Biology, Behavior, and Larval Morphology of *Salbia lotanalis* (Lepidoptera: Crambidae), a Potential Biological Control Agent of *Miconia calvescens* (Myrtales: Melastomataceae) From Costa Rica

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ABSTRACT The leaf roller *Salbia lotanalis* Druce (Lepidoptera: Crambidae), a potential biological control agent of *Miconia calvescens* de Candolle (Melastomataceae), was studied in Costa Rica. Larvae were collected from a field site near San José and the insect was reared in the laboratory to study its biology and behavior. Chaetotaxy and morphology of final-instar larvae were described. Using head capsule width measurements, we determined five larval instars in *S. lotanalis*. The insect was easily reared in the laboratory on *M. calvescens* seedlings and the life cycle of the insect was completed in 71.3 and 66.4 d for females and males, respectively. Dissection of ovarioles indicated that females could lay >400 eggs. Larvae are initially gregarious, but become solitary as third instars. First- to fourth-instar larvae prefer to use leaf rolls already formed by other larvae, but fifth-instar larvae prefer to make a new leaf roll rather than using leaf rolls already made and occupied by other larvae. Pupation occurs in leaves, where prepupae build a pupation chamber. Host-specificity tests, including larval feeding tests and two-choice and no-choice oviposition experiments in the laboratory, indicate that *S. lotanalis* has a narrow host range restricted to *Miconia* spp. and other Melastomaceae. Levels of parasitism in the native habitat of *S. lotanalis* in Costa Rica were low. In locations like Hawaii, where there are no native Melastomataceae, *S. lotanalis* has the potential of being an effective biological control agent against *M. calvescens*, but interference from resident natural enemies of Lepidoptera could be high.

KEY WORDS leaf roller, instar, host plant preference, host specificity, oviposition

Miconia calvescens de Candolle (Melastomataceae) is native to neotropical forests from southern Mexico to northern Argentina and Chile (Meyer and Florence 1996, Medeiros et al. 1997). Although its populations are scattered and relatively uncommon in its native habitat (Denslow et al. 1990, Ellison et al. 1993), *M. calvescens* is highly invasive in Australia, French Polynesia, and Hawaii, where it can form dense monospecific forests, causing heavy shade that excludes most species of native plants (Meyer and Florence 1996, Medeiros et al. 1997, Csurhes 1998).

Several control methods have been used to manage *M. calvescens* (Conant et al. 1997, Medeiros et al. 1997). Classical biological control via the introduction of natural enemies from the native habitat of *M. calvescens* is considered an essential tool for long-term management of this invasive species, especially in remote and highly invaded areas (Medeiros et al. 1997, Smith 2000, Denslow and Johnson 2006, Meyer and Fourdrigniez 2011). In Hawaii, lack of native Melastomataceae represents an advantage for the use of biological control programs against *M. calvescens*, as natural enemies could be used with a specificity restricted to this plant family (Smith 2000).

Several insects from Brazil and Costa Rica have been studied as potential biological control agents of *M. calvescens* (Burckhardt et al. 2005, 2006; Picanço et al. 2005; Badenes-Perez and Johnson 2007a,b, 2008, Allen 2010, Badenes-Perez et al. 2010, Morais et al. 2010a,b, Reichert et al. 2010, Chacon-Madrigal et al. 2012, Morais et al. 2012). Among these insects, *Salbia lotanalis* Druce (Lepidoptera: Crambidae) has been studied in its native habitat in Brazil and in Costa Rica (Castillo 2009; Morais et al. 2010b, 2012; Janzen and Hallwachs 2014; Badenes-Perez et al. 2014). The biology and behavior of *S. lotanalis* are still not well-known, although the studies by Morais et al. (2010, 2012) have provided substantial knowledge on the biology of this species and its potential as a biological control agent of *M. calvescens*.

The genus *Salbia* includes 35 species so far, most of which have not been studied beyond initial species descriptions (Munroe et al. 1995, Nuss et al. 2014). *S. lotanalis* is currently in the subfamily Spilomelinae, the largest in the superfamily Pyraloidea, which in-

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cludes several important economic pests of crops (Druce 1899, Hallman and Sanchez 1982, Pemberton and Cordo 2001). Two closely related species, *Salbia haemorrhoidalis* Guenée and *Ategumia matutinalis* Guenée (Lepidoptera: Crambidae), have been used for biological control of *Lantana camara* L. (Verbenaceae) and *Clidemia hirta* (L.) D. Don (Melastomataceae), respectively (Nakahara et al. 1992, Julien and Griffiths 1998, Broughton 2000, Conant 2002, Baars 2003).

Our objective was to study the biology and behavior of *S. lotanalis* in Costa Rica. We also described the morphology of final-instar larvae and conducted host specificity tests with ovipositing moths and larvae to examine the potential for biological control of *M. calvescens.*

Materials and Methods

Study Site. Larvae of *S. lotanalis* were collected from *M. calvescens* trees planted in 2003 at Sabanilla de Montes de Oca, in suburban San José, Costa Rica (09° 56′48.6″ N 84° 02′45.6″ O, 1,239 m above sea level). At the time of this study in 2006–2007, our Sabanilla plot (10 by 15 m) contained ≈80 *M. calvescens* ranging from 0.5 to 3 m in height. The site has an annual rainfall of 1,500–2,000 mm, with a dry season from December to April, typical of the Central Valley of Costa Rica (Valerio 1998). Insects were reared and evaluated in laboratory and greenhouse facilities at the nearby Universidad de Costa Rica, where temperature was 22 ± 3°C and relative humidity was 68 ± 5%.

Development and Behavior. To determine the number of instars of *S. lotanalis*, 138 larvae were collected from the field and placed in 70% ethanol. Head capsule width, measured as the distance between genae (Fig. 3A), was recorded for each larva using a stereomicroscope with a micrometer (Dyar 1890). Body length was measured for 25 final-instar larvae. Description of the final instar was prepared by making drawings of placement and number of setae, spiracles, and pinnacles.

Additional larvae were collected from the field and reared on 1-yr-old potted *M. calvescens* saplings. Upon pupation, individuals were moved to cylindrical paper carton (9 cm in diameter by 10 cm in height) and held until emergence of adults. Adults were transferred to cages (125 by 55 by 55 cm) containing a 1-yr-old *M. calvescens* sapling and 15% honey solution. Honey solutions were changed every 3 d. Biology and behavior of *S. lotanalis* was evaluated using greenhouse-reared eggs, larvae, prepupae, pupae, and adults.

Eggs. Five *M. calvescens* saplings, each placed in a cage (125 by 55 by 55 cm) with 3 mated female adults, were inspected daily for eggs over a period of 2 d. After oviposition, the color, shape, size, and distribution of eggs on plants was recorded, as well as the time from oviposition to hatching ($N = 60$).

Larvae. Potted *M. calvescens* with newly hatched larvae were observed daily to record development of instars, mortality, and behavior, including changes in gregarious versus solitary feeding and rolling of leaves. In total, 50 larvae were followed until the prepupal stage.

Larval preference for preexisting leaf rolls was evaluated using 5–10 larvae of each of the five instars (5 first-instar larvae and 10 larvae of each of the subsequent instars). Each larva was placed individually on a leaf with one roll made and occupied by another larva on a potted *M. calvescens* sapling. We observed larvae for 1 h, recording their movement. Leaf rolls also were inspected in the field for occupation by larvae of different instars. Five leaves were randomly collected from each of five trees (a total of 25 leaves).

Pupae. Site of pupation was recorded for 10 prepupal larvae placed on a *M. calvescens* sapling. For a total of 50 pupae, we measured body length and recorded sex, number of adults emerged, and days from pupation to adult emergence.

Adults. Timing of adult emergence was recorded for three observation periods: early morning (0600–0900 hours), late afternoon (1700–1900 hours), and night (1900 to 2400 hours). Longevity of adults was estimated based on 15 males and 15 females kept separately in two cages. Female fecundity was determined by dissecting 10 unmated adult females and counting the eggs in their ovaries. The food preference of adults of *S. lotanalis* was tested using three different food colorants (green, purple, and yellow) mixed with 10% sugar solution and a control without food colorant. Four vials, each with a different colorant treatment, were placed in the center of a cage (125 by 55 by 55 cm) with one *M. calvescens* sapling. Ten newly emerged *S. lotanalis* moths (six females and four males) were placed in each of the five replicate cages, and the number of times that each vial was chosen for feeding was recorded. Observations were conducted over a period of 3 d during the day (0700 to 1200 hours) and at night (1730 to 2400 hours). Voucher specimens of *S. lotanalis* were deposited in the Zoology Museum of the Department of Biology at the University of Costa Rica.

Host Specificity. Host specificity was evaluated using third- to fourth-instar *S. lotanalis* larvae and adult moths. Three larvae were placed on each plant of eight different species, and feeding was recorded after 48 h. Experiments were conducted in the laboratory using cages (125 by 55 by 55 cm) containing three potted plants of the species being tested (three replicate larval tests were conducted for each plant species). The species tested were *M. calvescens*, *Miconia argentea* (Swartz) de Candolle, *Miconia multispicata* Naudin, *Miconia palacea* Cogniaux, *Miconia theaezans* (Bonpland) Cogniaux, *Conostegia xalapensis* (Bonpland) D. Don (Melastomataceae), *Tradescantia zebrina* (Schinz) D. R. Hunt (Commelinaceae), and *Nephrolepis exaltata* (L.) Schott (Lomariopsidaceae).

We also conducted oviposition tests with adult moths in cages (125 by 55 by 55 cm) containing either two plants (*M. calvescens* and one other plant species) or one plant (no-choice test). The four species tested were *M. calvescens*, *M. theaezans*, *T. zebrina*, and *N. exaltata.* Each two-choice and no-choice test was replicated three times. Two mated pairs of moths were

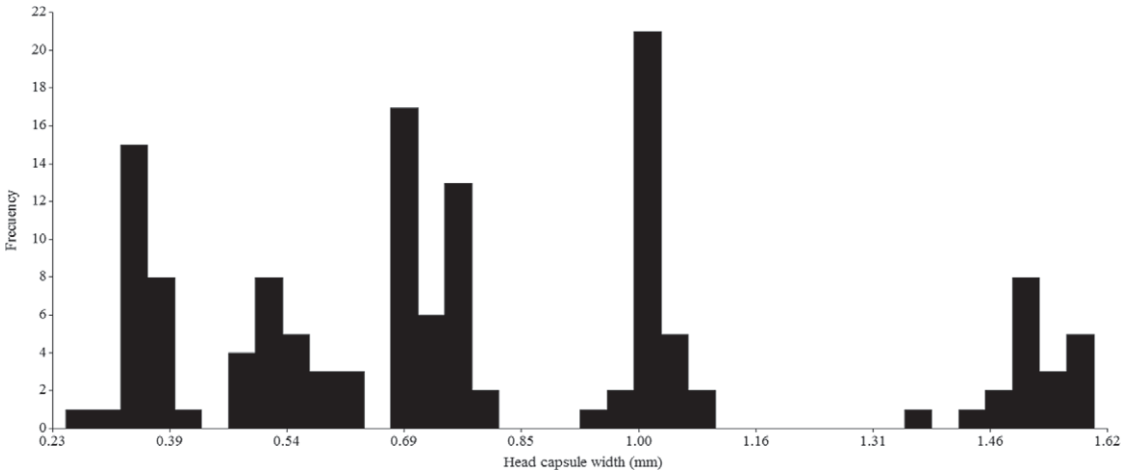

Fig. 1. Frequency distribution of head capsule widths of field-collected *S. lotanalis* larvae ($N = 138$).

released in each cage with a vial of 10% sugar solution. Eggs were counted after 24 h.

Parasitism. From 138 larvae collected from the study site, larvae that seemed to have stopped feeding—indicating possible parasitism—were placed individually with a small leaf of *M. calvescens* in a cylindrical carton (10 cm in diameter by 5 cm in height) closed with fine mesh. Other field-collected larvae were reared on potted plants until they pupated, when they were placed in cartons as described above to check for emerging parasitoids.

Statistical Analysis. Statistical analyses to compare differences in *S. lotanalis* biology between males and females, and feeding and oviposition preferences tests were conducted using a paired *t*-test. To determine the total number of larval instars in *S. lotanalis*, a cluster analysis was performed with the capsule width data using the *K*-means cluster analysis of SPSS (SPSS Inc. 2011, Chicago, IL). This cluster analysis was followed by a one-way analysis of variance and Tamhane's T2 test ($P \leq 0.05$) to separate means.

Results

Determination of Larval Instars. The frequency distribution of head capsule widths of *S. lotanalis* showed five separate peaks indicating five separate instars (Fig. 1), which was confirmed by the statistical analysis ($F = 3036.59$; df = 4, 137; $P \leq 0.0001$).

Development and Behavior. In the laboratory, at a temperature of 22 ± 3°C, the life cycle of *S. lotanalis* from oviposition to adult death was longer for females (71.3 ± 3.0) (mean ± SD) than males (66.4 ± 3.8; $t = 4.73$; df = 21; $P \leq 0.001$). From the 310 eggs laid in greenhouse cages, we obtained 300 larvae, 84 of which became pupae, from which 59 adults emerged (19% survival from egg to adult). Most mortality occurred between the third- and fourth-larval instar.

Eggs. Eggs of *S. lotanalis* were laid on the abaxial side of the leaves, either singly or in groups, often forming a chain along veins or borders of the leaf. Eggs are oval and flat, with a striated surface, and are mostly transparent, so the embryo can be seen through the chorion (Fig. 2A). Eggs measured 1.09 ± 0.09 mm in length (range: 0.80–1.50 mm) and 0.83 ± 0.06 mm in width (range: 0.63–1.00 mm; $N = 60$). Of the 310 eggs observed in the laboratory, 97% hatched, taking on average 7.4 d to hatch (Table 1).

Larvae. Laboratory-reared larvae developed through five stadia, with durations shown in Table 1. The larval head had black stemmata and was mostly transparent in first and second instars, becoming yellowish from the third instar onwards. The integument was yellow and transparent. In fifth instars, the prothoracic shield was brown, darker on the posterior and ventral part, with the ventral edge almost black. The mesothoracic pinnacles that contain setae D1 and D2 and SD1 and SD2 were nearly black (Fig. 3B). The eighth abdominal pinnacles containing seta SD1 were also black, with a clear region anteriorly (Fig. 3E). The rest of the pinnacles were yellowish (Fig. 3B–E). Spiracles in T1 and A8 were larger than the others. Crochets of fifth instars were triordinal (Fig. 3 F).

Larvae emerging from eggs on the same leaf aggregated and started feeding from the abaxial leaf surface, leaving the adaxial cuticle intact. Larvae wove silk threads between leaf veins, creating a tangle within which feces accumulated. Larvae typically fed starting from the leaf border and progressing toward the midrib. From the fourth instar onward, defoliation became more evident as larvae consumed the leaf lamina completely. In the laboratory, some leaves that were almost completely defoliated fell off the plant. However, larvae sometimes used silk threads to attach leaves to the stem and prevent sudden leaf fall (Fig. 2B).

As third instars, *S. lotanalis* started rolling the leaves with silk threads (Fig. 2C). Rolls were constructed and occupied by one or more larvae. Larvae fed from inside the roll, causing small dips and bumps to become visible on the outer surface. Feces accumulated inside the leaf roll. As larvae grew, they enlarged the

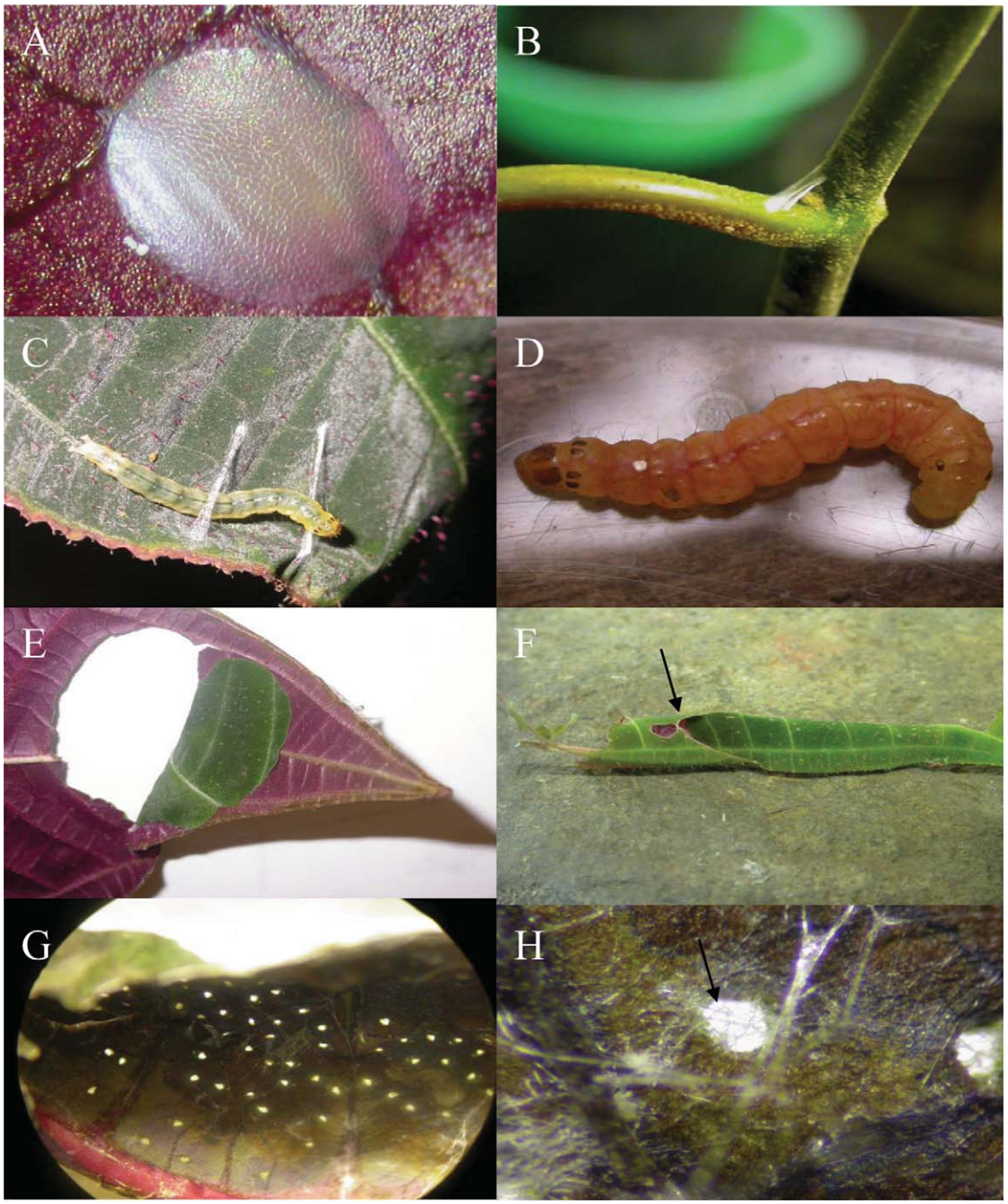

Fig. 2. Solitary egg (A), silk thread secreted by larvae to tie the leaf to the stem (B), fifth-instar caterpillar (C), prepupae (D), pupation chamber (E and F), and holes in pupation chamber of *S. lotanalis* (G and H).

existing leaf rolls with further tying. Early-instar larvae tended to reuse rolls when these were already available, even when still occupied by other larvae. Of the 25 rolls observed in the field, 13 contained larvae of several instars (first, second, and third).

We investigated leaf roll use further in the greenhouse, placing 5–10 larvae of each instar on leaves that already had a roll. Within 1 h, 100, 50, 60, 0, and 40% of first, second, third, fourth, and fifth instars, respectively, moved to the roll already present; the remaining larvae stayed immobile on leaves, except for fifth instars, 50% of which started a new roll.

Prepupae. Larvae turned light orange in color when prepupal (Fig. 2D). Soon after, they started building a pupation chamber by cutting a section of leaf, folding it over, and attaching it to the leaf with silk

Table 1. Duration of life stages of *S. lotanalis* reared on *M. calvescens* in the laboratory

Instar	*n*	Average ± SD (d)	Range (d)
Eggs	310	7.48 ± 0.7	7–9
L1	300	5.9 ± 1.2	4–7
L2	286	5.2 ± 1.8	3–9
L3	265	5.5 ± 0.7	4–7
L4	181	8.9 ± 3.4	4–12
L5	131	8.5 ± 2.7	4–11
Prepupa	86	3.6 ± 0.9	2–6
Pupa	59	13.8 ± 1.8	11–18
Adult	59	13.9 ± 1.0	12–17
Total	59	69.2 ± 4.1	67–77

thread. The pupation chamber could be either inside or outside of a leaf roll (Fig. 2E and F). Prepupae made small holes in the pupation chamber (Fig. 2G and H), presumably for air flow, then covered the inside of the chamber with fine silk thread (Fig. 2H).

Pupae. Pupae of *S. lotanalis* measured 12–14 mm in length (n = 10). They usually pupated on the leaves of *M. calvescens* as described above; however, in the laboratory, we recorded one instance of pupation in the substrate of the pot where *M. calvescens* was planted. Of the 84 laboratory-reared pupae, moths emerged from 70%, with 63% being female and 37% being male. Pupal duration was 13.5 ± 1.7 d for males (N = 22) and 13.4 ± 2.1 d for females (N = 37).

Adults. Emergence of adults from the pupa occurred at night, and we only observed adult emergence between 1900 and 2400 hours. Adults were

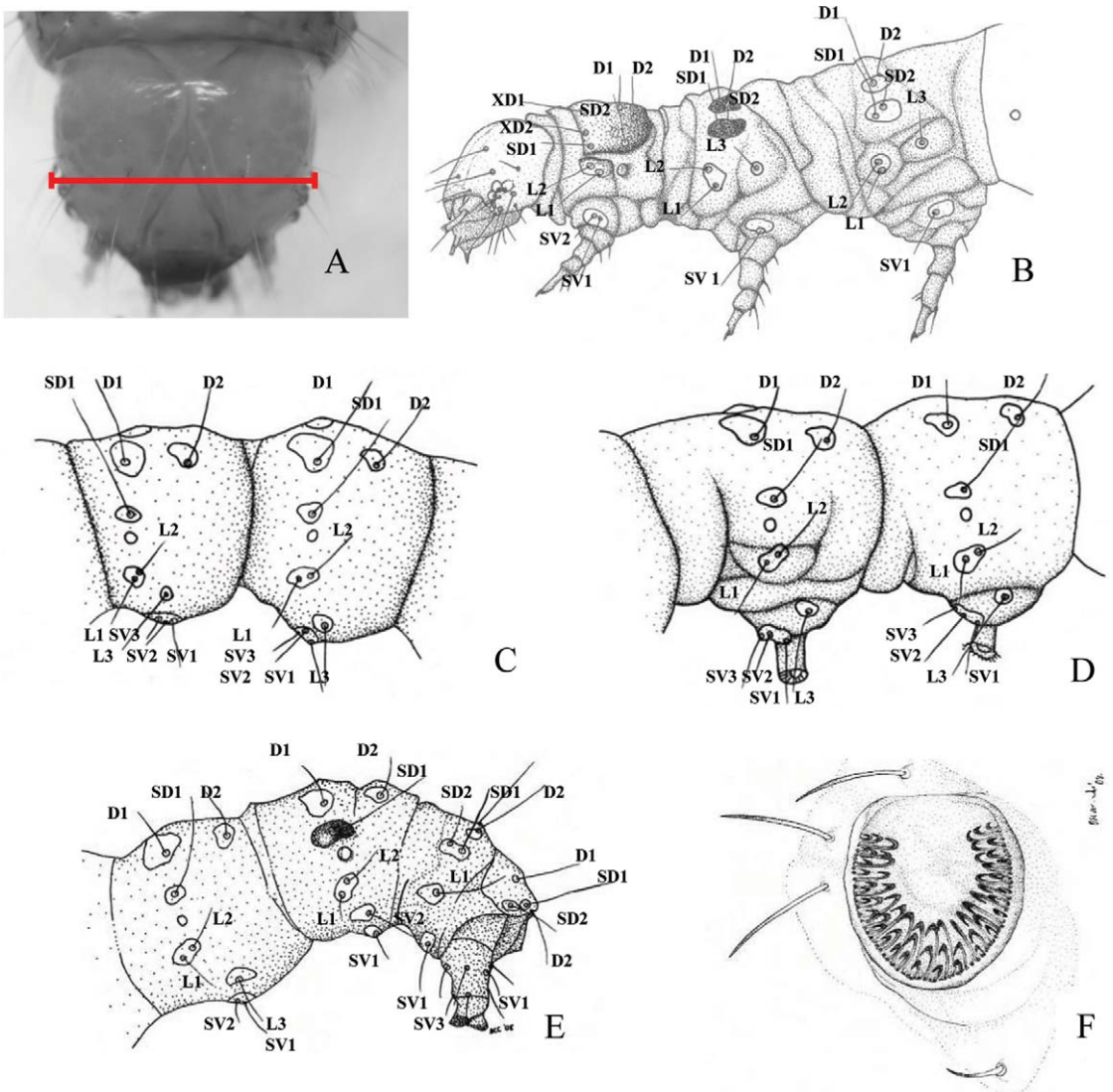

Fig. 3. Chaetotaxy of fifth-instar larvae of *S. lotanalis* and methodology to measure head capsule width: head capsule width measurement (A); head and thorax (B); first and second abdominal segments (C); fifth and sixth abdominal segments (D); eighth, ninth and tenth abdominal segments (E); and proleg (F). (Online figure in color.)

active immediately after emergence. With the food source of honey–water, males and females lived an average of 13.3 ± 1.0 and 14.1 ± 0.9 d (mean ± SD), respectively.

Adults were active primarily at dusk and during the night, remaining immobile on the abaxial side of *M. calvescens* leaves or on cage walls during the day (although feeding occurred at any time). Mating and oviposition occurred at night. The first eggs laid by females were usually placed singly, but subsequent eggs were laid in clusters of 2–50, typically in a straight line. Females had eight ovarioles (four on each of the two ovaries). From unmated females, we dissected two ovarioles with an average total of 102.4 ± 5.4 eggs (mean ± SD; $N = 10$), indicating each female could lay >400 eggs. In the 59 observed visits by adults, vials with the yellow sugar solution were the only ones selected for feeding. Green, purple, and uncolored vials were ignored.

Host Specificity. Third and fourth instars of *S. lotanalis* were able to feed on all Melastomataceae that we tested, including five species of *Miconia* and *C. xalapensis.* Larvae did not feed on the nonmelastomes *T. zebrina* and *N. exaltata.* In no-choice adult tests, *S. lotanalis* oviposited on *M. calvescens* (15.3 ± 9.0; mean eggs per day ± SD) and *M. theaezans* (16.7 ± 11.5), but not on the nonmelastomes *T. zebrina* and *N. exaltata.* In two-choice preference tests, *S. lotanalis* moths laid 1.5 times more eggs on *M. theaezans* than on *M. calvescens*, but this difference was not statistically significant ($t = 1.24$; df = 2; $P = 0.339$). *S. lotanalis* oviposited only on *M. calvescens* when it was simultaneously offered the nonmelastomes *T. zebrina* ($t = 4.91$; df = 2; $P = 0.039$) and *N. exaltata* ($t = 7.56$; df = 2; $P = 0.017$).

Parasitism. Rates of parasitism did not appear to be high in our sample of field-collected larvae, but several species of parasitoids were encountered. Four individuals of a *Bracon* sp. (Hymenoptera: Braconidae) emerged from one prepupa, and one *Meteorus* sp. (Hymenoptera: Braconidae) emerged from another prepupa. Four parasitized *S. lotanalis* pupae yielded each a different parasitoid: one *Hyphantrophaga virilis* Aldrich & Webber (Diptera: Tachinidae), one *Leurus caeruliventris* Cresson (Hymenoptera: Ichneumonidae), one *Brachymeria* sp. (Hymenoptera: Chalcididae), and one unidentified species of the subfamily Cryptinae (Hymenoptera: Ichneumonidae).

Discussion

This study provides new information on the biology, behavior, and morphology of *S. lotanalis.* Our results are generally consistent with observations of *S. lotanalis* in Brazil by Morais et al. (2010): eggs laid individually or in small groups, five larval instars, and a host range apparently restricted to Melastomataceae. In addition, we provide the first description of the fifth instar and document development and behavior from egg to adult. *S. lotanalis* males developed faster than females, which has been observed in other species of Pyraloidea (Galway and Purcell 2005). We found that *S. lotanalis* was relatively easy to rear in the laboratory on potted *M. calvescens*, an important consideration for a potential biocontrol agent. Morais et al. (2012) found that *S. lotanalis* could also be reared on *M. calvescens* leaves in plastic bags.

At our Costa Rica study site, different instars commonly occupied the same leaf roll, inducing high levels of damage from sustained oviposition and feeding. The gregariousness observed in *S. lotanalis* early instars has been observed in other Lepidoptera, including other species of Pyraloidea (Fitzgerald 1993, Zalucki et al. 2002, McAuslane 2005, Costa 2006). Gregariousness has several potential advantages, including more efficient feeding, improved defense, and temperature regulation (Fitzgerald 1993, Clark and Faeth 1997, Denno and Benrey 1997). Gregariousness in the early instars followed by solitary late instars allows avoidance of intraspecific competition, as larvae begin to feed more voraciously (Inouye and Johnson 2005). In *S. lotanalis*, declining gregariousness beginning with the third instar is associated with the formation of leaf rolls. Leaf roll reuse in early-instar larvae could provide shelter against predators and parasitoids for larvae that seem unable to make a roll. Besides providing shelter, leaf rolling could improve feeding and development of the larvae because leaf rolling has been shown to decrease leaf toughness and phenolics, while simultaneously increasing nitrogen concentrations (Fukui et al. 2002).

S. lotanalis was vulnerable to a variety of parasitoids in Costa Rica, which raises concerns that its effectiveness as a biocontrol agent might be compromised by biotic interference in Hawaii. Reimer and Beardsley (1988) reported up to 43% of parasitism of larvae of another crambid leaf roller, *A. matutinalis*, hampering its efficacy in Hawaii as a biocontrol of *C. hirta.* In our field collections, we found the species of *Brachymeria* and *Meteorus* parasitizing *S. lotanalis*, genera with representatives in Hawaii that are known to be broad generalists (Reimer and Beardsley 1988, Delvare 2006, Shaw 2006). In the case of *Brachymeria*, this genus includes not only parasitoids of Lepidoptera but also hyperparasitoids of Tachinidae (Delvare 2006). However, it is unclear whether the *Brachymeria* sp. that we found in this study was a parasitoid of *S. lotanalis*, given that it is also known to hyperparasitize Tachinidae, which we also found (*H. virilis*) attacking *S. lotanalis.*

Although preliminary, our tests provide further evidence that *S. lotanalis* has a host range restricted to Melastomataceae (Morais et al. 2012). Some of the *Miconia* spp. that we tested were recorded for the first time in Costa Rica as hosts for *S. lotanalis* (*M. calvescens*, *M. multispicata*, *M. palacea*, and *M. theaezans*), while others (*M. argentea* and *C. xalapensis*) have already been reported by Janzen and Hallwachs (2014). The exception to the record of *S. lotanalis* as a melastome specialist is one observation of larvae feeding on *Piper aduncum* L. (Piperaceae) (Janzen and Hallwachs 2014). *P. aduncum* is a neotropical species that does not occur in Hawaii, although it occurs in other Pacific Islands as a naturalized invasive species (Hartemink 1999). There are no native Melas-

tomataceae in Hawaii, but several species of this family have been introduced and have become invasive (Wester 1992), including *Tibouchina longifolia* (Vahl) Baillon ex Cogniaux and *C. hirta*, which also are recorded as hosts of *S. lotanalis* (Janzen and Hallwachs 2014).

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