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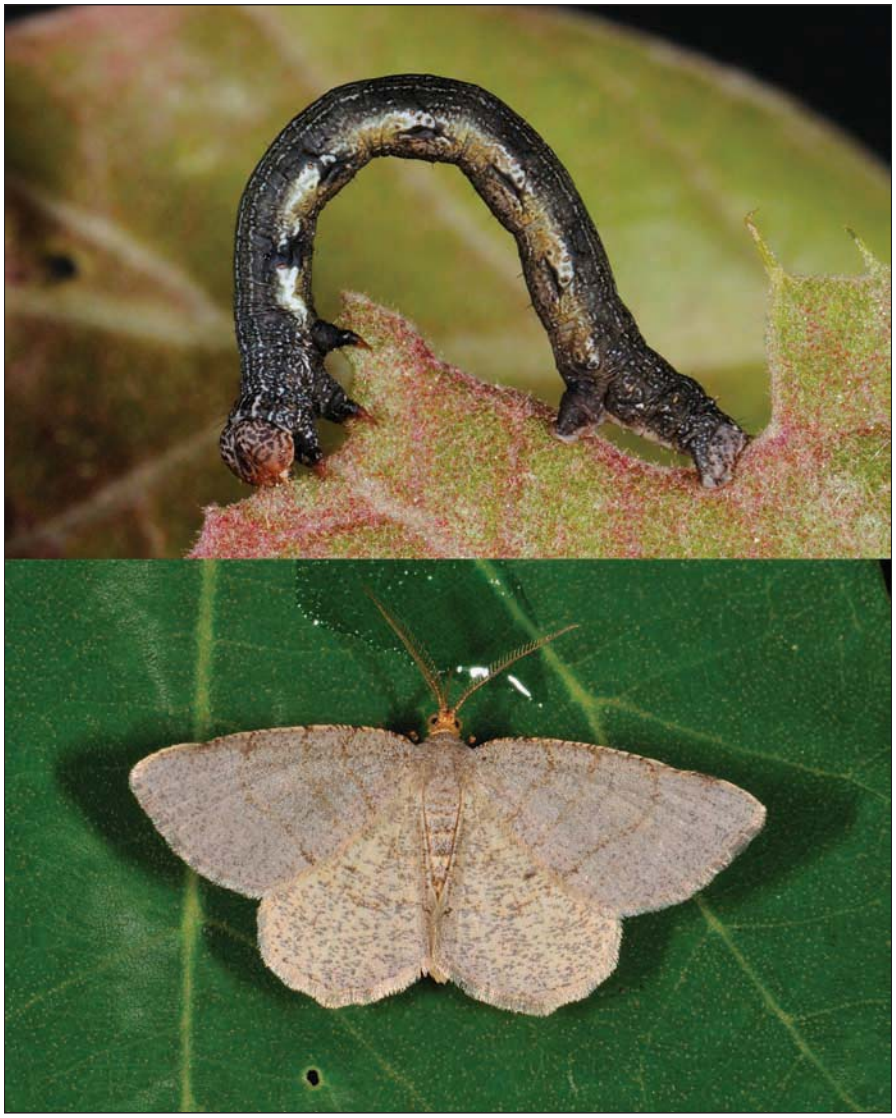

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Cover illustration: *Speranza exonerata* Ferguson, 2008: larva and adult male. Larva reared from egg (live female collected 8 July 2008), photographed in the lab 2 June 2009. Adult male reared from egg (live female collected 13 July 2009), photographed in the lab 23 June 2010. Live females collected near Myles Standish State Forest, in the town of Plymouth, Plymouth County, Massachusetts, USA. Photographs by Michael W. Nelson, Massachusetts Natural Heritage & Endangered Species Program. See article on page 77.

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THE LIFE HISTORY OF *SPERANZA EXONERATA* FERGUSON, 2008 (GEOMETRIDAE: ENNOMINAE: MACARIINI)

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ABSTRACT. *Speranza exonerata* Ferguson, 2008 (Geometridae: Ennominae: Macariini) is a stenotopic moth only known from the northeastern USA. This species was reared from ova obtained from captive females in 2008 and 2009; the immature stages and life history are described. Both a larval host plant experiment and the discovery of wild larvae demonstrate that *Speranza exonerata* feeds on oak (*Quercus* L.), and does not feed on blueberry (*Vaccinium* L.). Larvae feed on scrub oak (*Quercus ilicifolia* Wangenh.), including both leaves and catkins, and *Speranza exonerata* may be a specialist on new growth of this plant. Ova are dormant through late summer, autumn, and winter, and hatch in early spring. Larval development is rapid (3–4 weeks), and corresponds to the availability of new growth of scrub oak. The pupal period is also brief (1–2 weeks), with adult moths flying in early summer.

Additional key words: host plant, *Quercus ilicifolia*, rearing, specialist, *Vaccinium*

The first valid description of what is now known as *Speranza exonerata* was authored by Douglas C. Ferguson, and published posthumously in 2008, in Fascicle 17.2 of the Moths of North America series. In the same work, Ferguson transferred about 50 North American species from the genus *Itame* Hübner, "1816" [1823] to *Speranza* Curtis, 1828. Prior to the publication of Ferguson (2008), the existence of an undescribed species in the genus *Itame* in the northeastern USA was known to lepidopterists for decades. Forbes (1948) incorrectly applied the name *inceptaria* to this species. It was more recently known as *Itame* "sp. 1," or *Itame* "sp. 1 near *inextricata*," due to its apparent close relationship to *Speranza inextricata* (Walker, 1861). *Speranza inextricata* is a species of the southeastern USA, occurring in Florida and Georgia (Schweitzer et al. 2011).

The known geographic range of *Speranza exonerata* extends along the Atlantic Coastal Plain from southern Maine south to New Jersey, and in the Appalachian Mountains from New York and Pennsylvania south to West Virginia and Virginia (Schweitzer et al. 2011). Within this range it is spottily distributed, and only found in pitch pine (*Pinus rigida* Mill.)-scrub oak (*Quercus ilicifolia* Wangenh.) barrens, both on sandy soils and on rocky summits and ridges. The population of *Speranza exonerata* that is the subject of this study occurs in and near Myles Standish State Forest, in the town of Plymouth, Plymouth County, Massachusetts, USA. The habitat at the collection locality (Fig. 1) is sandplain pitch pine-scrub oak barrens with small, scattered pitch pines interspersed with scrub oak, lowbush blueberry (*Vaccinium angustifolium* Aiton and *V. pallidum* Aiton), bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), and heather (*Hudsonia* L.).

Previously, the life history of *Speranza exonerata* was unpublished, but speculation as to its larval host plant focused on scrub oak and lowbush blueberry. These plants are common in pitch pine-scrub oak barrens, where *Speranza exonerata* occurs, and many barrens Lepidoptera feed on one or both of these hosts (Wagner et al. 2003). However, because most *Speranza* are host specific (Ferguson 2008), it seemed unlikely that both scrub oak and lowbush blueberry could serve as larval hosts.

The hypothesis that *Speranza exonerata* feeds on lowbush blueberry seemed plausible because two closely related species, *Speranza brunneata* (Thunberg, 1784) and *Speranza sulphurea* (Packard, 1873), feed primarily on species of *Vaccinium* (Ferguson 2008). Moreover, a third closely related species, *Speranza amboflava* (Ferguson, 1953), is known to feed on another ericaceous plant, *Arctostaphylos uva-ursi* (Ferguson 2008). However, in 1999, Timothy McCabe (New York State Museum) found a single final instar larva of *Speranza exonerata* on *Quercus ilicifolia* in the Albany Pine Bush (Albany County, New York, USA). That single larval collection was the basis for listing *Quercus ilicifolia* as the larval host of *Speranza exonerata* (then "*Itame* sp. 1 near *inextricata*") in Wagner et al. (2003). Given no other evidence as to the larval host of *Speranza exonerata*, speculation that it feeds on lowbush blueberry persisted.

METHODS

Host plant experiment. On 3 July 2008, in pine barrens habitat near Myles Standish State Forest (Fig. 1), in the town of Plymouth, Plymouth County, Massachusetts, USA, three female *Speranza exonerata* were taken live at a mercury vapor light and sheet setup.

FIG. 1. Pitch pine-scrub oak barrens habitat of *Speranza exonerata* near Myles Standish State Forest, in the town of Plymouth, Plymouth County, Massachusetts, USA. Photographed 8 June 2009.

On 8 July 2008, four additional female *Speranza exonerata* were taken live at the same site with the same method. Each of the seven females was set up for oviposition in a separate plastic vial, each vial containing both a *Quercus ilicifolia* twig and a small strip of paper towel as oviposition substrates. Each female was also offered a small piece of cotton saturated with a solution of honey dissolved in water. Viable eggs were obtained from six of the seven females. The eggs were kept through the remainder of the summer and the autumn on a shaded outside porch for a natural temperature and light regime, and through the winter in sealed vials in a refrigerator. The eggs were returned to the porch in early spring.

In the spring of 2009, hatchling larvae from the six female *Speranza exonerata* obtained in 2008 were used in a larval host plant experiment, replicated six-fold. Eighteen hatchlings from each female were divided into three lots of six hatchlings, with each lot in a separate plastic vial. In each replicate, the first of the three lots was offered new growth (new leaves and catkins) of *Quercus ilicifolia*; the second lot was offered new growth (new leaves and flowers) of *Vaccinium pallidum*; and the third lot was offered new growth of both *Quercus ilicifolia* and *Vaccinium pallidum*. Rearing lots were kept on a shaded outside porch for a natural temperature and light regime. Every few days throughout the rearing process, each vial was cleaned of uneaten foliage and feculae, and fresh food of the same treatment offered (*Quercus*, *Vaccinium*, or *Quercus* plus *Vaccinium*). When larvae completed development, dry *Sphagnum* moss was added to the bottom of each vial as a pupation substrate.

Search for wild larvae. On 8 June 2009, foliage was beaten in the vicinity of where the female *Speranza exonerata* were taken the previous year (Fig. 1). A standard one meter square beating sheet was used to catch fallen insects. Beating was conducted for five hours while moving through the habitat.

Deposition of specimens. Both wild and reared adult moths were pinned and spread. Pupal shells were pinned. Ova, larvae, and pupae were preserved in 75% ethanol. Specimens were deposited at the Massachusetts Natural Heritage & Endangered Species Program Insect Collection and the University of Connecticut Insect Collection.

RESULTS

Host plant experiment. In the larval host plant experiment, it quickly became apparent that *Speranza exonerata* feeds on *Quercus*, and does not feed on *Vaccinium*. In each of the six lots (from six separate females) that were fed *Vaccinium*, the six hatchling larvae wandered about the inside of the plastic vial, and over the *Vaccinium* foliage and flowers, but did not feed. Occasionally a hatchling appeared to be "tasting" the *Vaccinium*, but no feeding occurred. Within several days, all six hatchling larvae in each of the six lots that were fed *Vaccinium* were dead. The *Vaccinium* foliage and flowers were examined closely for feeding damage, but none was apparent, and there were no feculae in any of the vials.

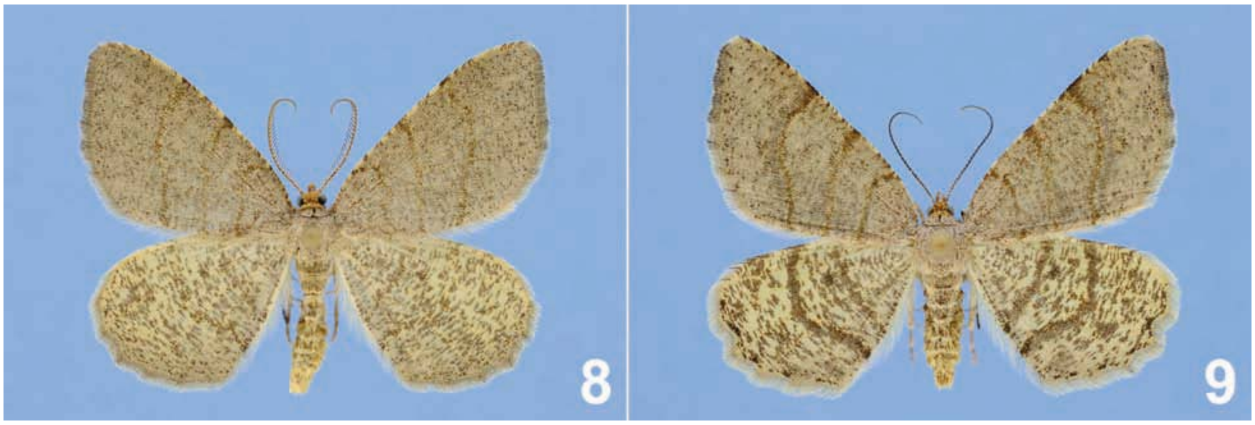
In contrast, in each of the six lots (from six separate females) that were fed *Quercus*, the hatchling larvae began to feed immediately, on both the new leaves and catkins. The larvae grew rapidly, and most larvae completed development and pupated within three to four weeks after hatching. In each of the six lots (from six separate females) that were fed both *Quercus* and *Vaccinium*, the hatchling larvae began to feed immediately on both the new leaves and catkins of *Quercus*, but ignored the new leaves and flowers of *Vaccinium*. Every few days when the vials were cleaned and fresh foliage offered to the *Quercus* plus *Vaccinium* lots, the old *Vaccinium* foliage and flowers were closely examined, but no feeding damage was ever observed. As with the lots fed only *Quercus*, the larvae in the lots fed *Quercus* plus *Vaccinium* grew rapidly, feeding on the *Quercus* alone, and most larvae completed development and pupated within three to four weeks after hatching.

Search for wild larvae. The search for wild larvae of *Speranza exonerata* on 8 June 2009 yielded only a single third instar larva (which was collected and reared to the adult stage), despite beating of vegetation for five hours throughout the habitat where the adult females had been taken at mercury vapor light the previous year.

FIGS. 2–7. **2.** *Speranza exonerata* egg, 0.64 mm long x 0.43 mm wide x 0.32 mm high. Photographed 15 May 2009. **3.** *Speranza exonerata* hatchling larva on catkin of *Quercus ilicifolia.* Larva 1.8 mm long, head capsule 0.23 mm wide. Photographed 21 May 2009. **4.** Third instar larva of *Speranza exonerata*, ≈ 7.0 mm long, head capsule 0.64 mm wide. Photographed 29 May 2009. **5.** Reared, early fifth instar larva of *Speranza exonerata*, ≈ 17 mm long, head capsule 1.6 mm wide. Photographed 6 June 2009. **6.** Wild, late fifth instar larva of *Speranza exonerata*, ≈ 24 mm long, head capsule 1.6 mm wide. Photo courtesy of David L. Wagner, photographed 2 June 2011. **7.** *Speranza exonerata* pupa, length ≈ 11 mm, width ≈ 3.6 mm at third abdominal segment. Photographed 27 June 2009.

Nevertheless, the larva was beaten from *Quercus ilicifolia*, and this observation, along with Timothy McCabe's 1999 collection in the Albany Pine Bush, provide evidence that *Quercus ilicifolia* is the larval host plant of *Speranza exonerata* in the wild. In addition, in the spring of 2011, David L. Wagner (University of Connecticut) found (and reared to adults) larvae of *Speranza exonerata* on *Quercus ilicifolia* growing in the Dwarf Pine Plains of eastern Long Island, New York, USA.

Description of immature stages. The following descriptions were written by examining living specimens and photos of living specimens, and later checked and expanded by examining preserved material. All



FIGS. 8–9. **8.** *Speranza exonerata*, adult male, reared in 2009. Wingspan 21 mm. **9.** *Speranza exonerata*, adult female, reared in 2009. Wingspan 21 mm.

specimens were from a population near Myles Standish State Forest, in the town of Plymouth, Plymouth County, Massachusetts, USA.

Egg (Fig. 2). Oblong and flattened, 0.64 mm long, 0.43 mm wide, 0.32 mm high (N = 8). Color pale green when laid, within several days becoming pale yellow and then pinkish orange. Chorion sculptured with pits and ridges with tiny white knobs. Egg turns dark a day before hatching, as color of first instar larva begins to show through chorion.

First instar larva (Fig. 3). Length 1.8 mm at hatching (N = 8), growing to 2.9 mm (N = 4). Head capsule 0.23 mm wide (N = 8), rounded, smooth and unsculptured, orangish brown in color. Antenna white. Body very pale olive green (almost white), with broad, black stripe on dorsum from T1 to A9 and matching black stripe on venter. Prothoracic shield and anal plate indistinct, concolorous with body. Legs tan.

Second instar larva. Growing to 5.6 mm in length (N = 4). Head capsule 0.42 mm wide (N = 8), rounded, smooth and unsculptured, tan in color (lighter than first instar), with mottling on vertex. Clypeus and labrum tan; antenna white. Body pale olive green in color, with faint white mottling and indistinct, narrow and broken, white middorsal stripe along entire length of body. Prothoracic shield and anal plate indistinct, concolorous with body. Legs tan.

Third instar larva (Fig. 4). Growing to 9.2 mm in length (N = 4). Head capsule 0.64 mm wide (N = 7), rounded, smooth and unsculptured, tan in color with darker mottling. Clypeus tan with white ventral margin; labrum tan; antenna white. Body pale olive green in color, with white mottling. Indistinct, narrow and broken, white middorsal and subdorsal stripes along entire length of body. Prothoracic shield and anal plate indistinct, concolorous with body. Legs gray or grayish tan, becoming black proximally late in the instar.

Fourth instar larva. Growing to 14 mm in length (N = 4). Head capsule 1.1 mm wide (N = 7), rounded, smooth and unsculptured, orangish to pinkish tan (peach colored) with black mottling on vertex, lobes, and frons (mottling occasionally very dense, even solid black, on vertex, front of lobes, and frons). Clypeus white, or tan with white ventral margin; labrum tan; antenna white. Body dark slate gray, with narrow and broken, white middorsal, addorsal, subdorsal, and lateral stripes along entire length of body. On A1 to A5 (sometimes also A6), lateral stripe broadening around, or slightly anterior to, each spiracle into a white patch, with black patch or spot ventrad and slightly posterior to white patch; often with yellowish green patch in subspiracular area between segments. Spiracles tan. Venter mottled gray, with indistinct, narrow and broken, white midventral and adventral stripes. Prothoracic shield and anal plate indistinct, concolorous with body. Legs black proximally, orangish to pinkish tan (peach colored) distally.

Fifth instar larva (Figs. 5 and 6). Growing to 24 mm in length (N = 4), 2.4 mm wide at fourth abdominal segment (N = 8). Head capsule 1.6 mm wide (N = 8), rounded, smooth and unsculptured, orangish to pinkish tan (peach colored) with black mottling on vertex, lobes, and frons (mottling occasionally very dense, even solid black, on vertex, front of lobes, and frons). Clypeus white, or tan with white ventral margin; labrum tan with dark brown edge at notch; mandible tan with dark brown cutting edge. Mandible with seven teeth on cutting edge, plus one small inner tooth. Antennal base white, distal segments tan. Head setae tan to brown in color; no setae unusually short or long, longest setae two times the height of spiracle on T1; seta A3 displaced dorsally toward vertex, well above seta A2 and stemma 1, nearly as high as seta L1. Body dark slate gray to black with narrow and broken, white middorsal, addorsal, subdorsal, supraspiracular, and lateral stripes along entire length of body. On A1 to A5 (sometimes also A6), lateral stripe broadening around, or slightly anterior to, each spiracle into a white patch, with black patch or spot ventrad and slightly posterior to white patch; often with yellowish green patch in subspiracular area between segments. Yellowish green patch of varying extent, occasionally covering most of subspiracular area and extending onto venter. Spiracles yellowish tan with black peritreme, those on T1 and A6–A8 larger than on A1–A5. Venter mottled, varying from brown to gray to black, with indistinct, narrow and broken, white midventral and adventral stripes. Prothoracic shield and anterior of anal plate indistinct, concolorous with body; posterior of anal plate, paraproct, and prolegs often tinged with pink. Legs black proximally, orangish to pinkish tan (peach colored) distally. Hypoproct and paraproct approximately equal in length, both one-third the length of anal plate. Crochets in biordinal homoideous mesoseries, in a single group with no medial lobe; 22–25 crochets on anterior proleg and 23–27 on anal proleg. Body setae tan to brown in color, occasionally more pigmented (dark brown or black); no setae unusually short or long, some on T1 longer than any on T2–T3 and some on A10 and prolegs longer than any on A1–A9, longest setae two and one-half times the height of spiracle on T1. On A1–A8, seta SD1 anterior to spiracle, seta L1 posterior, seta L2 anterior, and seta L3 posteroventrad, distances between SD1, L1, and L2 and spiracle each no more than half the distance between L3 and spiracle; A9 with setae D2, SD1, L1, and SV1 only, all four aligned from dorsum to subventer (none displaced anteriorly or posteriorly relative to others).

Pupa (Fig. 7). Length 11 mm, width 3.6 mm at third abdominal segment (N = 6). Fusiform; eye prominent; labrum hemispherical, length 0.72 of width (N = 6); labial palpus short, tonguelike, slightly longer than wide. Wing ending at posterior margin of fourth abdominal segment. Antenna and metathoracic leg equal in length, extending just beyond wing margin. Mesothoracic leg minutely shorter than antenna and metathoracic leg; proboscis slightly shorter than mesothoracic leg. Prothoracic leg ending in line with posterior margin of third abdominal segment. Prothoracic femur visible. Integument thin, yellowish to orangish brown on wings and other appendages; somewhat thicker and darker, orangish brown on head, thorax, and A1–A4; considerably thicker and darker brown on eyes and A5–A10. Integument smooth on wings, other appendages, head, and thorax.

Mesothoracic spiracle raised and elongate. A1–A8 sculptured with numerous minute pits; anterolateral surface of A5 most densely pitted, with integument thickened and darker brown; A9 and A10 smooth except for rough sculpturing around base of cremaster. Head with one pair of setae near dorsal margin of labrum and two pairs at vertex; T1–T3 each with two pairs of setae; A1 with one pair of setae (anterodorsal); A2–A3 each with two pairs (posterodorsal and anterolateral); A4 with four pairs (posterodorsal, anterolateral, posterolateral, and posteroventral); A5 with six pairs (posterodorsal, two anterolateral, posterolateral, anteroventral, and posteroventral); A6 with five pairs (posterodorsal, two anterolateral, posterolateral, and anteroventral); A7 with six pairs (posterodorsal, two anterolateral, posterolateral, anteroventral, and posteroventral); A8 with two pairs (anterolateral and posterolateral); A9–A10 with no setae. Cremaster with single pair of caudal spines.

DISCUSSION

Larval phenotype. Larvae of Macariini may develop a darker phenotype when reared in crowded or humid conditions (Wagner et al. 2001). This may have been the case with the larvae reared for this study, as they developed a darker phenotype (Fig. 5) than the wild larvae collected by D.L. Wagner (Fig. 6).

Life history and behavior. The life history description presented below is inferred primarily from observations of captive individuals, and it should be noted that behavior in the wild may differ.

Adult *Speranza exonerata* fly in late June and early July. The adult moths are completely nocturnal (Ferguson 2008; Schweitzer et al. 2011). Female moths affix their eggs to twigs of scrub oak (*Quercus ilicifolia*). Eggs are pale green when laid, but within several days after oviposition they change to pale yellow, and then to pinkish orange (Fig. 2). Ova remain dormant through the remainder of the summer and the following autumn and winter.

The eggs hatch in mid- to late May, and the hatchling larvae (Fig. 3) begin to feed on both catkins and new leaves of the host plant. While early instar larvae will feed on either catkins or leaves, there appears to be a preference for catkins in the first and second instars, transitioning to leaves in the third instar (Fig. 4) and thereafter. When feeding on catkins, the larvae will consume both the flower tissue and pollen. When feeding on leaves, first and second instar larvae scrape tissue from one surface of a leaf, leaving the leaf skeletonized on one side. By the third instar, larvae chew through both leaf surfaces and finer vascular tissues, leaving small holes. Scrub oak catkins are largely gone by the time larvae reach the fourth and fifth instars, and so late instar larvae feed mainly on new spring leaves, chewing in from a leaf edge.

When not feeding, early instar larvae either remain in the catkins, where they are well hidden, or sit on the underside of a leaf, where they often align themselves with the midrib. Late instars rest either on the underside of a leaf (again, often aligned with the midrib), or on a petiole or twig, where they assume the straight and upright posture of a geometrid twig mimic.

Larvae grow rapidly, and by early to mid-June reach the fifth and final instar (Figs. 5 and 6). Once fully grown (≈ 24 mm long), larvae descend from the host plant, and pupate in the leaf litter without spinning any sort of cocoon (Fig. 7). The pupal period is brief, with adults emerging one to two weeks after pupation (Figs. 8 and 9).

Conservation status. While it is not known whether *Speranza exonerata* can feed on species of oak other than scrub oak (*Quercus ilicifolia*), the apparent strict association with habitats dominated by scrub oak suggest that *Speranza exonerata* may be a scrub oak specialist. Scrub oak barrens are a rare, and in many places disappearing, natural community (Wagner et al. 2003, Schweitzer et al. 2011). Association with specialized and threatened habitat, along with a relatively limited geographic range, as well as decline and apparent disappearance from some of its former localities, were all factored into the current conservation status rank for *Speranza exonerata* of G3G4, or "vulnerable to apparently secure" (NatureServe 2014).

Conclusions. The distribution of *Speranza exonerata* in the southern Appalachian Mountains has not been well documented, and surveys targeting scrub oak balds in that region are needed. To determine if oaks other than scrub oak (*Quercus ilicifolia*) are fed upon, host plant experiments offering different species of oaks could be performed. It is worth noting, however, that the known geographic range of *Speranza exonerata* corresponds remarkably well with the geographic range of *Quercus ilicifolia*, further suggesting that it may be a scrub oak specialist. Moreover, the early spring phenology of *Speranza exonerata* larvae suggests that this species may require catkins and new growth of leaves for successful development.

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A NEW SUBSPECIES OF *ANTHANASSA* (NYMPHALIDAE: NYMPHALINAE: MELITAEINI) FROM SOUTHEASTERN BRAZIL

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ABSTRACT. A new subspecies of *Anthanassa drusilla*, ssp *rioverde*, is described from Minas Gerais, Southeastern Brazil. This new subspecies is isolated from all other known subspecies of *A. drusilla* by at least 2000 km, and its closest taxon based on wing pattern is *Anthanassa drusilla higginsi*, from Cerro Neblina, Venezuela. To our knowledge, the species is endemic to the region of Poços de Caldas Plateau (Minas Gerais), a region of high natural radiation and heavily impacted by mining. Since the entire geographic distribution and conservation status of this subspecies is unknown, it is highly recommended that immediate measures are taken to minimize the environmental impact on the area of occurrence of this butterfly.

Additional key words: Atlantic Forest, Phyciodina, Minas Gerais, Taxonomy

The knowledge of the butterfly fauna in Brazil is unevenly distributed through the territory, with a clear concentration in the Southeastern Region along the Atlantic Coast, in the Atlantic Forest domain (Brown & Freitas 1999, Santos et al. 2008). Not coincidentally, this is also the region in Brazil with higher human densities and with a longer history and intensity of anthropogenic disturbance (Brown & Brown 1992, Coimbra-Filho & Câmara 1996, Dean 1996). In the five centuries since the beginning of European colonization, more than 80% of the Atlantic Forest has been converted into pastures, fields and urban areas, and the remaining forest persists as highly fragmented landscapes (Ribeiro et al. 2009). As a consequence, several species of animals and plants in this region are threatened; for example, 51 out of the 55 species of Brazilian threatened butterflies are endemics of the Atlantic Forest, some of them facing real risks of extinction (Machado et al. 2008, Freitas et al. 2011, 2014, Freitas & Marini-Filho 2011).

In spite of the above scenario, there are still large forest remnants in SE Brazil, especially in the complex and heterogeneous landscapes in the montane regions of Serra do Mar and Serra da Mantiqueira, where butterfly diversity peaks in the Atlantic Forest biome (Brown & Freitas 2000). In these mountain ranges, several new butterfly taxa have been described in the last years (Freitas et al. 2012 and references therein), and new taxa are being discovered continuously with further field trips (Freitas 2010).

During an outing in a montane region in the state of Minas Gerais in February, 2011, the first author collected a female of an unknown Phyciodina (Fig. 2). A subsequent expedition to the same site on May 2014 resulted in three additional males collected. Based on facies, this proved to be an undescribed subspecies of *Anthanassa drusilla* (C. Felder & R. Felder, 1861), and also the first record of this species of *Anthanassa* Scudder, 1875 for Southeastern Brazil. The present paper describes this new subspecies and discusses the biogeographical and conservation implications of this discovery.

STUDY SITES AND METHODS

Adults were collected and studied in the field in the region of Pocinhos do Rio Verde, Caldas municipality, Minas Gerais, Southeastern Brazil, a montane region with altitudes varying from 1100 to 1700 m, which is part of the Poços de Caldas Plateau. The climate in the region is Cwb of Köppen's classification (Rezende et al. 2013), with average temperature of 18.2°C and mean annual rainfall of 1500 mm, with a dry winter and a wet summer. The region is mostly covered by a mosaic of Seasonal Semidecidual Montane Forest, Dense Ombrophilous High-Montane Forest and Mixed Ombrophilous Forest, including some altitudinal grasslands and rocky fields in the highest peaks (Rezende et al. 2013). The region is now highly fragmented, intermixed with pastures, small plantations including corn, coffee and grapevines and *Pinus* and *Eucalyptus* plantations. The whole region is considered of extreme biological importance and a conservation priority for several biological groups in Minas Gerais (Drummond et

Fig. 1. Habitat and live adults of *Anthanassa drusilla rioverde* in Pocinhos do Rio Verde, Caldas, MG, SE Brazil. **Above** – general view of the habitat in the type locality in Sítio Mar de Minas; **Below** – Two views of a living male landing in the vegetation near the forest edge. Photos by TML.

al. 2005). The specific collecting site was "Sítio Mar de Minas" (21°56'41.53"S, 46°24'41.09"W 1170–1190 m a.s.l.), an area of ca. 12 ha of secondary Seasonal Semidecidual Montane Forest neighbor to a large river (the "Rio Verde") (Fig. 1A).

Taxonomic nomenclature followed Lamas (2004) and Wahlberg & Freitas (2007). Species of *Anthanassa* were studied based on the material available in the Zoology Museum of Unicamp, and compared with the Lamas collection of neotropical butterfly type specimen photographs at the MUSM (also available online in Warren et al. 2013), representing most currently relevant names and recognized species of *Anthanassa* (Lamas, 2004), and also with the revision of Higgins (1981). The acronyms for the collections are: **DZUP**, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; **ZUEC**, Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil. The following abbreviations were used: FW: forewing; HW: hind wing; D: dorsal; V: ventral.

Genomic DNA was extracted from two legs of freshly caught butterflies, using Invisorb® Spin Tissue Mini Kit (STRATEC Molecular, Germany) in the laboratory at Campinas, and using the QIAgen DNeasy Tissue Kit (Qiagen, Hilden, Germany) in the laboratory at Turku. Four gene regions were sequenced according to published protocols (Wahlberg & Wheat 2008), these were cytochrome c oxidase I (COI, 1471 bp), elongation factor 1 alpha (EF1α, 1240 bp), ribosomal protein S5 (RpS5, 617 bp) and wingless (403 bp). Sequences were aligned with those of other *Anthanassa* obtained either in our laboratory or from GenBank (Table 2), comprising 6 out the 19 described species within *Anthanassa*.

The final matrix comprised 34 individuals of *Anthanassa* and two outgroups, (Table 1). Bayesian analyses (Huelsenbeck et al. 2001, 2002) were carried out for the combined data set under the model GTR+Γ+I, using the program MrBayes 3.2 (Ronquist & Huelsenbeck 2003). Four simultaneous chains were run for 10×10^6 generations for two runs, sampling trees

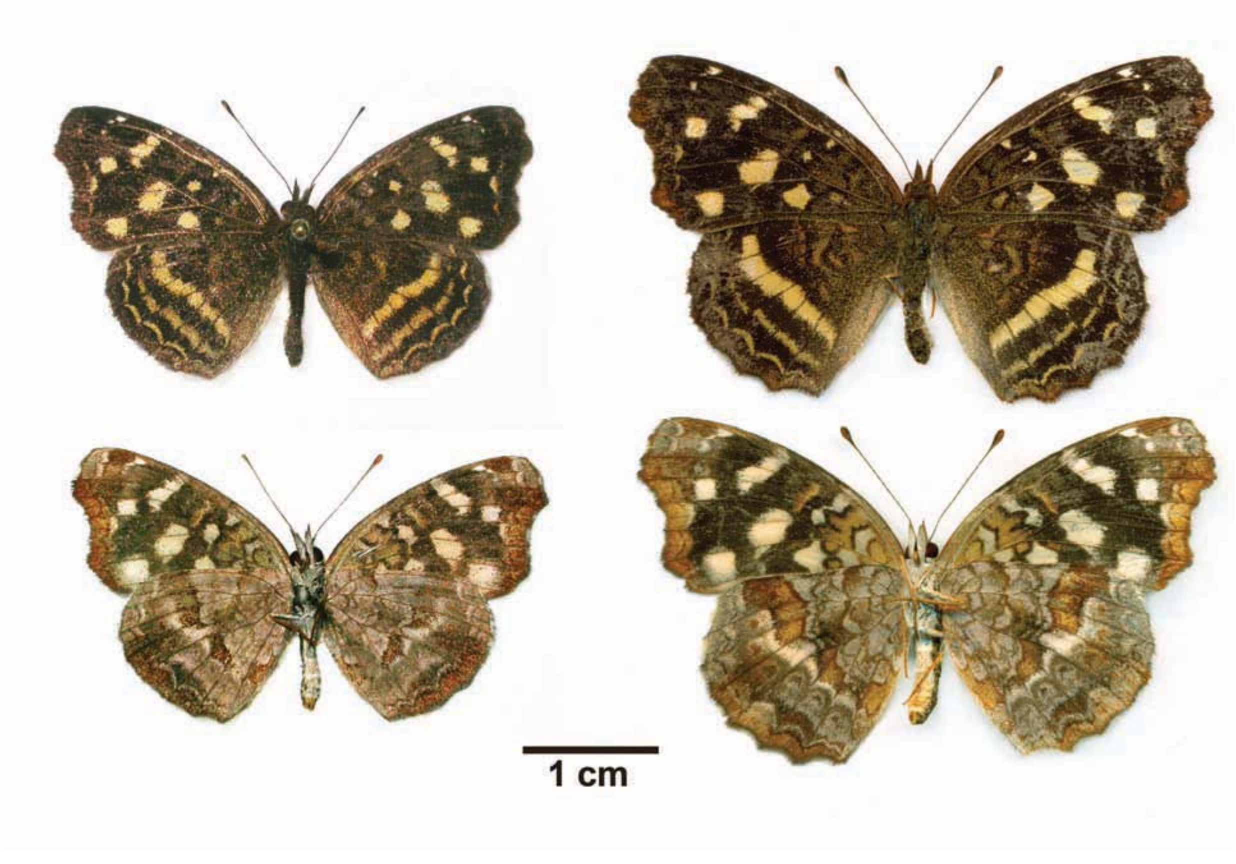

FIG. 2. Holotype male (left) and paratype female (right) of *Anthanassa drusilla rioverde.*

every 1,000 cycles. The first 2,500 trees were discarded as "burn in" based on when the runs had converged and reached equilibrium.

Anthanassa drusilla rioverde Freitas, **new subspecies**

(Figs. 1, 2)

Phyciodes drusilla (Felder, 1861) ssp.n.; Ebert 1969: 44, Appendix II

Diagnosis. Together with *Anthanassa drusilla higginsi* Neild 2008, this new subspecies can be distinguished from all other subspecies of *Anthanassa drusilla* by the median yellow patch in DFW, mostly confined from M_3 to Cu_2, only barely visible below the Cu_2 (this patch conspicuously extends through Cu_2 to the inner margin in all other subspecies, Higgins 1981, Neild 2008, Warren et al. 2014). This new subspecies can be easily distinguished from the similar *Anthanassa drusilla higginsi*, by the following characters: males much smaller (FW length 16–17 mm, compared with the 18-19.5 mm of *A. drusilla higginsi*, see Neild 2008); median patches in DFW larger and post median band in DHW broader than in *A. drusilla higginsi*; the submarginal lunule in space M_3– Cu_1 not as broad as in *A. drusilla higginsi*. Although the ventral pattern was considered useless for subspecific distinction (Neild 2008), the dark brown area on the forewing, from costa to the anal margin is darker and more expansive in *A. drusilla rioverde* compared to the other subspecies. In addition, *A. drusilla rioverde* is isolated from *A. drusilla higginsi* by more than 3,000 km (the latter was described from the region of Cerro Neblina, near the Brazil/Venezuela border).

Description: Male (Fig. 1). FW length 16-17 mm (n = 3), HW length 12–13 mm (n = 3). Eyes naked, entirely brown. Palpus length 2.0 times head height, brown with long brown hairs. Antenna 9 mm in length, shaft dark brown, club orange, conspicuously developed, with 9 antennomeres. Body brown, ventral abdomen white. Wings dorsal color dark brown with contrasting pale yellow markings; ventral wings with a variegated pattern with tones of brown, orange and beige, variable among individuals. Forewing outer margin conspicuously excavated; hind wing rounded, with subtle concavities in the intervenal spaces.

Female (Fig. 1): The only known female is very similar to the males, but much larger. FW length 21 mm (n = 1), HW length 16 mm (n = 1), antenna 9 mm.

Habitat, behavior and natural history. *A. drusilla rioverde* was observed flying in sunny patches near the forest edge, as several other Phyciodina recorded for the region. Males and females were observed flying in sunny patches from 10:00 to 15:00 h, occasionally visiting flowers of *Mikania micrantha* Kunth and *Bidens rubifolia* Kunth (Asteraceae). Oviposition was not observed, and the larval host plant is unknown. Ebert (1969: Appendix II) mentions this butterfly as rare to common from November to May near well preserved and secondary forests in altitudes from 1000 to 1400m, suggesting that the species is multivoltine, with multiple broods throughout the year.

Distribution. Besides the type locality, this subspecies was also mentioned by Ebert (1969) to occur in three different sites around Poços de Caldas (about 35 km North of the type locality).

Types: Holotype. Male (Fig. 2A) from Sítio Mar de Minas, Pocinhos do Rio Verde, Caldas, Minas Gerais, Brazil, deposited in the Museu de Zoologia da Unicamp (ZUEC), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. Labels on the holotype (four labels separated by transverse bars): / Holotypus/ B 884 – POCIN – 2/mai/2014, Sítio Mar de Minas, Pocinhos do Rio Verde, Caldas, MG: Brazil 21°56'41''S, 46°24'41''W, 02.V.2014, 1160–1200 m, André V. L. Freitas leg. / ZUEC LEP 8918 / DNA voucher – BLU 523 /

Paratypes (all from Minas Gerais, Brazil). ZUEC – 1 ♀ 19.II.2011 (DNA voucher PM23-03), (ZUEC-AVLF collection), 2 ♂♂ 02.V.2014 (DNA vouchers BLU 524, BLU 525), Sítio Mar de Minas, Pocinhos do Rio Verde, Caldas, André V. L. Freitas leg., ZUEC LEP 8919, ZUEC LEP 8920. **DZUP** – 1 ♂ 27.XI.1966, Poços de Caldas, 1250m, ex-coll. Ebert, DZ 30.902; 1 ♀, 27.IV.1967, Poços de Caldas, 1000m, ex-coll. Ebert, DZ 30.901; 5 ♂♂ 08.II.1963, Poços de Caldas, 1250m, ex-coll. Ebert, DZ 30.903, DZ 30.904, DZ 30.905, DZ 30.906, DZ 30.907; 1 ♂ 27.V.1967, Poços de Caldas, 1000m, ex-coll. Ebert, DZ 30.908; 3 ♂♂ 21.IV.1967, Poços de Caldas, 1000m, ex-coll. Ebert, DZ 30.909, DZ 30.868, DZ 30.869; 1 ♂ 11.IV.1967, Poços de Caldas, 1250m, ex-coll. Ebert, DZ 30.870; 1 ♂ 17.V.1963, Poços de Caldas, 1250m, ex-coll. Ebert, DZ 30.871; 1 ♂ 22.IV.1967, Poços de Caldas, 1250m, ex-coll. Ebert, DZ 30.872

Etymology. The subspecific name was given after the "Rio Verde", the main river in the type locality of this subspecies. A noun in apposition.

Phylogenetic relationships. Based on DNA sequences, the four individuals of *Anthanassa drusilla rioverde* group together with other *Anthanassa drusilla* individuals (Fig. 3), validating the description of the current taxon as a subspecies of *A. drusilla*.

Discussion

The importance of the present paper goes far beyond the description of a new taxon of Phyciodina in Southeastern Brazil, which by itself is surprising, since this is one of the most thoroughly collected regions for butterflies in Brazil (Santos et al. 2008). However, even more surprisingly, this is the first record of *Anthanassa drusilla* for Southern South America. *Anthanassa drusilla* is known to occur from Mexico through Central America and in the Andean region, in Venezuela, Colombia, Ecuador, Peru, Bolivia and Northwestern Brazil (Higgins 1981, Neild 2008, AVLF and K. S. Brown Jr., unpublished data), with one isolated subspecies in the region of Cerro Neblina (Venezuela) (Neild 2008). Based on the available data, the nearest subspecies to *A. drusilla rioverde* known so far are *Anthanassa drusilla verena* (Hewitson, 1864), from Cochabamba, Bolivia (ca. 2,000 km Northwest) and Acre, Brazil (ca. 3,000 km Northwest), and *A. drusilla higginsi*, from Cerro Neblina, Venezuela (ca. 3,000 km North) (Gareca et al. 2006, Neild 2008, AVLF and K. S. Brown Jr., unpublished data). This makes *A. drusilla rioverde* the most isolated subspecies of *A. drusilla*, and the only one from Southeastern South America. It is also worth noting that *A. drusilla rioverde* is much more similar to *A. drusilla higginsi* than to the geographically nearer *A. drusilla verena*. The reasons for the isolation

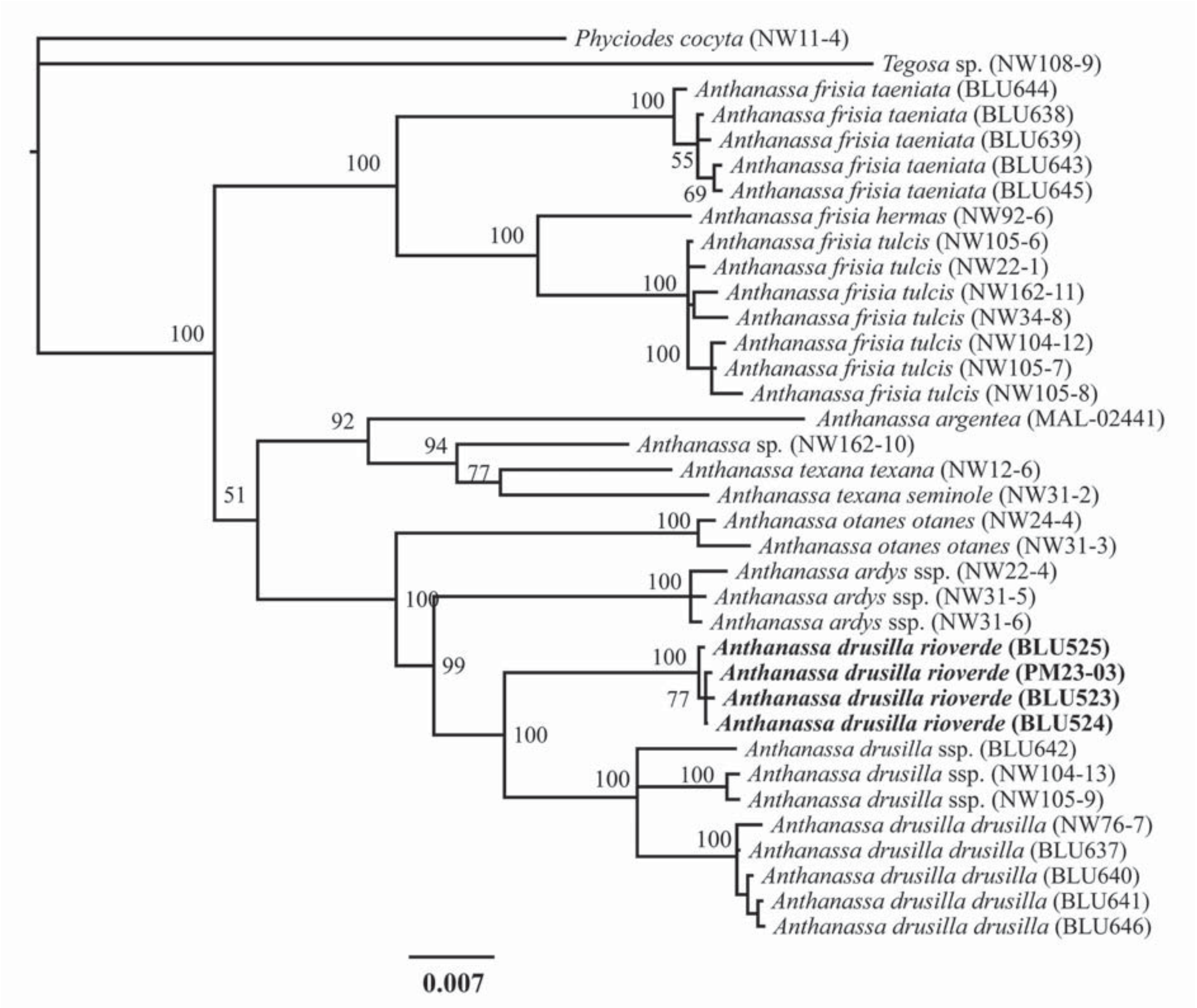

FIG. 3. Relationships within the genus *Anthanassa* analysed using Bayesian inference. Posterior probabilities of nodes are given near the branches.

of *A. drusilla rioverde* are unknown, and the similarity in wing pattern with *A. drusilla higginsi* cannot be assigned to kinship with the available information. A broader study, including samples of most species and subspecies in multiple localities is required to answer this and other questions about the distribution of the species in this genus, and to explain the isolation of *A. drusilla rioverde* in SE Brazil.

This subspecies is only known from the region of the Poços de Caldas plateau, in southwestern Minas Gerais (searches in three Brazilian museums resulted in no additional individuals found, except the listed paratypes from the H. Ebert collection, now deposited in the Universidade Federal do Paraná), a region considered of extreme biological importance, including several endemisms of plants and animals (Drummond et al. 2005, Machado et al. 2008, Martinelli & Moraes 2013), and a conservation priority in the Atlantic Forest (MMA 2000). The Poços de Caldas Plateau has been intensively surveyed because of its outstanding levels of natural radiation associated with a complex mixture of ores (Amaral et al. 1992). Consequently, the entire region of Poços de Caldas Plateau, has been highly impacted by mining of bauxite, uranium, and several other mineral deposits, with several socio-environmental impacts, and great injury to the local fauna and flora (Fernandes et al. 1995, Barros et al. 2012).

The type locality of *A. drusilla rioverde* lies within in the "Santuário Ecológico da Pedra Branca" (Pedra Branca Ecological Sanctuary), a protected area in the municipality of Caldas. However, despite its protected status, this region suffers continuously from heavy impacts arising from mining of syenite (an igneous rock used for several purposes in the region) (Conforti et al. 2007).

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

Code	Genus	Species	Subspecies	Country	Locality	COI	EF1a	wingless	RPS5
NW11-4	*Phyciodes*	*cocyta*	-----	Canada	Trail, B.C.	AF187755	AY090192	AY090158	GQ865486
NW108-9	*Tegosa*	*sp.*	-----	Brazil	Viamão, Rio Grande do Sul	EF493957	EF494015	EF493908	GQ865500
NW92-6	*Anthanassa*	*frisia*	*hermas*	Brazil	E. E. Jataí, Luis Antônio, SP	EF493929	EF493977	EF493870	KP172589
NW104-12	*Anthanassa*	*frisia*	*tulcis*	Panama	Forest Edge Gamboa	AY788612	AY788717	AY788478	KP172583
NW162-11	*Anthanassa*	*frisia*	*tulcis*	Mexico	Morales, Road Yautepec-Jojutla, km 8.5, CEPROBI	KP172561	KP172572	KP119834	KP172587
NW22-1	*Anthanassa*	*frisia*	*tulcis*	Costa Rica	Monteverde	AF187811	KP172573	KP119835	-----
NW34-8	*Anthanassa*	*frisia*	*tulcis*	Mexico	Manzanillo, Colima	AF187802	EF493978	EF493871	KP172588
NW105-6	*Anthanassa*	*frisia*	*tulcis*	Panama	Path to Gloria Alta, Chiriqui Grande - Almirante 9.5 km	KP172558	KP172569	KP119831	KP172584
NW105-7	*Anthanassa*	*frisia*	*tulcis*	Panama	Forest edge, Gamboa	KP172559	KP172570	KP119832	KP172585
NW105-8	*Anthanassa*	*frisia*	*tulcis*	Panama	Forest edge, Gamboa	KP172560	KP172571	KP119833	KP172586
BLU-638	*Anthanassa*	*frisia*	*taeniata*	Ecuador	Manabe, La Victoria, Km3 W Cascol	KP263381	KP297920	-----	KP297926
BLU-639	*Anthanassa*	*frisia*	*taeniata*	Ecuador	Loja Aeroporto, La Tola, Catamayo	KP263382	KP297921	-----	KP297927
BLU-643	*Anthanassa*	*frisia*	*taeniata*	Ecuador	Manabe, San Vicente de Loja, Rio Olón	KP263386	-----	-----	-----
BLU-644	*Anthanassa*	*frisia*	*taeniata*	Ecuador	El Oro, Destacamento Chacras	KP263387	-----	-----	-----
BLU-645	*Anthanassa*	*frisia*	*taeniata*	Ecuador	Loja, Km 22 road El Empalme - Loja	KP263388	-----	-----	-----
NW162-10	*Anthanassa*	sp.		Mexico	Morales, Road Yautepec-Jojutla, km 8.5, CEPROBI	KP172556	KP172568	KP119830	KP172574
NW12-6	*Anthanassa*	*texana*	*texana*	USA	Austin, Texas	AF187806	AY788716	AY788477	GQ865388
NW31-2	*Anthanassa*	*texana*	*seminole*	USA	Alachua Co., Florida	KP172557	-----	-----	-----
NW31-5	*Anthanassa*	*ardys*	ssp.	Costa Rica	Monteverde	KP172550	KP172562	KP119824	KP172576

TABLE 1. Continued

Code	Genus	Species	Subspecies	Country	Locality	COI	EF1a	wingless	RPS5
NW22-4	*Anthanassa*	*ardys*	ssp.	Costa Rica	Monteverde	AF187743	AY788713	AY788474	KP172575
NW31-6	*Anthanassa*	*ardys*	ssp.	Costa Rica	Monteverde	KP172551	KP172563	KP119825	KP172577
NW24-4	*Anthanassa*	*otanes*	*otanes*	Costa Rica	Monteverde	AF187790	AY788715	AY788476	KP172581
NW31-3	*Anthanassa*	*otanes*	*otanes*	Costa Rica	Monteverde	KP172555	KP172567	KP119829	KP172582
MAL-02441	*Anthanassa*	*argentea*	-----	Mexico	Campeche, Calakmul, Reserva de la Biosfera de Calakmul, Ejido Laguna Alvarado: ac ahual de selva baja	HM890823	-----	-----	-----
NW104-13	*Anthanassa*	*drusilla*	ssp.	Panama	Forest Edge, Gamboa	KP172552	KP172564	KP119826	KP172578
NW105-9	*Anthanassa*	*drusilla*	ssp.	Panama	Pipeline road	KP172553	KP172565	KP119827	KP172579
NW76-7	*Anthanassa*	*drusilla*	ssp.	Ecuador	Zapatta, near Esmeraldas, Esmeraldas	AY788611	AY788714	AY788475	KP172580
BLU-637	*Anthanassa*	*drusilla*	*drusilla*	Ecuador	Loja, Km 22 El Empalme - Loja Road	KP263380/ KP297918	KP297919	-----	KP297925
BLU-640	*Anthanassa*	*drusilla*	*drusilla*	Ecuador	Loja, Rio Inguna, Km5 road Zambe-Piñas	KP263383	KP297922	-----	KP297928
BLU-641	*Anthanassa*	*drusilla*	*drusilla*	Ecuador	Loja, Km2 road Las Chinchas-Zambe	KP263384	KP297923	-----	KP297929
BLU-646	*Anthanassa*	*drusilla*	*drusilla*	Ecuador	Loja, Reserva Jurupe, W Macará	KP263389	-----	-----	-----
BLU-642	*Anthanassa*	*drusilla*	ssp.	Ecuador	Carche Finca San Francisco	KP263385	KP297924	-----	KP297930
PM23-03	*Anthanassa*	*drusilla*	*rioverde*	Brazil	Pocinhos do Rio Verde, Caldas, Minas Gerais	KP172554	KP172566	KP119828	-----
BLU-523	*Anthanassa*	*drusilla*	*rioverde*	Brazil	Pocinhos do Rio Verde, Caldas, Minas Gerais	KP100172	KP100175	-----	KP100178
BLU-524	*Anthanassa*	*drusilla*	*rioverde*	Brazil	Pocinhos do Rio Verde, Caldas, Minas Gerais	KP100173	KP100176	-----	KP100179
BLU-525	*Anthanassa*	*drusilla*	*rioverde*	Brazil	Pocinhos do Rio Verde, Caldas, Minas Gerais	KP100174	KP100177	-----	KP100180

The entire distribution and conservation status of this subspecies is unknown. However, it has never been recorded in the many localities surveyed in the Mantiqueira range, which extends east and northward into the states of Rio de Janeiro and Minas Gerais, nor in the more extended Serra do Mar or the inland Serra do Espinhaço. Therefore at present we have to presume that this new subspecies is indeed endemic to the Poços de Caldas plateau and possible to adjoining ridges. Hence it is highly recommended that suggestions and guidelines of the ecological zoning of the area are followed (see Conforti et al. 2007). This will not only enhance protection of this notable new endemic butterfly, but also other threatened plants and animals of the entire region, several of which are of high conservation interest.

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STATUS OF *DANAUS PLEXIPPUS* POPULATION IN ARIZONA

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ABSTRACT. We report results of a ten year study to understand the distribution, breeding and migration of the monarch butterfly (*Danaus plexippus*) in Arizona. We observed breeding and migratory monarch populations throughout the state and small overwintering aggregations in some locations. Migration occurred to known migration destinations in both California and Mexico. We found that the destination is not random. Wind significantly affects whether migrating monarchs are recovered. This study provides new insights into the breeding, overwintering and migratory strategies of Arizona monarchs.

Additional key words: *Danaus plexippus*, Arizona, Southwest Monarch Study, Migration, Monarch Butterfly

While much is known about the monarch butterfly (*Danaus plexippus* L., Nymphalidae) migration and breeding in the eastern portion of North America, little is documented about the southwest United States. Through tagging studies, Urquhart (1987) concluded there were two monarch populations in North America. He identified an extensive "Eastern Population" overwintering in Mexico and a "Western Population" that overwinters in California as well as a resident population in Florida. Urquhart maintained that the two populations are not geographically isolated and migrants from west and east of the Rocky Mountains both move through river valleys especially in Idaho and Montana, particularly along the Snake River tributaries. He noted that it was likely that genetic material was also exchanged in other mountain passes. Monarchs west of the Rocky Mountains migrate to the coastal sites of California extending in smaller numbers to Baja California in Mexico (Leong et al. 2004). Howard et al. (2010) demonstrated that small numbers of monarchs also spend the winter along the Gulf coast and in Texas. Many have questioned if eastern and western monarchs are one population (Brower 2005). Recent genetic studies of migrating eastern and western monarchs support the hypothesis that they may form one admixed population (Lyons et al. 2012).

An early map of fall monarch western migration movement by Urquhart (1960) noted that Arizona was in an area with no reported collections or recorded observations. Later, Urquhart (1977) reported that few adult monarch butterflies were ever collected in Arizona and New Mexico. R. Bailowitz's (pers. comm.) database for Arizona butterflies listed 150 monarch sightings from 13 August 1975 to 7 October 1984 primarily in Santa Cruz and Cochise counties in southeast Arizona but also in smaller numbers in other counties across the state (Appendix 1). Urquhart (1987) posted observations from Louis Schellbach at the Grand Canyon reporting monarchs moving south through the state during the migration. In particular Schellbach observed monarchs flying south along U. S. Hwy 89 from Salt Lake City, Utah between two mountain ranges. Urquhart (1987) also recorded limited sightings of monarchs in Flagstaff, Arizona and Ridgefield, Utah. Bailowitz and Brock (1991) noted that monarchs were most common "during its southward migration, in late summer and early fall" in southeast Arizona.

Pyle (1996) travelled through Arizona during the fall migration while researching monarch movement and observed occasional monarchs in the southern part of the state flying to the south. R. Gilmore (pers. comm.) in October 1997 and again in 1998 noted monarchs flying north along the Colorado River at Lake Havasu then turning west along I-40 at Needles and flying west through the mountain pass into California. He also observed hundreds of dead monarchs on the front grills of semi-trucks parked at a truck stop near Kingman after driving east through the same pass. The Arizona

Sonora Desert Museum Migratory Pollinator Program on Monarch Butterflies (1999) research noted monarchs flying south along the San Pedro River through Guadalupe Canyon into Mexico. They also recorded monarchs flying south through Buenos Aires National Wildlife Refuge and Organ Pipe Cactus National Monument in southern Arizona continuing south across the border. The observations of Bailowitz, Brock, Pyle and the Arizona Sonora Desert Museum researchers provided evidence that some western monarchs may migrate to the Mexican overwintering sites and that not all Western monarchs fly to overwintering sites on the west coast (Pyle 1999, Brower and Pyle 2004). Observations of Pyle and Dingle et al. (2005) suggested the possibility of monarch migration flyways in eastern Arizona along the New Mexico border and San Pedro River as well as along the Colorado River on the western border.

There have been conflicting reports regarding monarch breeding in Arizona. A map of eastern and western monarch populations in Journey North (2011) excluded most of Arizona as monarch breeding habitats. Stevens and Frey (2010) studied monarch host plants and climate patterns in western North America and noted Arizona had 22 species of *Asclepias* according to their model that included only extreme western Arizona. Of these, in Arizona only *A. erosa*, *A. linaria*, *A. speciosa* and *A. tuberosa* had growing seasons extending to August and September to produce a migratory generation. Earlier Urquhart (1960) mentioned briefly that Louis Schellbach found monarch larvae feeding on native milkweed at the Grand Canyon but provided few additional details. Funk (1968) reported 48 monarch larvae on *Asclepias tuberosa*, not native to the lower elevation of Yuma, as well as six pupae and three adults in Yuma in December 1965. He observed oviposition on 16 January 1966 as well as 18 and 27 February 1966, although copulation was not observed. Bailowitz and Brock (1991) noted monarchs were common in the Canelo Hills in southeast Arizona where they seemed to breed and reported the primary food plant as *Asclepias asperula* in the nearby Huachuca Mountains. J. Brock (pers. comm.) found a female ovipositing on *Asclepias tuberosa* along Turkey Creek in Canelo on 1 June 1994. He returned on 16 June 1994 and found monarch larvae. Brower and Pyle (2004) noted a report of 65 monarchs on 2 August 2003 along the San Pedro River between Hereford and Palominos near a stand of *Asclepias subverticillata*.

Monarchs were observed during the winter months in Yuma and Tucson. Funk (1968) observed monarch adults flying in the Yuma area on warm days in January 1966. Bailowitz and Brock (1991) reported limited monarch sightings during the winter in the Tucson area. Brower and Pyle (2004) reported small numbers of monarchs during the winter months in the Yuma area and along the Colorado River as well as Tucson.

Brower and Pyle (2004) hypothesized that occasional east to west influxes of eastern monarch butterflies increased the western population. In 1996 a poor spring remigration in the eastern United States from Mexico was followed by a large population increase in the western monarch population the following fall. This shift correlated with a documented major westward wind pattern shift in March and April also affecting the warbler migration. Winds could have displaced monarchs into New Mexico and Arizona aiding the western California overwintering population recovery. In this scenario Arizona could be a flyway.

A unique annual weather phenomena in Arizona is the summer monsoon season from 15 June to 30 September. The normal dominating westerly winds shift to prevailing winds blowing from the south, southeast and east to the north, northwest and west. It is a time of frequent to daily intense storm activity with locally heavy rainfall and damaging winds. During September the winds aloft are unstable as the season ebbs and flows, but intense storms are triggered and amplified by increased pacific hurricane remnants or cold fronts sweeping through the state. This results in severe storms over large areas of the desert, particularly southeast and central Arizona (National Weather Service 2008). This arrival of the annual monsoon triggers the time of greatest insect activity as well as plant growth around the state and is particularly pronounced in southeast Arizona (Bailowitz and Brock 1991).

The natural history of the monarch in Arizona is fragmented and incomplete. This paper presents field observations of a citizen science study and the results of a tagging program that addresses both monarch breeding and heretofore unknown migratory movements of the monarch butterfly in Arizona.

MATERIALS AND METHODS

Early locations for exploration of *Danaus plexippus* absence/presence were based on data reports on the Southwest U.S./Northwest Mexico Leps list (1999) and personal communications with several butterfly enthusiasts in Arizona. Collections of *Asclepias* were researched in SEINet (Southwest Environmental Information Network 2014) database to locate possible breeding habitats. Opportunities for Citizen Scientists to participate in monitoring and tagging monarchs were publicized on the Boyce Thompson Arboretum website, newspaper articles and an occasional television feature.

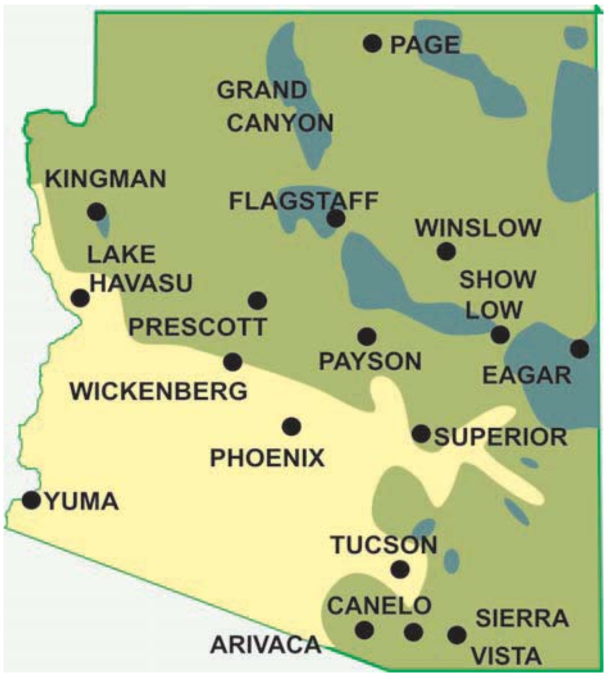


FIG. 1. Arizona climate zones. Blue indicates mountainous regions, Green, high desert and cool plateau highlands, Yellow, low and mid altitude desert.

In 2010 the Southwest Monarch Study web site was developed to promote tagging and monitoring opportunities as well as a Facebook page. Permits and/or permissions to enter, monitor and tag on private or government properties were acquired. Data collection of monarchs tagged or monitored in a site where it was unclear whether proper landowner permission had been obtained or later denied were omitted.

Tags were provided free of charge to volunteer citizen scientists to encourage active participation by the public. Tagging trips began in 2003 in southeast Arizona, known for the Sky Islands, rich in biologic diversity and density (Bailowitz and Brock 1991). Tags were purchased through Monarch Watch with Southwest Monarch Study contact information printed on the tags. The tags were made from a 2 mil all-weather white polyester facestock, paired with a 2 mil 3M adhesive layer. They were 8.89 mm in diameter and weigh less than 0.01g. From 2003 to 2011 the tags were blue; 2012 to 2014 the tags were white.

Sightings. The general public as Citizen Scientists was invited to monitor their own backyards and search natural areas for the presence of species of *Asclepias*, monarch breeding or migration activity and send in reports. In addition training workshops were held around the state. Sightings and photos of species of *Asclepias*, *Danaus plexippus* adults, eggs, larvae and pupae around Arizona and the Southwest were reported via email or posted to the Southwest Monarch Study Facebook page. Photo documentation was required for participants if they were new to monitoring to assure proper identification of adults or immatures due to the easy confusion with *Danaus gilippus*, queen butterflies, in the field. In addition, Southeast Arizona Butterfly Association (SEABA), Central Arizona Butterfly Association (CAzBA) and other butterfly lists were monitored for monarch sightings and reporters were contacted for details.

Breeding Habitats. Field trips were organized to investigate possible breeding habitats based on monarch sightings, *Asclepias* collections and reported riparian habitat. Protocols for identifying species of *Asclepias* were designed using herbarium and other resources (Kearney and Peebles, 1961, Woodson, 1954). For the purpose of this study we used the following divisions to identify elevations in Arizona: Low and Mid Altitude Desert (below 1,067 m) including Phoenix, Tucson, Lake Havasu, Parker and Yuma, High Altitude Desert and Cool Plateau Highlands (1,067 m to 1,829 m) including Prescott, Payson, Patagonia, Canelo and Sierra Vista, and Cold Mountainous Regions (above above 1,829 m) including Flagstaff, Pinetop/Lakeside, the Grand Canyon and Springerville/Eager (Davison, 1999) (Fig.1). When monarch breeding was noted, the location, date, weather conditions, species of *Asclepias*, and species of nectar in bloom were noted. In addition, mating, oviposition, eggs, larvae, pupae and adults were recorded. There were multiple visits to identify breeding habitats and to monitor field conditions.

Overwintering Monarchs. Monarch sightings during the winter months were recorded and possible habitats were explored for monarch absence/presence weekly. The number of adult monarchs, species of nectar, tree species used for night roosting, clustering, presence of milkweed as well as any copulation and presence of immatures were recorded for the season.

Field Methods: Tagging Wild Monarchs. Volunteer citizen scientists were trained in netting techniques, data collection and *Danaus plexippus* identification. Using a standard 46 to 61 cm (18 to 24 in.) deep insect net, live wild monarchs were captured for tagging, especially during summer and fall. Some monarchs were also captured by using fingers to lift them from flowers.

Date, name of tagger, tag number, and location, were recorded along with butterfly sex. The behavior at the time of tagging was recorded (such as nectaring including species of nectar plant if known), time of tagging and condition (freshly eclosed, excellent, good, fair, poor) were recorded on data sheets with room for additional comments. All were recorded as wild monarchs. After tagging, the butterflies were released. Any sightings of other *Danaus plexippus* already tagged in the field were recorded.

In addition to tagging, habitat conditions including species of *Asclepias* and nectar, approximate number of monarchs present, weather conditions and time of day were noted for further site analysis when possible. Starting in 2010, occasional sampling of monarchs was sent to Monarch Health at the University of Georgia for analysis of *Ophryocystis elektroscirrha* (OE) parasite load. Samples were tested for infection status by researchers at the University of Georgia associated with Project Monarch Health (www.monarchparasites.org). Samples were collected from monarchs by pressing transparent tape against adult monarch abdomens. Samples were scored for the presence/absence of OE infection based on the presence of > 100 parasite spores per sample following Bartel et al. (2011).

Field Methods: Tagging Farm Monarchs. In addition to tagging wild caught monarchs, each fall from 2004 to 2012, the Desert Botanical Garden (DBG) in Phoenix tagged and released up to 50 farmed monarch butterflies a week with the public. DBG purchased these monarchs from a butterfly breeder farm in California and all activity was conducted under appropriate USDA permits DBG obtained. Other limited additional opportunities arose to tag farmed monarchs in other settings such as butterfly events sponsored by local nature centers or churches who purchased farmed monarchs for special celebrations. The sponsors of the events and the farms where they purchased the butterflies were responsible for legal compliance. All farmed monarch tagging was conducted by the same method employed for wild monarchs except they were recorded as farm monarchs. We tested some of the farm monarchs purchased for special events for *Ophryocystis elektroscirrha* with the same protocols as Wild Monarchs. The Southwest Monarch Study never purchased farmed monarchs or was involved in monarch breeding.

TABLE 1: *Asclepias* Favored by *Danaus plexippus* by Climate Zone. **H** = Mountainous regions, **M** = High desert and cool plateau highlands, **L** = Low and mid altitude desert

H	M	L	
-	-	x	*A. albicans* **
-	x	x	*A. angustifolia* **
x	x	x	*A. asperula*
x	x	x	*A. engelmanniana*
-	-	x	*A. erosa*
-	x	x	*A. linaria* **
x	x	x	*A. nyctaginifolia*
x	x	-	*A. speciosa*
-	-	x	*A. subulata* * **
x	x	-	*A. subverticillata* *
x	x	-	*A. tuberosa*
-	-	x	*Funastrum cynanchoide* (*Sarcostemma cynanchoides*)

* primary *Asclepias* for breeding

** evergreen

FIG. 2. Mating monarchs on *Pinus ponderosa*, near an *Asclepias subverticillata* meadow, Maswik Lodge, Grand Canyon National Park South Rim. Photo by Bob Morris.

Peak Migration. The monarch migration is correlated with sun angle (sun's elevation above the horizon at solar noon) which is dependent on latitude and date. In the east, the leading edge of the monarch migration begins at a sun angle of 57° to 56° and ends at 47°, slowing then to a trickle in most years (O. R. Taylor pers. comm.). We compiled monarch sightings and tagging numbers to see if they increase during these periods. It has been observed that the peak migration occurs when the sun angle is 53° to 52° (Monarch Watch 2014). When tagged monarchs are recovered or sighted at overwintering sites in Mexico or California the sun angle at the time of tagging was determined using the NOAA Solar Calculator (2014) to compare with peak migration observations by latitude in the east.

Wind and Migration Destination. The shift in wind direction during the summer monsoon in Arizona, especially during the transitional period in September, could play a role in migration destination from southeast Arizona. Gibo and Pallett (1979) found that head winds, crosswinds, and tail winds affect monarch flight. The most efficient flight when favorable conditions are present for migrating monarchs is soaring by gliding in rising air thermals to conserve lipids. Lift can be generated by two means: thermal lift and slope lift. Thermal lift is frequently used by soaring birds as well as monarchs and occurs when air masses are heated by the sun. Slope lift occurs on the upwind side of mountain passes and occurs in hilly or mountainous terrain. While monarchs can soar and glide at many heights, the most common used is 300 m (Gibo 1981). Since southeast Arizona is most deeply affected by the moist monsoon wind shift and is also located in mountainous terrain we formulated two hypotheses regarding migration from this location.

Based on this information:

1. We predicted that monarchs tagged on a single day in southeast Arizona will travel to the same migration destination (California or Mexico).
2. We predicted that wind direction on the day of tagging in southeast Arizona affects whether a monarch was recovered.

We obtained wind speed and direction from the National Weather Service in Tucson (Thompson 2014). The wind data were interpolated to 305 m (1000 ft) intervals above ground level (AGL), based on twice-daily weather balloon releases in Tucson. The balloons were tracked via GPS to calculate wind speed and direction, and altitude was calculated from the air pressure. We standardized to the 0000 h UTC (1700 h MST) sounding at 305 m (1,000 ft) AGL.

RESULTS

Monarch Presence. Adult monarchs were reported in every month in some years in Arizona but at varying elevations. In warm winter years without a hard freeze (temperatures less than or equal to -2.7°C for two or more hours (NOAA, 2014)), monarchs were reported most commonly from September until mid-May in the lower desert elevations including Phoenix, Tucson, Yuma, Parker and Lake Havasu. In years with a hard freeze, monarch sightings plummeted until late March through May when a small number of monarch observations were reported. In the High Altitude Desert and Cool Plateau Highlands including Pine, Sedona, San Rafael Valley, Sierra Vista and Canelo, monarchs were reported in some years as early as the last week of March in the southeastern portion of the state but more commonly in July through October, sometimes longer with an extended favorable fall season. In the Cold Mountainous Regions including Flagstaff, the Grand Canyon and Springerville, monarchs were present from mid-June through September.

Breeding Habitats. Arizona has a variety of elevations providing diverse climates supporting many *Asclepias* species. Monarchs were seen ovipositing and eggs, larvae and pupae were observed on the following species of *Asclepias* in each plant climate zone. During the summer breeding season in the Cold Mountainous Regions of Arizona, *Asclepias subverticillata* was the primary host plant closely followed by *Asclepias speciosa*. In the High Altitude Desert and Cool Plateau Highlands elevations, *Asclepias subverticillata* was primary but other milkweeds were also utilized (Table 1). Evergreen milkweeds were host to mainly fall breeding monarchs in

TABLE 2: Breeding nectar. **H** = Mountainous regions, **M** = High desert and cool plateau highlands, **L** = Low and mid altitude desert.

H	M	L	Plant Name	Family Name	Common name
x	x	x	*Apocynum cannabinum*	Apocynaceae	Indian Hemp
x	x	x	*Asclepias* spp.	Apocynaceae	Milkweed
-	x	x	*Baccharis salicifolia*	Asteraceae	Seep Willow
x	x	-	*Carduus nutans*	Asteraceae	Nodding Thistle
x	x	x	*Cirsium* spp.	Asteraceae	Various Thistles
x	x	x	*Helianthus annuus*	Asteraceae	Common Sunflower
x	x	x	*Medicago sativa*	Fabaceae	Alfalfa
x	x	-	*Senecio flaccidus* var. *flaccidus*	Asteraceae	Threadleaf Groundsel
x	-	-	*Trifolium pinetorum*	Fabaceae	Cow Clover
x	-	-	*Verbena macdougalii*	Verbenaceae	New Mexico Vervain
-	-	x	*Vitex agnus-castus*	Lamiaceae	Lilac Chaste-Tree

FIG. 3. Monarch larva on *Asclepias subulata*, Chandler Environmental Center, Chandler, AZ, 28 September 2009 High temperature 38.8° C, Low temperature 17.7° C (Weather Underground). Photo by Gail Morris.

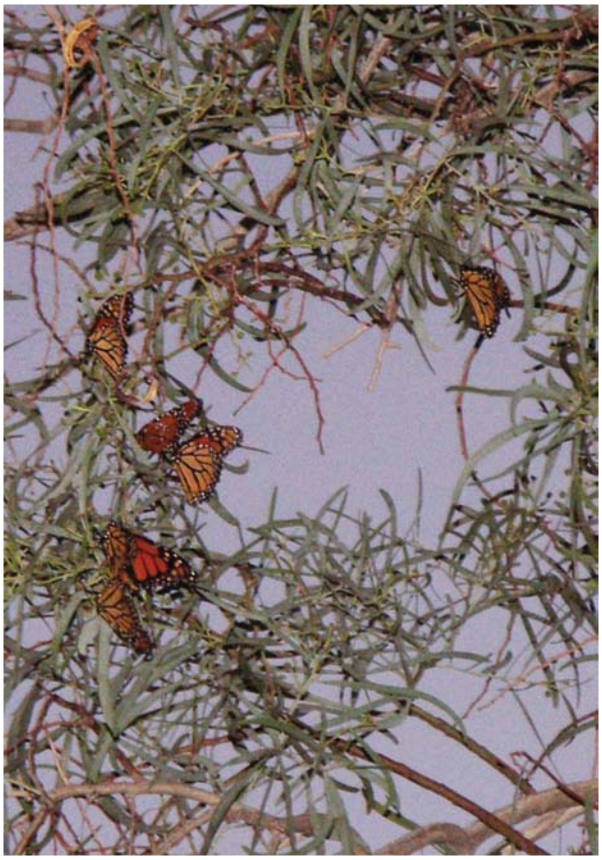


FIG. 4. Roosting *Danaus plexippus* and one *Danaus gilippus*, South Mountain, Phoenix, 11 November 2007. Photo by Tatsuyo Schultz.

TABLE 3: Clusters of migrating monarchs

Date	Location	Number of D. plexippus
11/7/2010	South Mountain, Phoenix	6 + 1 D. gilippus
11/21/2010	South Mountain, Phoenix	5
10/6/2012	Arivaca Cienega, Arivaca	20
10/27/2012	Rotary Park, Lake Havasu	60
9/28/2013	Montosa Canyon, Santa Rita Mountains	13
10/5/2013	Canelo	23
11/8/2013	Buckskin State Park, Parker	125
9/6/2014	South Rim, Grand Canyon	28
10/6/2014	Alamo Lake	12
10/12/2014	Alamo Lake	12

the Low and Mid Altitude Desert. In particular *Asclepias subulata* was heavily favored although *Asclepias angustifolia* was also used frequently in backyard gardens. Abundant summer monsoon rains triggered a second growing season in some years especially in the lower deserts. Eggs, immatures and monarch oviposition were frequently reported in the fall on *Asclepias nyctaginifolia*, *Asclepias asperula* and *Asclepias erosa* in addition to the evergreen milkweeds. There were no collections (SEINet 2015) or observations of *Asclepias curassavica* growing in roadside ditches or any other naturalized areas. This milkweed was limited to an irrigated garden specialty.

Most breeding areas in Arizona hosted two to three generations (sometimes more) in the High Altitude Desert and Cool Plateau Highlands during the summer months, allowing the monarch population to expand substantially at these locations before the fall migration. In particular Elgin, Turkey Creek and the San Rafael Valley in southeast Arizona had the largest monarch populations in the state. By mid-September it was not unusual to find over 100 monarch adults present in a 0.5 km^2 field along Turkey Creek as well as larvae and pupae. The greater Prescott area and Tonto Natural Bridge State Park in Pine also documented breeding in late July until September.

In the Cold Mountainous Regions monarchs usually successfully completed two generations before the fall migration. Monarchs were reported in Flagstaff at Buffalo Park with extensive fields of *Asclepias subverticillata*. Monarchs were recorded on the South Rim of the Grand Canyon flying out of the inner Canyon along Bright Angel Creek on the South Rim

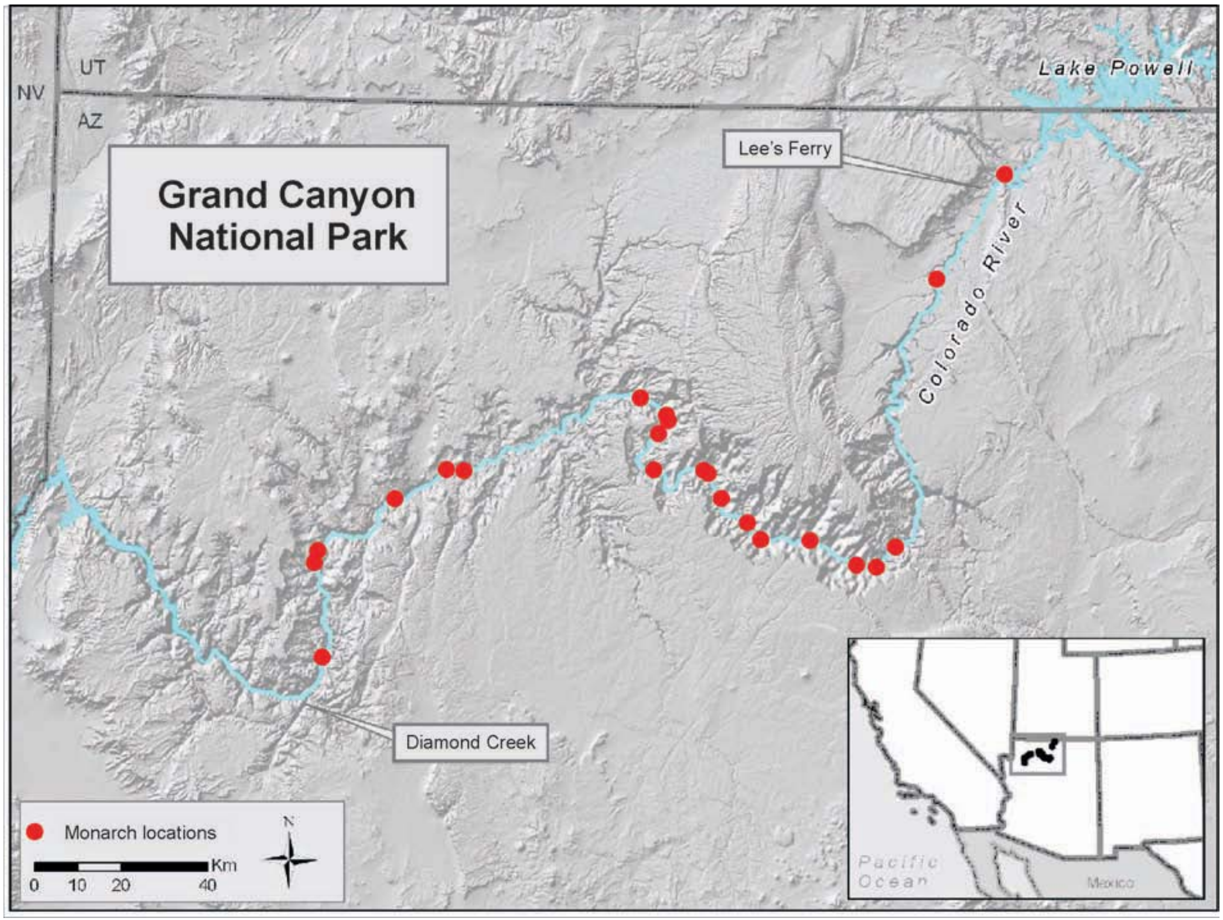


FIG. 5. Locations of monarch sightings on the Colorado River in the Grand Canyon between 23 October 2008 and 10 November 2008. Each red dot represents a GPS sighting. No monarchs were tagged in the park during this time period.

during July and August. Extensive oviposition, larvae and pupae were noted in low-lying, moist meadows filled with *Asclepias subverticillata* while breeding was documented in nearby Ponderosa Pines (Fig. 2). The White Mountains, including Pinetop/Lakeside, Springerville and Eager had abundant breeding primarily on *Asclepias subverticillata* and *Asclepias speciosa* in meadows and riparian areas. After the Wallow Fire in Springerville in the summer of 2011, monarchs were notably absent in July, but were present the second week of August and completed only one generation before leaving on their migration.

While limited reports of spring breeding were noted in the Low and Mid Altitude Deserts, fall was the premier breeding season in Phoenix, Yuma, Lake Havasu, Kofa Mountains and Tucson. In the final days of August through early September monarchs returned into the area and they were breeding with heavy oviposition documented (Fig. 3). Temperatures in the lower desert can still reach 43°C or above in some years in early September and egg, larvae, and pupae demise have been documented in years with high temperatures. In years of warm fall temperatures both migrating and breeding monarchs were observed in late September and October. Some locations documented one to two generations.

Breeding Season Nectar. *Asclepias* spp. in bloom was the favored nectar for breeding monarchs at all elevations. Monarchs were also observed feeding on additional nectar plants commonly in season (Table 2), a variety of trees in bloom such as *Prosopis velutina* (Fabaceae), Velvet Mesquite, and *Robinia neomexicana* (Fabaceae), New Mexico Locust, in addition to other lesser nectar sources. Monarchs were opportunists when nectar sources were limited and were seen nectaring on invasive species such as *Convolvulus arvensis* (Convolvulaceae), Field Bindweed, and *Tamarix chinensis* (Tamaricaceae), Salt Cedar. In home gardens zinnias, cosmos, sunflowers, tithonia, coreopsis and asters were favored.

Migration Sightings. Small, loose clusters of monarchs during the migration were occasionally

TABLE 4: Fall migration nectar. **H** = Mountainous regions, **M** = High desert and cool plateau highlands, **L** = Low and mid altitude desert.

H	**M**	**L**	**Plant Name**	**Family Name**	**Common name**
x	x	x			
-	x	x	*Baccharis salicifolia*	Asteraceae	Seep Willow
-	x	x	*Baccharis sarothroides*	Asteraceae	Desert Broom
-	-	x	*Bebbia juncea*	Asteraceae	Sweetbush
	x		*Bidens laevis*	Asteraceae	Smooth Beggartick (Marsh Sunflower)
x	x	-	*Carduus nutans*	Asteraceae	Nodding Thistle
x	x	-	*Ericameria (Chrysothamnus)* spp.	Asteraceae	Rabbit Brush *
x	x	x	*Cirsium* spp.	Asteraceae	Various Thistles
x	x	x	*Helianthus annuus*	Asteraceae	Common Sunflower *
x	x	-	*Senecio flaccidus* var. *flaccidus*	Asteraceae	Threadleaf Groundsel
x	x	x	*Verbesina encelioides*	Asteraceae	Golden Crownbeard
-	-	x	*Vitex agnus-castus*	Lamiaceae	Lilac Chaste-Tree

* Favored

reported (Fig. 4) as well as multiple monarch movement during September through November (Table 3). In addition there were late sightings of monarch movement along rivers such 16 monarchs along the Colorado River through the Grand Canyon in November 2008 (Fig. 5), one monarch at the Hassayampa River Preserve near Wickenburg (elevation 610 m) on 23 November 2014, and three monarchs on the Agua Fria at Rock Springs (elevation 610 m) on 9 December 2014.

Migration Nectar. Monarchs were observed to favor, but were not limited to, fall blooming species of *Asclepias* in bloom as well as other nectar plants (Table 4). In home gardens, fall blooming zinnias, cosmos, sunflowers, tithonia, coreopsis, ageratum and asters were favored.

Overwintering aggregations. Several small overwintering aggregations of 3 to 45 monarchs were found to spend the winter in the greater Phoenix area each year. Two sites were along the Salt River (Rio Salado Habitat Restoration Area and Tempe Marsh) and one was at Desert Botanical Garden in Phoenix. The populations at Desert Botanical Garden and Tempe Marsh were decimated by a hard freeze of -2°C on 31 December 2010. A second hard freeze of -2°C occurred one month later on 2 February 2011. The monarch population at Rio Salado Habitat Restoration Area was able to partially survive these conditions (Fig. 6). By weekly monitoring of nearby *Asclepias subulata* the Rio Salado overwintering monarchs appeared to be in diapause until early February (Fig. 7). In 2012 overwintering aggregations were also found at Singh

TABLE 5: *Ophryocystis elektroscirrha* (OE) infection rates

Year	**Total count**	**Zero**		**1 to 10**		**11 to 100**		**More than 100**	
2010	47	37	79%	2	4%	2	4%	6	13%
2011	115	110	96%	1	1%	1	1%	3	3%
2012	170	162	95%	1	1%	0	0%	7	4%
2013	44	44	100%	0	0%	0	0%	0	0%
2014	87	75	86%	5	6%	3	3%	4	5%
Total	463	428	92%	9	2%	6	1%	20	4%
Farm	14	9	64%	1	7%	0	0%	4	29%
Wild	449	419	93%	8	2%	6	1%	16	4%

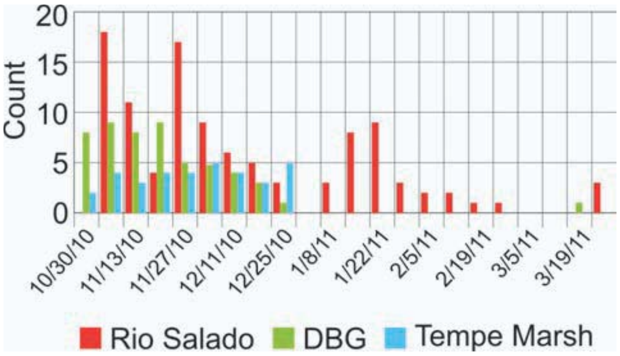


FIG. 6. Comparison of adult monarch sightings at three locations with overwintering monarchs pre and post freeze. A hard freeze occurred on 31 December 2010. Monarchs normally begin mating and dispersing early February.

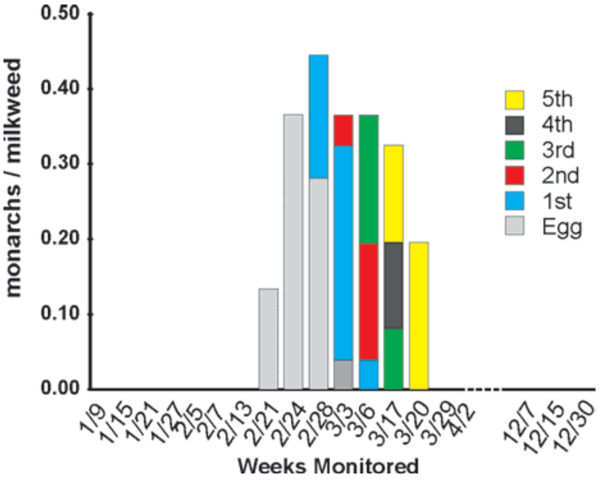


FIG. 7. Monarch Density. Monarch egg and larvae by instar, absence and presence at Rio Salado Habitat Restoration Area, Phoenix, Arizona, with weekly monitoring of thirty-two *Asclepias subulata* plants.

Farm in Scottsdale. Adult monarchs were tagged and monitored weekly. We found both breeding monarchs and a small number of monarchs that lived for three months indicating the possibility of a mixed population of breeding and nonbreeding monarchs. During the warm winter of 2013, three monarchs overwintered at Boyce Thompson Arboretum in Superior (elevation 735 m) in Eucalyptus (*Eucalyptus* spp.) trees. One was tagged on 26 October 2013 and sighted flying in the area on 26 January 2014. In most years winters were too cold for monarch survival at this location.

In warm winters without a hard freeze, small numbers of monarchs were reported in backyards in the greater Phoenix area, Tucson, and Yuma. In most years monarchs were also reported at the Arizona Sonora Desert Museum in Tucson. Trained docents tagged monarchs present at the museum. By the longevity of some tagged monarchs as well as photo documentation of others ovipositing, the monarchs appeared to be a mix of nonbreeding and breeding monarchs. The immature phase was as long as six to eight weeks in response to average night temperatures hovering near 1.6°C and low daytime temperatures. On warm days monarchs at Rio Salado Habitat Restoration Area and Tempe Marsh nectared primarily on *Baccharis salicifolia*, as well as *Bebbia juncea*, *Lycium* spp. and *Pluchea sericea* when available and stayed primarily in *Salix gooddingii* but also *Populus* spp. trees at night. Monarchs at the Desert Botanical Garden and Arizona Sonora Desert Museum visited a variety of winter garden flowers in addition to *Calliandra californica* and *Lycium* spp.

Small aggregations were also noted along the Colorado River from Parker to Lake Havasu including 125 monarchs found in *Acacia salicina* trees at Buckskin State Park in Parker along the Colorado on 8 November 2013. The following morning many flew south along the Colorado River. Later, 25 monarchs were found at the same location on 18 January 2014. One of approximately 60 monarchs sighted and later tagged on 27 October 2012 at Rotary Park in Lake Havasu along the Colorado River was spotted in the city of Lake Havasu on 17 February 2013, suggesting an overwintering population. Others tagged at the same time were observed flying north and a few also flew south along the Colorado River the following morning.

***Ophryocystis elektroscirrha*.** We submitted 463 samples to Monarch Health at the University of George to test for *Ophryocystis elektroscirrha* (OE). Results for the submitted specimen analysis indicate low levels of *Ophryocystis elektroscirrha* in Arizona (Table 5). Test results were provided in three levels: 1 to 10 spores (Level 1), 11 to 100 spores (Level 2) and 101 and above spores (Level 3). Level 3 is where the infected monarch likely acquired the infection as a larva and is the primary point of comparison as a heavily infected monarch. In Arizona, the number of Level 3 infections dropped from 13% in 2010 to 0% in 2013 and 5% in 2014. The Canelo breeding habitat in southeast Arizona had the highest level of Level 3 infected monarchs. Overall, 449 wild monarchs sampled had a 4% Level 3 infection rate. Fourteen farm monarchs tested had a 29% rate.

TABLE 6: Enumeration of recovered wild monarchs. Sun angle is the sun's elevation angle above the horizon at solar noon on the day of tagging, calculated with NOAA calculator http://www.esrl.noaa.gov/gmd/grad/solcalc/. Single-letter tags are wild monarchs.

TAG	Tagging date	Tagging Location	Sun Angle	Recovery Location
A	27 September 2007	Canelo	57	El Rosario
B	7 September 2008	San Rafael Valley	64	Ellwood Main
C	26 September 2008	Elgin	57	El Rosario
D	1 October 2008	Canelo	55	El Rosario
E	1 October 2008	Canelo	55	El Rosario
F	1 October 2008	Canelo	55	El Capulin
G	6 October 2008	San Rafael Valley	53	El Rosario
H	15 September 2010	Canelo	61	Halcyon CA
I	30 September 2010	Elgin	55	Cerro Pelon
J	30 September 2010	Elgin	55	Cerro Pelon
K	30 September 2010	Elgin	55	Macheros
L	19 November 2011	Chandler	37	Kino Bay
M	19 September 2012	Gardenerville	52	Santa Cruz
N	20 September 2012	Canelo	59	El Rosario
O	29 September 2012	Canelo	56	El Rosario
P	30 September 2012	Elgin	55	El Rosario
Q	2 October 2012	Canelo	55	El Rosario
R	2 October 2012	Canelo	55	El Rosario
S	8 September 2013	Elgin	64	El Rosario
T	14 September 2013	Canelo	62	Pismo Beach
U	15 September 2013	Canelo	61	Pismo Beach
V	15 September 2013	Hereford	61	Cayucos CA
W	20 September 2013	Elgin	59	San Simeon CA
X	20 September 2013	Elgin	59	Black Lake CA
Y	20 September 2014	Canelo	59	Big Sur
Z	22 September 2014	Canelo	58	Pacific Grove

Water. Migrating monarchs were reported mainly along water sources, especially rivers. The Colorado River in particular was heavily favored as a migration flyway through the Grand Canyon as well as below Lake Havasu as were the Little Colorado, San Pedro, Santa Cruz, Verde, Gila, Hassayampa, Bill Williams and Salt Rivers. Breeding and migrating monarchs were frequently found in larger densities near (but not limited to) water, including cienegas, rivers and creeks (especially flood plains), washes, roadside ditches and irrigated gardens. During periods of low humidity monarchs were frequently found puddling in moist soils and in shallow creeks and streams (Fig. 8).

Tagged monarchs. A total of 12,088 monarchs were tagged between 2003 and 2014 by 384 individuals in 276 locations. This includes 7,809 wild monarchs and 4,279 farmed monarchs; 7,133 were males, 4,662 were females, and sex was not reported for 293. In addition to tagging sites, 134 unique sighting locations of monarch adults and/or immatures were reported (Fig. 9).

Recoveries of tagged monarchs. Recoveries at the overwintering sites in Mexico were reported to

FIG. 8. Monarch drinking water from stream, Huachuca Mountains, 3 October 2012. Photo by Bob Herrmann.

volunteers of Southwest Monarch Study, Monarch Watch and others. The campesinos who live at the overwintering sites and actually found the tags were paid 50 pesos (about five dollars) per tag. Most monarch recoveries in Mexico were based on tags that were found on dead monarchs at each location. Only one female monarch spotted at Kino Bay, Sonora, was a live sighting. Recoveries in California were all from live monarchs sighted or photographed by citizen observers.

The total count of wild monarch recoveries was 15 in Mexico and 9 in California (Fig. 10a) (Table 6). In addition to the identified tagged monarchs, two blue Southwest Monarch Study tagged monarchs were spotted at Camp Pendleton in Oceanside, CA by David Marriott on 8 January 2009. However, despite repeated photographs, the tag numbers remained unreadable for these two tags. The number of recoveries in California varied by year:

- 2008 (3; including 2 unidentified tags at Camp Pendleton)
- 2009 (0)
- 2010 (1)
- 2011 (0)
- 2012 (0)
- 2013 (5; all tagged in the same week in southeast Arizona)
- 2014 (2; tagged 2 days apart in southeast Arizona)

There were 12 additional sightings in Arizona of wild tagged monarchs under 50 km from their tagging sites in Chandler, Canelo, Elgin, Gilbert, San Rafael Valley, Scottsdale, Springerville, and Tempe.

The total number of farm monarch recoveries was 5 in Mexico and 0 in California (Fig. 10b) (Table 7). One farmed monarch tagged at the Desert Botanical Garden in Phoenix flew northwest 34.3 km and was sighted in Sun City and later was re-sighted in Tonopah, 61.8 km to the southwest. There were 13 sightings of tagged farm monarchs from the Desert Botanical Gardens to the south and southeast under 50 km in Ahwatukee (3), Mesa (4), Chandler (3), and South Mountain (3).

From 2003 to 2011, the overall recovery rate was 1 recovery out of 564 monarchs tagged. The recovery rate nearly tripled for 2012 and 2013 becoming 1 recovery for every 198 monarchs tagged.

Wind and migration destination. Observation of data showed perfect concordance with our hypothesis that monarchs tagged in a single day in southeast Arizona would travel to the same overwintering location (Mexico or California). In every instance where multiple recovered monarchs were tagged on a single day, they all were recovered at the same location. This effect was statistically significant by Fisher's Exact test with ≤ 0.05, allowing us to reject the null hypothesis that migration direction is random.

Our hypothesis was that wind direction on the day of tagging in southeast Arizona affects whether the monarch was recovered. Results are shown in (Table 8) (Fig.11). We found wind direction does significantly affect whether the monarch was recovered by Fisher's Exact test with $p \leq 0.05$.

Peak Migration. The earliest two migrating monarchs recovered to date both had sun angles at the time of tagging of 64°. One was recovered at Ellwood Main in California, the other at El Rosario, Michoacan,

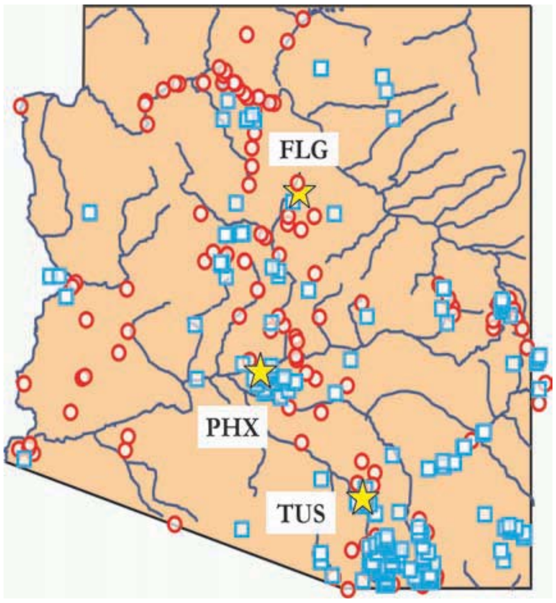
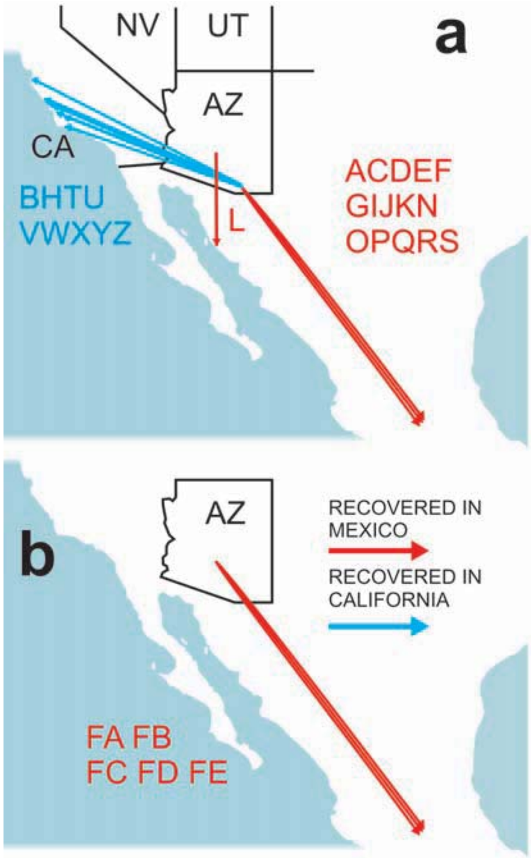


FIG. 9. Locations of Monarch Tagging and Sighting. Each blue square represents the location where one or more monarchs was tagged. Each red circle represents the location where one or more monarch sightings have been reported.



FIGS. 10a & 10b. Recovery Locations of Monarchs Tagged in Arizona. **a,** wild monarchs. **b,** farm monarchs. Letters next to each set of arrows individually identify the monarchs (Table 6; Table 7).

TABLE 7: Enumeration of recovered farm monarchs. Sun angle is the sun's elevation angle above the horizon at solar noon on the day of tagging, calculated with NOAA calculator http://www.esrl.noaa.gov/gmd/grad/solcalc/. Two-letter tags are farm monarchs.

TAG	Tagging date	Tagging Location	Sun Angle	Recovery Location
FA	8 October 2004	DBG	50	El Rosario
FB	4 October 2007	DBG	52	Cerro Pelon
FC	11 October 2007	DBG	49	Cerro Pelon
FD	14 October 2010	DBG	50	El Rosario
FE	4 October 2012	DBG	52	El Rosario

Mexico (Fig. 12). Both monarchs were freshly eclosed and tagged in the San Rafael Valley in southeast Arizona on 7 September 2008 and 8 September 2013, respectively. Most of the recoveries of tagged monarchs in Mexico are in alignment with migration observations for latitude in the east. Most California recoveries occurred before the times observed in the east. We had one late recovery of a freshly eclosed monarch tagged in Chandler on 19 November 2011 that was sighted in Kino Bay, Sonora, Mexico on 14 December 2011 that had been tagged with a sun angle of 37°. When we averaged all the tagging over the life of the study there is a surge of monarchs tagged the first week of October (Fig. 13).

DISCUSSION

Danaus plexippus was present and at times abundant in Arizona at different elevations throughout the year. Breeding populations were observed at all elevations seasonally and they utilized a variety of native species of *Asclepias*. Habitats were most numerous in riparian areas. Both adults and immatures were reported at all elevations. During the breeding season monarchs favored species of *Asclepias* for nectar as well as oviposition but also used other available nectar. We also identified migration nectar sources and learned *D. plexippus* favors riparian areas and rivers during their migration when available and sometimes were found puddling. Both breeding and migrating monarchs were frequently seen in city backyards and parks when *Asclepias* spp. and favored nectar were available. Backyard gardeners can help create rest stops for migration refueling.

The lower elevation deserts have small numbers of overwintering monarchs in warm winters without a hard freeze. They were recorded from 2009 onward every year and appear to be a regular occurrence. The largest aggregations were found at Rio Salado Habitat Restoration Area in Phoenix and there were other small locations along the Salt and Colorado Rivers. Yuma, Phoenix, Lake Havasu, Parker and Tucson areas also

TABLE 8. Tags and recoveries from southeast Arizona, broken down by wind direction at 305 m AGL (1,000 ft) at 1200 h GMT (1700 h MST) on the day of tagging.

Wind to	Wind from Compass Heading	Tags	Recoveries
SW	0° to 90°	415	0
NW	90° to 180°	752	10
NE	180° to 270°	1084	1
SE	270° to 360°	1945	13

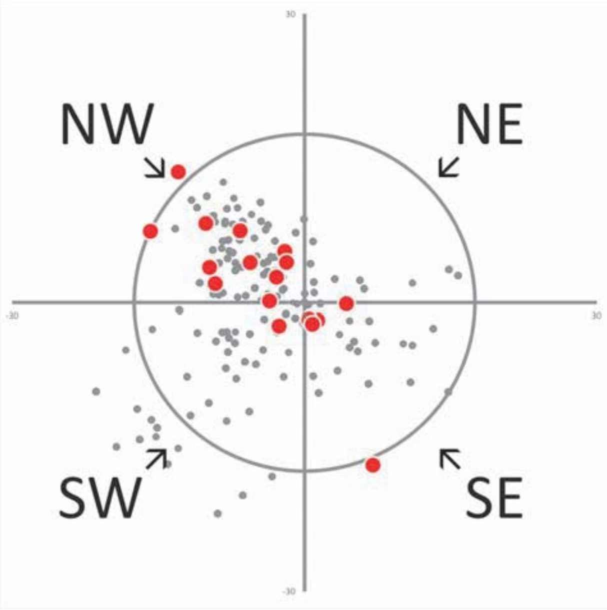


FIG. 11. Wind Speed and Direction on Day of Tagging. Each black dot represents the wind speed and direction at 305 m (1,000 ft) AGL (above ground level) on a day on which one or more monarchs was tagged. Red dots represent the same data for the days on which one or more recovered monarch was tagged. The speed is proportional to the distance from the center. The circle represents 9 m/sec. The direction of the wind is from each marker to the center.

reported winter monarch sightings. There were reports of limited monarch breeding during the winter but at other locations breeding was not evident. Native evergreen milkweeds were most common near these locations. With a record warm year in 2014 in Phoenix (National Weather Service 2015), especially in the fall, together with a general warming trend in recent years, it will be critical to monitor the effects on the overwintering numbers in the future.

Ophryocystis elektroscirrha levels were low in monarchs over the past five years in Arizona with an average rate of 4%. Monarchs were tested in breeding areas, during the migration, in overwintering aggregations and in backyard gardens throughout the year. While levels should continue to be monitored to detect a changing trend, current levels indicate this is not a serious threat to the monarch population at this time. Arizona has evergreen milkweeds utilized by the monarch population for both oviposition and nectaring, but they do not appear to contribute to a higher *Ophryocystis elektroscirrha* infection rate. Nor does the presence of *Asclepias curassavica* in occasional irrigated gardens. It is possible Arizona's high temperatures and low humidity limit the transmission of *Ophryocystis elektroscirrha*.

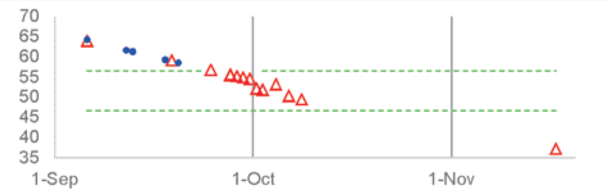


FIG. 12. Recoveries by sun angle (sun's elevation angle above the horizon at solar noon) on the day of tagging. Recoveries in Mexico are represented by red triangles; California by blue circles. Vertical axis is sun angle in degrees. Horizontal axis is the tagging date. Dashed green lines indicate elevation of 46.5° and 56.5°, the nominal values for the migration.

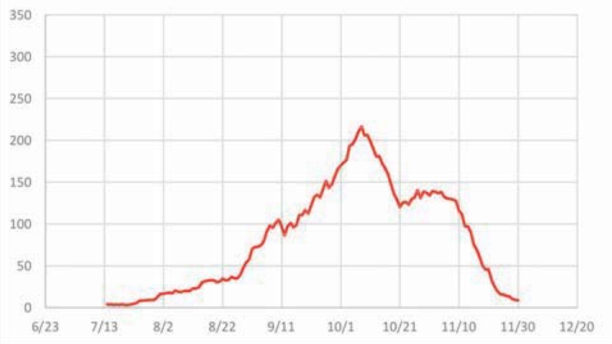


FIG. 13. Counts of monarchs tagged by date, sum of all years. The counts are displayed as a seven day running average to remove the artifacts caused by day of week.

Monarchs in Arizona migrate to known overwintering destinations in both Mexico and California while small numbers overwinter in the lower deserts in Phoenix, Tucson, Yuma, Parker and Lake Havasu. All the monarchs recovered in California were tagged in southeast Arizona near fields of abundant *Asclepias subverticillata*. Most of these early migrators appeared to be recently eclosed from local fields.

Winds play a significant role in the southeast Arizona monarch migration. When multiple monarchs were tagged at the same location and later recovered, they were always all found in California or all reported in Mexico, a significant finding. There were several sets of two or three recoveries from tagging on the same day. We were surprised when we plotted the recoveries on the radar chart (Figure 10) to learn that the direction of the wind determined if there would be a recovery. Each data point on the chart only represents the wind on a day where one or more monarchs was tagged. We discovered that almost all recoveries occurred when winds originated from the southeast or from the northwest. There were no recoveries when the wind blew from the northeast to the southwest, normally considered a favorable wind direction for the monarch migration in the east and only one when the wind was from the southwest. Continued monitoring of tagged recoveries will show if this pattern persists. We are developing a model that will describe the factors determining the migration destination. With more recoveries we will improve its accuracy.

The flyways of Arizona monarchs migrating to California are unknown. Frey and Schaffner (2004) found monarch movement in response to weather patterns at the California overwintering sites, especially in response to temperature and winds. Monarchs were observed moving north along the California coast from the southern coastal areas (Urquhart 1987). It is unknown if monarchs from Arizona fly west to reach the coast and then fly north to reach the location where they were sighted or directly northwest.

Our data indicates monarchs tagged in Phoenix migrate to Mexico but more tagging will help us learn if they also fly to California as well. More information is also needed about the migration destinations around the state, especially the northern and western portions. Western flight has been observed near Lake Havasu and Alamo Lake. While there has been extensive tagging at the Grand Canyon, Flagstaff, Prescott, Camp Verde, Springerville/Eager, Lake Havasu and other locations, we have not had recoveries at this time. Future recoveries may open up new understanding of migration destinations from these locations.

We found that farmed butterflies shipped from California to Arizona, tagged and released at the Desert Botanical Garden in Phoenix, flew to Mexico rather than returning to California. All five recoveries in Mexico were tagged during the time of predicted peak migration for latitude in Phoenix. Not all of the tagged farm monarchs migrated. In addition to the one farm monarch sighting in Sun City later reported in Tonopah, thirteen tagged farm monarchs were reported in locations to the southwest, south and southeast. Three tagged monarchs were spotted in the same yard in successive years on South Mountain, a slightly southwest flight path.

The migration window for *D. plexippus* in Arizona was larger than anticipated, with recoveries from monarchs tagged at the beginning of September with a sun angle of 64° to mid-November at 37°. While the largest number of recoveries occurred during the predicted range of 57° to 47°, most in this range migrated to Mexico. Earlier sun angle recoveries were mainly in California, but a few also migrated to Mexico. Baum and Mueller (2015) noted in the southern Great Plains there is a movement of reproductive monarchs into the area in August and September prior to the peak fall migration. F. X. Villablanca of Monarch Alert (pers. comm.) noted only 5% of monarchs at the California overwintering sites are reproductive. Furthermore, the longevity of a monarch tagged near Canelo in southeast Arizona on 20 September 2014 and sighted in Big Sur, California on 29 January 2015 gives additional credence that this monarch was in reproductive diapause. Based on these observations the migration appears to begin in early September through middle October in Arizona with occasional late migrators later.

Tagging recoveries increased from 1 of 564 monarchs to 1 of 198 monarchs tagged in 2012 and 2013. We learned using new tags every year increased our recoveries. Earlier tags were purchased in bulk to save cost but the adhesive decayed over time, especially when the tags were left in hot conditions. Purchasing new tags each year increased our recovery ratios.

Citizen science. The Southwest Monarch Study is a volunteer non-profit Citizen Science study. Volunteers spent endless hours in the field and used their own personal funds for nets, transportation and any lodging/camping fees. We forged working relationships with monarch experts across the country to create field strategies and protocols. There may be some who question the accuracy of the data we've collected. Droege (2007) notes that in many instances volunteers are more invested than paid college students who are in attendance for a few years and move on. Volunteer Citizen Scientists take their job collecting data more seriously and are more accurate. Volunteers come because they want to, not because they have to. Oberhauser et al. (2015) notes that the data generated in Citizen Science projects are carefully analyzed and provide an avenue to answer questions that would likely never be addressed in traditional academic research. Our continuing study of monarchs in the southwest has documented new insights about the breeding and migratory movements of *Danaus plexippus* in Arizona.

ACKNOWLEDGMENTS

Southwest Monarch Study volunteer Citizen Scientists spent time living with the monarchs in the fields of Arizona. They watched and observed, photographed when possible, and wrote detailed descriptions of their encounter including presence and absence. Their data is priceless and opens a new chapter in understanding monarch butterflies in Arizona. We've likely only scratched the surface of understanding monarch biology in the southwestern United States.

This study would not have been possible without the extraordinary hours in the field tagging, monitoring and recording data of over 300 volunteer citizen scientists. In particular we thank A. Grimaldi, J. Billings, L. Miller, K. Graves, T. Schultz, J. Zofrea, M. Miller, C. Palm-Gessner, R. Gessner, A. Burkhart, R. Rensch, B. Jensen, C. Overlock, L. Paetschow, R. Morris, M. Vandewater, P. Akers, C. Kondrat-Smith, M. Sanford, L. Jakse, W. Anderson, and P. Cherubini. We thank J. Brock, R. Bailowitz, M. Klinkel, R. Gillmore, A.Grkovich, SEABA and CAzBA for their historical documentations of monarchs in Arizona. We are grateful for the support and/or permission to access land for monitoring and tagging at Arizona State Parks, Coronado National Forest, City of

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Appendix 1: Arizona Monarch Sightings by Richard Bailowitz, 1975 to 1984

Date	County	Location	Date	County	Location
25 June 1976	Apache	Rte 273 s. of Springerville	23 October 1983	Pima	Quitobaquito, Organ Pipe CNM
15 July 1980	Apache	Springerville	28 January 1984	Pima	Elkhorn Ranch, Baboquivaris
7 July 1981	Apache	South Fk Ranch, White Mtns	25 August 1984	Pima	Elkhorn Ranch, Baboquivaris
13 August 1975	Cochise	Chiricahua Mtns	1 September 1984	Pima	4M W Arivaca
31 May 1976	Cochise	Parker Cyn Lake	1 September 1984	Pima	Fraguita Wash, S of Arivaca
27 June 1976	Cochise	Chiricahua Mtns	5 October 1984	Pima	Arivaca Cienega
9 August 1978	Cochise	Cottonwood Cyn, Peloncillos	21 August 1979	Pinal	Oracle Junction
12 August 1978	Cochise	Parker Canyon	11 October 1975	Sta.Cruz	Sycamore Cyn, Atascosas
17 September 1978	Cochise	Chiricahua Mtns	4 September 1976	Sta.Cruz	west of Pena Blanca Lake
24 September 1978	Cochise	below Parker Canyon dam	18 August 1977	Sta.Cruz	Sonoita Creek
20 October 1979	Cochise	Ash Springs, Perillas	20 August 1977	Sta.Cruz	Sycamore Cyn, Atascosas
20 October 1979	Cochise	Leslie Cyn	27 August 1977	Sta.Cruz	12 M S Sonoita
27 April 1980	Cochise	San Bernardino Ranch	3 September 1977	Sta.Cruz	Patagonia
8 August 1980	Cochise	San Bernardino Ranch	11 September 1977	Sta.Cruz	Sonoita Creek
24 August 1980	Cochise	Guadalupe Cyn	17 September 1977	Sta.Cruz	Sycamore Cyn, Atascosas
27 September 1980	Cochise	San Bernardino Ranch	20 November 1977	Sta.Cruz	Flux Cyn, Patagonia Mtns
4 October 1980	Cochise	French Joe Cyn, Whetstones	3 December 1977	Sta.Cruz	Sonoita Creek
26 October 1980	Cochise	San Bernardino Ranch	11 December 1977	Sta.Cruz	3M SW Patagonia
25 April 1981	Cochise	Leslie Cyn, Swisshelm Mtns	5 February 1978	Sta.Cruz	Rock Corral Cyn, Tumacacori Mtns
24 May 1981	Cochise	Reiley Cyn, Winchester Mtns	25 February 1978	Sta.Cruz	3M SW Patagonia
19 July 1981	Cochise	Montezuma Cyn, Huachucas	14 May 1978	Sta.Cruz	Sheehy Sprgs, San Rafael Vly
22 July 1981	Cochise	Babacomari Ranch	11 August 1978	Sta.Cruz	Sycamore Cyn
29 July 1981	Cochise	Babacomari Ranch	13 August 1978	Sta.Cruz	Sycamore Cyn, Atascosas
5 August 1981	Cochise	Babacomari Ranch	18 August 1978	Sta.Cruz	Sonoita Creek
9 August 1981	Cochise	Babacomari Ranch	19 August 1978	Sta.Cruz	Flux Cyn, Patagonias
12 August 1981	Cochise	San Bernardino Ranch	21 August 1978	Sta.Cruz	Rock Corral Cyn, Tumacacoris
26 August 1981	Cochise	Babacomari Ranch	23 August 1978	Sta.Cruz	lower Sycamore Cyn
5 September 1981	Cochise	San Bernardino Ranch	2 September 1978	Sta.Cruz	Sycamore Cyn, Atascosas
5 September 1981	Cochise	Guadalupe Cyn	1 October 1978	Sta.Cruz	Sonoita Creek
6 September 1981	Cochise	Leslie Cyn, Swisshelms	7 October 1978	Sta.Cruz	Sycamore Cyn, Atascosas
27 September 1981	Cochise	San Bernardino Ranch	15 October 1978	Sta.Cruz	Washington Pass, Patagonias
1 November 1981	Cochise	Guadalupe Cyn	22 October 1978	Sta.Cruz	Patagonia
5 September 1982	Cochise	Ash Sprgs, Perilla Mtns	22 July 1979	Sta.Cruz	Sonoita Creek
19 September 1982	Cochise	Dixie Cyn, Mule Mtns	29 September 1979	Sta.Cruz	Mt.Hopkins, Sta.Ritas
23 October 1982	Cochise	Bisbee	26 May 1980	Sta.Cruz	Grosvenor Hills

Appendix 1: Arizona Monarch Sightings by Richard Bailowitz, 1975 to 1984 (continued)

Date	County	Location	Date	County	Location
21 August 1983	Cochise	Ash Cyn, Huachuca Mtns	11 August 1980	Sta.Cruz	Sycamore Cyn
10 September 1983	Cochise	Guadalupe Cyn	6 September 1980	Sta.Cruz	Sonoita Creek, below dam
10 September 1983	Cochise	Leslie Cyn, Swisshelms	2 November 1980	Sta.Cruz	Sycamore Cyn
11 September 1983	Cochise	W.Turkey Ck, Chiricahuas	11 November 1980	Sta.Cruz	Patagonia
11 September 1983	Cochise	Stronghold Cyn, Dragoons	29 March 1981	Sta.Cruz	California Gulch
15 October 1983	Cochise	east of Elfrida	5 April 1981	Sta.Cruz	5M SW Patagonia
16 October 1983	Cochise	Guadalupe Cyn	2 May 1981	Sta.Cruz	5M SW Patagonia
13 November 1983	Cochise	San Pedro R, 3M S St.David	3 May 1981	Sta.Cruz	California Gulch
11 August 1984	Cochise	Palominas	25 July 1981	Sta.Cruz	Babacomari Ranch
8 September 1984	Cochise	Parker Cyn, Canelo Hills	8 August 1981	Sta.Cruz	5M SW Patagonia
8 September 1984	Cochise	Garden Cyn, Huachucas	16 August 1981	Sta.Cruz	California Gulch
15 September 1984	Cochise	Swisshelm Mtns, due E of Elfrida	19 September 1981	Sta.Cruz	Babacomari Ranch
15 September 1984	Cochise	Leslie Cyn, Swisshelm Mtns	8 April 1982	Sta.Cruz	California Gulch
16 September 1984	Cochise	Guadalupe Cyn, Peloncillo Mtns	4 September 1982	Sta.Cruz	O'Donnell Cyn, Canelo Hills
16 September 1984	Cochise	Cottonwood Cyn, Peloncillos	12 September 1982	Sta.Cruz	Research Ranch, Elgin
24 June 1976	Coconino	Parks	18 September 1982	Sta.Cruz	Research Ranch, Elgin
21 July 1976	Coconino	De Motte Camp, Kaibab	25 September 1982	Sta.Cruz	A.W.Research Ranch, Elgin
14 September 1976	Coconino	Schultz Pass, San Fran Pks	9 October 1982	Sta.Cruz	Research Ranch, Elgin
27 September 1975	Gila	Tonto Nat'l Bridge	10 October 1982	Sta.Cruz	California Gulch
14 August 1976	Gila	12 M E Payson	15 October 1982	Sta.Cruz	Research Ranch, Elgin
15 May 1982	Gila	Cherry Ck, Sierra Anchas	30 October 1982	Sta.Cruz	Research Ranch, Elgin
23 September 1979	Graham	High Creek Cyn, Galiuros	6 November 1982	Sta.Cruz	Research Ranch, Elgin
31 May 1980	Graham	20M SW Thatcher	13 November 1982	Sta.Cruz	Post Cyn, Canelo Hills
15 July 1983	Graham	Nantak Rim, Pt. of Pines	28 May 1983	Sta.Cruz	Research Ranch, Elgin
8 August 1978	Greenlee	Big Lue Mtns	3 September 1983	Sta.Cruz	Research Ranch, Elgin
17 July 1979	Greenlee	White Mule Cyn, Big Lue Mtns	4 September 1983	Sta.Cruz	Sonoita Ck, 5M SW Patagonia
17 July 1980	Greenlee	Blue River	18 September 1983	Sta.Cruz	Research Ranch, Elgin
2 August 1980	Greenlee	Campbell Blue river	9 October 1983	Sta.Cruz	Rock Corral, Tumacacori Mtns
7 October 1984	LaPaz	north side, Harquahala Pk	21 October 1983	Sta.Cruz	California Gulch
20 July 1976	Mohave	Colorado City	11 November 1983	Sta.Cruz	Research Ranch, Elgin
29 July 1980	Mohave	Littlefield	5 August 1984	Sta.Cruz	Warsaw Cyn, Atascosa Mtns
29 July 1980	Mohave	Colorado City	26 August 1984	Sta.Cruz	Sycamore Cyn
25 June 1976	Navajo	east of Show Low	2 September 1984	Sta.Cruz	Sonoita Ck, 5M SW Patagonia
17 July 1983	Navajo	2M S Alchesay Fish Hatchery	10 September 1975	Yavapai	west side Mingus Mtn
6 September 1976	Pima	Box Canyon, Sta.Ritas	23 May 1976	Yavapai	Mingus Mtn
28 May 1978	Pima	Arivaca	24 August 1976	Yavapai	Yarnell
9 September 1978	Pima	3M W Arivaca	28 September 1976	Yavapai	nr Cleator
7 October 1979	Pima	Cienega Creek	16 August 1983	Yavapai	3M S Seligman
31 July 1981	Pima	Bear Cyn, Sta.Catalinas	10 October 1976	Yuma	north of San Luis
7 November 1981	Pima	Bull Pasture, Organ Pipe CNM			

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NOTES ON THE DEMOGRAPHY, LIFE HISTORY, AND BEHAVIOR OF THE WHITE MOUNTAIN ARCTIC BUTTERFLY (*OENEIS MELISSA SEMIDEA*)

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ABSTRACT. The White Mountain Arctic butterfly [WMA; *Oeneis melissa semidea* (Say, 1828)] is endemic to the alpine zone of the Presidential Range of the White Mountains, New Hampshire, USA. Although it has been listed as "imperiled", many biological characteristics of the WMA important for its conservation assessment and management are unknown. We conducted field studies in 2011 and 2012 to further characterize the WMA's demography, life history, and behavior. In both years, adults emerged in mid-June and occurred on Mts. Washington and Jefferson in association with Bigelow's sedge (*Carex bigelowii*). On both mountains, adult numbers generally were very low, suggesting that the population has declined considerably since its first description. Adults dispersed among some of the meadows on Mt. Washington, but we were unable to confirm if they moved between Mts. Washington and Jefferson. Adults generally congregated on rocky ledges and out-croppings, where males employed both perching and patrolling mate-locating strategies. In addition to elevation (high points in the landscape), adults used other cues when choosing sites at which to congregate. Finally, although many other *Oeneis* species engage in male territoriality, our observations suggest that WMA males are not truly territorial.

Additional key words: alpine, conservation, territoriality, lek, dispersal

The White Mountain arctic [WMA; *Oeneis melissa* semidea (Say)] is endemic to the alpine zone of the Presidential Range of the White Mountains, New Hampshire, USA. Within this area, populations are confirmed only on Mts. Washington and Jefferson, where adults are localized in alpine meadows dominated by Bigelow's sedge (*Carex bigelowii* Torr. ex Schwein), the sole larval host plant of the WMA (Scudder 1889, Anthony 1970, McFarland 2003). Because of its rarity and severely restricted range, the WMA has been listed as threatened and imperiled at state and global levels, respectively (New Hampshire Fish and Game Department 2005).

To date, most of our biological and demographic knowledge of the WMA comes from the initial descriptions of Scudder (1881, 1889, 1891, 1901). Since then, only Anthony (1970) and McFarland (2003) have attempted to systematically monitor or study the WMA, and Anthony (1970) deemed his own study to be inconclusive. Consequently, many aspects of the WMA's biology and behavior remain unconfirmed or unknown. For instance, an estimate of present-day population size is lacking. Furthermore, although the WMA population is purportedly spatially structured into isolated fragments (Anthony 1970; McFarland 2003), adult dispersal capacity and patterns have never been determined. Finally, WMA males appear to aggregate in leks where they await the arrival of females (McFarland 2003), but the mating system has never been definitively characterized. Current, detailed knowledge of such demographic and behavioral characteristics will be critical for the continuing conservation assessment and management of the WMA.

Over two field seasons, we attempted to further quantify the WMA's behavior and demography in the context of its conservation. However, consistent with the experiences of Anthony (1970) and McFarland (2003), making systematic and quantifiable observations of the WMA proved challenging: access to adults required long hikes, and the steep and rocky terrain made following or capturing adults very difficult. Mount Washington also routinely experiences harsh and unpredictable weather, and hence a limited number of days were suitable for adult butterfly activity. Nevertheless, we made some novel observations significant to the WMA's conservation that we summarize here.

FIELD METHODS

We conducted field studies from 22 June–14 July, 2011, and 22 June–15 July, 2012. Each year, the area that we surveyed included the alpine meadows described by Anthony (1970) (Cow Pasture, Bigelow Lawn, and Gulf Tanks on Mt. Washington; and Monticello Lawn on Mt. Jefferson), but also encompassed most of the intervening and adjacent areas containing Bigelow's sedge (Figure 1). Following rough transects, we surveyed each meadow at least every other day, or as weather permitted. In total, Cow Pasture, Bigelow Lawn, Gulf Tanks, and Monticello Lawn were surveyed 9, 5, 5, and 1 times, respectively, in 2011; and 9, 4, 7, and 2 times, respectively, in 2012. Because the weather conditions on Mt. Washington are variable and subject to rapid change, the number of days we were able to survey and the amount of time spent surveying in each meadow on any given day was highly variable.

TABLE 1. Summary of *Oeneis melissa semidea* adult capture data.

					Recapture Distance (m)			Days to Recapture		
Year	**Captured**	**Males**	**Females**	**Recaptures**	**mean**	**min**	**max**	**mean**	**min**	**max**
2011	187	126	61	8	305.7	28.1	787.0	5	1	8
2012	182	110	69	8	66.3	14.8	172.0	2	1	7

As such, our surveys were unavoidably biased, and thus we were unable to accurately estimate several adult population characteristics (e.g., overall size and density, density by meadow, sex ratio).

During surveys, we employed mark-release-recapture in an attempt to assess adult distribution, movements, longevity, and population size. To uniquely mark individuals, we applied small dots to the ventral wing surface of one side of the body with water-based, colored (red, green, blue, or yellow) paint markers (Sharpie® poster-paint) using a position-based numbered coding system (Southwood 1980).

Occasionally, we searched for eggs, larvae, and pupae at the bases of sedge plants or under small, moveable rocks.

RESULTS AND DISCUSSION

Adult Life History and Demography. Adults were present for the duration of each study period. Based on the degree of wing wear of the first individuals captured, adults likely first emerged on ~22 June in 2011, and may have emerged as early as 15 June in 2012. By the end of each study period, approximately 85% of adults demonstrated some degree of wing wear, indicating that they were near the end of their flight period. We estimate the flight periods were approximately 30 and 36 days in duration in 2011 and 2012, respectively.

Adults were located in almost every sedge-containing area of the Mt. Washington alpine zone. Similarly, adults were located in association with Bigelow's sedge on Mt. Jefferson, but were concentrated southeast of the summit (Fig. 1). On both mountains, adult density generally decreased with decreasing elevation, and the beginning of the krummholz (i.e., tree line) marked the limit of adult distribution. We did not locate any eggs, larvae, or pupae, which was unsurprising as WMA life stages other than adults have rarely been observed, even with intense search effort (Scudder 1881, 1889). To our knowledge, there is only a single report of a WMA egg observed in the field (Scudder 1889). Scudder (1881, 1889, 1891) often caged WMA females on Bigelow's sedge plants, and reported that females typically deposited single eggs loosely around the bases of the plants among the leaf litter or on loose sticks (Scudder 1881, 1891). White Mountain arctic larvae and pupae also have been located in the field but only with intense search effort. Larvae feed at night and rest during the day in between or under rocks (Scudder 1874, 1889), and pupation occurs under rocks, moss, or just below the soil surface (Scudder 1874, 1889).

In total, 187 and 182 adults were marked in 2011 and 2012, respectively (Table 1). Each year, the ratio of males to females caught was approximately 2:1 (Table 1). Very few recaptures were made (8 each year; Table 1), precluding an accurate estimate of population size. However, the WMA population certainly has declined dramatically since its earliest descriptions. At the turn of the last century, Scudder (1901) encountered a large and robust WMA population, claiming that "During the entire month of July the butterflies swarm over the rocks and sedgy plateaus of the upper summits…" and that "…hundreds, perhaps thousands, are annually captured by enthusiastic collectors…". In stark contrast, we discovered that WMA adults were low in numbers and localized. As McFarland (2003) reported, we could survey large areas and encounter only one or two adults until reaching an area of congregation. These congregations typically only contained 10–15 adults. Because of a lack of study, the specific causes of the WMA population decline remain unclear, but may include climate change (Parmesan 2006, Konviĉka et al. 2010), a decline in the abundance of Bigelow's sedge, population genetic factors (Gradish, unpublished data), and/or historical over-collecting of adults. However, additional research on the WMA (e.g., phenology, habitat use) in relation to historical changes to the Mt. Washington alpine zone and Bigelow's sedge is necessary to identify the specific cause(s) of the WMA population decline.

Although the WMA emerges annually, it likely is biennial (i.e., requires 2 years for development) (McFarland 2003), as is the case for all other *Oeneis* species (Scott 1986, Layberry et al. 2001). Most biennial insects emerge every year over parts of their range (Heliövaara and Väisänen 1984, Scott 1986, Heliövaara et al. 1994, Kankare et al. 2002), and these seemingly annual emergences are assumed to represent two sympatric, allochronic cohorts (i.e., one emerging in odd-numbered years and the other emerging in even-numbered years) (Scott 1986, Heliövaara et al. 1994, Kankare et al. 2002). The WMA also is presumably structured into two allochronic cohorts (Scudder 1889). Where sympatric, allochronic cohorts of biennial insects exist, one cohort usually is consistently less common (Masters 1974, Mikkola 1976, Heliövaara and Väisänen 1984, Scott 1986, Heliövaara et al. 1988, Sperling 1993, Kankare et al. 2002). Despite our almost identical capture rates each year, the total number of adults we observed (i.e., adults that we caught and adults that we observed but failed to catch) during our surveys in 2012 seemed comparatively lower, but despite this, our capture rates were almost identical both years. Because of our initial field experience in 2011, we were more proficient at capturing adults (i.e., we knew where to locate them and how to most effectively net them) during our second field season. As such, we believe that the adult population in 2012 was smaller, but we caught a comparatively larger proportion of it, resulting in a similar capture rate each year. Therefore, the WMA even-year cohort may be smaller; however, additional monitoring will be required to confirm this.

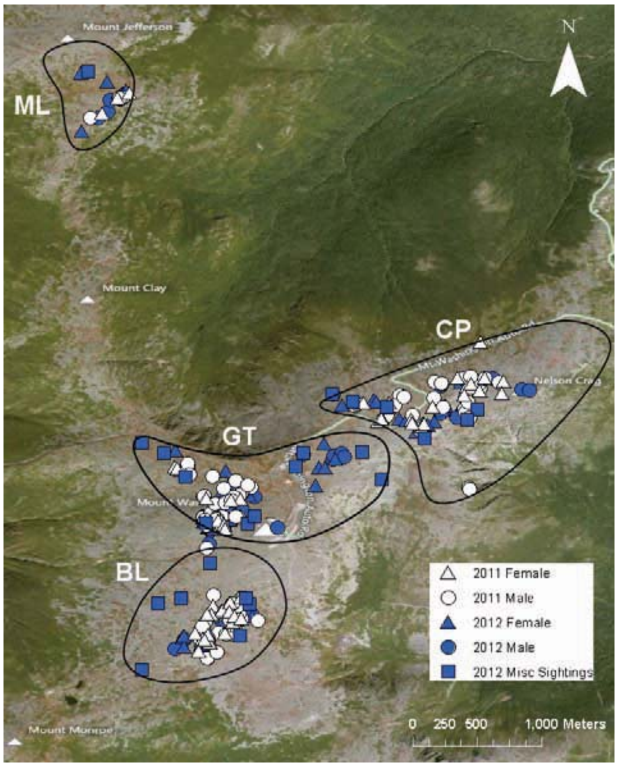

FIG. 1. Distribution of adult *Oeneis melissa semidea* on the alpine zone of Mts. Washington and Jefferson, New Hampshire, USA, determined by mark-release-recapture. Black lines indicate the areas surveyed for adults [Bigelow Lawn (BL), Gulf Tanks (GT), Cow Pasture (CP), and Monticello Lawn (ML)]. Triangles indicate locations where individual females were captured, circles where individual males were captured, and squares where an adult was sighted, but not captured. White and blue points indicate that the capture or sighting was made in 2011 and 2012, respectively.

The average time between capture and recapture of an adult was 5 and 2 days in 2011 and 2012, respectively, with a maximum of 8 days (Table 1). The average distance between capture and recapture of an adult was 306 and 66 m in 2011 and 2012, respectively (Table 1). In 2011, a male originally captured at Gulf Tanks was recaptured 787 m away at Bigelow Lawn. The distance that this male covered indicates that adults are capable of dispersing among all meadows on Mt. Washington. Although we did not directly observe dispersal between Cow Pasture and the other two meadows, we routinely encountered adults in areas among all three meadows. Thus the populations in the meadows of Mt. Washington are likely not isolated from each other as suggested by Anthony (1970). However, it remains unclear if adults actively disperse between Mt. Washington and Mt. Jefferson. These mountains are separated by the Great Gulf ravine (approximately 2.5 km wide when measured between Cow Pasture and Monticello Lawn), which adults may be unwilling or unable to cross. Yet, adults may occasionally be carried between these two areas by the wind (Anthony 1970). We did not observe adult movement between these mountains, but this could reflect in part the low numbers of adults that we marked on Mt. Jefferson (8 and 12 in 2011 and 2012, respectively).

Until recently, the WMA has been reported only from Mt. Washington and Mt. Jefferson. However, McFarland (2003) observed one adult on Mt. Monroe in 2002 and noted the presence of suitable habitat. On 11 July 2012, a hiker familiar with the WMA encountered an adult on the southern slope of Mt. Monroe (E. Elinski, pers. comm.). We were unable to survey this area, and thus it remains unclear whether adults consistently occur on Mt. Monroe.

General Adult Behavior and Mating System. Adults were most active on sunny days with winds below 30 km/h. However, even under cloudy skies with winds up to 60 km/h, some adults would fly if disturbed. Adults were wary and had strong and rapid flight: we occasionally observed them flying into 40–50 km/h winds to avoid capture. As reported by Scudder (1889), they frequently dove or crawled deep into rock piles if repeatedly disturbed or if we attempted to net them from directly above while they basked. Following capture and marking, we gently placed adults on a rock, where they typically basked briefly before flying away. White Mountain Arctic adults rarely nectar, but have been observed feeding on Moss Campion (Silene acaulis), Mountain Sandwort (*Arenaria groenlandica*), and various *Vaccinium* spp. (Scudder 1901, McFarland 2003). In 2011, we observed one female nectaring from Mountain Cranberry (*Vaccinium vitis-idaea*).

Adults generally congregated on rocky ridges or small rocky outcroppings. These were typically characterized by a relatively flat area of sedge on the uphill side of a rocky ledge that bordered a rocky slope. The drop in elevation below the ledge was usually steep in the case of ridges, but rather slight in the case of small outcroppings. As is the case for other *Oeneis* species (Guppy 1962, Troubridge et al. 1982), this use of raised landscape features by the WMA has been interpreted as hilltopping (McFarland 2003), a mate-encounter system in which males congregate at high points in the landscape where they await the arrival of females (Shields 1967, Baughman and Murphy 1988). However, the ledges occupied by WMAs were often not the most elevated in relation to the surrounding area. For instance, the north slope of the Mt. Washington summit contains numerous ridges along a drop in elevation of approximately 120 m. Males and females routinely occurred on all of these ridges and occasionally on the rocky slopes between them. Moreover, adults frequently were found on small ridges or outcroppings at the bases of large slopes, despite the presence of seemingly identical habitat upslope. In Colorado, *Oeneis chryxus* (Doubleday) displays similar behaviour, congregating on slopes of varying elevation (Daily et al. 1991). The authors hypothesized that where males choose to congregate in a given season is dictated by female distribution and movement, and that to intercept females, males align themselves with bare areas that females were likely to move towards. Rather than simply congregating at high points in the landscape, it appears the WMA also uses additional visual cues when choosing areas in which to congregate.

Congregated WMA males appeared to use a combination of perching and patrolling as mate-locating strategies, as described by Scott (1974). They frequently perched on rocks and alternated between lateral basking and spontaneous (i.e., initiated without obvious stimulus or disturbance), presumably patrolling, flights. Males also engaged in spiral flights with passing conspecifics and other flying insects. Other butterfly species (Suzuki 1976, Lederhouse 1982, Alcock 1983), including some *Oeneis* species (Dunlop 1962, Guppy 1962, Masters et al. 1967, Daily et al. 1991, Clayton and Petr 1992), engage in a similar suite of behaviors, and these behaviors have been interpreted by some authors as male territoriality associated with a lek mating system (Dunlop 1962, Guppy 1962, Masters et al. 1967, Lederhouse 1982, Alcock 1983, Knapton 1985, Clayton and Petr 1992, McFarland 2003). Yet the behaviour of the WMA differed both from some other *Oeneis* species and the definitional criteria for lekking (Bradbury 1981, Baker 1983). First, while territories of true lekking species remain fixed for several days in succession or longer (Baker 1983), the sites occupied by individual WMA males were not temporally stable. As an example, during an extended period of favorable weather between 9 and 13 July, 2012, we were able to conduct daily surveys of a ridge in Cow Pasture where adults consistently occurred. Each day, we observed 10–15 adults, 85–95% of which we were able to capture and mark. Despite our high capture rate, we only made two recaptures on subsequent days, even on the fifth visit. Furthermore, approximately 90% of the adults captured each day showed at least some wing wear, indicating that although these adults had clearly emerged at least a few days prior to capture, we had not previously encountered them at that site. Thus, either the adults were resident on the ridge continuously but a large proportion of them were inactive on any given day, or most adults moved away from the ridge. In contrast, *Oeneis chryxus* males consistently occupy the same sites for many days in succession, which is typical for lek-forming species (Dunlop 1962, Knapton 1985).

Second, the area occupied and/or patrolled by individual males often overlapped with other males without stimulating aggression between them. Males often perched within 2 m of each other, but also occasionally perched and basked directly beside each other on the same rock. Patrolling flights usually were of short distances (< 2m from point of initiation), but some individuals would fly and resume perching at a new site up to 15 m away. In either case, the area patrolled by a given male routinely contained multiple perching males. True butterfly territories typically contain only the resident male (Dunlop 1962, Lederhouse 1982, Knapton 1985), and 'intruders' are promptly driven away by the resident male (Davies 1978, Lederhouse 1982).

Third, following any type of flight, WMA males frequently did not return to the same rock or site from which they departed. Conversely, other purportedly territorial butterfly species (Lederhouse 1982, Wickman and Wiklund 1983), including *O. chryxus* (Knapton 1985, Daily et al. 1991), consistently return to their original perch immediately following patrolling or spiral flights.

Fourth, although spiral flights may be interpreted as a form of territorial defense (Lederhouse 1982, Alcock 1983), others view such flights as investigative, being used facilitate mate recognition (Scott 1974, Suzuki

1976, Daily et al. 1991, Clayton and Petr 1992). This latter explanation appears applicable to the WMA, as spiral flights often occurred between males and females, and, in three cases, ended immediately in copulation.

Fifth, male territories at leks are by definition devoid of oviposition and feeding sites (Bradbury 1981), yet areas of WMA male congregation contained both. The rocks on which males perched were almost invariably surrounded by Bigelow's sedge, the purported ovipositional site for females and larval host plant (Scudder1891, 1901). Many flowering plants also occurred in these areas, including Mountain Cranberry and Mountain Sandwort, on which WMA adults occasionally feed.

Thus, although at first glance the WMA appeared to display behaviors typical of hilltopping and lekking species, our more in-depth observations indicate otherwise. As has been suggested for other perching butterflies displaying similar behavior (Scott 1974, 1986, Suzuki 1976), it appears that the WMA is not truly territorial. Further study will be required to determine the specific abiotic or biotic cues for WMA adult congregation, and to further characterize its mating behavior.

In conclusion, while quantifiable study of the WMA was unsuccessful, we did gain some novel insight into its life history and behavior. First, we were able to obtain information on the WMA's adult distribution and dispersal behavior. Although the localized meadow populations likely are not isolated from each other, the population as a whole appears to be in decline. Second, we were able to better characterize its male mate-locating behavior, which involves male aggregation on rocky ledges but none of the other traits of leks. This system seems to be different from that of other species of the genus *Oeneis*. Not only does this study contribute to our knowledge of *Oeneis* butterflies in general, but this information also should aid the WMA's conservation assessment and recovery efforts.

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THE FUNEREAL DUSKYWING, *ERYNNIS FUNERALIS* (HESPERIIDAE): SEASONAL RANGE EXPANSION INTO EASTERN NORTH AMERICA

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ABSTRACT. The accepted normal range of the funereal duskywing skipper, *Erynnis funeralis* (Hesperiidae), is generally considered to be the southwestern United States, Mexico, Central America, and western South America from Colombia to northern Argentina and Chile. According to various records, however, adult *funeralis* have been observed in a variety of locations throughout the eastern half of central North America, sometimes thousands of kilometers outside its accepted range. These individuals are usually conceptualized as non-reproductive strays, but different lines of evidence (e.g. the observations of both males and females, the fresh condition of most adults, the recurrence of observations in the same locations at similar times of year in different years) suggest that *funeralis* regularly establishes seasonal breeding populations in the eastern half of central North America. To test this hypothesis, I examined reports of observations of *funeralis* throughout this region for evidence of 1) regular as opposed to random presence in the East, 2) eastern as opposed to western eclosion, 3) regular as opposed to random expansion throughout the East, and 4) reproductive activity. The results revealed evidence of all four phenomena. Consequently, I concluded that instead of being conceptualized as an irregular, non-reproducing stray, *funeralis* should be conceptualized as a regular seasonal immigrant that establishes temporary breeding populations in the eastern half of central North America during the warmer months of the year.

Additional key words: *Erynnis*, Lepidoptera migration, reproductive behavior, skippers

The accepted normal range of the funereal duskywing skipper, *Erynnis funeralis* (Scud. & Burg.) (Hesperiidae), is generally considered to be the southwestern United States, Mexico, Central America, and western South America from Colombia to northern Argentina and Chile (Burns 1964 pp. 174–175). In the southwestern United States, its accepted range is considered to be southern California, Arizona, southern New Mexico, and Texas. Individuals found somewhat outside this range (i.e. southern Nevada, Utah, and Colorado in the West; Oklahoma, Nebraska, and Kansas in the Plains; and western Louisiana and Arkansas in the South) are considered to be uncommon, but still within *funeralis*'s accepted range.

According to various records, however, *funeralis* has been observed in a variety of locations throughout the eastern half of central North America, sometimes thousands of kilometers outside its accepted range. The record for such far-flung sightings appears to be one from Avondale Farm Preserve, Waverly (Washington Co.), Rhode Island (Koehn 2011 p. 145), some 3000 km from the focal point of *funeralis*'s typical U.S. range in the Southwest. Although observations of *funeralis* in the eastern half of central North America are uncommon, they are sufficiently numerous to provoke interest regarding their significance.

In the literature, *funeralis* is persistently described as a "stray" when discovered outside its accepted range (e.g. Hall 1936, Scott 1986 p. 492, Heitzman & Heitzman 1987 p. 32, Shull 1987 p. 41, Tuttle 2004 p. 49, LeGrand & Howard 2010, Koehn 2011 p. 145, Belth 2013 p. 82, Neese 2013). This characterization implies that its occurrence in the East is not only irregular, but also non-reproductive in nature. Exceptions to this perception include Bouseman et al. (2006 p. 56), who acknowledge that *funeralis* may occasionally establish temporary breeding population as far east as Illinois, but overwhelmingly, the presence of *funeralis* in the eastern half of central North America is viewed as an anomaly. The possibility that its occurrence there may be something more than accidental is generally not considered. Various lines of evidence, however, suggest that *funeralis* regularly establishes seasonal breeding populations in the East.

First, the data indicate that both male and female adults have been observed (e.g. Shull 1987 p. 41, Hanson et al. 2002, Bouseman et al. 2006 p. 57, Reese 2007, Arvin 2010, Bolin 2010, Brees 2010a, Brown 2010, Ennis 2010, Huf 2010, Legler et al. 2010, LeGrand & Howard 2010, Mann 2010, 2012, Rehm 2010a,b, Schulte 2010,"Stone Lark" 2010, Trently 2010a, Williams 2010, Yomeyer 2010, Cavasin 2012, Davis 2012, Geiser 2012, Lubahn 2012, Shively 2012, Spitzer 2012, Lotts & Naberhaus 2013a,c; Fig. 1). This suggests that individuals of one sex are not merely wandering outside their accepted range because of some sex-specific behavior. Instead, the appearance of both sexes suggests that *funeralis*'s presence outside its accepted range is related to the behavior of the species in general. Both male and female adults are obviously required to establish a breeding population, so the presence of both sexes by itself suggests this possibility.

Second, the majority of adult *funeralis* collected, photographed, or otherwise reported in the East have

FIG. 1. *Erynnis funeralis* in west central Indiana. Female (**a**) dorsal view, (**b**) ventral view, Terre Haute (Vigo Co.), Indiana, 15 September 2003, 1647 h., taking nectar from *Perilla frutescens* (L.) Britt. (Lamiaceae) at the author's home. This individual displayed little if any wing wear, suggesting it had recently eclosed and, therefore, came from a local breeding population. The majority of *funeralis* encountered in the eastern half of central North America have been found in similar condition. Species and sex identified by John M. Burns. Photos copyright © Roger Carpenter.

been found in remarkably fresh condition (see previous paragraph for examples; in addition, see Ziebol & Homeyer 2007, Koehn 2011 p. 101, Lamond 2011, and Wormington 2012 for comments). Indeed, some observers have not only remarked about their immaculate state, but also marveled that they could remain in "mint" condition after having flown what are presumed to be great distances (Lamond 2011). The condition of these adults, however, suggests that they had recently eclosed and, consequently, would not have had the time required to travel hundreds, let alone thousands, of kilometers to the eastern locations where they were sighted. It is more logical to assume that most if not all of these adults were, in fact, the products of breeding populations that had become established much closer to where they were observed.

Third, various reports from the East indicate that not one but two or more adults have been observed in the same place at the same time. Examples of such sightings include one from Shaw Nature Reserve (Franklin Co.), MO on 10 July 2010 in which two adults were observed flying together (Homeyer 2010); one from the vicinity of Tamms (Alexander Co.), IL in which three males were collected between 18 and 20 September 1999 (Wiker, pers. com.); and one from Point Pelee National Park (Essex Co.), ON on 13 September 2010 in which three adults were observed flying together (Koehn 2011 p. 101). Because *funeralis* is not known to migrate en masse, the occurrence of two or more *funeralis* together so far outside its accepted range is consistent less with the idea that (presumably isolated) individuals have strayed outside their normal range than with the idea that groups of adults are eclosing in the same place at the same time.

Fourth, in similar fashion, various reports indicate that *funeralis* tends to be observed in the same locations at similar times of year in different years. For example, *funeralis* has been observed at Point Pelee National Park during the late summer-early fall of 1990, 1992, 2010, 2011, and 2012 (Layberry et al. 1998 p. 40, Koehn 2011 p. 101, 2012 p. 82, Cavasin 2012, Mann 2012, Wormington 2012). Other examples include Tippecanoe Co., IN during early/mid-August 2010 and 2012 (Arvin 2010, Belth pers. com.) and Dane Co., WI in mid-/late August 2007 and 2010 (Reese 2007, Legler et al. 2010). This type of pattern is consistent less with random straying than with regular expansion that causes *funeralis* to arrive at specific eastern locations at similar times of year.

The purpose of the present study, then, was to determine whether *funeralis* is merely straying, in random fashion, outside its accepted range or regularly expanding its range and establishing breeding populations when conditions become favorable. I hypothesized that if the latter were true, then the *funeralis* observations from the East should display the following characteristics:

1. Observations should occur in many if not most years, suggesting regular as opposed to random presence in the East;
2. Observations should indicate that, in general, adults had eclosed relatively close to where they were observed, as suggested by a) excellent wing condition in many adults and b) observations of two or more adults in the same location in the same year in a species that does not appear to swarm;
3. Observations should indicate regular expansion throughout the eastern half of central North America during the warmer months of the year, as suggested by a) observations of adults in similar locations at similar times of year in different years, b) in general, a regular as opposed to random pattern of movement

FIG. 2. Idealized range expansion pattern, based on data from all years, of *E. funeralis* throughout the eastern half of central North America from late spring to early fall. Polygons enclose outermost first observations of the year for specific counties reported through the end of five successive months: 5 = May; 6 = June; 7 = July; 8 = August; 9 = September. (New Hanover Co., NC and Escambia Co., FL observations occurred in October.)

from west to east, c) a relatively constant rate of expansion from month to month, and d) similarities in the pattern of movement from year to year;

4. Observations should indicate the occurrence of breeding activity, as suggested by a) an overall sex ratio of 1:1, b) evidence of different stages of the life cycle, and c) regularly spaced increases in the number of adult observations, consistent with the production of successive generations.

METHODS AND MATERIALS

I analyzed observations of *funeralis* from the eastern half of North America derived from the following sources: Hall (1936), the Lepidopterists' Society Season Summary reports (1960-2013), Burns (1964), Shull (1987), Layberry et al. (1998), Belth (2013); the websites Bug Guide (VanDyk 2013), Butterflies and Moths of North America (Lotts & Naberhaus 2013a; Opler et al. 2013); Butterflies of North Carolina (LeGrand & Howard 2010), Butterflies of Ontario (Cavasin 2013), Illinois Butterfly Monitoring Network (2013), North American Butterfly Association (2013), North American Moth Photographers Group (Patterson 2013), and Wisconsin Butterflies (Reese 2013); the blogs '*Burg Birder* (Mann 2013) and *Exploring the Remnants* (Brees 2010); the online forums Illinois Birders' Forum (Neise 2013) and Ontario Butterflies (2013); the photo sharing pages of Kevin Arvin (2010), Bruce Bolin (2010), Mark Brown (2010), Allan Trently (2010a), and Urs Geiser (2012); personal communication with Jeffrey Belth, John Burns, Myron Cole, and James Wiker and personal observation.

Because I focused on *funeralis*'s movements outside its accepted range, I excluded data from the following states, based on the *funeralis* range map given in Burns (1964 Fig. 23): California, Arizona, New Mexico, Texas, and Oklahoma. In addition, I excluded data from states west of a line separating the Plains States from the eastern states as well as from Arkansas and Louisiana to control for the possibility of random movement of individuals within as opposed to outside the accepted *funeralis* range. The final data set included observations from the states of Alabama (1), Florida (12), Georgia (1), Illinois (24), Indiana (8), Iowa (6), Kentucky (4), Michigan (1), Mississippi (4), Missouri (16), North Carolina (2), Ohio (1), Pennsylvania (2), Rhode Island (1), South Carolina (1), Tennessee (7), West Virginia (1), and Wisconsin (7) as well as the province of Ontario (27) for a total of 126 observations. Data from the remaining eastern states and provinces were unavailable. Different subsets of this primary data set were used in various analyses depending on the type of information available for individual observations.

Observations by Year.

The number of reported observations of *funeralis* per year was totaled. In addition, the median number of observations per year, the median year of the observations, and the median day of the observations (corrected for multiple observations in a specific county in a specific year) were calculated.

Eclosion near Location Observed.

Wing condition. I evaluated the wing conditions of as many adults as possible as a proxy for adult age and, by inference, distance traveled during the adult stage. I examined photographs of live, unhandled adults in which the dorsal sides of all four wings were clearly visible to determine levels of wing wear. I rated the condition of each wing on a scale ranging from 0 (missing) to 5 (perfect) in 0.1 increments for finer discrimination. The ratings for the four wings were then averaged to yield total wing condition scores both for individuals and for wing type (RFW, RHW, LFW, LHW). One-way ANOVA was performed to determine if wing condition differed by wing type.

Same location/single year observations. I analyzed observations of *funeralis* in the East for instances of two or more observations in the same location in the same year. "Same location" was operationally defined as the same county or adjacent counties if the observations took place within 50 km of each other (the average length of a county in the United States).

Range Expansion.

Same location/different year observations. I analyzed observations of *funeralis* in the East for instances of observations in the same location in different years. "Same location" was operationally defined as it was in the same location/single year observation analysis.

General movement. I derived an idealized model of *funeralis*'s expansion throughout the East by plotting the first observation of the year reported for a particular county on a county-level map of the eastern United States then drawing the smallest possible polygon around the outermost observations for successive 1-month periods beginning with all observations through the end of May and ending with those through the end of October. The data were analyzed for outlying values by dividing the distance of the observation in kilometers from the focal point of *funeralis*'s range in the United States by the day of the year of the observation and converting the resulting values to *z*-scores. Because *funeralis*'s perennial range in the United States is concentrated in the Southwest (see dot map in Burns 1964 Fig. 23), I operationally defined the focal point of its range as Phoenix, AZ (33.500°N, 112.083°W). Outlying values were eliminated from the expansion model.

Expansion rate. I estimated the average rate of *funeralis*'s expansion throughout the eastern half of central North America using the method that Davis and Howard (2005) employed to determine the rate at which *Danaus plexippus* that overwinter in Mexico recolonize the eastern half of central North America in the spring. After determining the extent of the species' range (in km^2) for successive, equally spaced time periods, the net increase in range from one period to the next is calculated. The square root of the increase is then divided by the number of days in the period to estimate the average rate of expansion (in km/d). Periods of one month were used in the present study.

Single-year movement. Because 2010 appeared to be unusually rich in *funeralis* observations (n = 43), providing an adequate sample for detailed single-year analysis, I performed correlation and regression analyses to measure the relationship between the day of the year on which the 2010 observations occurred and the distance from Phoenix at which they occurred. To be counted in this analysis, an observation had to include 1) the location at which the observation occurred (to the county level or better) and 2) the specific date on which the observation occurred. For counties where two or more observations occurred, I included only the first observation for the year. I estimated the coordinates of each observation using the most accurate information available. This information included 1) specific locations (e.g. an observer's residence), 2) general locations (e.g. a city or a state park), or 3) county-level locations (e.g.

Boone Co., IA). In cases 2 and 3, the geographical center of the location was determined and used. Then, using Google Earth (2010), I measured the distance in kilometers (and cardinal direction in degrees) from Phoenix to the location of the observation.

2010 vs. non-2010 comparison. To determine if the 2010 and non-2010 data significantly differed, I compared the mean distance of the observations from Phoenix, the mean cardinal direction of the observations from Phoenix, and the median day of the observations. For the distance and direction comparisons, I used *t*-tests, while for the median day comparison, I used the Mann-Whitney *U*-test. (All tests were two-tailed.)

Eastward and northward movement. I calculated the median easternmost longitude and the median northernmost latitude of the observations, respectively. In addition, I calculated the correlations between year and 1) easternmost longitude at which *funeralis* was observed and 2) northernmost latitude at which *funeralis* was observed. (All tests were two-tailed.)

Reproductive Behavior.

Sex ratio. I estimated the overall sex ratio of the *funeralis* that have been observed in the East by ascertaining the sexes of as many photographed and collected individuals as possible. I assumed that an adequate sample of such individuals would be representative of the proportion of males vs. females in the East, since eastern photographers and collectors appear to focus on acquiring images or specimens of the species rather than of a particular sex. The binomial test (two tailed), assuming a 0.5 probability, was used to determine if the proportion of the two sexes differed from the expected 1:1 ratio.

Life cycle observations. I examined the available records for observations of mating, oviposition, eggs, larvae, pupae, and eclosing adults as indicators of breeding activity.

Generational trends. I totaled the observations for successive 15-day periods beginning with the first dated observation and ending with the last to determine the presence or absence of regularly spaced peaks in adult observations suggestive of breeding activity.

Statistical analyses were performed using SPSS v20.0 software (IBM Corp. 2011).

RESULTS

Observations by Year.

Observations reported before 1990 were sporadic with one observation reported in 1963, 1974, and 1979, respectively, two in 1975, and three in 1914. Hall (1936) reported the collection of a *funeralis* in Crawfordsville (Montgomery Co.), IN sometime in the early 1930s but did not give an exact date. Observations reported after 1990 were more constant with at least one observation reported each year between 1990 and 1992 as well as between 1998 and 2014 (except for 2013). In addition, at least one observation was reported as far east as the Illinois-Indiana border each year between 1998 and 2014 (except for 2013). The median number of observations per year (n = 112) was 1.5 and ranged from 1 to 43. The median year of the observations was 2010 and ranged from 1914 to 2014. The majority of the observations (92.9%) occurred in 1990 or after. The corrected median day of the observations (n = 80) was day 214 (= 2 August, 365-day calendar) and ranged from 20 April to 30 October.

Eclosion near Location Observed.

Wing condition. The mean wing condition rating for all individuals examined (n = 36) was 4.97 (SD = 0.08). Twenty-nine individuals (80.6%) received a rating of 5.0, while the remaining seven (19.4%) received ratings that ranged from 4.58 to 4.98. Mean ratings for each wing were RFW = 4.98 (SD = 0.05), RHW = 4.97 (SD = 0.07), LFW = 4.98 (SD = 0.05), and LHW = 4.92 (SD = 0.25). The lower LHW mean and higher standard deviation resulted primarily from one individual (Lotts & Naberhaus 2013c) that received a LHW score of 3.5 because of a large linear tear extending from the LHW outer margin to the discal area. When this individual's LHW score was removed, the LHW mean/standard deviation (n = 35) became more similar to those for the other three wings (mean = 4.98, SD = 0.05). The difference in wing condition by wing type was not significant, $F(3, 105) = 0.72$, $P = .542$.

Same location/single year observations. The results of the same-location/single-year observation analysis are presented in Table 1. Thirteen one-county/two-county units reported two or more observations of *funeralis* in the same year.

Range Expansion.

Same location/different year observations. The results of the same-location/different-year observation analysis are presented in Table 2. Eleven one-county/two-county units reported at least one observation of *funeralis* per year in two or more years.

General movement. From an initial subsample of 66 observations, one observation from Clark State Forest (Clark Co.), IN on 20 April 1991 (Belth 2013 p. 82, pers. com.) was eliminated because it was revealed to be an outlier (distance/day, $z = 3.96$; second highest, $z = 2.27$). The resulting data set, then, contained 65 observations. Because there was only one remaining observation for April (Benton Co., MO, 27 April 1975, Lotts & Naberhaus 2013b), and this observation occurred late in

TABLE 1. *Erynnis funeralis* Observations in the Same Location in the Same Year

State/Province	County/Counties	Year [Number]
Florida	Escambia (Pensacola)	1914 [4]
Illinois	Alexander	1999 [4]
Illinois	Henderson/Fulton	2010 [2]
Illinois	Lake/McHenry	2010 [2]
Illinois	Will	2010 [2]
Illinois	Clay/Fayette	2012 [2]
Illinois	Lake/Cook	2011 [2]
Iowa	Decatur/Ringgold	2010 [2]
Missouri	Calloway/Boone	2010 [2]
Missouri	St. Charles/St. Louis	2010 [2]
Tennessee	Lauderdale	2010 [2]
Wisconsin	Dane	2010 [2]
Ontario	Essex (Point Pelee Natl. Park)	2010 [10]

Note: Specific locations within counties (when applicable) are given in parentheses.

the month, I included this value in the polygon for May. A dot map of these observations is presented in Fig. 2. The mean coordinates for the observations (n = 65) were 38.88°N, 88.02°W (SE Jasper Co., IL).

Expansion rate. The expansion rates for the five months analyzed (June-October) were June = 15.9 km/d, July = 26.4 km/d, August = 25.3 km/d, September = 24.8 km/d, and October = 11.9 km/d, resulting in a median expansion rate of 24.8 km/d.

Single-year movement (2010). Before performing analyses, I eliminated one observation from Will Co., IL, 26 September (already seen 5 September); one from Dane Co., WI, 30 October (already seen 27 August); one from Lauderdale, Co., TN, 16 August (already seen 31 July); and nine from Point Pelee National Park, ON that occurred after the initial 5 September observation. In addition, I counted the observation of two *funeralis* at Shaw Nature Reserve in Franklin Co., MO on 10 July as one observation. The resulting data set, then, contained 30 observations.

Correlation analysis revealed a positive correlation between day of observation and distance of observation from Phoenix, $r = .655$, df = 28, $P < .0001$. Regression analysis revealed that a linear model provided the best fit to the data. The equation of the best-fitting line was $y = 10.55x - 77.73$, where x = day and y = distance from Phoenix in km. A scatterplot of the 2010 data is presented in Fig. 3.

2010 and non-2010 comparison. Mean distances of the observations from Phoenix for the 2010 and non-2010 data were 2263.19 km (SD = 491.03) and 2417.08 km (SD = 404.49), respectively. The difference was not significant, $t = 1.526$, df = 79, $P = .131$. The mean cardinal directions of the observations from Phoenix were 63.38° (SD = 8.49) and 67.77° (SD = 11.04) or roughly ENE (= 67.50°). The difference was not significant, $t = 1.875$, df = 79, $P = .065$. The median days of the observations were days 214.5 (range = 177-281) and 217.0 (range 117-294), respectively (2 August and 5 August, respectively, 365-day calendar). The difference was not significant, $U = 743.0$, $z = -0.210$, $P = .834$.

Eastward and northward movement. The median easternmost longitude of the observations was 82.32°W (range = 71.84°-87.97°W). The correlation between year (1990-1992, 1998-2012, 2014) and easternmost longitude at which *funeralis* was observed was not significant, $r = .089$, df = 17, $P = .717$. The median northernmost latitude of the observations was 42.51°N (range = 30.77°-46.77°N). The correlation between year (1990-1992, 1998-2012, 2014) and northernmost latitude at which *funeralis* was observed was not significant, $r = -.005$, df = 17, $P = .984$.

Reproductive Behavior.

Sex ratio. The examination of the available records in which sex was or could be determined (n = 39) revealed 24 males and 15 females. The resulting sex ratio (M:F) was 1.60:1. This ratio did not differ significantly from the expected 1:1 sex ratio, $P = .200$.

Life cycle observations. An examination of the available records revealed no observations of mated pairs, eggs, larvae, pupae, or eclosing adults. One photograph by Spitzer (2012) taken on 5 May 2012 at Lake Bloomington (McLean Co.), IL, however, appeared to show a female *funeralis* ovipositing on *Lathyrus* sp. (Fabaceae), which is in the same family as *funeralis*'s primary larval hosts.

Generational trends. A bar graph of the number of observations during successive 15-day periods (n = 107) is presented in Fig. 4. The graph revealed two primary peaks in adult observations occurring around early/mid-July and mid-/late September and a secondary peak occurring around mid-August.

DISCUSSION

The results of the present study suggest that *E. funeralis* is not randomly straying into the eastern half of central North America, but regularly expanding its range during the warmer months and establishing breeding populations in that region. Several facts argue in favor of this interpretation:

1. Adults were reported as far east as the Illinois-Indiana border every year except one between 1998 and 2014, suggesting regular as opposed to random presence in the East;
2. The majority of adults encountered in the East have been in excellent condition, suggesting that they had not traveled the long distances they are usually assumed to travel. In addition, the multiple observations of two or more adults in the same location in the same year in a species that does not appear to swarm further suggests that these adults had eclosed relatively close to where they were observed;
3. Data from all years suggest regular as opposed to random expansion throughout the East, as indicated by a) the appearance of adults in the same locations at similar times of year in different years (Table 2 and Fig. 2), b) the relatively constant expansion rate of ~25 km/d between July and September, and c) the similarities between the 2010 and non-2010 data;
4. Evidence of reproductive behavior in the East, as indicated by a) an overall sex ratio of 1:1, consistent with that of breeding populations, b) an observation of a female *funeralis* ovipositing on a legume, implying more widespread reproductive activity, and c) regularly spaced increases in adult observations, consistent with the production of at least two eastern generations per year.

Given these facts, *E. funeralis* should be conceptualized as a regular seasonal immigrant that establishes temporary breeding grounds in the East rather than as the irregular, non-reproducing stray that it is usually considered to be.

As far as the low number of records of *funeralis* in the East is concerned, several factors may be involved. First, the data suggest that *funeralis* may penetrate into the eastern half of central North America to varying degrees each year. The dot map (Fig. 2) reveals a disproportionate number of observations in the more western states (e.g. Illinois, Iowa, Missouri, Tennessee, Wisconsin), suggesting that *funeralis* does not typically penetrate into the more eastern states and provinces. Therefore, the low number of reports from the more eastern reaches of central North America may reflect actual absence in many years.

Second, eastern populations of *funeralis* may typically be smaller or more diffuse than those of other seasonal immigrants, which means that observers would be unlikely to encounter it most years in spite of its presence. For example, in some years *funeralis* has been

TABLE 2. *Erynnis funeralis* Observations in the Same Location in Different Years

State/Province	County/Counties	Date
Florida	Alachua	30 SEP 2003
		21 OCT 2005
Illinois	Alexander	18 SEP 1999
		16 OCT 2011
Illinois	La Salle (Matthiessen State Park)	23 JUL 2004
		1 JUL 2012
Illinois	Lake*	9 AUG 2010
		5 JUN 2012
Indiana	Bartholomew/ Brown	27 JUL 2004
		29 JUL 2014
Indiana	Tippecanoe	6 AUG 2010
		18 AUG 2012
North Carolina	Brunswick/ New Hanover	7 OCT 2000
		4 AUG 2010
Wisconsin	Dane	13 AUG 2007
		27 AUG 2010
Ontario	Essex (Point Pelee Natl. Park)	6/14 OCT 1990**
		23 SEP 1992
		5 SEP 2010
		12 AUG 2011
		7 JUL 2012
Ontario	York	27 AUG 1998
		12 AUG 1999
		6 OCT 2002
		17 AUG 2006
		12 AUG 2008
Ontario	Halton	8 OCT 2010
		15 AUG 2012

Note: Only the first observation in a specific county for a specific year is given. Specific locations within counties (when applicable) are given in parentheses. *E. funeralis was also observed in 2011, but the specific date was not available in the record consulted. **Layberry et al. (1998 p. 40) give 6 October; Preston (1991 p. 28) gives 14 October.

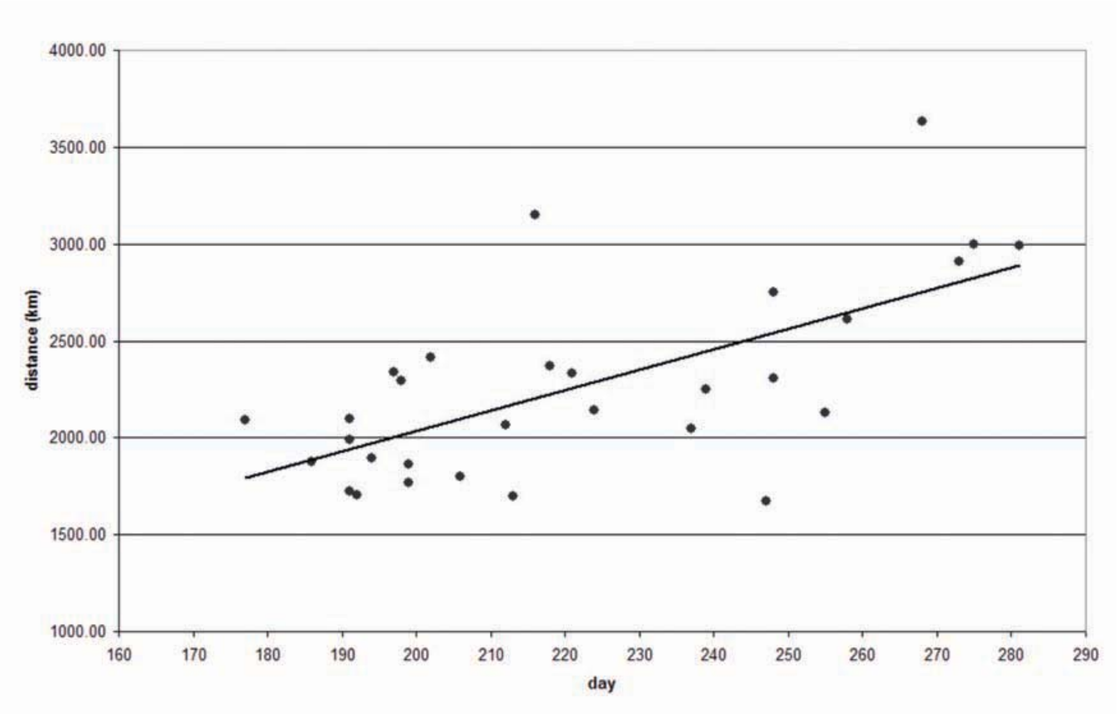

FIG. 3. Scatterplot of day of year (365-day calendar) of observations of *E. funeralis* vs. distance (km) of observations from Phoenix, AZ (33.500°N, 112.083°W).

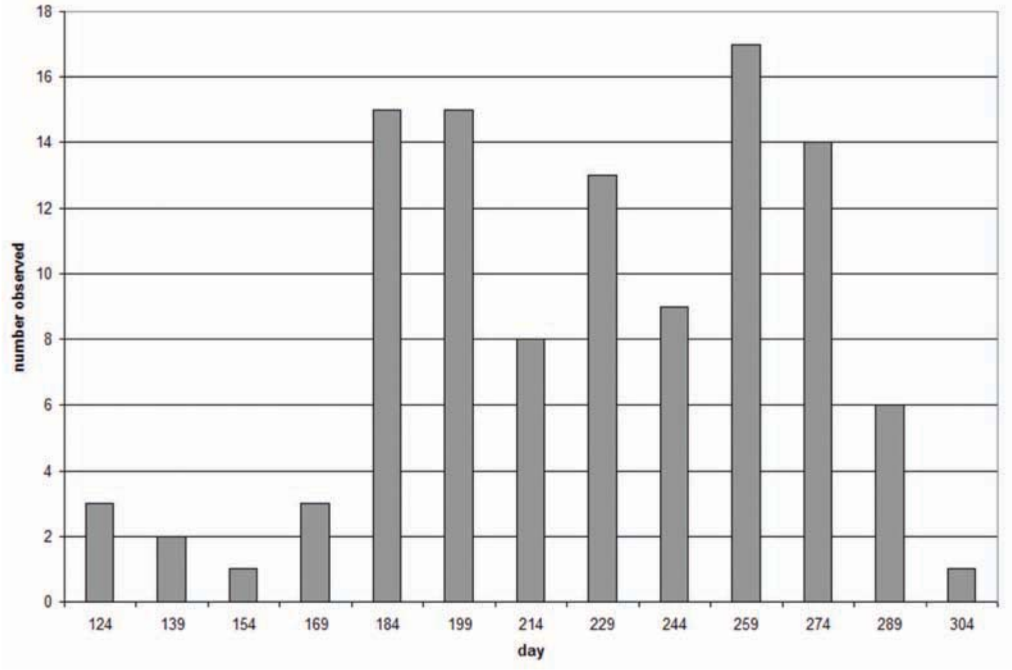

FIG. 4. Number of observations of *E. funeralis* in the East during successive 15-day intervals (365-day calendar, n = 107). Days given are median days for ranges.

reported exclusively from more eastern states or provinces (e.g. Ontario in 1990, 1992, 2006, and 2008; North Carolina in 2000; Florida in 2005), suggesting it was also present farther west in those years but remained undetected.

Third, *funeralis* is not a "showy" species, being small and having a stereotypically "moth-like" appearance, so the average (and even knowledgeable) person may tend to overlook it. In addition, if the white hindwing fringe that distinguishes *funeralis* from all other *Erynnis* species found in the East is missing, then *funeralis* can easily be mistaken for one of the dark-fringed species expected for the region. Consequently, an unknown number of *funeralis* may have been observed or collected in the East but misidentified as dark-fringed members of the genus.

In spite of rare reports of *funeralis* in the East by mid-spring (e.g. Clark Co., IN, 20 April 1991), the available evidence suggests that in the United States, *funeralis* does not overwinter outside the Southwest. *Erynnis* species overwinter during the larval stage (Burns 1964 p. 14), and although some members of the genus are cold-adapted (e.g. *horatius, juvenalis, baptisiae* etc.), not all *Erynnis* species are (Burns, pers. com.). The fact that *funeralis* is typically found in tropical and subtropical environments suggests that it may not be able to survive the northern winters. In addition, the fact that *funeralis* adults do not appear throughout the northern and eastern United States within a short period of time in the spring further suggests they are not overwintering there.

Extrapolating backward using the expansion rate estimate, one scenario suggests that *funeralis* begins to disperse from its perennial range in the Southwest sometime in mid- to late April. This time frame is consistent with the onset of expansion of various warm-adapted butterfly species into the more northern regions of central North America (e.g. *D. plexippus*). Spreading out from its perennial range in the Southwest, a *funeralis* migration wave moving ENE at an average rate of 25 km/d could easily reach the western edge of the Midwest by June (when records there generally start appearing). Of course, *funeralis* originating farther east, traveling faster, or both could arrive earlier, possibly explaining some eastern observations that have occurred earlier than expected (e.g. Clark Co., IN, 20 April 1991). *E. funeralis* appears to reach the ultimate extent of its expansion by late September-early October, stopped by natural barriers (e.g. the Appalachian Mountains, the Atlantic Ocean) in the east and probably by developing thermal barriers to the north.

The 2010 expansion of *funeralis* appears to have attracted special attention (e.g. LeGrand & Howard 2010), but the data presented here suggest that it was different in quantity, not quality. *E. funeralis* appeared to be especially numerous that year, presumably causing observers to take special note of it. The 2010 and non-2010 comparisons suggest, however, that *funeralis* behaves roughly the same way in different years.

One question that the present study cannot fully answer is that of how far individual adult *funeralis* can and do travel within their lifetimes. How the 25-km/d expansion rate estimate relates to the vagility of individual adult *funeralis* is unclear. This figure includes the lag time required for stationary pre-adult development, which suggests that adult *funeralis* travel faster and farther than the 25-km/d estimate indicates. Only mark-release-recapture studies assessing the vagility of adult *funeralis* will settle the issue.

Another question that the present study cannot fully address is the extent to which climate change is affecting *funeralis*'s northward movements. Apart from one observation from Whitefish Point (Chippewa Co.), MI (46.77°N) on 18 August 2001 (Tuttle 2002 p. 48), *funeralis* has not been reported north of 44°N. In general, the northern limit of *funeralis*'s summer range is about 43°N, a figure that has remained fairly constant for at least 50 years. To answer the question of the possible effects of climate change on *funeralis*'s migratory behavior, data with better coverage of the northern United States and southern Canada would be required.

The primary peaks in adult observations that occur in early/mid-July and mid-/late September suggest the production of at least two eastern generations per year. *E. funeralis* is multivoltine, producing three generations per year (Burns 1964 p. 175 & Fig. 24). The July and September increases may represent the emergence of adults that are the first- and second-generation offspring, respectively, of adults that began migrating northeastward in late spring. Consequently, the midsummer and early fall observations in the East, respectively, appear to be those of second- and third-flight individuals, not first-flight ones. The secondary peak in mid-August may be an artifact of combining data from different years, which is suggested by the greater number of observations in July and September 2010 than in mid-August of that year (see Fig. 3).

The results of the present study are tentative and much additional data need to be gathered to determine the full extent and nature of *funeralis*'s movements throughout the eastern half of central North America during the warmer months. The implication of the results, however, is that *funeralis*'s presence in that region has been misunderstood. Far from being the occasional vagrant it is usually presumed to be, *funeralis* appears in fact to be a regular seasonal resident of the eastern reaches of central North America whose presence in that region during the warmer months is much less random than has traditionally been considered.

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WIND TUNNEL STUDIES OF TEMPERATURE DEPENDENCE AND BEHAVIOR OF BUTTERFLIES IN THE CONTEXT OF HABITAT EDGES

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ABSTRACT. Wind tunnel studies provide a valuable experimental approach that can be used to investigate the influence of specific environmental parameters and to make generalizations about insect behavior. In this study, we designed an experiment to test the sensitivity of butterflies to isolated environmental parameters in the context of understanding edge responses. We tested the behavior of 21 different butterfly species in response to certain stimuli, including food source, feeder color, temperature, and UV light. Certain butterfly species (e.g. *Heliconius melpomene* and *Papilio polytes*) were particularly active in the wind tunnel setup. All butterfly species tested preferred blue feeders over white, yellow or pink. Investigation of the UV content of the different feeders and the butterflies' preferred nectar plant showed a similar wavelength response, which could indicate a UV preference in butterflies. We also observed species-dependent temperature preferences. *Papilio lowii* had a significant preference for the warm side (36.0°C) of the wind tunnel, whereas *Papilio polytes* showed a significant preference for the cold side (25.3°C).

Additional key words: flight, training, UV, perception, experiments

Wind tunnel studies have long been used to investigate animal flight (e.g. Pennycuick 1968, Tucker 1968). The biggest advantage of wind tunnel use is the ability to simplify a complex natural environment and allow for controllable and repeatable measurements. To ensure non-biased results of a lab or wind tunnel study, the experimental design needs to be adjusted carefully to represent conditions pertinent to the research question. Previous training and behavioral testing of the study species or individual can be essential for the success of the experiment (e.g. Pennycuick 1968). However, training butterflies presents a different set of challenges than training vertebrates, like birds or bats, and the butterflies' perception and learning capabilities need to be taken into account. Current studies by van Dyck (e.g., 2011) acknowledge a species' perception of its environment and highlight the importance of incorporating this species-specific perception when applying research questions to natural environments.

Our study was designed to investigate the sensitivity of butterflies to environmental parameters in the context of edge responses. Current habitat restorations aim to restore the function of original ecosystems and one measure of restoration success is the composition of the insect community. Butterflies are particularly good indicators because they are easily identifiable and are associated with the plant community both as herbivores and pollinators (e.g., Kremen 1992, Brown & Freitas 2000, Shepherd & Debinski 2005). However, some grassland butterfly species react strongly to the presence of habitat edges and show differential probabilities for crossing edges between different land cover types (e.g., road, treeline, field, or crop) (Ries & Debinski 2001). The landscape today in most parts of the developed world is highly fragmented and these behavioral responses to edges could influence the dispersal and recolonization of restored habitats by butterfly species, thereby affecting the function of the restored ecosystem.

The conceptual model driving our wind tunnel experiment combines free flight in the context of a simplified environment to allow assessment of choice. By allowing the butterflies to fly freely in a confined space, an opportunity is provided for the researcher to evaluate selection for or against a particular environmental variable. The wind tunnel test section is divided into two parts, with one environmental parameter (e.g., temperature) varying across the two parts of the wind tunnel. An identical food source in each compartment is provided and the butterflies' preference is observed, recorded, and analyzed. Certain prerequisites, however, need to be achieved to promote the success of the experiments. The butterflies need to be acclimatized to the wind tunnel conditions and be willing to fly around the wind tunnel and feed from the offered food source. This involves prior training of the butterflies and appropriate environmental conditions to keep the butterflies active. To ensure the validity of the experiment, it is further necessary that the two compartments of the wind tunnel are identical except for the parameter to be tested. For example, if the test involves an artificial food source, the two sides of the chamber should not vary in smell, food quality, amount, etc. Here we present preliminary results with a focus on developing an experimental protocol that will provide a basis for future butterfly behavioral research using wind tunnels.

MATERIALS AND METHODS

Butterfly species. Table 1 provides an overview of the 21 butterfly species tested in the wind tunnel. The butterflies were supplied from the butterfly house of the Reiman Gardens at Iowa State University, where they were reared from caterpillars. All caterpillars were obtained from commercial butterfly farms and were most likely reared in captivity for several generations. Butterflies taken straight out of the rearing chamber where they had recently emerged were generally inactive for about 24 h. Active butterflies caught in the butterfly house needed a couple of hours to adjust to wind tunnel conditions. The most success (i.e., the most activity) was attained by keeping individuals in the wind tunnel for several consecutive days. The tested species were selected depending on availability at the Reiman Gardens and encompassed a broad variety of both native and foreign species, different body and wing sizes, as well as fast and slow flying species. This allowed us to assess a wide variety of potential behavioral differences within the wind tunnel. The butterfly behavior is summarized in Table 1 and an assessment of the suitability of the species for these kinds of wind tunnel experiments is described. Two species, *Heliconius melpomene* and *Papilio polytes*, were by far the most active and displayed the desired feeding behavior. All other tested longwings showed similar activity levels and behavior, indicating a general suitability of this genus for wind tunnel experiments. Even by keeping individuals in the wind tunnel for several days and showing them the food source (extending the proboscis into the artificial nectar), some species did not accept the artificial food source or were not active and stayed in one spot.

TABLE 1: Butterfly species tested in the wind tunnel. The number of total individuals tested in the wind tunnel includes both the individuals that were only tested for a single day and the individuals that were used for repeated tests. The number of individuals that were used for repeated tests is displayed in a separate column with the number of days they spent in the wind tunnel in brackets.

Species	**# total individuals**	**# individuals (repeated tests)**	**Performance**	**Suitability**
Athyma perius	2		sit mostly	more tests needed
Battus philenor	1		moderately active	possibly
Cethosia cyane	2		mostly sits nectars sitting	more tests needed
Graphium agamemnon	7	6 (3)	sit mostly	no
Heliconius charitonius	5		moderately active	possibly
Heliconius doris	2	2 (4)	active	possibly
Heliconius melpomene	11	5 (5)	very active nectars sitting	yes
Heliconius numata	1	1 (5)	active	possibly
Hypolimnas bolina	2		sit mostly	no
Idea leuconoe	10		slow flight nectars sitting	possibly
Junonia coenia	5	5 (3)	sit mostly do not accept feeder	no
Morpho peleides	2		sit mostly feeds on rotten fruit	no
Papilio dardanus	3		erratic flight	more tests needed
Papilio demodocus	8		moderately active	possibly
Papilio lowii	4	2 (3)	mostly sits	no
Papilio nireus	1			more tests needed
Papilio ophidicephalus	1		sit mostly	more tests needed
Papilio polytes	28	11 (3)	very active nectars in flight	yes
Papilio rumanzovia	2			more tests needed
Papilio torquatus	2	2 (2)	sit mostly	no
Parides iphidamas	10		moderately active	possibly

Wind tunnel. The wind tunnel used for our temperature study was an open return wind tunnel, which followed the design described by Miller and Roelofs (1978). The original setup had a flat bottom plate and two plexiglass sheets bent around the top, resulting in a half round test section of about 0.89 m diameter and 2.5 m length. Our setup was modified to a rectangular configuration and measured about 1.1 × 1.2 × 2.5 m (see Fig. 1). Two wooden boxes at the beginning of the test section housed the head of a floor fan and four turbulence dampers of decreasing mesh size to straighten the flow. A variable autotransformer (Variac) enabled the control of the wind speed from 0 to 1.8 m/s. Six lights were installed at the top of the test section; the four downstream lights had 60 W incandescent light bulbs and the two upstream lights had 60 W fluorescent light bulbs, mimicking day light conditions (5500K).

Food source. One of the most crucial components of the experiment is the acceptance of the food source by the butterflies, so that they voluntarily chose to feed in the artificial environment. Offering a known nectar plant of the butterflies was a powerful attractant and the butterflies came to feed at once. A nectar plant, however, is less quantifiable with respect to the resource value to the butterfly (e.g., small differences in smell intensity, nectar amount, or sugar content would influence the butterflies choice) and is therefore not as ideal for experimental purposes. For that reason, several artificial feeders were also tested in the wind tunnel. The most successful model for artificial feeders was achieved by mimicking a natural food source. Nectar was offered from several “artificial flowers” (plastic birthday candle holders that came in various colors) that were mounted on a wooden rod stuck through and suspended by the divider. Cut pieces of *Passiflora incarnata* leaves were attached to the wooden rod and seemed to attract the butterflies to the nectar source, even when plant pieces were wilted (Fig. 1B). We observed a preference of the butterflies to feed from the blue candle holders over all other colors (yellow, pink and white), but this was not statistically tested. When all colors were offered, most butterflies would only feed from the blue feeders. Replacing the artificial flowers with only blue ones increased the feeding activity substantially. There was no noticeable preference between honey water and lemon/lime Gatorade mix as a food source.

Colored Light Responses. The other explored stimulus was colored light. Color vision of butterflies and the species-dependent preference for certain colors has been shown in previous studies (e.g., Kelber & Pfaff 1999, Kinoshita et al. 1999). Given this information, four different colored LED lights (yellow, red, blues and purple) and two laser pointers (green and purple) were set up to either shine close to the food source or

Fig. 1. Wind tunnel setup from upstream (**1A**), showing the fan and wooden box with turbulence dampers; inside of the wind tunnel (**1B**) with wooded divider and feeding rod with plant materials. Window (0.3 × 0.4 m) on side and opening on downstream end allowed researchers to handle butterflies and other materials placed in the wind tunnel.

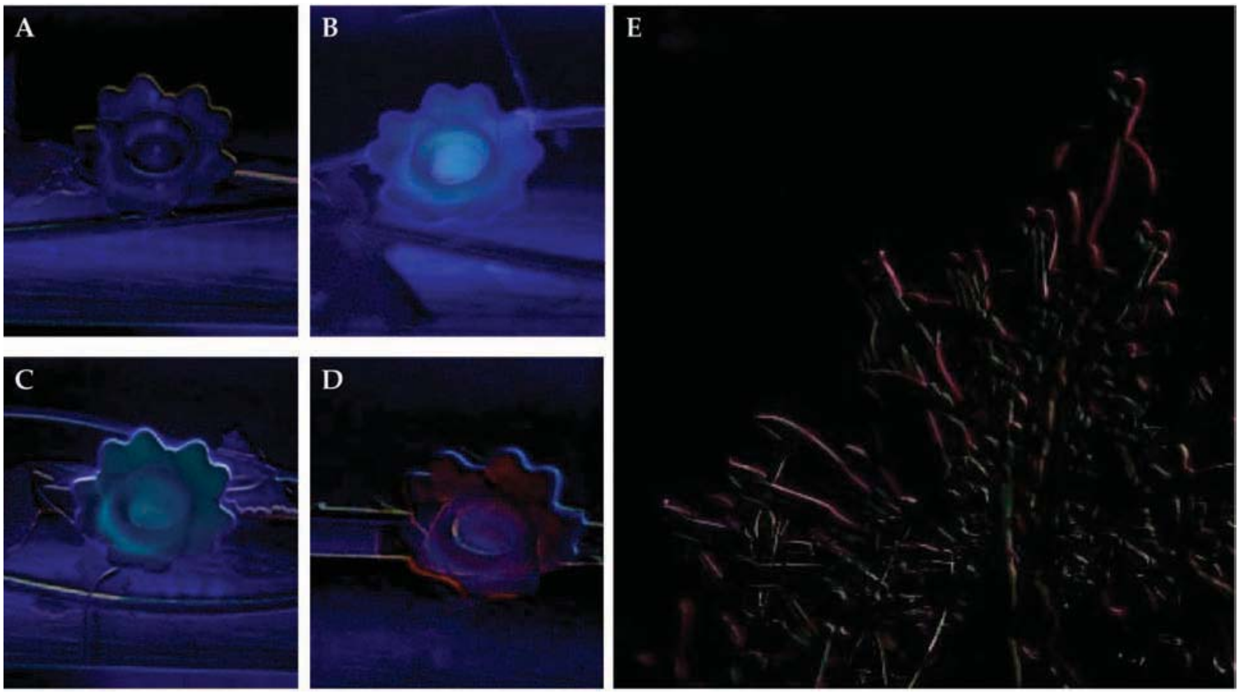

FIG. 2: UV reflectance of the four different birthday candle holders (**2A**) yellow, (**2B**) pink, (**2C**) white and (**2D**) blue; UV reflectance of the firespike (*Odontonema strictum*), a flower that the butterflies frequently nectar from in the butterfly wing (**2E**).

illuminate the feeder (Eppendorf cup) and the butterflies response was recorded.

UV sensitivity. One of the receptors in butterfly compound eyes is UV sensitive (300nm) (e.g., Menzel 1979, Arikawa et al. 1987, Briscoe & Chittka 2001). The reaction to purple light and the preference of blue artificial flowers could indicate an increased sensitivity of butterfly eyes to responses in the UV spectrum. To test the UV response of the setup compared to a natural environment, we took UV response pictures of the setup, and specifically the artificial flowers, and compared those to UV response pictures from nectar flowers from the butterfly house at Reiman Gardens. To filter out only the UV component in these pictures, two images were taken with a digital SLR camera (Nikon D90), one under normal light conditions and one with illumination from a UV light source (Ultrafire UV-365nm flashlight). These images and were subtracted from each other using the image processing toolbox in Matlab (R2011b, The MathWorks Inc., Natick, MA).

Temperature sensitivity. For the temperature study, the wind tunnel was divided into two sections (see Fig. 1B). Two space heaters in the back box of the wind tunnel allowed for separate temperature control of the two compartments. Mean temperatures on the cold side were 25.3°C and 36.0°C on the warm side. This temperature range is within the temperature range that is required for butterflies to achieve optimal wing muscle temperature to sustain flight (e.g., Watt 1968). Warmer temperatures used in this experiment correspond to temperatures that a butterfly might experience over heated roads in the summer in the Midwestern U.S., while lower temperatures correspond to temperatures over prairie or fields within the same season and geographic location. The temperature was randomly varied between trials relative to the two sides to avoid side bias and learning effect of the butterflies. Experiments were conducted for 11 days, which consisted of three test sets where the same individuals were kept in the wind tunnel and their behavior observed for 3–5 consecutive days. A logistic regression was used to analyze the data. The model included species and side as fixed effects, and the butterfly measurement group as a random effect to account for the correlation of consecutive measurement days with the same individuals.

RESULTS

Colored Light Responses. The LED lights did not inflict a strong response in the butterflies, although a slight attraction could be observed in some species: *Heliconius melpomene* was attracted to yellow and red, *Idea leuconoe* to blue and purple and *Papilio demodocus* to red and purple light. However, all tested species (*Battus philenor, Heliconius charitonius, Heliconius melpomene, Idea leuconoe, Papilio dardanus, Papilio demodocus, Papilio polytes* and *Parides iphidamas*) reacted strongly to the purple laser. The reaction ranged from turning of the head, antennae movement or wing fluttering when the laser was pointed close to the head. *Heliconius charitonius* would fly away when the laser pointed close to the butterfly. *Idea leuconoe* and *Papilio polytes* would fly or land close to the purple laser spot when pointed to a food source or on the wind tunnel wall.

UV sensitivity. The UV sensitivity test revealed two interesting facts: first, a tape residue located at the wind tunnel wall had attracted the attention of the butterflies during previous observations and showed a high UV reflectance in the pictures; second, the UV response of the artificial flowers differed quite substantially between the colors of the candle holders (Fig. 2). The yellow candle holders showed basically no UV content (Fig. 2A), while both pink and white candle holders had a strong UV reflectance in the blue and green spectrum (Fig. 2B and 2C respectively). Surprisingly, the blue candle holders showed a UV content (Fig. 2D) that showed a similar spectrum to firespike (*Odontonema strictum*) in the butterfly wing, which is used as a nectar plant for the butterflies at Reiman Gardens (Fig. 2E). It is visible as red color in the subtracted images.

Temperature sensitivity. The temperature study showed that on average all butterfly species examined spent 49.9% of the time on the cold side, 44.0% of the time on the warm side and 6.0% in the back of the wind tunnel section, without temperature division. Species level analyses revealed some species-dependent temperature preferences (Table 2). Two butterfly species (*Graphium agamemnon* and *Junonia coenia*) showed no temperature preference, with a probability of choosing the warm side of 0.50 (p = n.s.) and 0.52 (p = n.s.), respectively. Two species had a preference for warm temperature. *Papilio lowii* had a marginally significant probability of 0.89 (p = 0.05) and *Papilio torquatus* had a non-significant probability of 0.60 for choosing the warm side. Conversely, two tested species had a preference for the cold side. *Papilio polytes* had a significant probability of 0.39 for (p < 0.05) for choosing the warm side and *Heliconius* spp. had a non-significant probability of 0.43. Depending on the time of the day and weather condition, there was a strong preference for the right side of the wind tunnel over the left side, regardless of temperature setting, which was taken into account in the general linear model.

Discussion and conclusion

The behavioral tests show the importance of both testing different species and training individuals in the wind tunnel prior to experiments. Species dependent behavioral differences and cognitive abilities can affect the activity levels, feeding and flight behavior of the butterflies in wind tunnels. Several tested butterfly species seem to be unsuitable for wind tunnel experiments, because they did not fly in the confined space. This is not surprising, but should be taken into account when designing a wind tunnel experiment and selecting suitable species. Light intensity and food source are important factors to keep butterflies active. Mimicking a natural food source was the most successful strategy to attract butterflies to the offered feeder. Olfactory or visual signals can increase the butterflies' attraction, as long as those additional signals do not introduce unwanted variation into the experiment. Signals in the UV spectrum might have contributed to the acceptance of an artificial feeder. Our experiments highlight the importance of a controlled environment, where only one tested variable can be adjusted. We found that even a slight change in light intensity in the lab environment due to outside weather conditions could bias the outcome of a behavioral study.

This study was designed to examine the underlying reasons for butterfly edge responses by combining aspects of conservation biology and biomechanics. Certain grassland butterfly species react strongly to the presence of habitat edges (e.g., Ries & Debinski 2001), yet little is know about the physiological reasons for such an edge response. In the controlled environment of a wind tunnel we can test the sensitivity of butterflies to

Table 2: Summary of least squares means analysis of temperature dependence for six butterfly species.

Species	DF	t Value	Pr > |t|	Mean
Graphium agamemnon	144	0.27	0.7850	0.5248
Heliconius spp.	144	-1.51	0.1331	0.4321
Junonia coenia	144	-0.05	0.9585	0.4967
Papilio lowii	144	1.97	0.0513	0.8927
Papilio polytes	144	-2.08	0.0397	0.3933
Papilio torquatus	144	0.92	0.3594	0.6001

isolated parameters that could potentially inflict an edge response, such as ground structure, temperature, light intensity, turbulence, etc.

Although some insects can regulate their body temperature through biochemical processes, butterflies are dependent on ambient temperature (e.g. May 1979). Like all flying insects, butterflies need a certain minimum temperature for their wing muscles to function. They are often observed basking in the sun to increase their thoracic temperature to working conditions. On the other hand, insects can also overheat when ambient temperature increases (e.g. Watt, 1968, May 1979). One could therefore argue that the reason for butterflies to avoid crossing a habitat edge might be related to a temperature difference between different habitats. For example, the temperature over a road on a bright summer day is much higher than the temperature over prairie grassland. To test this hypothesis, we observed whether butterflies had a temperature preference within the temperature range their flight muscles can operate (~25–44°C, Douglas 1986). In our temperature study, we accounted for side preferences to eliminate the effect of light intensity and weather changes. The side effect also accounted for inactive individuals. If ignored, the stationary behavior of some butterflies could have biased the results if they chose a side and stayed there regardless of the tested variable (in this case, temperature). Our results also highlight the fact that butterfly activity in the wind tunnel depends strongly on the tested species and individual. Many species are not willing to fly in the confined space of a wind tunnel. In such cases, the behavior of a butterfly in the field cannot readily be replicated in a wind tunnel. We were, however, able to show a clear species-dependent temperature preference for some butterfly species. This is a promising result, demonstrating that our experimental design is suitable to study the sensitivity of different butterfly species to environmental parameters. Although these results, which are mostly based on exotic species, cannot be directly applied to the edge response in native Midwestern butterflies, they provide validation of a technique. Future research will allow us to test these same analytical methods on native grassland-dependent species.

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REVIEW OF *EUCERATIA* WALSINGHAM (LEPIDOPTERA, YPSOLOPHIDAE) WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT. The genus *Euceratia* is reviewed by the re-descriptions of two known species, *E. castella* and *E. securella,* and the description of a new species from California, *E. intermedia* n. sp. *Euceratia* is compared to other genera of Ypsolophidae. Diagnostic characters are provided for the three species of *Euceratia* and their distribution in the Nearctic Region is discussed. Imagoes and genitalia of all the species of *Euceratia* are illustrated.

Additional key words: Canada, Ditrysia, North America, USA, Yponomeutoidea

The Nearctic genus *Euceratia* was described by Walsingham (1881) for two species, *E. castella* and *E. securella*, from California, USA. It was originally assigned to Tineidae, in which most primitive micromoths were included by authors. Meyrick (1914) and Fletcher (1929) transferred the genus to Plutellidae, based on superficial features. Kyrki (1984) revised the systematic position of *Euceratia* and found that it is associated with *Ypsolopha*. Kyrki (1990) finally assigned the genus to Ypsolophidae.

The two *Euceratia* described by Walsingham (1881) are still the only known species of the genus. Both of these share the characteristic labial palpi that Walsingham (1881) highlighted with relatively lengthy description. Heppner (1984) assigned *Calantica argentea* Busck, 1913 to *Euceratia*. This Mexican species differs from *Euceratia* in the characters of labial palpus and genitalia. Friese (1960) assigned the species to *Niphonympha* (Yponomeutidae). It is known that the larvae of *Euceratia* are leaf tiers on snowberries (*Symphoricarpos*) and honeysuckles (*Lonicera*) of Caprifoliaceae (Powell and Opler 2009).

The aims of this paper are to redescribe *Euceratia* and its two known species, *E. castella* and *E. securella*, and to describe a new congener from California. In addition, the distribution of the three species of *Euceratia* is discussed and compared with those of other ypsolophid genera.

MATERIALS AND METHODS

Pinned specimens from five institutional collections were examined. The abbreviations of these and other relevant depositories are as follows:

ANSP: Academy of Natural Sciences of Drexel University, Philadelphia, USA;
BMNH: Natural History Museum (formerly British Museum of Natural History), London, UK;
EMEC: Essig Museum of Entomology, University of California, Berkeley, USA;
MCA: Museum of Comparative Zoology, Harvard University, Cambridge, USA;
USNM: United States National Museum of Natural History, Washington DC, USA;
YPM: Yale Peabody Museum of Natural History, New Haven, USA.

Other abbreviations used in the specimen data include:

BL: black light; Co.: county; ft.: feet; gen. no.: genitalia slide number; Is.: island; mi: mile; Mt.: mount; Mts.: mountains; MVL: mercury vapor lamp; UVL: ultraviolet light; and WL: white light.

Verbatim label data are provided only for primary types. The marks '/' in the label data indicate line breaks. The genitalia slides were prepared according to Clarke (1941), except that chlorazol black was used for staining and euparal resin was used for permanent slide mounting. The wing venation slides were prepared according to Hodges (2005). Terminology follows Klots (1970) for genitalia and Wootton (1979) for wing venation. The names of host plants follow the Plant List (http://www.theplantlist.org/).

Taxonomic Accounts

Ypsolophidae: Ypsolophinae
EUCERATIA Walsingham, 1881

Euceratia Walsingham, 1881: 310.
Type species: *Euceratia castella* Walsingham, 1881, by subsequent designation by Fletcher (1929).

Diagnosis. This genus is similar to *Phrealcia* Chrétien, 1900 in the external appearance and the female genitalia, especially the presence of a band-like, scobinate signum. *Euceratia*, however, differs from the latter in having the porrect labial palpi longer than the head (as long as or shorter than the head in *Phrealcia*).

Redescription. *Head* (Fig. 1) – Vestiture of vertex and frons rough with piliform scales; ocelli present [Walsingham (1881) erroneously stated that *Euceratia* lacks ocelli]. Antenna filiform in both sexes, annulated, naked ventrally. Labial palpus porrect, 3× as long as head, 1st segment 1/5 as long as 2nd, with piliform-scale tuft ventrally; 2nd segment as long as 3rd, with piliform-scale tuft ventrally, scales of tuft longer distally; 3rd segment duster-like with piliform scales. Maxillary palpus short, 1-segmented [Walsingham's (1881) observation that maxillary palpi are absent in *Euceratia* is not correct].

Thorax – Patagium comprising piliform scales. Forewing subtriangular, with oblique termen; pterostigma spanning near 1/2 of costa and vein R. Forewing venation (Figs. 2 & 3) with Sc reaching margin near 2/3 of costa; R arising from near middle of radius; Rs$_{1\text{-}3}$ reaching margin above apex; Rs$_1$ arising from anterior margin of accessory cell at 4/5 length of cell; Rs$_1$ nearly parallel to Rs$_2$; Rs$_2$ and Rs$_3$ close basally, then divergent; Rs$_4$ reaching margin below apex at the anterior 1/5 of termen; M with 3 branches; M$_1$ and M$_2$ slightly divergent; M$_2$ nearly equidistant from M$_1$ and from M$_3$; CuA$_1$ and M$_3$ connate basally (*E. securella*) or equidistant as CuA$_1$ and CuA$_2$ (*E. intermedia* n. sp.); CuA$_2$ nearly straight; CuP vestigial as fold in basal 4/5; basal fork of 1A+2A near 1/4 of length. Hindwing venation (Figs. 2 & 3) with Sc+R$_1$ reaching margin at 4/5 of costa; Rs reaching margin above apex, stalked with M$_1$ in posterior 2/5 (*E. securella*) or 3/5 (*E. intermedia* n. sp.); M stem vestigial, as a short branch; M$_2$ nearly parallel to M$_3$; M$_3$ close to CuA$_1$ basally and then divergent; CuA$_1$ nearly parallel to CuA$_2$; CuP present in posterior half (*E. securella*) or entire (*E. intermedia* n. sp.); 1A+2A slightly divergent from CuP in distal 1/3, with basal fork 1/5 of length.

Abdomen – Sternum II (Fig. 4) with apodeme and venula 4× longer than transverse ridge; venula arched in anterior half; transverse ridge present at level of anterior 2/5 of venula. Pleuron VIII (Fig. 5) expanding to posteriorly, semicircular; interspace between pleural lobes slightly emarginated. Male genitalia (Figs. 15–17) with uncus trapezoidal or subtriangular; socius with small spine on apex; subscaphium present; valva subrectangular, round apically, densely setose in distal 3/4; anellus with minute thorns. Phallus with spinulate cornutal zones. Female genitalia (Figs. 18–20) with ovipositor telescopic, with two subdivisions; apophysis posterioris with Y-fork basally; ductus bursae slender; signum band-like, scobinate.

Included species
Euceratia castella Walsingham, 1881
Euceratia intermedia n. sp.
Euceratia securella Walsingham, 1881

Euceratia castella Walsingham
Figs. 6–8, 15, 18
Euceratia castella Walsingham, 1881: 310.

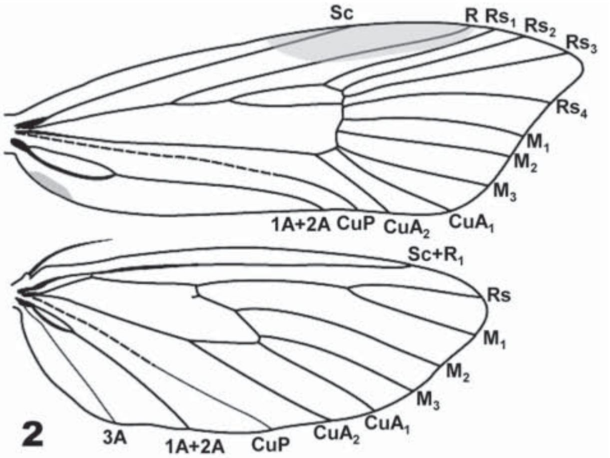
Diagnosis. This species is superficially similar to an yponomeutid species, *Eucalantica polita* (Walsingham) but differs from the latter in having the longer labial palpi and by the lack of a reddish brown dorsal patch on the forewings. Also, the tergites of *Eucalantica* possess spiniform setae which are absent in *Euceratia*.

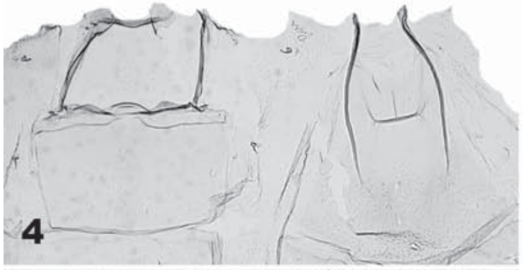
Redescription. *Head* – Vertex and frons white. Antenna 1/2 as long as forewing; scape white; first three flagellomeres with white annulation; remaining flagellomeres dark brown. Labial palpus white, sparsely intermixed with dark brown-tipped, white scales.

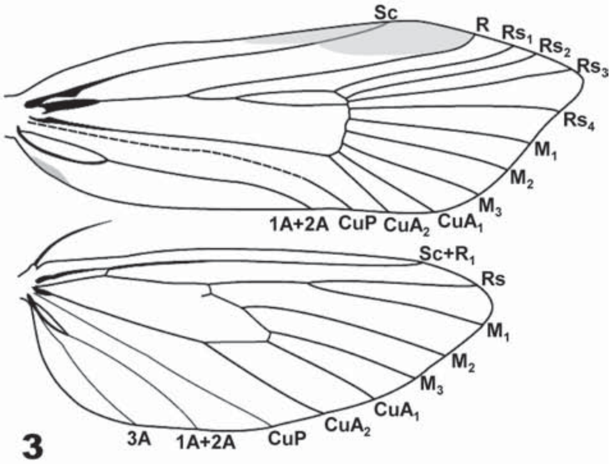
Thorax – Patagium, tegula and mesonotum white. All legs white or yellowish white. Forewing length 6.8–10.1 mm (n = 10), white, slightly broadened to termen; apex narrowly round; a small black spot present on distal 1/2 of CuP; dark brown scales scattered in various density, depending on individuals; a small black spot at the lower angle of discal cell usually present, but sometimes absent (Fig. 7); dark yellow, intermittent postmedian line and striation in distal area sometimes present (Fig. 8); scales of fringe white with dark brown tip. Hindwing dark brownish gray, suffused with white in basal and posterior areas; marginal scales white, with pale dark brown tip; fringe white, tinged with pale gray in anterior area.

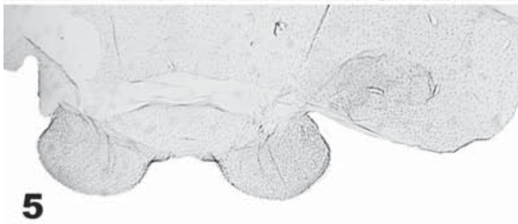
Abdomen – Terga white; sterna yellowish white. Male genitalia (Fig. 15) with uncus subtrapezoidal; socius slender, 4× longer than uncus. Tegumen wide, trapezoidal, 1/2 as long as socius. Valva subrectangular, round apically, densely setose in distal 2/3; sacculus round in basal half, sparsely setose. Vinculum nearly straight anteriorly; saccus elongate, slightly broadened in distal half, as long as socius. Phallus 2.5× longer than valva, straight, slender, slightly broadened anteriorly; two cornutal zones 1/10 as long as phallus. Female genitalia (Fig. 18) with ovipositor 1.5× longer than corpus bursae. Apophyses posteriores 2× longer than apophyses anteriores. Ductus bursae narrow, bowl-shaped near ostium bursae, 3× longer than corpus bursae. Corpus bursae ovate; signum on posterior 3/5 of corpus bursae.

Types. Lectotype [designated by Sohn (2015a)] – male, "Type" [round label with red borders], "Russian R/ Sonoma Co./ CALIFORNIA/ 19.V. 1871/ Wlsm", "Walsingham/ Collection./ 1910-427", "NG *Euceratia*/ *castella* Wlsm/ TYPE" [hand-written], "*Euceratia*/ *castella*, Wlsm./ P.Z.S.Lond. p. 311. Tf. 35'13 1881/ TYPE ♂ figd. & descr." [hand-written on label with black borders], detached abdomen in a gelatin capsule attached with the specimen, BMNH.





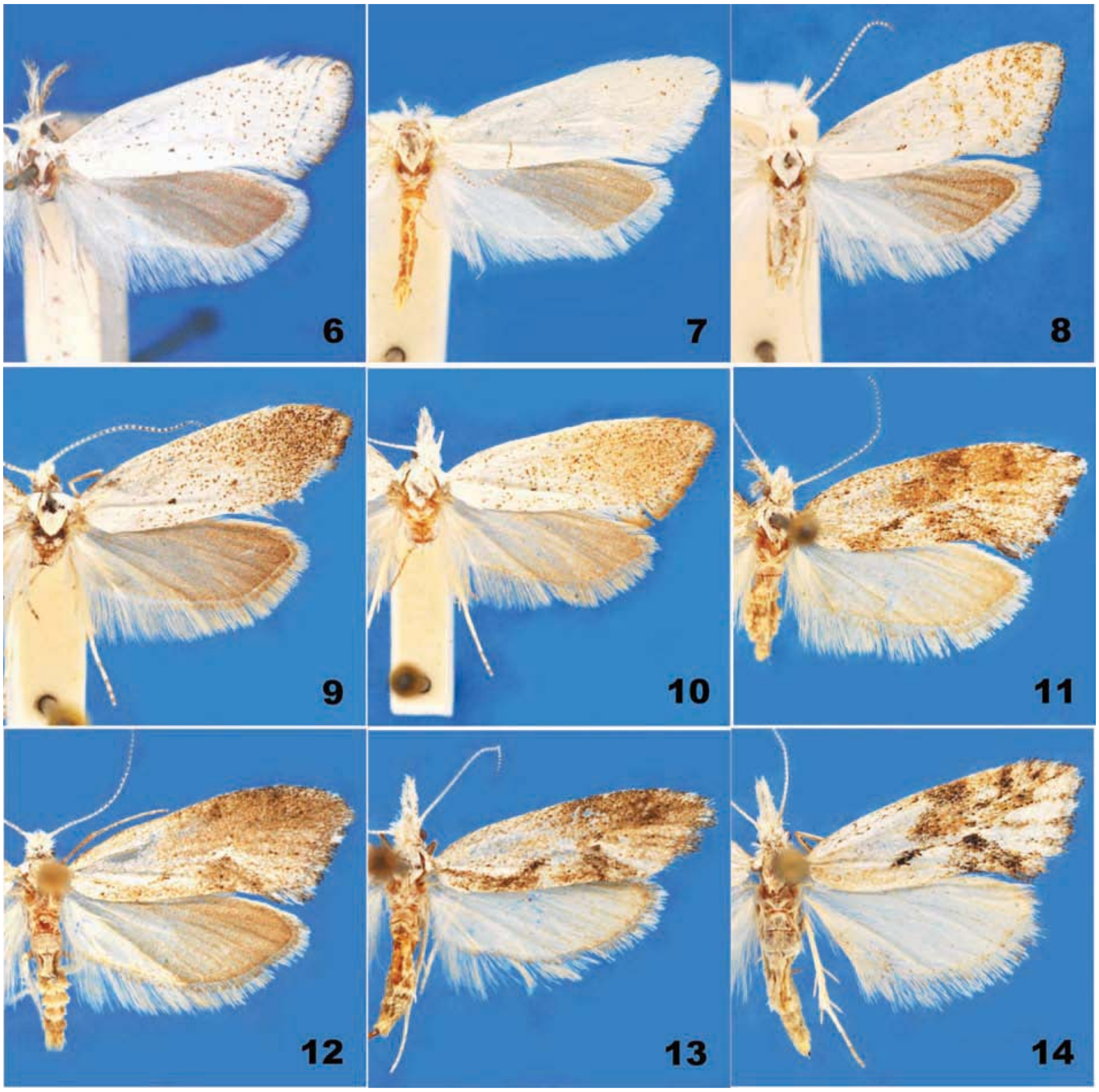




FIGS. 1–5. Generic characters of *Euceratia*. **1.** Head of *E. securella*, lateral view. **2.** Wing venation of *E. securella*. **3.** Wing venation of *E. intermedia*. **4.** Abdominal segment I and II of *E. securella*, tergite I in left, sternite II in right. **5.** Abdominal segment VIII of *E. securella*, tergite and pleural lobes in left, sternite in right.

Paralectotypes – USA: CALIFORNIA: San Francisco: 1♂, 1♀ , [no date & collector], MCZ. Walsingham (1881) described *Euceratia castella*, based on "several specimens near San Francisco and on Mount Shasta." Three specimens listed here were the only representatives of Walsingham's syntypes of *E. castella* which could be traced.

Materials examined. CANADA: BRITISH COLUMBIA: Vancouver Is.: Duncan, 2♀, [no date] (AW Hanham), USNM; Quamichan District [near Duncan]: 1♂, 15-31 May "192" (AW Hanham), USNM; Victoria: 1♂, 13 June 1901 (AW Hanham), USNM; 2♂, 4 June 1910 (AJ Croker), USNM; 1♂, 12 June 1920 (EH Blackmore), USNM; 1♂, 1♀, 5 July 1920, USNM; 2♂, 30 May 1921 (WR Carter), USNM; 4♂, 6 June 1922, USNM; 1♂, 1♀, 6 July 1923 (JF Clarke), USNM; Wellington: 1♂, 1♀, [no date] (GW Taylor), USNM. **USA: CALIFORNIA**: Alameda Co.: Berkeley: 3♂, 6 May 1921 (EO Essig), USNM; 1♂, 26 May 1921, USNM; 1♂, 18 May 1931 (D Meadows), USNM; Hayward: 1♂, 17 May 1966 (AJ Slater), EMEC; Northeast Oakland: Piedmont Pines: 1♀, 19 June 1962 (PD Hurd), EMEC; Northeast Oakland: Berkeley Hills: 1400 ft.: 1♀, 10 May 1962 (J Powell), EMEC; Tilden Park: 2♀, no date (DL Wagner), rearing no. LII-IV-79, reared from *Symphoricarpos*, emerged on 1 June 1979 & 8 May 1979, EMEC; 1♀, 17 April 1969 (PA Opler), rearing no. 69D34, reared from *Symphoricarpos* (?), emerged on 14 May 1969, EMEC; [no specific locality]: 1♂, 1♀, June (CV Riley), reared from *Symphoricarpos mollis*, USNM; 20♂, 19♀, 11-20 May 1908 (GR Pilate), USNM; 3♂, 2♀, 22 May 1908, ANSP; 1♀, 4 June 1908, USNM. **Alpine Co**.: Carson River: 8 mi south of Markleeville: 1♂, 22 June 1962 (J Powell), EMEC. **Calaveras Co.**: Mokelumne Hill: 1500 ft.: 1♀, June [no year], USNM. **Contra Costa Co.**: Lafayette: 1♂, 2 June 1960 (J Powell), at BL, EMEC; Orinda: 1♂, 4 June 1957 (SF Cook Jr), at light; 1♀, 9 June 1957, EMEC. **El Dorado Co.**: Blodgett Forest: 14 mi east of Georgetown: 1♀, 21 June 1982 (JA DeBenedictis), at UVL, EMEC; Lake Tahoe: Deer Park Springs: 2♂, 24-30 June [no year], USNM; 2♂, 2♀, 1-7 July [no year], USNM; 3♂, 1♀, 8-15 July [no year], USNM; Pilot Creek: 1♀, 8 July 1967 (WJ Turner), EMEC. **Glenn Co.**: 5 mi north of Black Butte: 6200 ft.: 1♂, 19 June 1956, EMEC. **Inyo Co.**: [no specific locality]: 1♀, 1-15 June 1922 (OC Poling), USNM. **Kern Co.**: Tehachapi Mt. Park: 5600 ft.: 1♀, 18 June 1989 (J Powell), at BL, EMEC. Lake Co.: Summit Elk Mt.: 1♂, 2 July 1949 (CC & UN Lankar), USNM. Los Angeles Co.: "La Puerta Valley", 1♀, [no date], USNM; Tujunga: 1♂, 14 May 1940 (C Henne), YPM. **Marin Co.**: Phoenix Lake, 2♂, 7-8 April 1927 (HH



FIGS. 6–14. Adults of *Euceratia*. **Figs. 6–8.** *E. castella*. **6.** male, holotype, California, Sonoma Co. **7.** male, California, Mono Co. **8.** male, California, San Mateo Co. **Figs. 9–10.** *E. intermedia*. **9.** male, paratype, California, Del Puerto Canyon. **10.** female, paratype, California, San Luis Obispo Co. **Figs. 11–14.** *E. securella*. **11.** female, California, Lake Co. **12.** male, California, San Diego Co. **13.** female, California, Orange Co. **14.** female, California, Humboldt Co.

Kelfer), reared from *Symphoricarpos raceniosus*, ANSP. **Mendocino Co.**: 4 mi south of Hopland: 1♀, 9 May 1961 (J Powell), EMEC. **Modoc Co**.: Warner Mts.: 3 mi east of Davis Creek: 5500 ft.: 2♂, 8♀, 8-15 July 1922 (AW Lindsey), USNM. Mono Co.: 4 mi east of Monitor Pass: 1♂, 30 June 1962 (J Powell), EMEC. **Monterey Co.**: Carmel Valley: 1♀, 30 May 1997 (J Kruse & J Powell), at BL, EMEC. **Napa Co.**: Soda Creek: 2♂, 1♀, 22 March 1933 (Keifer), USNM; 3♂, 3♀, 27 April 1934 (Keifer), USNM. **Nevada Co.**: Donner Summit: 7200 ft.: 1♂, 11 July 1979, EMEC. Placer Co.: Colfax: 1♀, April [no year] (AH Vachell), USNM; Ward Creek: 2 mi south of Tahoe City: 2♂, 3♀, 26 July 1969 (N Westerland), USNM. **Plumas Co**.: 1♂, 3♀, 16-23 June [no year], USNM. **San Bernardino Co.**: San Bernardino Mts.: 3000 ft.: 1♀, 9 May 1931 (CM Dammers), USNM; 1♂, 16 June 1933, USNM. **San Luis Obispo Co.**: 3 mi west of Paso Robles: 1♂, 28 April 1968 (D Veirs & J Powell), at light, EMEC. **San Mateo Co.**: San Bruno Mt.: 1♂, 18 March 1983 (JA DeBenedictis), rearing no. JADeB No. 83077-C, reared from *Symphoricarpos albus*, emerged on 6 April 1983, EMEC; 2♂, 3♀, 1 March 1985, rearing no. JADeB No. 85C2, reared from *Symphoricarpos albus*, emerged on 1-2 April 1985, gen. no. EMEC-JCS-031 (♀), EMEC; 1♀, 22 March 1985 (JB Whitfield & JA DeBenedictis), rearing no. JBW No. 85C22, reared from *Symphoricarpos*, emerged on 5 April 1985, EMEC. **Santa**

Cruz Co.: Big Basin [erroneously given as San Francisco Co.]: 3♀, 18 June 1971 (E Jäckh), USNM. **Sierra Co.**: 1 mi east of Bassetts: 1♂, 29 June 2002 (J Powell). **Siskiyou Co.**: 5 mi east of McCloud: 1♂, 7 July 1957 (J Powell), EMEC; 1♂, 14 July 1962, EMEC; Mt. Shasta City: 2♂, 24-26 June 1958 (J Powell), EMEC; Shasta Retreat: 1♂, 4♀, 8-15 June [no year], USNM; 3♀, 16-23 June [no year], USNM. **Sonoma Co.**: 0.5 mi east of Forestville: 1♂, 26 May 1966 (J Powell), EMEC; [no specific locality]: 6♂, 6♀, 10-25 May [no year] (AH Wachell), USNM. **Tuolumne Co.**: Kennedy Meadows: 1♂, 3 July 1959 (PA Opler), EMEC; Big Oak Flat: 1♀, 12 June 1961 (J Powell), EMEC. **Tulare Co.**: Mineral King: 1♂, 24-30 June [no year], USNM; 2♀, 8-15 July [no year], USNM; 2♂, 2♀, 16-23 July [no year], USNM; 2♂, 24-31 July [no year], USNM; 1♀, 1-7 August [no year], USNM; Monarch Meadows: 8000 ft.: 1♂, 17 July 1917, ANSP;1♂, 4♀, 8-14 July [no year], USNM; 1♂, 1♀, 16-23 July [no year], USNM; 1♀, 8-15 Aug. [no year], USNM. **IDAHO: Boise Co.**: Cold Spring Creek: 5 mi west of Idaho City: 1♂, 9 June 1976 (JFG Clarke), USNM. **Bonner Co.**: Priest River Experimental Forest: 2500 ft.: 2♂, 19-20 June 1979 (DC Ferguson), USNM. **Elmore Co.**: Sawtooth National Forest Station: 4900 ft.: 1♀, 13 July 1969, USNM. **Latah Co.**: Moscow Mt.: 1♂, [no date] (CV Piper), USNM. **OREGON: Baker Co**.: Big Lookout Mt.: 1♂, 4♀, 13 July 1974 (JH Baker), USNM; Spring Creek: 1♀, 7 August 1962 (JH Baker), USNM; 1♀, 7 July 1970, USNM; 1♂, 11 July 1972, USNM. **Grant Co.**: Ritter: 4200 ft.: 2♂, 3♀, 17-20 July 1962, USNM. **Hood River Co.**: 7 mi west of Hood, 1♀, 14 June 1963 (RW), at light, gen. no. EMEC-JCS-032, EMEC. **Jackson Co.**: Kane Creek: 5 air mi south of Gold Hill: 1♂, 22 June 2000 (J Powell & D Rubinoff), at BL, gen. no. EMEC-JCS-035, EMEC; Mt. Ashland: 6650 ft., 2♂, 1♀, 27 July 1990 (R Robbins), USNM. **Josephine Co.**: 2 mi east of Merlin: 7♂, 2♀, 27 May 1970 (JFG Clarke), USNM. **Linn Co.**: 8 mi west of Mill City, 2♂, 1♀, July 1963 (SG Jewett), USNM. **Marion Co.**: Salem: 2♂, 2♀, 2 June 1961 (K Goeden), USNM. **Wasco Co.**: The Dalles: 2♂, 2♀, 3 June 1970 (JFG Clarke), USNM. **Washington Co**.: Forest Grove: 1♀, May 1923 (SE Keen), reared from *Symphoricarpos* sp., USNM; 5♂, 6♀, 1-11 May 1925 (SE Keen), reared from *Symphoricarpos albus*, USNM; 6♂, 3♀, 24-30 April 1925 (SE Keen), reared from *Symphoricarpos albus*, USNM; Portland: 3♀, [no date] (CV Piper), USNM; 1♀, 12 June 1931 (JF Clarke), USNM. **Yamhill Co.**: Williamson State Park: 1♂, 9 June 1962 (CWO Brien), EMEC. **WASHINGTON: Clallam Co.**: Tumwater Creek: 4 mi southwest of Port Angeles: 1♂, 17 July 2002 (J Powell), at BL, gen. no. EMEC-JCS-037, EMEC. **Ferry Co.**: Bodie Mt.: 5200 ft.: 3♂, 24 July 1962 (JFG Clarke), USNM; Sherman Pass: 5600 ft.: 1♀, 23 July 1962 (JFG Clarke), USNM. **Grays Harbor Co.**: Hoquiam: 1♀, 2 June 1904 (Burke), USNM. Klickitat Co.: Lyle: 1♂, 9 June 1931 (JF Clarke), USNM. **Mason Co.**: Shelton: 1♂, 20 June 1931 (JF Clarke), USNM. **San Juan Co.**: Deer Harbor: Orcas Island: 1♂, 1♀, 14 July 2002 (J Powell), gen. no. EMEC-JCS-036 (♀), EMEC. **Stevens Co**.: Kettle Falls: 2600 ft.: 4♂, 3♀, 20 July 1962 (JFG Clarke), USNM. **Thurston Co.**: Rochester: 1♀, 13 June 1929 (WW Baker), USNM; 1♂, 26 June 1929, USNM. **Whatcom Co**.: Bellingham: 1♀, 11 June 1922 (JF Clarke), USNM; 1♂, 25 June 1950, USNM; Chuckanut Bay: 1♀, 23 June 1955 (JFG Clarke), USNM. **Whitman Co.**: Pullman: 1♀, 10 July 1891 (CV Piper), USNM; 1♂, 8 June 1930 (JF Clarke), USNM; 1♀, 6 June 1933, USNM.

Distribution. Canada (British Columbia) and USA (California, Idaho, Oregon, Washington).

Host plants. Caprifoliaceae – *Lonicera* spp., *Symphoricarpos albus* (L.) S. F. Blake, and *S. mollis* Nutt. (Powell and Opler 2009; this study). Miller and Hammond (2003) listed *Quercus garryana* Douglas ex Hook. as a host plant of *E. castella*. This record seems questionable. Boulton (2004) extensively surveyed the caterpillars feeding on Garry oak (*Q. garryana*) and common snowberry (*Symphoricarpos albus*) from British Columbia and found that the larvae of *E. castella* were collected exclusively from the latter plant.

Remarks. This species shows some variations in the forewing patterns. These variations appear not to be correlated with gender, habitat, or flight time. The larvae are found in March and April and the adult moths are flying from late April to August (Powell and Opler 2009). It is the most widely distributed species of *Euceratia* (Fig. 21). The collecting locality of the lectotype specimen was given as "Russuian R[iver], Sonoma Co." which, however, was not one of the type series Walsingham reported, i.e. "near San Francisco and Mt. Shasta." There is no evidence that the Russian River specimen was recognized by Walsingham as one of the "Types." It can be argued that the "near San Francisco" record (Walsingham 1881) is equivalent to the Russian River of Sonoma County given on the type label.

Euceratia intermedia Sohn et Powell, **new species**

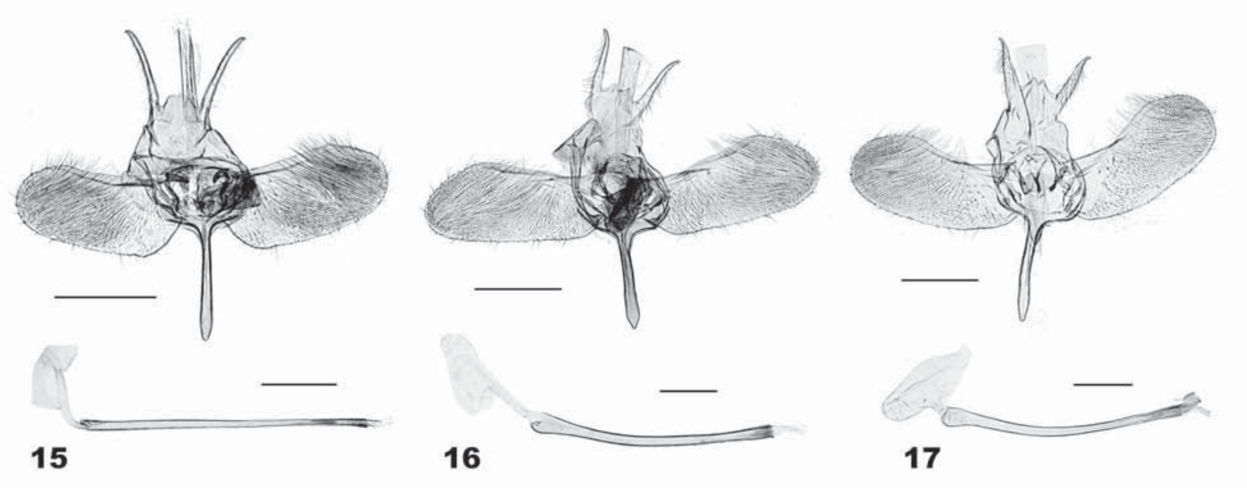
Figs. 9, 10, 16, 19

Diagnosis. This species is similar to its two congeners, *E. castella* and *E. securella*, but differs from them as follows: (a) the posterior half of forewing is densely irrorated with brown scales in *E. intermedia* and *E. securella* but sparsely intermixed with dark brown dots or yellowish brown mottling in *E. castella*; (b) dark brown markings are present on the forewing of *E. securella* but absent on those of *E. intermedia* and *E. castella*; (c) in the male genitalia, the saccular angulation is less profound in *E. intermedia* and *E. securella* than in *E. castella*; (d) the apex of the valva is more narrowly round in *E. intermedia* than in *E. castella* and *E. securella*; (e) the phallus is straight in *E. castella* but slightly curved in *E. intermedia* and *E. securella*; and (f) in the female genitalia, the signum of *E. intermedia* is longer than that of *E. securella*, but shorter than that of *E. castella*.

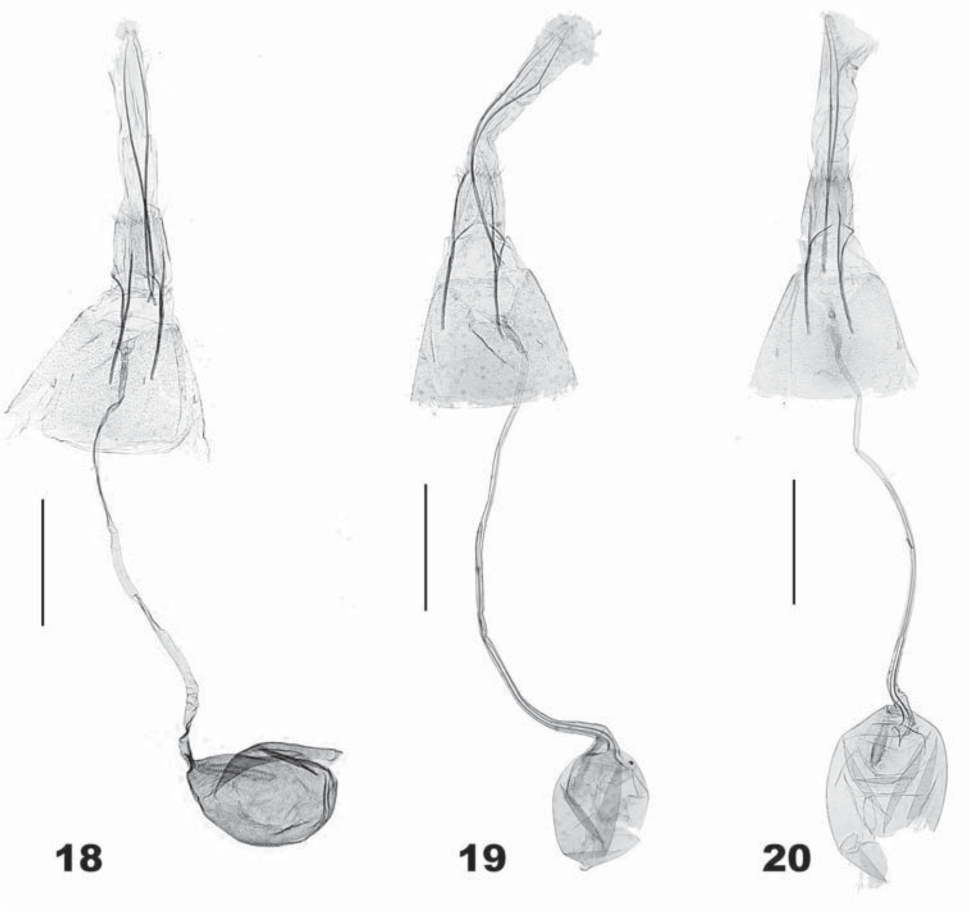
Description. *Head* – Vertex and frons white. Antenna 1/2 as long as forewing; scape white; first three flagellomeres with white annulation; remaining flagellomeres dark brown. Labial palpus with 1st segment white; 2nd segment brownish white laterally, white mesally, a few scales with dark brown tips; scales of 3rd segment white, with dark brown tips.

Thorax – Patagium, tegula and mesonotum white. Fore- and midleg with coxa brownish white; femur and tibia dark brownish gray on exterior surface, white on interior surface; tarsomere dark brownish gray with a white ring distally. Hindleg brownish white; tarsomeres with white ring distally. Forewing length 9.2–11.1 mm (n = 10), white, tinged with pale brownish gray in distal area; apex slightly acuminate; dark brown scales scattered sparsely in basal area, more densely to termen; a small black spot present on distal 1/2 of CuP; scales of fringe brownish gray with brownish black tip. Hindwing brownish gray, paler to base; fringe pale brownish gray.

Abdomen – Terga gray; sterna pale gray. Male genitalia (Fig. 16) with uncus elliptical, extending posteriorly, bifid apically; socius slightly broadened to base, slightly curved in distal 1/5. Tegumen trapezoidal, as long as uncus. Valva rectangular, slightly broadened distally, angulate at distal end of costa, narrowly round apically, densely setose in entire area; sacculus convex. Vinculum slightly convex anteromarginally, angulate laterally; saccus broadened distally. Phallus 2.3× longer than valva, slightly curved at basal 1/3, broadened in basal 1/5; cornutal zone 1/10 as long as phallus. Female genitalia (Fig. 19) with ovipositor 2× longer than corpus bursae. Apophyses



Figs. 15–17. Male genitalia of *Euceratia*. **15.** *E. castella*. **16.** *E. intermedia*, paratype. **17**. *E. securella*. Scale bars = 0.5 mm.



Figs. 18–20. Female genitalia of *Euceratia*. **18.** *E. castella*. **19.** *E. intermedia*, paratype. **20.** *E. securella*. Scale bars = 1 mm.

posteriores 2× longer than apophyses anteriores. Ductus bursae 3.3× longer than corpus bursae, slender, slightly broadened to corpus bursae, granulate in posterior 1/8; antrum near ostium bursae, thimble-shaped. Corpus bursae globular; signum on posterior half of corpus bursae.

Type. Holotype – male, "HOLOTYPE/ *Euceratia intermedia*/ SOHN & POWELL " [red label circumscribed with black lines], "[Stanislaus Co.] Del Puerto C[an]y[o]n./ 20 mi. W. Patterson/ Calif[ornia] IV.30.63", "J. Powell/ Collector", detached abdomen in a gelatin capsule attached with the specimen, EMEC. **Paratypes** (15♂, 3♀) – **USA: CALIFORNIA**: **Kern Co.**: Havilah: 1♂, 8-15 June [no year], USNM. **Marin Co.**: Alpine Lake: 1♂, 28 May 1960 (J Powell), EMEC. **Placer Co.**: Cisco: 1♂, 1 June 1905 (AH Vachell), USNM; Colfax: 2♂, 1♀, May [no year] (VH Vachell), USNM. **San Benito Co.**: 2 mi northeast of New Idria, 1♂, 24 April 1964 (J Powell), wing slide no. SJC-W003, EMEC. **San Luis Obispo Co.**: 2 mi northeast from Pozo, La Panza Camp, 1♂, 29 April 1962 (J Powell), EMEC; Pozo: 1♂, 1♀, 27 April 1962 (J Powell), gen. no. EMEC-JCS-034 (♀), EMEC. **Santa Barbara Co.**: 2 mi south of Buellton: 1♂, 12 May 1965 (J Powell), EMEC; Los Prietos: 1♂, 23 April 1966 (AJ Slater), gen. no. EMEC-JCS-033, EMEC. **Stanislaus Co.**: Del Puerto Canyon: 20 mi west of Patterson: 1♂, same as holotype, EMEC; Del Puerto Creek: 900-1200 ft.: 1♂, 14 April 1973 (M Chinn), "Insect Survey Specimen #" 154079, EMEC; 1♂, 13 April 1980 (K Standow), "Insect Survey Specimen #" 274968, EMEC. **Tulare Co.**: 5 mi northeast of Springville, 1♂, 14 May 1963 (CA Toschi), EMEC; Camp KEEP near Paso Park: 1440 m: 1♂, 23-24 June 1995 (J Powell), at BL, EMEC. **Tuolumne Co.** (?): Yosemite: 1♀, 5 June 1924 (HG Dyar), USNM.

Distribution. USA (California).

Host plants. Unknown.

Etymology. The species name is derived from two Latin terms '*inter*' and '*medius*' meaning "between" and "middle" respectively and refers to the overall appearance of this new species, which is intermediate between *Euceratia castella* and *E. securella*.

Euceratia securella Walsingham, 1881
Figs. 11–14, 17, 20

Euceratia securella Walsingham, 1881: 311.

Diagnosis. This species is similar to a European species, *Phrealcia eximiella* (Rebel), but differs from the latter in having longer labial palpi, a more slender phallus, and a narrower ductus bursae.

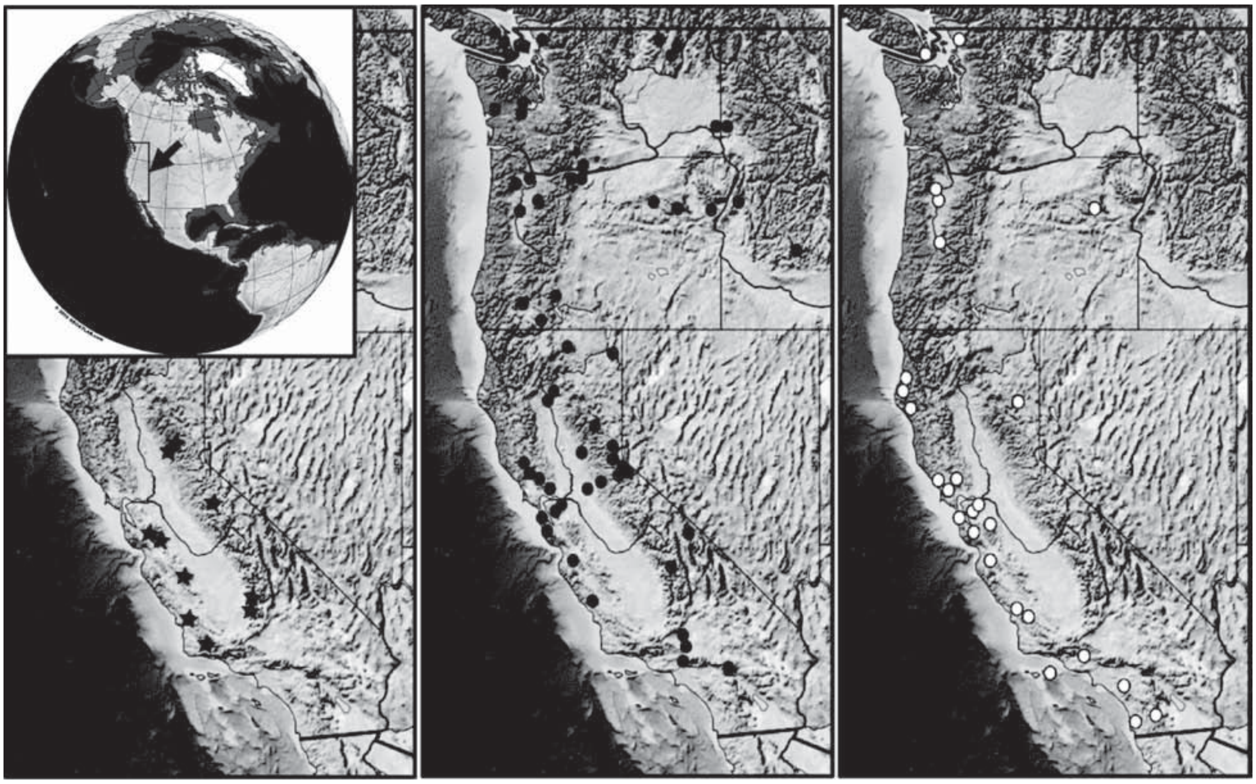
Redescription. *Head* – Vertex brownish white, sparsely intermixed with pale brown scales; frons pale brown. Antenna 2/3 as long as forewing; scape and first three flagellomeres brownish white, occasionally peppered with dark brown; remaining flagellomeres dark brown, with brownish white annulation. Labial palpus with 1st segment white, tinged with pale brown dorsally; scales of 2nd and 3rd segments pale brown, darkened to tips laterally, brownish white, with dark brown tips mesally.

Thorax – Patagium brownish white; tegula brownish white in inner half, pale or dark brown in outer half; mesonotum brownish white, occasionally peppered with dark brown, tinged with dark brown medially. Foreleg with coxa dark brownish gray on exterior surface, pale brownish gray on interior surface; femur to tarsus dark brownish gray; each tarsomere with a white ring terminally. Midleg with coxa brown on exterior surface, brownish white on interior surface; femur to tarsus brownish gray dorsally, pale brown ventrally; each tarsomere with a white ring terminally. Hindleg with coxa to femur brownish gray; femur pale brownish gray, sparsely intermixed with gray scales; each tarsomere brownish gray, with a white ring terminally. Forewing length 9.1–11.6 mm (n = 10), white to pale brownish gray; an oblique black bar connecting basal 1/3 of dorsum with terminal 1/3 of lower margin of discal cell present in variable width, depending on individual; a small black spot present at the lower end of discal cell; dark brown costal strigulae sometimes present (Figs. 13, 14); dark brown tornal patch variable in size, depending on individual; fringes dark brownish gray, irregularly intermittent with white. Hindwings brownish white; marginal shade brownish gray; fringe pale brownish gray, tinged with yellowish gray in inner margin.

Abdomen – Terga brownish gray; sterna brownish white. Male genitalia (Fig. 17) with uncus rectangular, convex posteriorly, bifid apically; socius broadened basally, falcate apically. Tegumen rectangular, as long as uncus. Valva slightly curved to costa, slightly broadened to apex, densely setose in distal 4/5; sacculus broadly round in basal 1/2. Vinculum nearly straight anteromarginally, nearly angulate laterally; saccus slightly broadened in distal 1/3. Phallus 2.3× longer than valva, slightly curved medially, broadened in anterior 1/7; cornutal zone 1/10 as long as phallus. Female genitalia (Fig. 20) with ovipositor 1.2× as long as corpus bursae. Apophyses posteriores 2.2× longer than apophyses anteriores. Ductus bursae slender, funnel-like near ostium bursae, granulate between posterior 1/9 and 2/9, 2.3× longer than corpus bursae; antrum at posterior 1/17 of ductus bursae, short, cylindrical. Corpus bursae elliptical; signum 1/4 as long as corpus bursae.

Types. Lectotype [designated by Sohn (2015a)] – male, "Type" [round label with red borders], "head of Dry Creek/ Mendocino Co./ CALIFORNIA/ 24.V. 1871/ Wlsm", "Walsingham/ Collection./ 1910-427", "*Euceratia*/ *securella* Wlsm/ TYPE Cala" [hand-written], "- lf – fwing/ TYPE COLL./ Cab. 12 Dr. 5", "*Euceratia*/ *securella*, Wlsm./ PZS. Lond. p. 311. pt 35'14 1881./ TYPE ♂ figd & descri." [hand-written on label with black borders], left forewing missing, BMNH. **Paralectotypes – USA: CALIFORNIA**: Sonoma: 1♂, [no date & collector], MCZ. Walsingham (1881) described *E. securella*, based on 17 specimens collected from Sonoma Co., California. We were able to locate only two of those.

Materials examined. CANADA: BRITISH COLUMBIA: Victoria: 1♂, 13 June 1903, USNM; 1♂, 1♀, 28 June 1921 (WR Carter), USNM; 1♀, 21 July 1921, USNM; 1♂, 24 June 1922, USNM; 1♀, 7 July 1922, USNM; 5♂, 3♀, 16-19 June 1923, USNM; 4♀, 12 July 1923, USNM. **USA: CALIFORNIA: Alameda Co.**: Del Valle Lake: 1♀, 2 February 1984 (J Powell), rearing no. 84820, reared from *Symphoricarpos albus*, emerged on 6 March 1984, EMEC; Northeast Oakland: Berkeley Hills: 1400 ft.: 1♂, 17 April 1962 (J Powell), EMEC; 1♂, 10 May 1962, EMEC; Tilden Park: 1♂, 28 May 1979 (DL Wagner), EMEC. [no specific locality]: 1♂, 28 March 1914 (S Jose), USNM. Contra Costa Co.: Lafayette, 1♀, 20 April 1969 (PA Opler), reared from *Symphoricarpos albus*, EMEC; 2 mi southwest of Moraga, 2♂, 8 June 1979 (DeBenedictis & Wagner), EMEC; Orinda: 1♂, 20 May 1957 (SF Cook, Jr), EMEC; 1♀, 4 June 1957, EMEC. **Humboldt Co.**: Arcata: 1♂, 30 June 1969 (J Powell), at light, EMEC; 1♂, 15 July 1969, EMEC; Blair's Ranch: Redwood Creek: 1♂, 10 June [no year] (HS Barber), USNM; Kneeland: 69 Prairie Lane: 1800 ft.: 1♀, 14 July 2001 (RS Wielgus), at UVL and MVL, EMEC; 1♀, 24 July 2001, EMEC; 1♀, 12 July 2002, gen. no. EMEC-JCS-056, EMEC; 1♀, 29 July 2002, EMEC; 1♂, 10 July 2005 (RS Wielgus), at UVL & WL, EMEC; Scotia: 1♀, 20 May [no year] (HS Barber), USNM. **Lake Co.**: Adams Springs: 1♀, 31 May 1982 (JA DeBenedictis), EMEC; 1 mi northeast of Cobb: 1♀, 5 June 1980 (J Powell), EMEC. **Marin Co.**: 2 mi southeast of Inverness, Inverness Ridge, 1♀, 15 May 1970 (JA Powell), at light, EMEC. **Mendocino Co.**: 1 mi north of Piercy: 2♂, 4♀, 20-23 May 1976 (Dietz, Chemsak & Powell), EMEC. **Monterey Co.**: Carmel Valley: 1♀, 30 May 1997 (J Kruse & J Powell), at BL, EMEC; near Jamesburg: 1♂, 3 May 1958 (J Powell), at light, EMEC. **Napa Co.**: Diamond Mt.: 3 air km south of Calistoga: 520 m: 1♂, 1♀, 21-23 May 1993 (J Powell), at light, gen. no. EMEC-JCS-058 (♂), EMEC. **Orange Co.**: Silverado: 1♂, 30 March 1968 (J Powell), EMEC; Silverado Canyon: Santa Ana Mts.: 1650 ft.: 1♂, 12 May 1979 (GA Marsh), at WL, EMEC; 2♀, 26-28 May 1979, EMEC. **San Diego Co.**: 3 mi east of Julian: 4♂, 14-15 June 1998 (N Bloomfield), at BL, USNM; MCAS Miramar: San Clemente Canyon: 2♂, 5 April 1998 (N Bloomfield), wing slide no. SJC-W004, EMEC &



Figs. 21–23. Distribution maps of the three species of *Euceratia*. **21.** *E. intermedia* (box and arrow in inset = the area covered in figures 21–23). **22.** *E. castella*. **23.** *E. securella*. Maps from Wikimedia Commons and GEOATLAS.com.

USNM; 1♂, 21 April 1998, EMEC; NAS Miramar 2: 1♀, 15 March 1997 (N Bloomfield), USNM; NAS Miramar 9: 1♀, 22 March 1997 (N Bloomfield), at BL, gen. no. USNM-115067, USNM; NAS Miramar 10: 1♂, 1♀, 15 April 1997 (N Bloomfield), USNM; San Clemente Canyon: USMC Air Station: 4♂, 2♀, 13-15 May 2011 (N Bloomfield), at BL, USNM. **San Francisco Co.**: [no specific locality]: 1♀, 20 July 1971 (E Jäckh), USNM. **San Luis Obispo Co.**: Alamo Creek, 16 air km east of Nipomo, 1♀, 8 April 2004 (J Powell), at BL, EMEC; 12 mi northeast of Pozo, La Panza Camp, 1♂, 2 May 1962 (J Powell), EMEC; 2♀, 2 June 1962, at light, gen. no. EMEC-JCS-055 & 062, EMEC; 1♂, 25 April 1968 (D Veirs), EMEC; Pozo: 1♀, 4 May 1962 (J Powell), EMEC: York Mt.: 8 mi west of Templeton: 2♂, 27 April 1968 (P Opler), EMEC. **Santa Barbara Co.**: Santa Cruz Island: Central Valley: 2♀, 25-28 April 1966 (J Powell), at light, EMEC; Field Station Headquarter: 1♂, 21-24 May 1984, EMEC; Islay Canyon Road: 165 m: 1♀, 1 May 2000 (J Powell), at BL, EMEC; La Cascada: 1♀, 23 April 2001 (J Powell), at BL, EMEC; 2♀, 1 May 2000, at BL, EMEC; Prisoners Harbor Creek: 50 m: 1♂, 1 May 1966 (J Powell), EMEC; 2♀, 5 May 2000 (J Powell & M Myers), EMEC; University of California Field Station: 76 m: 2♀, 1-7 May 2000 (J Powell & P Hart), at BL, EMEC. **Santa Clara Co.**: Herbert Creek: 3 mi west of New Almaden: 1♂, 1♀, 28 April 1969 (PA Opler), gen. no. EMEC-JCS-059 (♂), EMEC; 1♀, 19 April 1989 (J Powell & M Prentice), EMEC; New Almaden: 1♀, 28 September 1965 (P Opler), EMEC; [no specific locality]: 1♂, 1♀, [no date], USNM. **Sonoma Co.**: 1 mi southeast of Plantation, 1♂, 6 June 1979 (J Powell), EMEC; Plantation: 1♀, 30 June 1967 (P Opler), EMEC; [no specific locality]: 9♂, 4♀, 10-25 May [no year] (AH Vachell), ANSP & USNM. OREGON: **Clackamas Co.**: near Wilsonville: 1♂, 16 June 1982 (DL Wagner), EMEC. **Jackson Co.**: Kane Creek: 5 air mi south of Gold Hill: 1♀, 22 June 2000 (J Powell & D Rubinoff), at BL, EMEC. **Lane Co.**: near Dexter: Elijah Bristow State Park: 1♂, 1♀, 15 June 1985 (J Powell), EMEC. **Yamhill Co.**: Williamson State Park: 1♂, 1♀, 25 June 1975 (J Powell & P Opler), EMEC. **WASHINGTON: Whatcom Co.**: Bellingham: 2♂, 25 June 1950 (JFG Clarke), USNM.

Distribution. Canada (British Columbia) and USA (California, Oregon, Washington).

Host plants. Caprifoliaceae – *Lonicera* spp., including *L. involucrata* (Richardson) Banks ex Spreng., and *Symphoricarpos albus* (L.) S. F. Blake (Miller and Hammond 2003; Powell and Opler 2009).

Remarks. This species shows some variations in the forewing patterns. These variations appear to be unrelated to gender, habitat, or flight time. Distribution of this species (Fig. 23) largely overlaps with that of *Euceratia castella* but is rather congregated toward the west and extends slightly farther south. Both species often coexist in foothill canyons (Powell and Opler 2009).

Discussion

The wing venation and genital features of *Euceratia* strongly suggest their association with Ypsolophinae. In addition to *Euceratia*, Ypsolophinae currently includes four three genera: *Bhadorcosma* Moriuti, *Phrealcia* Chrétien, and *Ypsolopha* Latreille. No phylogenetic relationships of these five genera have been proposed. Interestingly, all genera except for *Ypsolopha* possess the same type of signum which is a simple, scobinate band without any transverse ridge. The signum of *Ypsolopha* possesses a single or two transverse ridges.

This may indicate that *Ypsolopha* is more advanced than other genera, including *Euceratia*.

Of the ypsolophine genera, *Ypsolopha* occurs worldwide, while other four genera are locally restricted. The distribution of *Euceratia* is limited to the New World, in contrast to those of *Bhadorcosma* and *Phrealcia* which span the Palearctic and Oriental Regions and Madagascar. It is notable that *Euceratia* shows several similarities with *Phrealcia*. The latter genus currently includes eight species occurring in Eurasia (Sohn 2015b, in press). Superficial resemblance between *Euceratia securella* and *Phrealcia eximiella* seems especially interesting but their relatedness needs to be verified with phylogenetic approaches.

No clear geographical separation was found for the three species of *Euceratia*. Of those, *Euceratia intermedia* occurs in the smallest range, exclusively California. *Euceratia castella* shows the broadest distribution, extending from British Columbia to southern California. Powell and Opler (2009) observed that *E. securella* ranges farther south than *E. castella*. Our data, however, show that both species have just a minor difference in their southernmost limits in distribution. *Euceratia securella* is, however, absent in Idaho where *E. castella* occurs. Near sympatry of three congeners of *Euceratia* presents an intriguing question as to what factors have led to their speciation.

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A NATURAL FOODPLANT FOR *DIRPHIA TARQUINA* (SATURNIIDAE: HEMILEUCINAE) IN SURINAM*E*

Additional key words: Surinam, Hemileucinae, Hypericaceae Vismia, *cayennensis*

Dirphia tarquinia (Saturniidae: Hemileucinae) was described by Cramer in 1775 from Suriname and is distributed from Peru through Venezuela, Trinidad and the Guianas to Brazil (Quesnel 1978, Lemaire 2002). Records for Suriname are few: near the Lucie river, July–August 1926 (southern Suriname, primary forest); Saramacca sluice, December 1970 (north, secondary vegetation); Raleighvallen, March 2014 (central, primary forest).

Although its natural foodplants are not known, the species can be reared on *Salix* (Salicaceae) and *Prunus armeniaca* (Rosaceae) (Lemaire 2002, Lampe 2010). We describe a natural foodplant for *D. tarquinia* from Suriname.

On 16 January 2005 the first author discovered, 1 km along a sandy track from Colakreek to Republiek, about 40 km south of Paramaribo, savanna area, six larvae of a saturniid (Fig. 1a) at about 2 m above ground on the leaves of a tree, known in Suriname as 'uma pinya' or 'blengitiwiri' (van Andel & Ruysschaert 2011). By providing the leaves of this tree as their only food, all larvae were reared to adults according to standard methods. A botanical collection was made of the foodplant (voucher Gernaat023, Herbarium Naturalis Biodiversity Center).

The adults turned out to be *D. tarquinia* (Fig. 1). The foodplant was subsequently identified as *Vismia cayennensis* (Jacq.) Persoon (Hypericaceae) (Fig. 2).

FIG. 1: Life history of *Dirphia tarquinia* on *Vismia cayennensis*, Colakreek-Republiek, Suriname; **a**: gregarious larvae on foodplant, 16-01-2005. Note opposite leaves and glandular punctations at the underside of leaves; **b**: last instar larvae (03-03-2005); **c**: pupa (below) cut out of cocoon (above) (13-04-2005); **d**: eclosed male (20-10-2005).

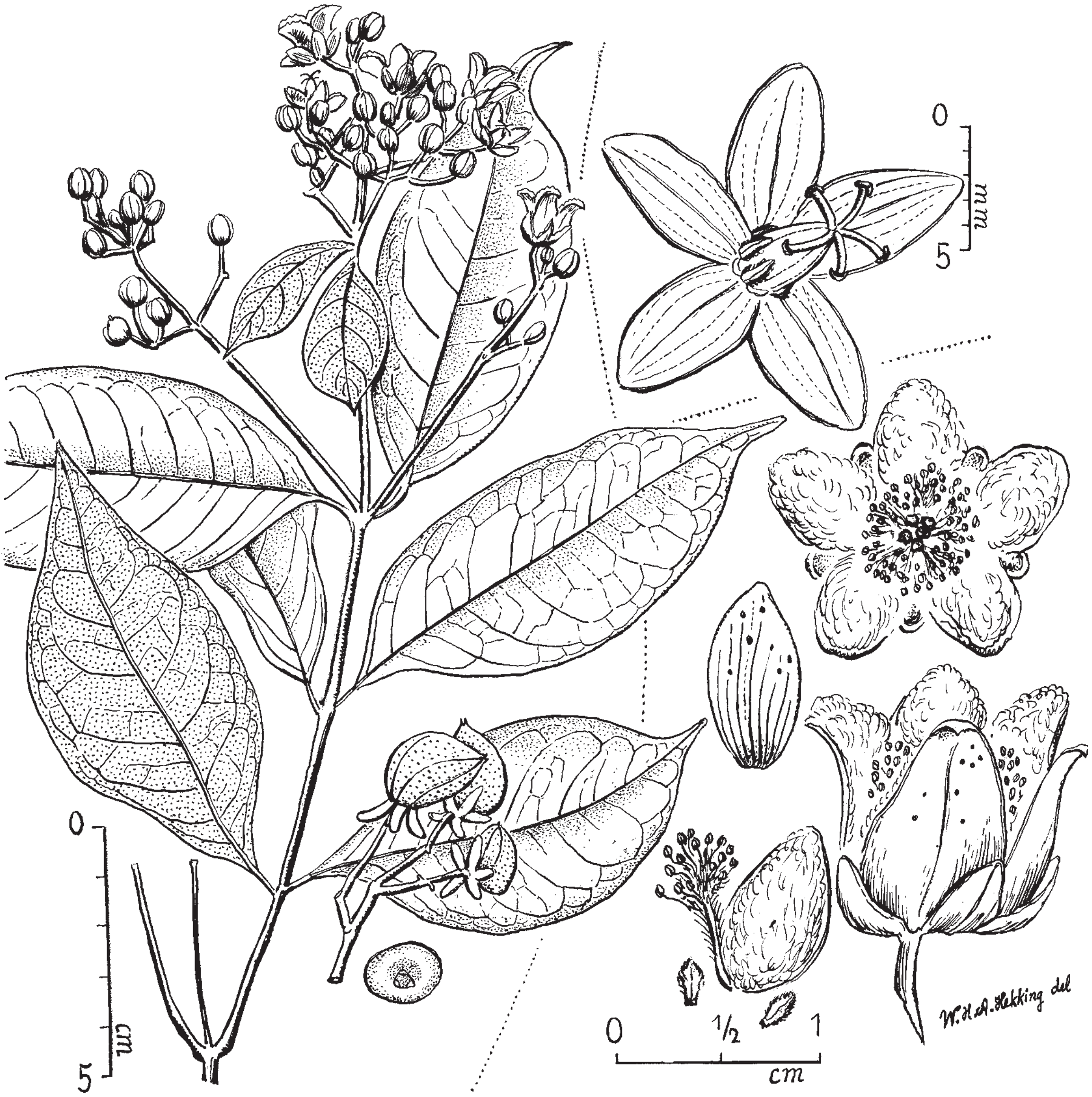

FIG. 2: *Vismia cayennensis*. Left: branch with opposite leaves, inflorescence and berries (below right); right: details of flowers (drawing by W.H.A. Hekking, Naturalis Biodiversity Center).

Description: Shrub or tree to 8 m, with orange latex. Leaves opposite, 8–13 × 2,5–4 cm; base and apex acute; both sides green and glabrous with black glandular dots; light orange-brown after drying. Inflorescence terminal. Flowers bisexual, 5-merous; sepals green, ovate; petals yellowish-green, woolly inside with white hairs; stamens numerous, fused into 5 bundles, ovary 5-locular, 5 orange styles. Berry cylindrical, green to red, about 1 cm long, crowned by styles. Seeds numerous, cylindrical, wartlike. *Vismia cayennensis* is distributed in Venezuela, Trinidad, the Guianas, Bolivia and the Brazilian Amazon region. In Suriname, it is common in secondary and riverine forest, and on savanna along creeks (van Roosmalen 1985). In French Guiana, flowering takes place in September and October (Mori et al. 2002).

Although the genus *Dirphia* comprises more than 40 species, the natural foodplants are only known for a few. These are quite diverse and belong to the Anacardiaceae, Araucariaceae, Fabaceae, Juglandaceae, Meliaceae, Myrsinaceae or Myrtaceae (Lemaire 2002). Further data are needed to assess the importance of *Vismia* and the Hypericaceae as foodplants for *Dirphia* and other Saturniids. As the geographical range of *D. tarquinia* is greater than that of *V. cayennensis*, other natural foodplants for *D. tarquinia* are obviously used.

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AN AMERICAN BLUE IN CUBA, THE FIRST WEST INDIAN RECORD OF *CUPIDO* SCHRANK (LEPIDOPTERA, LYCAENIDAE, POLYOMMATINAE).

Additional key words: colonization, Cuba, Florida, potential host plants, Southern United States, Yucatán

The genus *Cupido* Schrank 1801 includes two species inhabiting continental America, *C. amyntula* (Boisduval, 1852) and *C. comyntas* (Godart, [1824]) (Warren et al. 2012). Their ranges occupy the western United States and Canada, in the first case, and southern Canada and the eastern United States to Costa Rica in the second (Glassberg 1999; Warren et al. 2012). There are no records of *Cupido* species from the West Indian islands.

On July 4th 2014 a worn specimen of a tailed polyommatine lycaenid was collected near midday at the entrance of "Las Maravillas de Viñales" pathway, 200 m high, Viñales municipality, Pinar del Río province, Cuba. The specimen was perching about half a meter above the ground on the tip of a *Stachytarpheta* bush. Five hours later, about 4:30 pm, a second nearly fresh specimen was captured a few meters away perching on a leaf of an unidentified herbaceous plant about 10 centimeters high from the ground. The specimens were quickly differentiated from other known Cuban Polyommatinae due to their tailed hindwings and the reduced size of underside pattern spots. The only other Cuban member of this subfamily having tails is *Pseudochrysops bornoi yateritas* Smith & Hernández, 1992 which is confined to the semi desert Southeastern coast of the Guantánamo province (Alayo & Hernández 1987; Smith & Hernández 1992; Matthews et al. 2012). Others lycaenids at the collecting site were *Leptotes cassius theonus* (Lucas), *Hemiargus hanno filenus* (Poey), *Strymon limenia* (Hewitson), *Ministrymon azia* (Hewitson), and remarkably *Strymon martialis* (Herrich-Schäffer) for which previous Cuban records were restricted to coastal areas (Alayo & Hernández 1987; Smith et al. 1994). This is the second inland record for *S. martialis* after that from Camagüey, central-eastern Cuba, by Fernández (2007).

The specimens, deposited in the Insitute of Ecology and Systematics, were identified as males of *Cupido comyntas* (Fig. 1) by comparison with pictures at the Butterflies of America website (Warren et al. 2012) and pictures and characters at Glassberg (1999). The collecting site is a moderately disturbed shrubby area surrounded by relatively well preserved natural habitats, mainly limestone semideciduous forest. The species seems to have had a successful colonization event since the inland location of the site is 20 km distant from the nearest point from the North coast and more than 130 km from the Westernmost point of Cuba, the tip of the Guanahacabibes peninsula. The species in Cuba is probably using host plants belonging to most of genera that *comyntas* uses in Florida and mentioned by Heppner et al. (2007) including *Desmodium* Desv., *Galactia* P. Browne, *Medicago* L., *Trifolium* L., and *Vicia* L. The species arrival to Cuba probably took place in the last decade since works published in the previous one that treated the butterfly fauna of Western Cuba didn't mention it (Smith & Hernández 1992; Hernández et al. 1994; Roque-Albelo 1994; Roque-Albelo et al. 1995; Hernández et al. 1995; Núñez & Barro 2003).

Without additional information it is difficult to establish the arrival point. The lack of known colonization point, together with the absence of females, makes it difficult to correctly assign the specimens to one of the three described subspecies of *C. comyntas*. However, almost surely the species could reach Cuba from the Yucatán peninsula since at the other point closest to Western Cuba, South Florida, were inhabits

FIG. 1. Male specimens of *Everes comyntas* collected at *"Las Maravillas de Viñales"* pathway, Viñales municipality, Pinar del Río province, Cuba. Left column specimen collected near midday, right column specimen collected 4:30 pm, on July 4, 2014.

the nominate subspecies it is very rare (Calhoun 1997). This hypothesis is reinforced when comparing the specimens collected in Cuba which have reduced orange spots at the hindwings underside, as in *C. comyntas texana*, that inhabits Yucatán, and unlike these at *C. c. comyntas*.

Although the presence of *Cupido comyntas* in Cuba is surprising, there is a long history of colonizing events by butterflies that reached Cuba from adjacent continental areas, such as the Yucatán and Southern United States, during the twentieth century. Species that successfully extended their distribution to Cuba during that time are *Euptoieta claudia* (Cramer), *Phyciodes phaon* (Edwards), *Eurema boisduvaliana* (Felder & Felder), *Aguna claxon* Evans, and *Anteos clorinde* (Godart) among others (Sánchez & Villalba 1934; Torre 1943; Alayo & Hernández 1987). During the same time other species reached Cuba as vagrants or established for short periods of time only to disappear later: *Colias eurytheme* Boisduval, *Pontia protodice* (Boisduval & Leconte), *Libytheana carinenta bachmani* (Kirtland), and *Polygonia interrogationis* (Fabricius), among others (Sánchez & Villalba 1934; Torre 1943; Zayas & García 1965; Núñez & Barro 2003).

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FIRST RECORD OF *EUCHLORON MEGAERA* (LINNAEUS, 1758) (SPHINGIDAE) FROM SEYCHELLES

Additional key words: ephemeral population; faunal affinities, vagrant

The Seychelles Archipelago comprises 115 islands in the western Indian Ocean. Along with Madagascar, Comoros, Réunion, Mauritius and Rodrigues these islands form the Malagasy subregion, which is part of the Afrotropical biogeographical region. The Seychelles experience a tropical humid climate (Walsh 1984), and can be broadly divided into the northern granitic and southern coral islands (Braithwaite 1984) (Fig. 1). The granitic islands, along with the two coral islands of Bird and Denis, make up the inner Seychelles islands. The Lepidoptera fauna of the Seychelles can be considered fairly well-known, with much historical and recent work been done (Matyot 2005; Gerlach & Matyot 2006). This paper presents a new hawkmoth record for Seychelles. Furthermore, an updated biogeographical checklist of all known Seychelles hawkmoth species is provided.

A single specimen of the large hawkmoth *Euchloron megaera megaera* (Linnaeus, 1758) (Fig. 2) was collected on the 27 October 2005 adjacent to the Veuve Special Nature Reserve on the granitic Seychelles island of La Digue at La Passé (Fig. 1: inset map). The specimen was found resting on a white coloured wall at 0730 h. The specimen is housed in the private collection of the author. The Veuve Special Nature Reserve was set up in 1982 to protect the last remaining population of the Critically Endangered Seychelles Black Paradise-flycatcher, *Terpsiphone corvina* (Newton, 1867) (Aves: Muscicapidae) (Currie 2002), locally known as 'Veuve'. The reserve lies on the western plateau of the island and was originally covered with marshland, and extensive indigenous forests dominated by *Calophyllum inophyllum* L. (Calophyllaceae) and *Terminalia catappa*

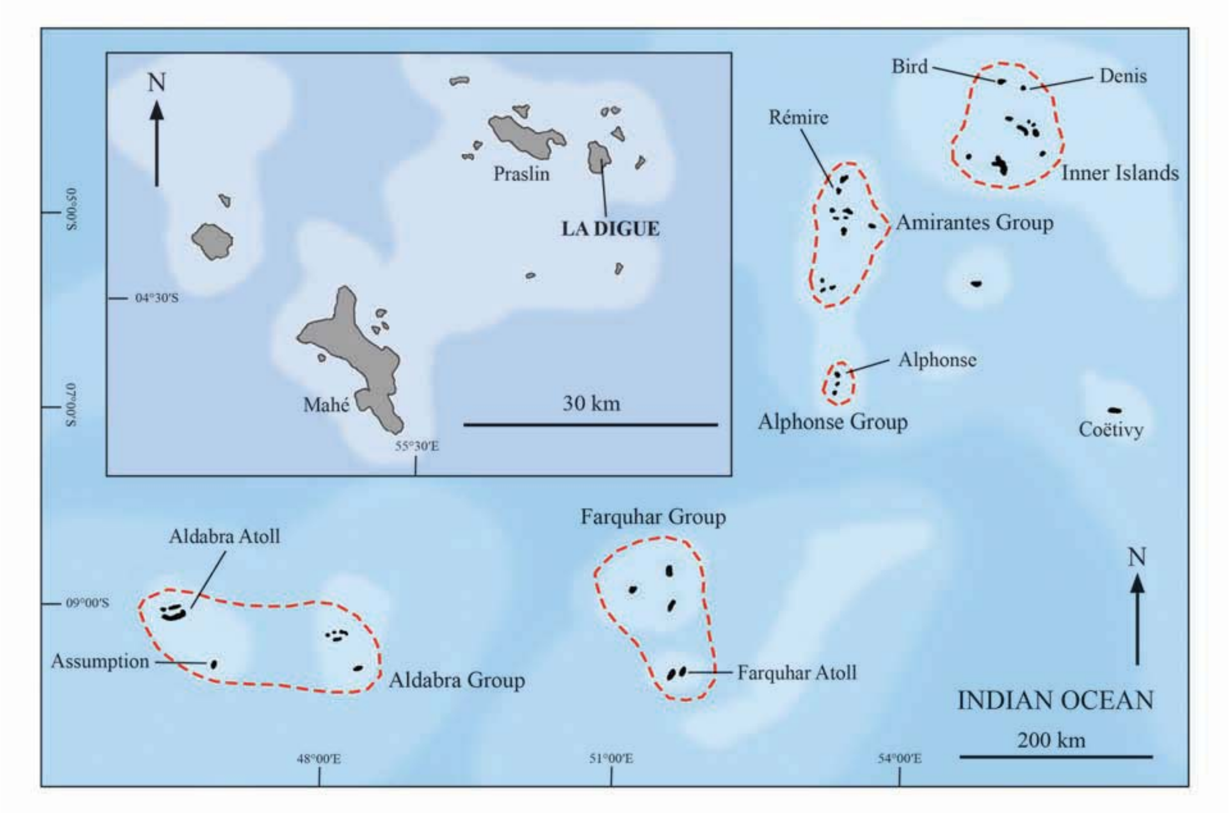

FIG. 1. The Seychelles Archipelago, with detailed inset map of the granitic islands showing the position of La Digue. La Digue lies within the Inner Islands.

TABLE 1. Distribution and faunal affinities of the Seychelles hawkmoths. **C** = Comoros; **Ma** = Madagascar; **R** = Réunion; **M** = Mauritius; **A** = Continental Africa; **SE** = Seychelles Endemic; **X** = taxon present in geographic area; **(X)** = taxon present as different subspecies in geographic area. Taxon distribution based on Carcasson (1967); Lawrence (2009); Matyot (2005); Pinhey (1962).

Seychelles taxon	**C**	**Ma**	**R**	**M**	**A**	**SE**
Acherontia atrops (Linnaeus, 1758)	X	X	X	X	X	-
Agrius convolvuli (Linnaeus, 1758)	X	X	X	X	X	
Batocnema cocquerelii aldabrensis Aurivillius, 1905 Note 1	(X)	(X)	-	-	-	X
Cephonodes hylas virescens (Wallegren, 1865)	X	X	-	-	X	-
Cephonodes tamsi Griveaud, 1960	-	-	-	-	-	X
Daphnis nerii (Linnaeus, 1758)	X	X	X	X	X	-
Euchloron megaera megaera (Linnaeus, 1758)	(X)	(X)	-	-	X	-
Hippotion aurora aurora Rothschild & Jordan, 1903 Note 2	-	X	-	-	-	-
Hippotion aurora delicatum Rothschild & Jordan, 1915 Note 2	-	-	-	-	-	X
Hippotion celerio (Linnaeus, 1758)	X	X	X	X	X	-
Hippotion eson (Cramer, 1779)	X	X	X	X	X	-
Hippotion geryon (Boisduval, 1875)	X	X	-	-	-	-
Hippotion osiris (Dalman, 1823)	-	X	-	-	X	-
Macroglossum alluaudi De Joannis, 1893	-	-	-	-	-	X
Nephele leighi Joicey & Talbot, 1921	-	-	-	-	-	X
Temnora peckoveri (Butler, 1877)	-	X	-	-	-	-

Note 1 *B. c. aldabrensis* is known from a single specimen collected in 1895 on Aldabra (Matyot 2005). The Madagsacan subspecies is *occidentalis* Griveaud, 1971. Two subspecies are found in Comoros, *comorana* Rothschild & Jordan, 1903 on Grande Comore and *anjounensis* Viette, 1982 on Anjouan. The Aldabra subspecies is poorly known and further specimens are required to confirm its subspecies status.

Note 2 Subspecies *aurora* occurs on Madagascar, and has been listed as occurring on the island of Assumption (south of Aldabra Atoll) in Seychelles by Carcasson (1967). The source of this record is unknown (I. Kitching pers. com.). Subspecies *delicatum* is listed as occurring on the islands of Coëtivy, Alphonse, Rémire, Assumption and Farquhar Atoll (Matyot 2005). Subspecies *gloriosana* Rothschild & Jordan, 1915 occurs on the Glorioso Islands north of Madagascar. This species is not widely collected and further work on its taxonomy is required.

L. (Combretaceae) trees. Most of the original vegetation has been removed or degraded, with wetland drainage, agricultural and urban development being significant anthropogenic threats (Skerrett et al. 2001). Although this hawkmoth is easily identifiable it can be confused with the smaller but similar looking *Basiothia medea* (Fabricius, 1781).

Two other species of hawkmoths have been recorded from La Digue. These are *Acherontia atropos* (Linnaeus, 1758) (Fletcher 1910) and *Cephonodes tamsi* Griveaud, 1960 (Mazzei 2009). *C. tamsi* is endemic to the granitic Seychelles islands where it is Red-Listed as Critically Endangered (Gerlach & Matyot 2006).

Larvae of *E. megaera* are polyphagous on numerous species within the plant family Vitaceae. *E. m. megaera* larvae have been recorded on *Cissus* sp. and *Vitis* sp. (Kroon 1999). In Seychelles, these plant genera are

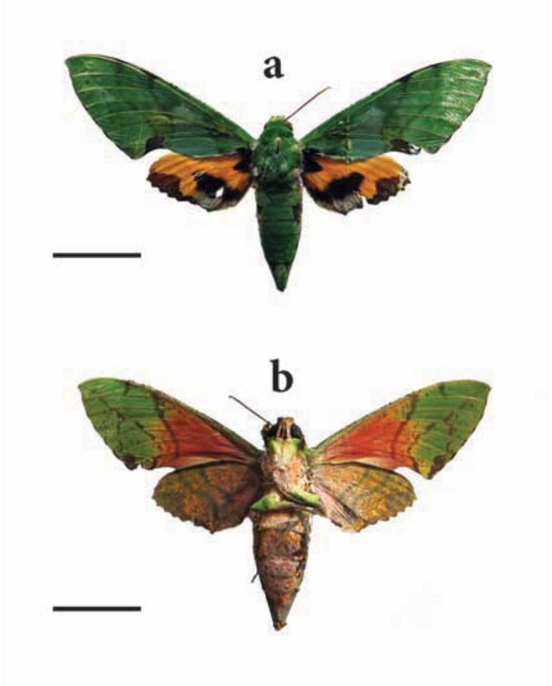

FIG. 2: **a)** *Euchloron megaera megaera* dorsal surface. **b)** *Euchloron megaera megaera* ventral surface. Specimen collected on La Digue 27 October 2005 (Photos: J.M. Lawrence). Scale bar = 2 cm.

represented by *C. rotundifolia* (Forskk.) Vahl and *V. vinifera* L. respectively. *V. vinifera* has been recorded on Mahé and Praslin, and *C. rotundifolia* occurs on Mahé (Friedmann 2011). However, there are no records of these plants on La Digue so far.

Euchloron megaera is widespread across the Afrotropical region where five subspecies are recognised: 1) *E. m. megaera* (Linnaeus, 1758) occurs throughout most of Africa south of the Sahara, including Grand Comore in the Comoros; 2) *E. m. asiatica* (Haxaire & Melichar, 2009) is found in Yemen; 3) *E. m. lacordairei* (Boisduval, 1833) occurs on Madagascar and the Comoro islands of Mayotte, Mohèli and Anjouan; 4) *E. m. orhanti* (Haxaire, 2010) is found on Rèunion; 5) *E. m. serrai* (Darge, 1970) is restricted to São Tomé off the west coast of Africa.

Interestingly, the Seychelles specimen belongs to the African mainland subspecies and not the Madagascan or Réunion subspecies. Whether this moth has been previously overlooked by researchers or the species was recently introduced is unknown. It may represent a vagrant specimen or an ephemeral population. An analysis of the faunal affinities of the Seychelles butterfly fauna found that the granitic islands shared a closer affinity to continental Africa than to Madagascar or Comoros (Lawrence 2014), suggesting that natural arrival of this species in Seychelles cannot be dismissed.

This record increases the number of hawkmoth species found in Seychelles to 15. One species is represented by two subspecies making the total number of taxa 16 (Table 1), of which 31.25% are endemic (i.e. three species and two subspecies). Five taxa are widespread across the Afrotropical region including the Malagasy subregion, and three species are confined to the Malagasy subregion.

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