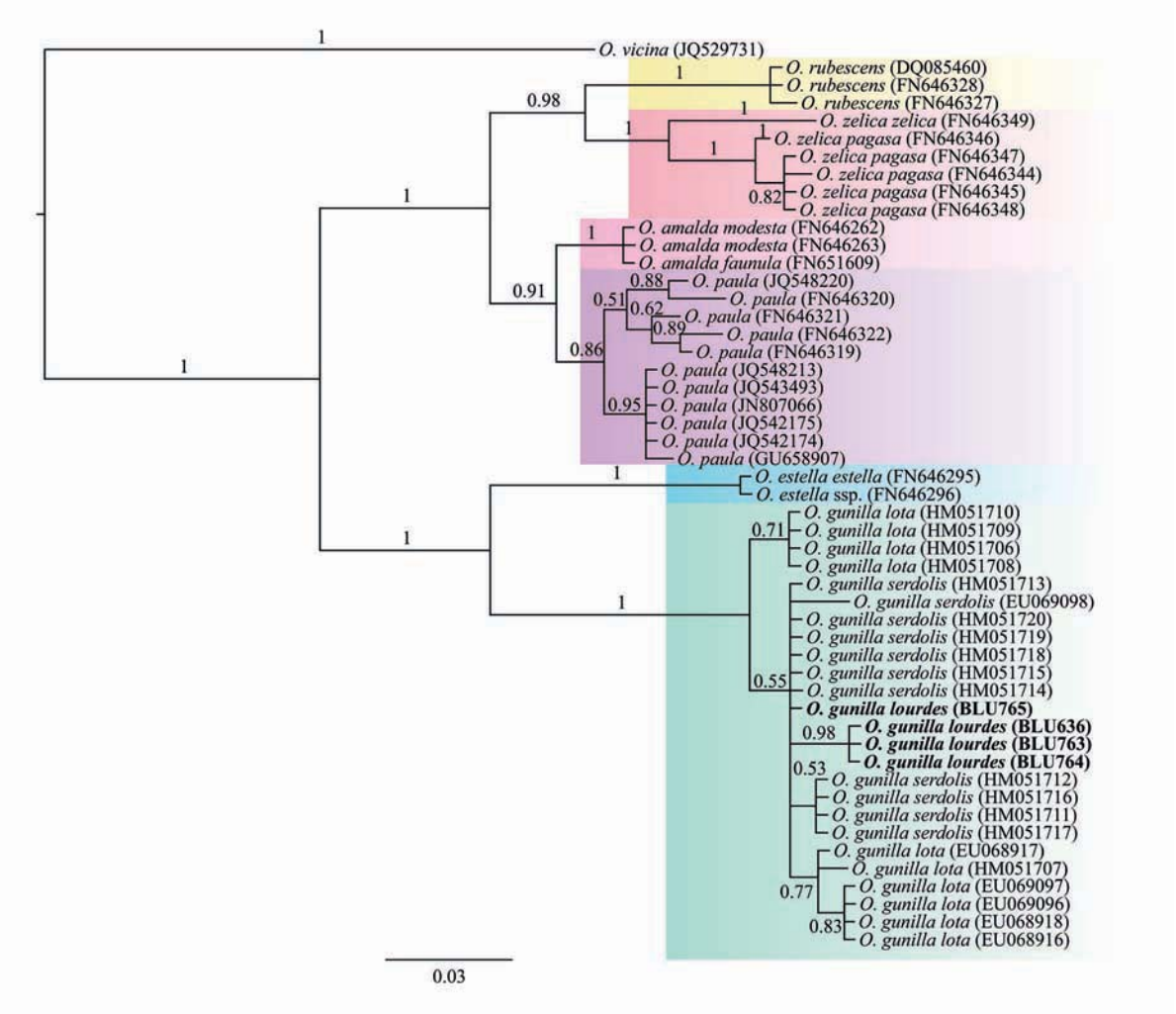


FIG. 3. Bayesian Inference tree for the "*amalda*" species group of *Oleria*, including the four specimens of *Oleria gunilla lourdes* **new ssp**. Posterior probabilities of nodes are presented below the nodes.

the same locality, not a single species with a similar mimetic pattern was observed, an unexpected fact considering that local convergence in mimetic patterns has been long known for aposematic butterflies (Müller 1879). Most strikingly, the extent of orange wing markings in this subspecies is one of the largest within the whole tribe, mirrored in very few other ithomiines (Warren et al. 2015). Although no other local Ithomiini converge in mimicry pattern with *O. gunilla lourdes*, candidate co-mimic butterflies not reported in the type locality could include some Riodinidae, such as species of *Stalachtis* Hübner, 1818, or classical mimetic Pieridae such as *Dismorphia theucharila* (E. Doubleday, 1848). This atypical situation surely deserves further investigation in depth, including additional fieldwork to uncover possible sympatric mimetic species of *O. gunilla lourdes*.

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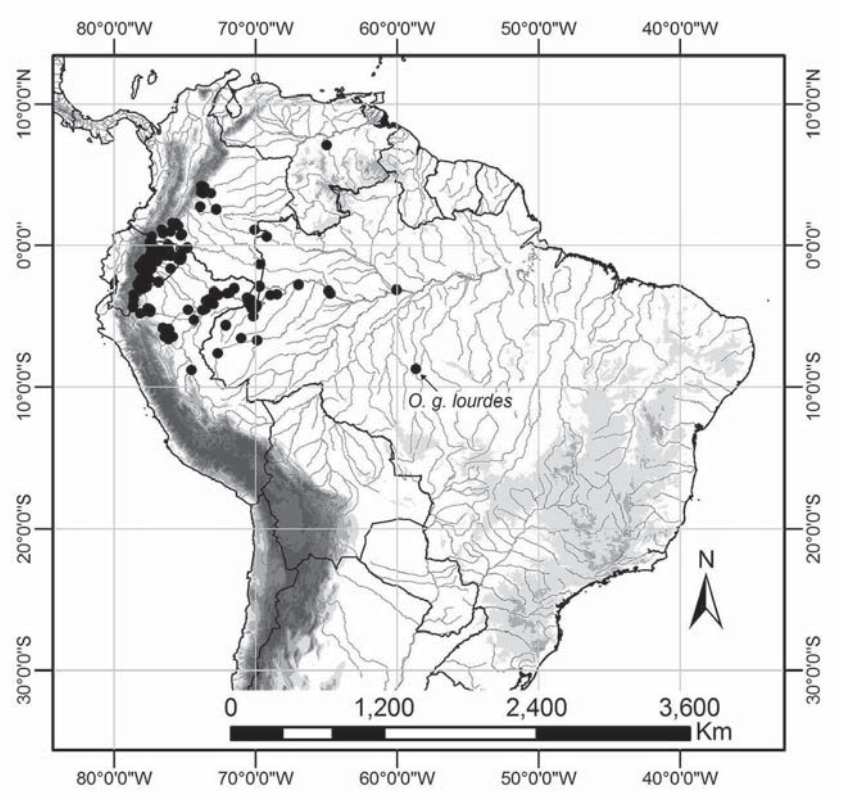


FIG. 4. Distribution of the ithomiine species belonging to the AURELIANA mimicry pattern in the Neotropics (solid circles). The location of the type locality of *O. gunilla lourdes* is indicated.

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IMPACT OF THE INVASIVE WEED *LANTANA CAMARA* (VERBENACEAE) ON BUTTERFLY BEHAVIOUR AND HABITAT USE IN A TROPICAL FOREST IN INDIA.

RAVI M. JAMBHEKAR[1,2*] AND KAVITA ISVARAN[2]

[1]University of Pune, Department of Environmental Sciences, Pune 411007. India.
[2]Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012. India
*Corresponding author: ravijambhekar04@gmail.com

ABSTRACT. Invasive species are thought to influence native biodiversity through a wide range of direct and indirect effects. We examined the influence of an invasive plant, *Lantana camara*, on butterfly assemblages in a tropical forest in India. *Lantana camara* typically dominates the understorey in invaded areas and might therefore reduce the availability of resources and microhabitats essential for butterflies. We hypothesized that butterflies would show reduced use of lantana-dominated habitat when compared with native vegetation. We evaluated such reduced habitat use by testing for (1) reduced levels of behaviours other than feeding and (2) fewer butterfly species and individuals in lantana-dominated habitat patches. To test these expectations, three plots of 30 × 30 meters each were laid in lantana-dominated and native-vegetation patches. In total, three plots in native-vegetation and three in lantana-dominated habitat were marked. Butterfly behaviour was measured through focal-animal follows, and abundance and species numbers were investigated using point sampling inside these plots. We found that butterflies showed substantial behavioural differences between lantana-dominated and native-vegetation plots, indicating a possiblity that the invaded patches were relatively less suitable for several butterfly activities. Furthermore, fewer butterfly species and individuals were seen in lantana-dominated compared with native-vegetation habitat, indicating that lantana invasion results in reduced suitability of a habitat. Whether local behavioural effects of invasive plants, such as reduced habitat use, can lead ultimately to reduced population sizes and local extinctions will need to be examined.

Additional key words: Invasive species, butterflies, tropics.

Invasive alien species are considered to be a major threat to native biodiversity (Calvero and García-Berthou 2005). One such invasive plant species, *Lantana camara* (henceforth lantana), was introduced into India in the 1800s as an ornamental plant (Kohli et al. 2006), and is amongst the most widespread terrestrial invasive species in India today (Love et al. 2009). Lantana is also one of the hundred most invasive species globally (Lowe et al. 2000). Despite its importance, the effect of lantana on native faunal diversity is poorly understood. Existing studies focus on patterns in the spread of lantana (e.g., Sundaram and Hiremath 2012); and its effect on native plants (e.g., Gooden et al. 2009, Ramaswami and Sukumar 2011, Sharma and Raghubanshi 2007) and ecosystem properties, such as propensity to fire (Hiremath and Sundaram 2005). Indeed, more generally, relatively little is known about the potential impacts of invasive plants on higher trophic levels (see Gerber et al. 2008).

We studied the impact of lantana on butterflies, an important set of floral pollinators (Radar et al. 2015). While there is some information on how invasive plants may influence temperate butterfly assemblages (e.g., Moron et al. 2009, Preston et al. 2012), very little is known regarding the effects of invasive plants on tropical butterflies (Bonebrake et al. 2010). The effect of lantana on butterflies is likely to be complex. As lantana flowers abundantly and, in many parts of India, almost throughout the year, the nectar resources provided by lantana may benefit butterfly species able to make use of this resource. Several relatively large butterfly species feed on lantana nectar (Boggs et al.1981, Schemske 1976, Kunte 2008). However, lantana does not provide other resources needed by butterflies. For example, to our knowledge, there is no evidence in the literature for the use of lantana by native butterflies as larval host plants. The lack of suitable resources, other than nectar (adult forage), may be further exacerbated by the typical pattern of lantana spread in a habitat. Lantana displaces native vegetation in the understorey and heavily infests areas, thereby reducing native-vegetation abundance and diversity in an area (Sharma et al. 2005). Since most of the larval host-plants of the butterflies are native plant species this reduction could negatively influence butterflies by reducing the abundance and diversity in resources and microhabitats required by butterflies: butterflies require a complex mixture of nectar plants, larval host plants, puddling areas, basking and resting places (Sharp and Parks 1974), and butterfly diversity is thought to correlate positively with habitat heterogeneity (Tews et al. 2004).

We examined the influence of heavy lantana infestation on butterfly behaviour and habitat use in a tropical forest in India. As described previously, while lantana-dominated habitat may provide nectar resources for adults, they may not be as rich in other required resources, such as larval host plants. We therefore hypothesized that butterflies show reduced use of lantana-dominated habitat when compared with

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native vegetation. Two ways in which reduced habitat use by butterflies may manifest itself are (1) through reduced levels of behaviours (basking, flying, resting and territorial chases) other than feeding behaviour (since lantana is a rich nectar source) in lantana-dominated habitat compared with native vegetation; and (2) through fewer butterfly species and individuals occurring in lantana-dominated habitat. To test these predictions, we compared butterfly behaviour and the number of different butterfly species seen using a forest site. We also compared butterfly abundance in habitat dominated by lantana with those in native vegetation habitats.

METHODS

Study Sites

The study was carried out in Biligiri Rangaswamy Temple Tiger Reserve (77°–77°66' E, and 11° 47'–12° 09' N), hereafter 'BRT', located in Chamarajanagar district in the Indian state of Karnataka. The sanctuary, 540 km^2 in area, is composed of small hills and valleys. Dry-deciduous and moist-deciduous forest cover most parts of the sanctuary, with scrub forest at lower elevations around the periphery of the sanctuary, patches of riparian, semi-evergreen, evergreen and shola forests on the hill tops. Lantana has invaded throughout the study area extensively including forest gaps, road edges and also the understorey in all forest types (Sundaram and Hiremath 2012).

Study plots were laid in moist-deciduous (MDF) and semi-evergreen (SEF) forest types as these generally have high lantana density (Krishnaswamy et al. 2004, Sundaram and Hiremath 2012) and also cover a large area in BRT. Within each forest type, two kinds of habitats were identified: (i) native vegetation with little (< 1% in 30 × 30 m) or no lantana in the undergrowth and (ii) vegetation dominated by lantana in the undergrowth. In these two habitats, plots measuring 30 × 30 m were marked using measuring tapes and coloured tags. In total, three plots in native-vegetation (two SEF and one MDF) and three in lantana-dominated (one SEF and two MDF) habitat were marked (Table 1). Both native-vegetation and lantana-dominated plots had similar tree abundance and primarily differed in the understorey composition (Tables 1 and 2). Two colour morphs of lantana were present in the study plots: one with pink and yellow flowers and the other with orange flowers, and the plants were around 1.5–2 meters tall. The study was conducted from February (late winter) to April (summer) in 2011 and 2012. At this study site, butterfly activity and abundance are high during two seasons – February–March and October-November (post-monsoon). Our study covered the Feb–March peak butterfly activity, but the post-monsoon season could not be studied because the study area experiences extended monsoons and retreating monsoons, which makes it difficult to study butterfly behaviour.

Behavioural observations

Observations were carried out from 0900–1700 hrs. In each plot, focal-animal sampling was combined with instantaneous sampling and all-occurrences sampling (Altmann 1974) to quantify butterfly behaviour. Each sampling session at a plot lasted one-two hours during which the plot was walked thoroughly and individuals were chosen for focal-animal follows. Only one individual per species was sampled during a sampling session to avoid sampling the same individual twice.

Nineteen butterfly species, which were relatively common, well-distributed across the study area, and seen throughout the year, were chosen as target species to study butterfly behaviour (Kunte et al. 2013). These were *Ariadne ariadne*, *Danaus genutia*, *Hypolimnas bolina*, *Hypolimnas misippus*, *Junonia hierta*, *Junonia iphita*, *Junonia lemonias*, *Junonia orithya*, *Kaniska canace*, *Leptosia nina*, *Neptis hylas*, *Pantoporia hordonia*, *Parantica aglea*, *Phalanta phalantha*, *Pseudozizeeria maha*, *Tirumala limniace*, *Ypthima baldus*, *Ypthima huebneri* and *Zizula hylax*.

Instantaneous sampling of focal individuals was used to record broad behavioural activities. At different locations in a plot, individuals encountered of target species were followed. During each focal follow, a single individual was followed for a maximum of five minutes and its activity was recorded every thirty seconds. The pursuit was stopped if the individual left the plot or was no longer visible. The four activities recorded were (1) flying: air borne, hovering; (2) feeding: inserting proboscis into a flower; (3) resting: stationary on a surface with wings closed; (4) basking: stationary on a surface in a sunlit patch with wings held open.

All-occurrences sampling on focal individuals was used to quantify behavioural events. During the focal follows described previously, all occurrences of chases (flying with or behind another individual) were recorded. Chases were used as a measure of interactions with conspecifics and heterospecifics.

Butterfly habitat use

To quantify differences between habitats in butterfly abundance and the number of different butterfly species using that habitat, each plot was divided into four quadrants and in each quadrant the number of butterfly species and butterfly abundance were measured through point samples. During a sampling session at a plot, at each point (one point per quadrant), the species identity of all the butterflies seen within a

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radius of 3 metres was recorded for a period of two minutes (the 3 m distance chosen based on the visibility in the plots and the period was kept short to minimise counting the same individual more than once). The data on species and individuals were pooled across the set of four point samples (one in each quadrant) to constitute one sample for a plot. Such samples were collected at different times of the day (0900 – 1700 hrs) for each plot. Approximately 114 hours of sampling effort were invested in behavioural and habitat use observations and yielded 513 focal follows for behavioural analyses and 73 samples for habitat-use analyses.

Plant diversity estimation.

Plant diversity in the study plots was measured in March 2012. The species identity of all trees and shrubs in each 30 × 30 m study plot was recorded. For small herbaceous plants, a central 5 m radius area was delineated within each study plot, and three 50 × 50 cm sub-plots were laid at random within this 5 m radius area. In the lantana-dominated habitat patches, the number of stems of lantana was counted in a central 5 × 5 m sub-plot within each 30 x 30 m study plot.

Analysis

In the behavioural analyses, first data from all species were pooled together and analysed. Behavioural activities—basking, resting, feeding and flying—were summarised as the proportion of scans in a focal follow for which that activity was recorded. The proportion of scans is a measure of the relative time spent in that activity and ranges from 0 to 1. Conspecific chase, an event, was summarised as chase rate—the number of chases recorded during a focal follow divided by the length of time of the focal follow and represented as chases per fifteen minutes. Since these behavioural data were not normally distributed, means and bootstrapped confidence intervals (calculated from 10,000 re-samples) are shown as descriptive statistics. Each of the four activities was analysed separately using a Generalised Linear Model (GLM) with binomial errors with the proportion of scans showing that activity as the response variable, and with forest type (SEF/MDF), lantana level (native, lantana-dominated), and an interaction between forest type and lantana level as predictors. Each focal follow was a data point in these analyses. Binomial errors were used as the response variable was a proportion (number of scans showing a particular activity out of a given total). As initial model-fitting indicated overdispersion, quasibinomial error structure was assumed and model coefficients were tested using the more conservative F tests (Crawley 2007). Model simplification through backwards deletion was carried out to arrive at the minimal adequate model (Crawley 2012). Chase rate was similarly analysed using a GLM with negative binomial errors, with the number of chases recorded during a focal follow as the response variable and the duration of the focal follow included as an offset to account for variation in sampling time. Species-wise analyses were not conducted because sample sizes for individual species across the different habitat and forest type categories under comparison were limited.

In the analysis of butterfly habitat use, (a) the number of different butterfly species recorded during a sampling session (species number), and (b) the number of individuals (all species together) recorded during a sampling session (abundance) were used as measures of the use of a habitat by butterflies. The data from individual point samples in each of the four quadrants in a plot for a given sampling session were pooled together to yield a data point (i.e., 4 point samples, one in each quadrant, constitute one data point). As the data on species number and butterfly abundance were not normally distributed, means and bootstrapped confidence intervals (calculated from 10000 re-samples) are shown as descriptive statistics. The number of butterfly species recorded during a sampling session was analysed using a GLM with Poisson errors (chosen as the response variable consists of counts). Forest type (SEF/MDF), lantana level (native, lantana-dominated), and the interaction between forest type and lantana level were included as predictors. Model simplification through backwards deletion was carried out to arrive at the minimal adequate model. Butterfly abundance (the number of individuals recorded during a sampling session) was similarly analysed in a GLM with negative Binomial errors (chosen because the abundance count data were overdispersed due to some samples with large values of abundance; Crawley 2012).

Note that in the behaviour and the species-number and abundance analyses, the individual data-point is a focal-animal sample or a point-sample session respectively, and not a plot. The plots were used to delimit representative habitat patches in which behavioural and habitat use observations were recorded. These analyses assume that the plots are a good representation of the larger forest and care was taken, by using previous information on species composition, to lay plots in habitat patches representative of the forest types and levels of lantana infestation. Care was also taken to invest substantial sampling effort to obtain robust sample sizes of butterfly behaviour and abundances in these plots (Table 2). The generality of inferences regarding association of behaviour and habitat use with lantana infestation and with forest type is well-supported because behaviour, species-number and abundance samples were obtained from three study

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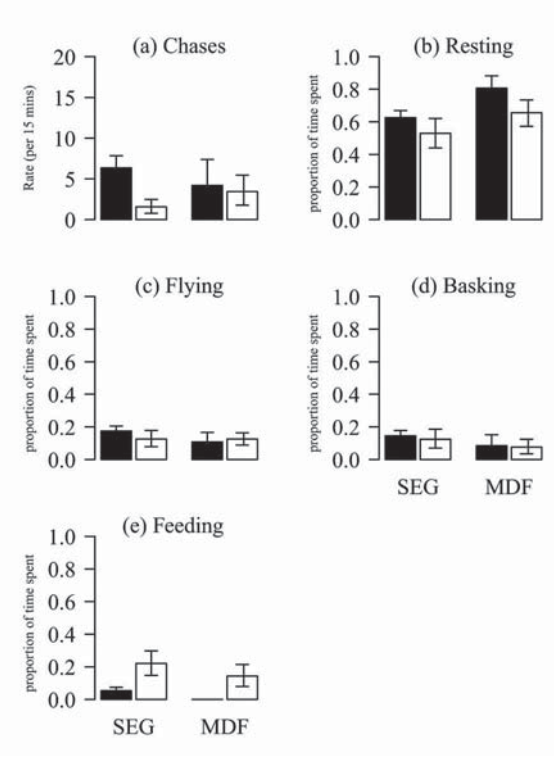


FIG. 1. Variation in butterfly behaviour between lantana-dominated habitat (white bars) and native vegetation with very little or no lantana (black bars) in the two forest types: frequency of chases (number of chases per 15 minutes) (a) and the proportion of time spent in resting (b), flying (c), basking (d) and feeding (e) activities. Error bars represent bootstrapped 95% confidence intervals.

patches for each category (three lantana-dominated vs. three native-vegetation plots and three MDF vs. three SEF respectively). However, the inferences regarding the interaction between lantana infestation and forest type are exploratory, since behaviour, species-number and abundance samples were obtained from only one habitat patch each of lantana-dominated habitat in SEF and native vegetation in MDF. Constraints in time and the area that could be covered during the study restricted the number of study plots. We checked whether our results were robust to potential non-independence in samples from a plot, by fitting generalised linear mixed-effects models (GLMM) with plot identity as a random effect to incorporate the repeated-measures structure in the sampling. Results from GLMMs were qualitatively similar and corroborated the main analyses. R software was used to analyse the data (R development core team 2011).

Shannon's diversity index was used to represent woody plant diversity (trees and shrubs pooled together) and herb diversity. Data from the three 50 × 50 cm quadrats within each 30 × 30 m study plot were pooled to calculate herb species richness, abundance and diversity for each study plot.

RESULTS

Behavioural analyses with all species pooled

Butterfly behaviour varied between the two forest types, and with the level of lantana infestation. Of the four behavioural activities, resting was most commonly seen and basking and feeding were relatively rare (proportion of focal follows with zeroes for feeding = 0.87, basking = 0.74, flying = 0.55, resting = 0.18, chase rate = 0.68; N = 513 focal follows).

Butterflies spent a lower proportion of time resting in lantana-dominated habitat than in native-vegetation habitat (GLM, $F = 5.58$, df = 1, $P = 0.018$, Fig. 1), and a higher proportion of time resting in MDF than in SEF ($F = 16.82$, df = 1, $P < 0.005$). The interaction between lantana and forest type was not significant ($F = 0.16$, df = 1, $P = 0.685$).

Butterflies spent a lower proportion of time flying in lantana-dominated habitat than in native vegetation ($F = 4.16$, df = 1, $P = 0.041$, Fig. 1), and a higher proportion of time flying in SEF than in MDF ($F = 3.90$, df = 1, $P = 0.048$), with no statistically significant interaction between lantana level and forest type ($F = 2.11$, df = 1, $P = 0.146$).

The proportion of time spent basking by butterflies was similar between lantana-dominated habitat and native vegetation ($F = 0.08$, df = 1, $P = 0.077$). The proportion of time spent basking was greater in SEF than in MDF ($F = 6.30$, df = 1, $P = 0.012$). The interaction between forest type and lantana level was not significant ($F = 0.009$, df = 1, $P = 0.924$).

Conspecific chases were fewer in lantana-dominated habitat than in native vegetation ($\chi^2 = 10.90$, df = 1, $P = 0.009$, Fig. 1), and did not vary significantly with forest type ($\chi^2 = 0.09$, df = 1, $P = 0.756$). The interaction between lantana and forest type tended to significance ($\chi^2 = 3.78$, df = 1, $P = 0.051$), indicating that the difference in chase rate between lantana-dominated habitat and native vegetation may be greater in SEF than in MDF.

In contrast to the other behaviours, the proportion of time spent feeding was greater in lantana-dominated habitat than in native-vegetation habitat and this difference was larger in MDF as indicated by the statistically significant interaction between lantana level and forest type ($F = 5.25$, df = 1, $P = 0.023$)

Use of lantana-infested and native habitats by butterfly species

The number of species and the number of individuals seen during a sampling session were used as measures

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of the use of a habitat by butterflies. A total of 74 species was observed during the entire study. Of these, 65 species were recorded from SEF and 41 species were observed in MDF. A total of 58 species was observed in native-vegetation habitat and 43 species in lantana-dominated habitat.

The number of species seen during a sampling session varied with the level of lantana infestation and forest type. The number of species observed during a sampling session was greater in native vegetation than in lantana-dominated habitat (GLM, $\chi^2 = 4.191$, df = 1, $P = 0.041$) and greater in SEF than in MDF ($\chi^2 = 44.617$, df = 1, $P < 0.00001$, Fig. 2a).

Butterfly abundance during a sampling session was greater in native vegetation than in lantana-dominated habitat in SEF, whereas this difference was much smaller in MDF (GLM interaction term, $\chi^2 = 6.965$, df = 1, $P = 0.008$, Fig. 2b).

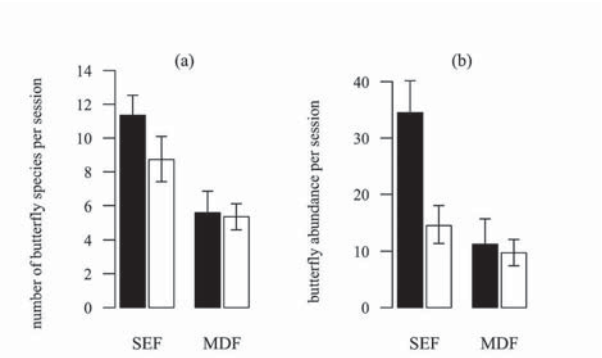


FIG. 2. Variation in butterfly habitat-use between lantana-dominated habitat (white bars) versus native vegetation with very little or no lantana (black bars) in the two forest types: comparison of the number of species (a) and butterfly abundance (b) recorded during a sampling session. Error bars represent bootstrapped 95% confidence intervals.

Plant diversity

Plant species richness for woody species (trees and shrubs) was roughly similar in lantana-dominated (range = 3–11) as well as native vegetation plots (range = 5–16) but the abundance of woody species differed greatly between these two habitats. In lantana-dominated plots, lantana was by far the most abundant woody species resulting in very uneven relative abundances of woody species. Accordingly, Shannon's diversity index was consistently higher for native vegetation plots (2.01–2.61) than for the lantana-dominated plots (1.4–1.6). Herb species richness and species diversity were also higher in native vegetation plots than in lantana-dominated plots (Table 2).

DISCUSSION

Our results from both behavioural observations and estimates of butterfly species numbers and abundances support the hypothesis that butterflies show reduced use of habitat patches dominated with the invasive weed, lantana, compared with patches with native vegetation. As expected, the proportion of time spent feeding was higher but the proportion of time spent in most other activities—resting, flying and conspecific interactions—was lower in lantana-dominated habitat. In addition, the number of species seen during a sampling session and butterfly abundances were lower in lantana-dominated patches. However, the differences in butterfly species-numbers and abundances were mainly seen in SEF. Taken together, these findings suggest a possible way in which an invasive plant may negatively affect native-butterfly assemblages: lantana by heavily infesting a habitat patch may reduce the resources and microhabitats important for different butterfly species. This can result in butterflies' obtaining only a part of their resources and habitat required for different activities in lantana-dominated habitats, consequently reducing their use of the invaded habitats.

Lantana infestation and butterfly behaviour

Several behaviours measured—resting, flying and conspecific interactions—were more commonly seen in native vegetation than in habitat dominated with lantana. Butterflies spent a higher proportion of time resting in native habitat. In native vegetation, butterflies (e.g., *Ariadne ariadne, Junonia iphita, Junonia lemonias, Pseudozizeeria maha, Ypthima huebneri*, and *Zizula hylax*), typically with cryptically-coloured hind wings, were seen resting on the ground or in the leaf litter, where they appeared well-camouflaged against the background; similar observations have been recorded for other butterfly species (e.g., *Vanessa atalanta*, Bitzer and Shaw 1979). It is possible that lantana-dominated habitat is not as suitable as native vegetation for crypsis as lantana forms a contrasting, thick, and almost continuous understorey vegetation cover that appears to be difficult to penetrate and find cryptic places for resting.

Chases, used as an indicator of species interactions, were similarly fewer in lantana-dominated habitat than in native vegetation. There are several possible reasons. First, if butterfly abundance is lower in lantana-dominated habitat (as we discuss below), perhaps because it is less suitable for activities, such as oviposition, encounter rates between conspecifics is likely to be reduced, resulting in fewer interactions. Second, more specifically, if these chases represent territorial behaviour (as seen in several previous studies; Baker 1972, Davies 1978), and if encounter rates with

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TABLE 1. Description of vegetation in the study plots in the two forest types in BRT along with sample sizes for behavioural follows and habitat-use in 2011 and 2012. Sample sizes for behaviour (NB = Number of focal follows for measuring behaviour) and habitat use (NS = Number of sampling sessions for butterfly species-numbers and abundance) are also shown for each study plot in 2011 and 2012.

Plot No.	Forest type	Habitat type (Level of lantana cover)	Description	NB	NS
1	Semi-Evergreen	Native (Very little or no lantana)	Dominant trees: *Cipadessa baccifera, Elaeocarpus serratus, Ficus amplissima, Maesa indica, Randia* spp., *Syzygium cumini*, and *Terminalia bellirica*. Understorey: *Bidens pilosa, Cyanotis tuberosa, Desmodium repandum, Olea glandulifera, Sida rhombifolia*, and *Strobilanthes* spp	65 (2011) 87 (2012)	8 (2011) 12 (2012)
2	Semi-Evergreen	Native (Very little or no lantana)	Dominant trees: *Bombax ceiba, Grewia tiliifolia, Maesa indica, Phyllanthus emblica, Pterocarpus marsupium and Terminalia bellirica*. Understorey: *Adinoflora* spp., *Ageratum conyzoides, Cyanotis tuberosa, Desmodium repandum* and *Sida rhombifolia*.	80 (2011) 67 (2012)	9 (2011) 10 (2012)
3	Semi-Evergreen	Lantana-dominated (High lantana density)	Dominant trees: *Maesa indica, Persea macrantha* and *Viburnum punctatum*, Understorey: *Lantana camara*	43 (2011) 37 (2011)	7 (2011) 7 (2012)
4	Moist Deciduous	Native (Very little or no lantana)	Dominant trees: *Randia* spp., *Tectona grandis*, and *Terminalia bellerica*. Understorey: Grasses	50 (2012)	13 (2012)
5	Moist Deciduous	Lantana-dominated (High lantana density)	Dominant trees: *Randia* spp., *Solanaceace* spp., *Syzygium cumini*, and T*erminalia bellerica*. Understorey: *Lantana camara, Adinoflora* spp., *Bidens pilosa, Sida rhombifolia* and grasses.	48 (2012)	12 (2012)
6	Moist Deciduous	Lantana-dominated (High lantana density)	Dominant trees: *Mangifera indica* and *Terminalia bellerica*. Understorey: *Lantana camara, Bidens pilosa, Sida rhombifolia* and grasses.	36 (2012)	9 (2012)

females is low in lantana-dominated habitat for reasons such as those mentioned previously, then it may not be economical for males to invest in maintaining territories in such habitat. Butterflies spent a higher proportion of time flying in native vegetation and, although statistically not significant, the proportion of time basking was also different in the expected direction. Basking and feeding were relatively rare (see Results) and hence need further investigation to confirm observed patterns.

Feeding was the only activity on which butterflies spent a larger proportion of time in lantana-dominated habitat than in native vegetation. Lantana is known to be a nectar resource used by butterflies (Arévalo 2005, Schemske 1976, Kunte 2008) and since it is a dominant shrub flowering almost throughout the year (Kohli et al. 2006) it is likely to be an important nectar resource. The low proportion of time spent feeding in native vegetation could be due to the seasonality in the flowering of native herbs, shrubs and trees (Bhatt and Murli 2001). By feeding regularly on lantana, native butterflies may aid in lantana pollination and its spread in the area. This could negatively affect their populations if lantana displaces the remaining areas of native vegetation, which include larval host plants, but is not itself suitable larval host plants. On the other hand, lantana can act as an important nectar resource for adult butterflies. Invasive plants may not always influence native biodiversity negatively and positive influences on phytophagous insects have been described (Rodriguez 2006). The relative importance of these different

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potential processes by which an invasive plant, such as lantana, may influence butterfly behaviour and ecology is yet to be examined.

Butterfly behaviour also differed between the two forest types. Butterflies spent more time basking in SEF than in MDF and more time resting in MDF than in SEF. This pattern might be explained by the lower temperatures in the SEF (unpublished data) as a result of which butterflies might have to bask for longer to maintain optimum body temperature. Also, butterflies spent more time feeding in SEF than in MDF, perhaps because nectar resources are greater in the dry season in SEF than in MDF. In MDF, both native plants and lantana flowered throughout the study period, but showed comparatively lower levels of flowering than did SEF. These findings relate to one major season of butterfly activity during the year. Further work is needed to confirm whether these behavioural differences are also seen in the post-monsoon season, another period of substantial butterfly activity. Overall, our findings on butterfly behaviour in relation to lantana infestation suggest that lantana is commonly used as a food resource but may be less suitable for many other activities.

Lantana infestation and habitat use by butterflies. We predicted that because of the unsuitability of lantana-dominated areas for many butterfly activities, habitat use by butterflies should be lower in lantana-dominated areas than in native vegetation. We used butterfly abundance and the number of species recorded during a sampling session as two measures of butterfly habitat use. We find clear evidence for reduced butterfly abundance and reduced number of species in lantana-dominated habitat in SEF. The trend was similar in MDF but not as clear. There are several possible reasons for this difference between forest types: perhaps the butterfly community in MDF was more robust to habitat changes driven by lantana invasion compared with the community in SEF; alternatively, lantana extent may have been greater in MDF than in SEF, which may have already resulted in a reduced butterfly community in MDF, thereby depressing any difference in butterfly habitat use between lantana-dominated and native-vegetation patches within MDF; The total number of species and the average number of species seen during a sampling session was greater in SEF than in MDF, but how much of this difference reflects differences in lantana spread

TABLE 2. Vegetation patterns in the native and lantana-dominated study plots in the two forest types in BRT. Species richness, abundance, and Shannon's Index of diversity are shown for woody species and herbs. Tree abundance includes lantana stems in 30 x 30 m plots in lantana dominated plots. Sample sizes for behaviour (NB = Number of focal follows for measuring behaviour) and habitat use (NS = Number of sampling sessions for butterfly species-numbers and abundance) are also shown for each study plot.

Plot No.	Forest type	Habitat type (Level of lantana cover)	Tree Richness	Tree Abundance	Shannon's Index (Trees)	Herb Richness	Herb Abundance	Shannon's Index (Herbs)	NB	NS
1	Semi-Evergreen	Native (Very little or no lantana)	16	49	3.01	17	143	2.61	152	20
2	Semi-Evergreen	Native (Very little or no lantana)	11	29	3.15	10	103	2.1	147	19
3	Semi-Evergreen	Lantana-dominated (High lantana density)	11	253	0.31	7	40	1.5	80	14
4	Moist Deciduous	Native (Very little or no lantana)	5	15	1.4	9	28	2.01	50	13
5	Moist Deciduous	Lantana-dominated (High lantana density)	5	273	0.24	6	21	1.6	48	12
6	Moist Deciduous	Lantana-dominated (High lantana density)	3	233	0.07	5	22	1.4	48	9

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and how much other ecological differences between the two forest types remains to be examined. While other studies have examined the effect of disturbance on butterfly diversity within a particular forest type (Hill et al. 1995; Spitzer et al. 1997), relatively few have examined how butterfly behaviour, habitat use and diversity vary between different types of forest within the same landscape.

Our results from comparing butterfly behaviour and habitat use in lantana-dominated and native-vegetation habitats suggest a mechanism by which an invasive plant may influence native butterfly assemblages. Lantana by dominating native habitat may reduce habitat heterogeneity and thus reduce the suitability of the habitat for native butterflies. For example, our behavioural findings suggest that lantana-dominated habitat is not as suitable as native vegetation habitat for several activities, including resting, flying and conspecific interactions. Furthermore, lantana-dominated habitat will inevitably have reduced larval host-plant abundance because lantana forms dense thickets displacing understorey vegetation, which include larval host plants, and lantana is itself apparently not used as a host plant. Larval host plants form an important part of the life cycle of butterflies and many aspects of adult butterfly habitat use (e.g., the search for oviposition sites by adult females, mate-searching and territorial behaviour) are closely linked to host-plant abundance. Our observations on plant diversity inside our study plots indicate that plant species diversity in lantana-dominated plots was lower than that in native vegetation plots. We do not have a comprehensive list of larval host plants from the study area, in part because most information regarding larval host plants is anecdotal for most Indian butterflies (Kunte et al. 2013). Thus, the reduced plant diversity in the lantana-dominated plots is likely to represent reduced host-plant abundance, which may have contributed to the reduced use of lantana-dominated habitat by adult butterflies in our study.

In the long term, a reduction in the use of lantana-dominated habitat could lead to a reduction in butterfly population sizes and ultimately butterfly diversity and abundance. While studies of butterfly behaviour in invaded and uninvaded habitat patches are scarce, studies of habitat use and populations, largely of temperate butterfly species report reduced habitat use (e.g., Severns and Warren 2008); reductions, even local extinctions in butterfly populations (e.g., Preston et al. 2012); and declines in diversity and abundance (e.g., Collinge et al. 2003, Moron et al. 2009, Valtonen et al. 2006) following the invasion of an area by exotic plants. Several of these studies link these reductions with a reduction in native plant abundance and diversity (Moron et al.2009), or more specifically with a decline in larval and adult resources (Preston et al. 2012, Severns and Warren 2008) as a result of the invasion.

Heavy infestation of areas is a characteristic for many invasive species (Newsom and Noble 1986); therefore, the process suggested by the findings from our study, that is, reduced habitat use by butterflies, as a result of lantana causing reduced resource and microhabitat abundance and diversity and corresponding poorer suitability for important activities, is likely to be general. Whether these local behavioural effects can lead ultimately to reduced population sizes and local extinctions will need to be examined.

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NOTES ON THE EARLY STAGES OF *ANTICHLORIS ERIPHIA* (EREBIDAE: ARCTIINAE) IN SURINAME

Additional key words: Arctiini, Canna, Maranta, Surinam, Neotropics

The genus *Antichloris* Hübner, 1818 (Erebidae: Arctiinae: Arctiini: Ctenuchina) has 27 species and is distributed from Mexico to Bolivia and Brazil with one species in Cuba and one in Guadeloupe (Draudt 1917, Schaus 1938, Field 1975, Chalumeau & Delplanque 1978). Two species (*A. eriphia* (Fabricius, 1777) and *A. viridis* Druce, 1884) are known pests in banana plantations and have been reported from western countries as an accidental import with bananas (Lempke 1968, Field 1975, Barnett 1986). *A. eriphia* is distributed from Ecuador and Colombia to Bolivia, Paraguay and SE Brazil (Draudt 1917, Watanabe 2007). Although Sepp (1843–1848, pp. 145–146, pl. 69) figured the early stages from Suriname, to our knowledge these have not been described in detail.

On 15 July 2015 in a garden at the Mathoeralaan, Paramaribo, Suriname (5°49'15.91"N, 55°12'21.97"W, 6 m asl), the second author observed a small, white-haired larva on a *Canna* x *generalis* L.H. Bailey & E.Z. Bailey (Cannaceae) (Fig. 1a). A herbarium voucher (Vandenheuvel001) was collected and deposited at the herbarium of Naturalis Biodiversity Center in Leiden, the Netherlands. The larva was reared and fed only with leaves of the host plant. Larval length was measured from the anterior end of the head capsule to the anal plate. Stages were photographed with a Nikon D300s camera, an AF Micro Nikkor 105 mm 1:2.8 D lens and a SB-800 flash. Photographs were made in NEF-format and converted to TIF-files in the same color space after minor retouching and adjustments of exposure, contrast and sharpening.

Antepenultimate instar (Fig 1b). General appearance of a white body with varying hues of dark green due to ingested plant matter and many tufts of long, soft, light gray to white setae. Head capsule pale orange, details of head obscured due to setae. Thorax and abdomen creamy white to light gray, lateral and subventral areas as well as intersegmental membranes light orange-brown; irregular middorsal light orange-brown stripe, interrupted on caudal one third to half of each segment; caudally on abdominal segments bordering intersegmental membrane a vaguely demarcated, narrow white transverse band extending unto subdorsal area. T1 with light gray prothoracic shield and subventral verruca with short, barbed setae. T2 and T3 with light gray subdorsal, lateral and subventral verrucae; subdorsal verrucae of both sides connected by a sharply demarcated, transverse "bridge," slightly concave anteriorly; subdorsal verrucae with many soft setae, some as long as five body segments, bearing multiple barbs and, interspersed with these, some dark gray, non-barbed setae of similar length; lateral and subventral verrucae with barbed setae. Abdomen with light gray to white prolegs on A3–A6 and A10. On A1–A8, dorsally a small verruca on anterior half of segment close to middorsal stripe, bearing non-barbed setae, about one third the length of an abdominal segment; subdorsally on caudal half of segment a larger verruca with multiple, non-barbed setae, 50–100% the length of an abdominal segment, as well as up to four soft, non-barbed, slightly curled, dark gray setae, on A1–A6 about half as long as an abdominal segment and on A7–A8 up to two segments long; laterally on anterior half of the segment, a large verruca with short (equivalent to about half a body segment), non-barbed setae, as well as long (up to five body segments), barbed setae projecting inferolaterally; subventrally and above proleg when present, a small verruca with barbed setae projecting inferolaterally. On A9, the small dorsal verrucae close to the midline are missing. Anal plate white.

When found on 15 July 2015, the larva was 18 mm long, solitary, inactive, exposed on the upperside of a leaf, about midway between the central vein and the leaf margin. In the evening it fed, producing round, oval or triangular holes in the leaf. On 16 July, the larva was 14 mm long, inactive, its body whitish, probably due to having voided its digestive system. It molted in the morning of 17 July.

Penultimate instar (Fig. 1c–e). Head capsule: vertices and frons light orange, no spines or scoli; at base of frons on either side a red-brown spot; clypeus light orange, anteclypeus red-brown with dark brown spots; labrum white with upper side convex, maximum width 63% of base of clypeus, length 88% of maximum width, cleft to 21% of length; six stemmata, stemmata 2–4 dark purple-red, others gray, stemma 3 the largest and nearer to 4 than to 2, 5 shifted ventrally and rostrally toward antennal base and nearer to 6 than to 4; basal and apical segments of antennae transparent light gray, middle segment light yellow. Thorax and abdomen in newly molted larva creamy white to light yellow with

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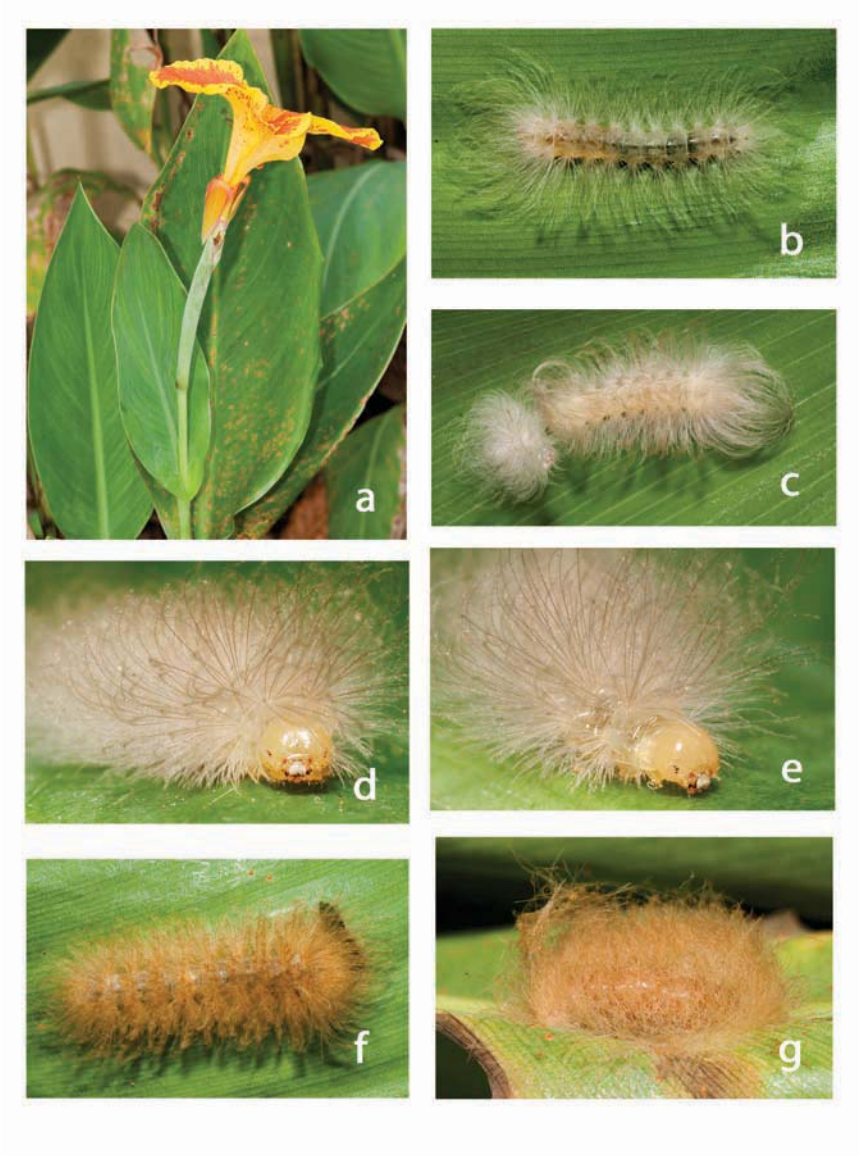


FIG. 1: Host plant and late larval stages of *Antichloris eriphia* (Fabricius, 1776) in Paramaribo, Suriname. **a**: *Canna* x *generalis* L.H. Bailey & E.Z. Bailey; **b**: antepenultimate instar (18 mm, head at left), 15 July 2015; **c**: newly molted penultimate instar (15 mm, exuviae at left, head at right), 17 July 2015; **d**: penultimate larva (24 mm), anterior view, 20 July 2015; **e**: penultimate larva, anterolateral view, 20 July 2015, note subdorsal, lateral and subventral verrucae on T2; **f**: ultimate instar (31 mm, head at right), 24 July 2015; **g**: cocoon (length 21 mm, height 12 mm) with pupa, 30 July 2015. Photographs by second author.

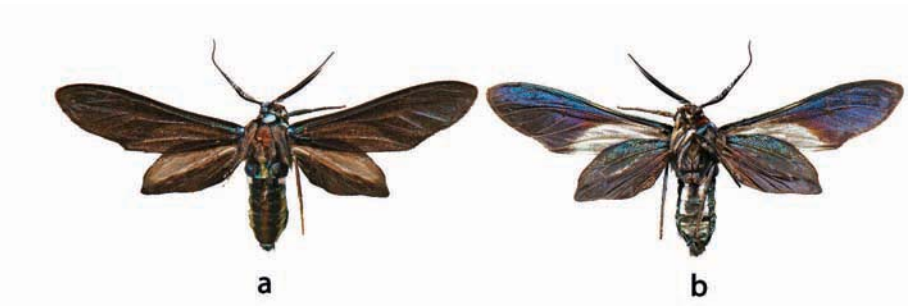


FIG. 2: Eclosed male *Antichloris eriphia* (Fabricius, 1776) (forewing length 18 mm, wingspan 38 mm; antennae mended) in Paramaribo, Suriname. **a**: dorsal view; **b**: ventral view. Specimen deposited in Naturalis Biodiversity Center, Leiden, Netherlands.

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irregular light brown areas laterally, brown middorsal stripe present on anterior one third on A2–A3 and restricted to oval brown spot on A5–A8. After some feeding bouts, the lateral and subventral area was light orange, the (sub)dorsum mottled gray- green, the middorsal stripe from T3 to A8 dark green and the white transverse bands caudally on A1–A7 had reappeared, anteriorly vaguely and caudally sharply demarcated. Dorsally on A5, anteriorly on either side of the middorsal stripe, a paired, oval, creamy white structure shining through, probably the testes. Distribution of verrucae as in previous instar. Up to ten, curled, dark gray setae, about two segments long, with multiple tiny barbs arise from the subdorsal verrucae on T2–A8; otherwise, setae as in previous instar.

In the morning of 17 July, the larva measured 15 mm long (Fig. 1c). From 12.15 to 12.20 hrs, it consumed its exuviae. In the evening, it measured 17 mm long and started feeding from the Canna leaf. On 18 July, the larva moved about considerably and fed little during the day, in the evening it had returned to the *Canna* leaf. On subsequent days, it stayed on the host plant and fed mainly during the evening and night. On 19 July, its length was 20 mm and on 20 July 24 mm. On 21 July, the larva was 18 mm long, inactive, with a white body after having voided its digestive system. It molted during the night.

Ultimate instar (Fig. 1f). Body and verrucae as in previous instar. The dark gray setae and part of the white setae of previous instars had been replaced by red-brown setae, which arose from all verrucae and were greatly increased in number; the distal third to half curved back from vertical except on T2–A1, where the curve was directed anteriorly.

On 22 July the larva remained largely inactive. During the next days it ate well. On 23 July it measured 28 mm long and on 24 July 31 mm. On 27 July, it had stopped eating, was inactive and measured 26 mm long.

Pupa and cocoon (Fig. 1g). In the morning of 28 July, the larva had made a light red-brown cocoon (length 21 mm, height 12 mm), that was attached to the upperside of the *Canna* leaf. The wall of the cocoon consisted of rather loosely interwoven setae of all types, not specifically directed outwards. On 30 July, the larva turned into a light-colored 14 mm pupa. On 6 August the pupa had darkened.

Imago (Fig. 2). In the morning of 7 August, a male *Antichloris eriphia* eclosed (forewing length 18 mm, wingspan 38 mm). Some diagnostic features (after Hampson (1898)): Overall appearance black, diffused with deep metallic bronze-green, especially abdomen. **Head**: proboscis well developed; first segment of labial palpi largely and second segment at its base covered with creamy-white setae. **Thorax**: lateroventrally on T1 a tuft of bright red setae; innerside of legs white-yellow including base of coxa. **Abdomen**: A1 expanded dorsolaterally ("lateral tubercles"); middorsally a longitudinal green band; dorsolaterally a white spot on A2; laterally a green band from A3 to A9; subventrally from A2 to A4 broad, white bands, on A5 and A6 only caudally. **Hindwing** (males only): outer margin acute opposite cell; rostral half pale gray with long setae.

Duration of stages. Antepenultimate instar at least 2 days, penultimate instar 5 days, ultimate instar 6 days, pupa 11 days.

For *A. eriphia*, the following host plants have been recorded: *Canna indica* L. (Brazil), *Musa* sp. (British isles), *Musa* x *paradisiaca* L. (Musaceae) and *Plantago* sp. (Plantaginaceae) (cosmopolitan) (Robinson et al. 2010) as well as *Heliconia latispatha* Benth. (Heliconiaceae) (SE Brazil) (Watanabe 2007). The host plant we found, *Canna* x *generalis*, is a cultivar related to *C. indica* and widely used as an ornamental plant. For Suriname, Sepp mentioned and figured "Indiaansche Tayer," *Maranta arundinacea* L. (Marantaceae) (arrowroot) (Sepp 1848, p. 145, van Andel & Ruysschaert 2011). He also mentioned "Jurca-bessies," probably referring to "yorka pesi", *Senna occidentalis* (L.) Link (Fabaceae). The latter record requires confirmation as the relationship between Fabaceae and Zingiberales is quite distant.

Only on 18 July, the *A. eriphia* larva exhibited some wandering, but otherwise remained on the host plant. Therefore, we had no evidence for individual polyphagy. Additional research is required to document the early larval stages, possible larval variation and parasitoids.

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HAJO B.P.E. GERNAAT *(corresponding author), Department of Taxonomy and Systematics, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; email: hajo.gernaat@naturalis.nl*; JOKE VAN DEN HEUVEL, *Marcusstraat 6, Paramaribo, Suriname; email: jokevandenheuvel58@gmail.com*; FRANS BARTEN, *Mozartlaan 3, 5283 KA Boxtel, The Netherlands; email: frans@fransbartel.nl;* TINDE VAN ANDEL, *National Herbarium, Naturalis Biodiversity Center; email: Tinde.vanAndel@naturalis.nl.*

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KEITH S. SUMMERVILLE, Editor
Department of Environmental Science and Policy
Drake University
2507 University Ave., 131 Olin Hall
Des Moines, Iowa 50311-4505
ksummerville@drake.edu

PEG TOLIVER, Layout Editor
Natural Imprints
1003 Dillon Drive
Normal, Illinois 61761
naturimp@mtco.com

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