

The Life History and Shelter Building Behavior of Vettius Coryna Coryna Hewitson, 1866 in Eastern Ecuador (Lepidoptera: Hesperiidae: Hesperiinae)

Authors: Greeney, Harold F., and Warren, Andrew D.

Source: Journal of Insect Science, 9(32): 1-9

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.009.3201

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

ı



The life history and shelter building behavior of Vettius coryna coryna Hewitson, 1866 in eastern Ecuador (Lepidoptera: Hesperiidae: Hesperiinae)

Harold F. Greeney I,a and Andrew D. Warren^{2,b}

Abstract

We describe all life-stages of Vettius coryna tewitson, 1866 in eastern Ecuador. The details of larval shelter structure and associated shelter building behavior are described and illustrated, as observed on two grass species (Poaceae). We provide brief observations on *V. coryna* adult behavior and a review of known life history information for other species of Vettius Godman, 1901.

Keywords: Andes, larva, larval shelter, pupa, skipper **Correspondence:** ^arevmmoss@yahoo.com, ^bandy@butterfliesofamerica.com

Received: 8 April 2008 | Accepted: 23 June 2008 | Published: 2 June 2009

Associate Editor: Jim Miller was editor of this paper

Copyright: This is an open access paper. We use the Creative Commons Attribution 3.0 license that permits unrestricted use, provided that

the paper is properly attributed.

ISSN: 1536-2442 | Volume 9, Number 32

Cite this paper as:

Greeney HF, Warren AD. 2009. The life history and shelter building behavior of Vettius coryna coryna Hewitson, 1866 in eastern Ecuador (Lepidoptera: Hesperiidae: Hesperiinae). 9pp. Journal of Insect Science 9:32, available online: insectscience.org/9.32

¹ Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador c/o 721 Foch y Amazonas, Quito, Ecuador

² McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, P.O. Box 112710, Gainesville, Florida 32611

² Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apdo. Postal 70-399, México, D.F. 04510 México

Introduction

The genus Vettius Godman, 1901 contains 22 small to medium-sized skipper species, confined to the Neotropics (Evans 1955, Mielke 2004, 2005). The wings of most are rather showy, usually with white spots or patches on a dark background, as well as highlights of yellow, orange, or in the Vettius coryna (Hewitson, 1866) species group, metallic silver (Figure 2b). The V. coryna group (Evans 1955) includes four taxa of uncertain taxonomic status: V. argentus H. A. Freeman, 1969 described from Chiapas, Mexico, V. conkaEvans, 1955 described from Guatemala, V. catargyra (C. Felder & R. Felder, 1867) described from Venezuela, and *V. coryna* described from "Amazons." These taxa differ primarily in the number and size of the white forewing spots, especially those located within the discal cell. In the most recent treatment (Mielke 2004, 2005), coryna, catagryra and conka are treated as subspecies of *V. coryna* following Evans (1955), while argentus is given full species status. Nevertheless, the taxonomy of the Vettius coryna group requires careful study to determine the actual relationships of the four included taxa.

Vettius coryna coryna (Figure 2b), distributed throughout the Andes from Venezuela south to Bolivia (Bebee 1951; Evans 1955), is usually found at elevations above 1500 m and commonly occurs up to 2400 m in Peru (Lamas 2003:33). It is quite common and is frequently collected, presumably because of its attractive, mostly silvered ventral surface. The taxon has been illustrated in color in several widely available identification guides (Smart 1984; Lewis 1987; Piñas and Manzano 1997; Lamas 2003). However, the results presented here are the first published notes on the immature stages of V. c. coryna. We hope our study will contribute to a better understanding of systematics within the V. coryna group, as well as to relationships between the V. coryna group and other members of Vettius.

Materials and Methods

We made all collections and observations of adults and immatures of *V. c. coryna* in eastern Ecuador, at the Yanayacu Biological Station and Center for Creative Studies (YBS; 00°35.95'S, 77°53.40'W), located at an elevation of 2150 m in the Quijos Valley, Napo Province, on the eastern slope of the Andes Mountains. The study site is located approximately five kilometers west of the town of Cosanga and is adjacent to the Cabañas San Isidro preserve of over 2000 hectares of primary cloud forest, bordered by cattle pasture and other disturbed habitats (see Valencia 1995; Greeney et al. 2006).

On 23 November, 1999, HFG visited disturbed forest adjacent to a large cattle pasture and there collected seven early instars, two fourth instars and one fifth (final) instar of *V. c. coryna* on two grass species (Poaceae):

Pennisetum tristachyon (Kunth) Spreng., and a species of Paspalum L., either P. peniculatum L. or P. jurgensii Hack. We transported larvae in plastic bags to the YBS and reared them in separate, small, plastic containers. We added fresh foodplant daily. Subsequently, we discovered numerous larvae in similar situations at the study site, and treated them as described above. We observed larvae of all stadia in the field as well as in the lab, but made descriptions of shelter building behavior exclusively in the field prior to collection. Terminology for shelter types follows Greeney and Jones (2003). We observed more than 200 larvae, and reared a total of 33 larvae to adult eclosion. Voucher material is deposited in the collections of the authors, as well as at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida (Gainesville).

Results

Egg (Diameter = 0.9 mm; n = 1)

Dome-shaped, white to pale yellow, appearing smooth but with minute web-like sculpturing forming pentagons and hexagons that cover nearly the entire surface; area around micropyle smooth.

Larval behavior

Larvae were encountered during all months of the year; all instars constructed and rested in leaf shelters. All instars forcibly ejected frass from the anus, directing it away from the shelter; no frass was encountered inside larval shelters.

First instar (Figure 1c; n = 20+)

Head appearing smooth, but with fine reticulations and a sparse covering of short, pale setae visible under magnification, shape nearly round to slightly triangular, epicranial suture not prominent, color dark brown to black; body varying from pale, translucent yellow-white to pale emerald-green, color dependent on gut contents at time of observation; overall shape tubular, abdominal segments slightly laterally produced laterally (Figure 1c); pronotum narrow, extending to edge of dorsal area, similar in color to head.

Second instar (Figure Ia; n = 20+; body length = to 6 mm)

Extremely similar to first instar, except body now appearing nearly parallel-sided in dorsal view.

Third instar (Figure 1b; n = 30+; development time = 10-12 days; body length = to 11 mm)

Similar to second instar, except near end of 3rd instar body develops two subdorsal, longitudinal white lines, extending from T2 to A8, two faint, thin dorsolateral white lines extend from T3 to A7; all markings faint.

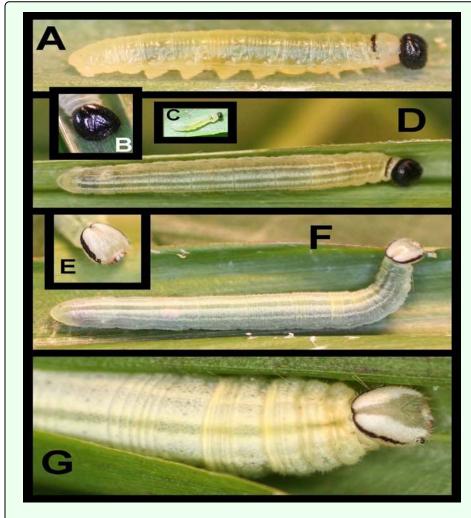


Figure 1. Larvae of *Vettius coryna coryna* at YBS (Napo Province, Ecuador, 2100 m). a) Premolt 2^{nd} instar; b) 3^{rd} instar head; c) 1st instar; d) 4th instar; e) head of 5th instar; f-g) 5th instar.

Fourth instar (Figure 1d; n = 42; development time = 11-14 days; body length = to 19 mm)

Head appearing smooth, but with fine reticulations when viewed under magnification (as described for earlier instars), roundly triangular with a slight epicranial suture, usually entirely dark brown to black, but in some individuals with a pair of pale, inverted, elongate, triangular spots at apex on either side of suture, and another pair of smaller triangular spots just posterior to stemmata; body elongate, parallel-sided, constricted slightly at T1 and T2, tubular when stretched out or feeding, but widest around A3 and slightly hunch-backed in appearance when resting; ground color emerald-green to pale yellow with four narrow, pale, powdery-white, longitudinal stripes, the dorsal pair slightly wider, extending from T2 to A10, two fainter stripes running sub-dorsally from T3 to A8; males with a pair of blue-green or yellow-green, kidney to oval-shaped testes visible through cuticle on either side of midline around A6-A7; pronotum thin, dark brown to black, extending to ventral edge of subdorsal area; a pale purple-red ventral prothoracic "neck" gland present; when probed, larvae rear back on prolegs and evert prothoracic gland with head tipped back.

Fifth instar (Figures le-Ig; n = 41; 21-23 days; to 28 mm)

Head sub-triangular; epicranial suture translucent green-white with black bands running laterally from ocular area and meeting dorsally, two broader, white bands anterior to black bands that do not meet dorsally; clypeus bright white to yellow-white, mandibles black; body similar to fourth instar except lacking a strongly scleritized pronotum, markings bolder though becoming less visible as an overall dusting of white to yellow-white develops later in instar; skin folds (especially inter-segmental ones) appearing as white to yellow-white bands; as larva develops and nears pupation, a thick coating of white waxy flocculence appears in four patches on ventral surface of A7 and A8; eversible prothoracic gland present (see description of fourth instar); anal comb lightly sclerotized, roughly scallop-shaped, bearing 19 short spines; a single

individual molted into a sixth instar, which was similar in appearance to 5th instar.

Pupa (Figures 2a, 2c-2d; n = 32; 25-28 days; 27-32 mm)

Elongate, roughly cylindrical, tapering toward cremaster; a prominent, flattened, triangular, anteriorly-directed horn arising between eyes; abdomen and wing pads with a light dusting of white waxy flocculence [as in late 5th instars (above)]; proboscis sheath detached beyond wing pads and extending to base of cremaster; ground color clear lime-green, changing to white or yellow-white several days after pupation; a pair of thin stripes dorsally, extending from prothorax to base of cremaster (which is clear white); two similar sub-dorsal stripes, extending from A1 to A8 (where they become faint); some specimens with faint white dashes sub-dorsally on pronotum behind eyes; 3–4 days before adult eclosion, eyes darken to brown and wing pads become bright orange; 1 day

before eclosion, thorax and head darken to black, abdomen develops a dark mid-dorsal stripe, and adult wing pattern becomes visible through cuticle.

Larval shelters (Figures 3-4)

Terminology for shelter types follows Greeney and Jones (2003). First instar (n = 27): larvae construct a Group I, type two, no-cut fold shelter by curling one edge of the leaf margin onto the dorsal surface of the leaf. Feeding begins immediately on the shelter lid, which allows it to be silked more tightly to the surface of the leaf, giving it the appearance of having been formed by a single cut into the leaf margin (Group II, type six, one-cut fold shelter; Figure 3a). Immediately after construction, the shelter is tubular in cross section and thinly dome-shaped when viewed from above. Once feeding begins, the shelter becomes a flattened pocket, appearing as an elongate triangle when viewed from above (Figure 3a). All first instar shelters were located at the apices of leaf blades.

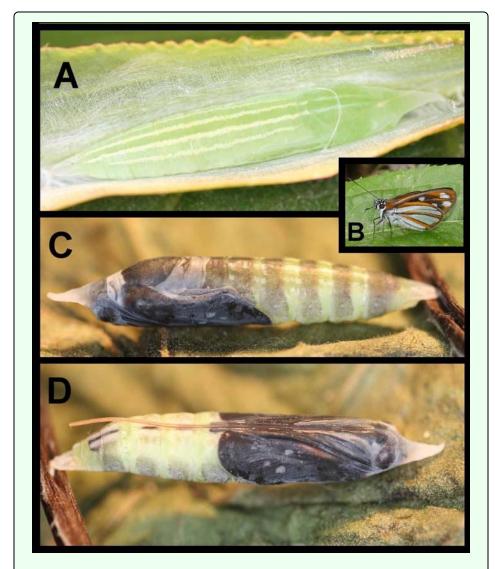


Figure 2. Pupa and adult of *Vettius coryna* coryna at YBS. a) Freshly formed pupa; b) adult; c-d) mature pupa with pharate adult visible through cuticle.

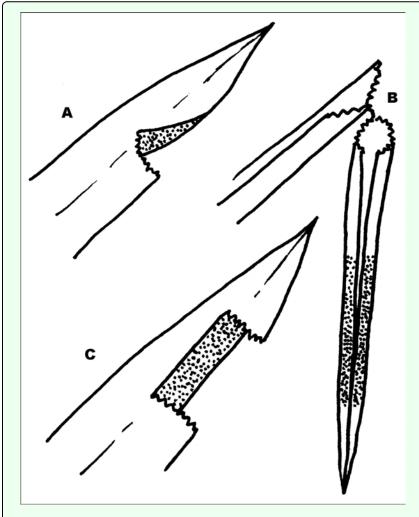


Figure 3. Larval shelters of *Vettius coryna coryna* at YBS. a) Shelter constructed by Ist instar; b) shelter constructed 4th/5th instar; c) Shelter constructed by 3rd instar.

Second instar (n = 26): larvae continue to utilize their initial shelters. Third instar (n = 29): larvae were also found in no-cut fold shelters, but the shelters were generally much larger than those constructed during earlier instars. As described for first instar shelters, third instar shelters begin as a simple curl onto the dorsal surface of the leaf, and after feeding begins, take on an elongate triangular to roughly rectangular shape (Figures 3c, 4a). For both the first and second shelter constructed, feeding damage surrounding the shelter quickly obscures its original form. Fourth instar (n = 37): larvae were all found in Group III, type eight, two-cut fold shelters. Two major cuts were made from opposite sides of the leaf, nearly meeting at the midvein. Opposing leaf margins were drawn together with silk to form a shallow pocket, then a tiny positioning cut was made near the base of the leaf midvein, causing it to weaken and hang in a vertical position (Figures 3b, 4b, 4c). Little or no silk was found around these positioning cuts. Major cuts and the positioning cut were made in the leaf's basal third. Fifth instar (n = 31): shelter construction was similar to that described for the fourth instar.

However, some curled with age, giving the shelter a tubular (rather than flattened) overall shape. Among fifth instar larvae continuously monitored in the field (n = 27), 21 built new shelters immediately prior to or immediately after molting. The remaining 6 constructed a fourth shelter. Pupal shelter: Only two pupae were encountered in the field. One was located in a shelter away from the foodplant, constructed with a living leaf of *Chusquea* Kunth (Poaceae). The other was found in a shelter made from an undamaged leaf of the foodplant. These shelters were Group I, type 2, no-cut fold shelters. Opposing leaf margins were drawn downward and slightly together, forming an inverted, open, canoe-shaped tent. The pupa was attached upside down to the ventral side of the leaf. Several heavy ties of sealing silk were located above and below the pupa in addition to many small ties crossing the midvein along the entire length of the shelter. A silk girdle crossed the thorax, and the cremaster was attached to one of the small crossties along the mid-vein.

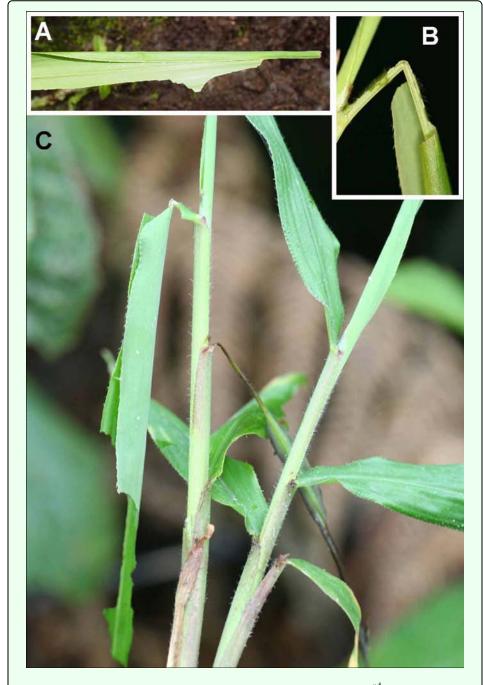


Figure 4. Larval shelters of *Vettius coryna coryna* at YBS. a) Shelter built by 3^{rd} instar; b) detail of positioning cuts at base of foodplant leaf; c) in situ 5^{th} instar shelter.

Adult behavior

Adults of *Vettius c. coryna* (Figure 2b) are common throughout the year at YBS. They are most frequently found along road cuts and in large clearings within the forest. Both sexes visit a variety of flowers, including species of *Heppiella* Regel. (Gesneriaceae), *Prunella* L. (Lamiaceae), *Verbena* L. (Verbenaceae), *Fuchsia* L. (Onagraceae), *Baccharis* L., *Munnozia* Ruiz & Pav., *Erato* DC., and *Adenostemma* J. R. Forst. & G. Forst. (Asteraceae). During overcast days and in early morning, adults are often seen basking on the upper surfaces of

leaves with their hindwings spread and their forewings mostly closed. Males remain on perches throughout the day, usually no higher than two meters above the ground. They fly out to inspect butterflies of all sizes, including individuals many times larger than themselves. Females search for oviposition sites during periods of full sun from 10:00 to 14:00 hrs, touching down briefly on the upper surfaces of narrow-bladed grasses, and pausing occasionally to bask. A single oviposition event was witnessed on 31 July 2001, at 11:30 hrs. After basking for several minutes, the female flew to the base of a nearby

clump of grasses and curled her abdomen under a young leaf-blade to lay a single egg on its undersurface. She then flew rapidly out of the area.

Discussion

Larval foodplants have been reported for the following Vettius species: V. fantasos (Cramer, 1780), V. tertianus (Herrich-Schäffer, 1869), V. lucretius (Latreille, [1824]), V. diversa (Herrich-Schäffer, 1869), V. artona (Hewitson, 1868), V. diana (Plötz, 1886), V. marcus (Fabricius, 1787), V. lafrenaye (Latreille, 1824), and V. aurelius (Plötz, 1882). For V. fantasos, Sepp (1847) noted Panicum ramosum L. (Poaceae), as a larval foodplant, as repeated by Hayward (1947). Draudt (1924) noted that the "green larvae live on grasses such as *Panicum ramosum*." Later, Kendall (1976) reported V. fantasos larvae from Tamaulipas, Mexico, feeding on "Lasiacis sp. (? ruscifolia)," but changed that determination in Kendall and McGuire (1984) to "Lasiacis sp., probably divaricata (L.)" (Poaceae). Kendall and McGuire (1984) speculate that Arnudo donax L. or Phragmites australis (Cav.) Trin. ex Steud. (both Poaceae) may serve as suitable hosts in south Texas. Recently, Janzen and Hallwachs (2007) reported Lasiacis sorghoidea (Desv. ex Hamilton) A.S. Hitch. & Chase, and Lasiacis procerrima (Hack.) A.S. Hitch. & Chase (both Poaceae) as popular larval foodplants for V. fantasos in Guanacaste Costa Rica, but also recorded Lasiacis ruscifolia (Kunth) A.S. Hitch. & Chase, two undetermined species of Lasiacis (Griseb.) A.S. Hitch., Olyra latifolia L., Panicum trichidiachne Doell, and Panicum trichoides Sw. (all Poaceae) as additional larval foodplants used by *V. fantasos* in the region.

Moss (1949) was the first to report a larval foodplant for V. tertianus (repeated by Silva et al. 1968). He reared one adult from a species of Scleria Berg. (Cyperaceae), and briefly described the pupa as being "brown and rounded at the extremities and is tightly packed in a closed web." Orivel and Dejean (2000) described and illustrated the life cycle of V. tertianus, found on Aechmea mertensii (G. Mey.) Schult. (Bromeliaceae) in French Guiana. A brief description of the egg and late instar was given, along with photos of the egg, second and last instars, and pupa. The authors also investigated a possible association between immatures of V. tertianus and various species of ants. Janzen and Hallwachs (2007) reported another bromeliad (Bromeliaceae), Catopsis nutans (Sw.) Griseb., as a larval foodplant for V. tertianus in Guanacaste, Costa Rica.

Moss (1949) provided a brief description of the larva of *V. lucretius*, which he regularly found at the fruit market at Pará, Brazil, living "amongst the sharp-spined leaves which grow at the top of the pineapple fruits" (Bromeliaceae). Moss' entire description of the larva of *V. lucretius* and its habits was reproduced by Brown and Heineman (1972).

Reported larval foodplants for other species of Vettius include "palmeiras" (Arecaceae) for V. diversa (K. Brown 1992), Bromelia L. (Bromeliaceae) for V. artona (Zikán and Zikán 1968) and V. diana diana (Zikán and Zikán 1968, repeated by Silva et al. 1968), "palmeira marajá," or Bactris Jacq. ex Scop. (Arecaceae), for V. marcus (Silva et al. 1968), and "bambú añao e tawuara" (Silva et al. 1968) or "taquara' (Guadua? sp.)" (Zikán and Zikán 1968) (Poaceae) for V. lafrenaye lafrenaye. In addition, Janzen and Hallwachs (2007) reported larval foodplants for Vettius lafrenaye pica (Herrich-Schäffer, 1869), including Olyra latifolia and an unidentified grass (both Poceae); Vettius diversa maeon (Mabille, 1891), including Lasiacis ruscifolia, an undetermined Lasiacis species, and another undetermined grass (all Poaceae); Vettius coryna conka Evans, 1955, including Lasiacis nigra Davidse, Lasiacis rhizophora (E. Fourn.) A.S. Hitch. & Chase, *Lasiacis ruscifolia*, and an undetermined grass species; and Vettius aurelius (Plötz, 1882), including five species of Lasiacis, Oplismenus hirtellus (L.) P. Beauv., Panicum trichidiachne, Pharus parvifolius Nash, Urochloa arrecta (Hack. ex T. Dur. & Schinz) O. Morrone & F. Zuloaga, and two undetermined species of grass.

Larvae of many hesperiine skippers are polyphagous, yet tend to feed on monocots with similar structural characteristics (Scott 1992). Plant architecture may be a constraint for foodplant suitability to skippers such as V. c. coryna that build elaborate larval shelters. Indeed, the two grass species upon which we have found V. c. coryna larvae are similar in that both are relatively long-bladed with a pronounced petiole, and both are slightly to moderately pubescent. However, Paspalum sp. is a low-growing grass, rarely taller than 60cm, with blades roughly 15-20 cm in length. Pennisetum tristachyon, on the other hand, is often over two meters tall, with blades roughly 30-70 cm in length. Both grasses are found exclusively in areas of forest disturbance. We would not be surprised to discover that V. c. coryna utilizes different grasses as larval foodplants in other parts of its range. In western Ecuador (Pichincha Province), we have encountered V. c. coryna where neither Paspalum nor Pennisetum occur, although other (undetermined) long-bladed, moderately pubescent grasses were present.

Vettius coryna coryna is one of many tropical skippers whose life history was previously undescribed, despite the abundance of adults and immatures in disturbed areas. Life history data can be extremely valuable for testing phylogenetic hypotheses, when adequate comparative information is available (e.g., Judd 1998). For Vettius, a genus containing no fewer than 22 species, much additional work remains before we can assemble enough character information to place the observations presented here into a phylogenetic or revisionary context. It is our hope that this study will encourage similar observations on the life histories of common but poorly known tropical skippers.

Acknowledgments

We are grateful to Dr. Richard Halse (Oregon State University) for determining the larval foodplants of V. c. coryna, and to Dr. Olaf H. H. Mielke (Universidade Federal do Paraná) for copies of and information on literature cited. We thank Chris Aldassay, Rudy Gelis, Jenny Getty, Josh Richman, and Paul Martin for assistance in the field. Thanks to George T. Austin, Thomas C. Emmel, Jacqueline Y. and Lee D. Miller and Andrei Sourakov (McGuire Center for Lepidoptera and Biodiversity) for providing research facilities and collections access to A.D.W. Many thanks to David J. and Sally J. Warren, Richard S. Peigler, Roy O. Kendall, and Phil Ackery for providing literature. We gratefully acknowledge the support of John V. and the late Ruth Ann Moore, Tim Metz, Jay Peltz, and the Humbolt Crew, as well as the National Science Foundation (NSF DEB-0346729). Additional funding was provided to A.D.W. through NSF Doctoral Dissertation Improvement Grant DEB-039005, and DGAPA-UNAM (Mexico City). Annette Aiello and an anonymous reviewer greatly improved this manuscript with their comments and careful revisions. Additionally, we acknowledge the PBNHS for their ongoing support of our field studies. This is publication no. 158 of the Yanayacu Natural History Research Group.

Editor's note

Paper copies of this article will be deposited in the following libraries. Senckenberg Library, Frankfurt Germany; National Museum of Natural History, Paris, France; Field Museum of Natural History, Chicago, Illinois USA; the University of Wisconsin, Madison, USA; the University of Arizona, Tucson, Arizona USA; Smithsonian Institution Libraries, Washington D.C. USA; The Linnean Society, London, England.

References

- Beebe CW. 1951. Migration of Nymphalidae (Nymphalinae), Brassolidae, Morphidae, Libytheidae, Satyridae, Riodinidae, Lycaenidae and Hesperiidae (Butterflies) through Portachuelo Pass, Rancho Grande, north-central Venezuela. Zoologica 36: 1-15.
- Brown FM, Heineman B. 1972. Jamaica and its Butterflies. E. W. Classey Ltd.
- Brown KS. 1992. Borboletas da Serra do Japi: diversidade, hábitats, recursos alimentares e variação temporal. In: Morellato LPC, editor. 142-187. História Natural da Serra do Japi, Ecología e Preservação de uma Área Florestal no Sudeste do Brasil. Universidade Estadual de Campinas, Campinas, Brazil. História Natural da Serra do Japi, Ecología e Preservação de uma Área Florestal no Sudeste do Brasil. Universidade Estadual de Campinas, Campinas, Brazil.

- Draudt M. 1917–1924. Grypocera. In: Seitz A, editor. 833-1056. Grossschmetterlinge der Erde 5: Die Amerikanischen Tagfalter, Alfred Kernen. Grossschmetterlinge der Erde 5: Die Amerikanischen Tagfalter, Alfred Kernen.
- Evans WH. 1955. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV (groups H to P), Hesperiinae and Megathyminae. British Museum, London.
- Greeney HF, Dobbs RC, Diaz GIC, Kerr S, Hayhurst JG. 2006.

 Breeding biology of the Green-fronted Lancebill (Doryfera ludovicae) in eastern Ecuador. Omitologia Neotropical 17: 321-331.
- Greeney HF, Jones M. 2003. Shelter building in the Hesperiidae: A classification scheme for larval shelters. Journal of Research on the Lepidoptera 37: 27-36.
- Hayward KJ. 1947. Hesperioidea Argentina XVI. Acta Zoologica Lilloana 4: 5-54.
- Janzen DH, Hallwachs W. 2007. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica http://janzen.sas.upenn.edu
- Judd DD. 1998. Exploring component stability using life-stage concordance in Sabethine mosquitoes (Diptera: Culicidae). Cladistics 14: 63-93.
- Kendall RO. 1976. Larval foodplants for thirty species of skippers (Lepidoptera: Hesperiidae) from Mexico. Bulletin of the Allyn Museum 39: 1-9.
- Kendall RO, McGuire WW. 1984. Some new and rare records of Lepidoptera found in Texas. Bulletin of the Allyn Museum 86: 1-49.
- Lamas G. 2003. Las Mariposas de Machu Picchu. Guía ilustrada de las Mariposas del Santuario Histórico Machu Picchu, Cuzco, Perú. PROFONANPE, Lima, Peru.
- Lewis HL. 1987. Butterflies of the World. Harrison House.
- Mielke OHH. In: Lamas G, editor. In: Heppner JB, editor. 2004. Hesperiidae. Checklist: Part 4A. Hesperioidea - Papilionoidea. Atlas of Neotropical Lepidoptera, Scientific Publishers.
- Mielke OHH. 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera). Sociedade Brasileira de Zoologia, Curitiba, Paraná, Brazil.
- Moss AM. 1949. Biological notes on some Hesperiidae of Pará and the Amazon (Lep. Rhop.). *Acta Zoologica Lilloana* 7: 27-79.
- Orivel J, Dejean A. 2000. Myrmecophily in Hesperiidae. The case of Vettius tertianus in ant gardens. Compte Rendu Hebdomadaire des Seances de l'Academie des Sciences (Sciences de la Vie) 323: 705-715.
- Pinas FRSJ, Manzano IP. 1997. Mariposas del Ecuador. Vol. 1, Géneros. Pontifica Universidad Católica del Ecuador, Quito, Ecuador.
- Scott JA. 1992. Hostplant records for butterflies and skippers (mostly from Colorado) 1959–1991, with new life histories and notes on oviposition, immatures, and ecology. *Papilio (new series)* 6: 1-171.
- Sepp J. In: Sceller HJ, Wichers JG, editors. 1847. Natuarlijke Historie van Surinamsche Vlinders, naar het leven geteekend/Papilions de Surinam dessinés d'aprés nature. Amsterdam. Jan Christian Sepp en Zoon 1: 185-192.

- Silva AGd'A, Gonçalves CR, Galvão DM, Gonçalves AJL, Gomes J, Silva MN, Simoni L. 1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil seus parasitos e predadores. Edição ampliada do "3° catálogo dos insetos que vivem nas plantas do Brasil" de autoria do Prof. A. M. da Costa Lima. Parte II. Insetos, hospedeiros e inimigos naturais. Indice de insetos e índice de plantas. Ministério da Agricultura, Rio de Janiero, Brazil.
- Smart P. 1984. The illustrated encyclopedia of the butterfly world. Chartwell Books, Inc.
- Valencia RR. 1995. Composition and structure of an Andean forest fragment in eastern Ecuador. In: Churchill S, Balslev H, Forero E, Luteyn JL, editors. Biodiversity and conservation of Neotropical montane forests, pp. 239-249. The New York Botanical Garden.
- Zikán JF, Zikán W. 1968. Inseto-fauna do Itatiaia e da Mantiqueira. III. Lepidoptera. *Pesquisa Agropecuária Brasileira* (Agronomia) 3: 45-109.