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The Occurrence and Behaviors of North American Fireflies (Coleoptera: Lampyridae) on Milkweed, *Asclepias syriaca* L.

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Abstract

At four sites spanning a general triangle with 50–100 km legs in East Tennessee over a six-week period in July and August 2013, 56 fireflies, male and female, from four species and three genera were associated with common milkweed, *Asclepias syriaca* L. *Photinus pyralis* (L.), *Photinus cooki* Green, *Pyropyga minuta* LeConte, and an determined species of *Photuris* Dejean repeatedly exhibited seven common behaviors of nectaring from individual blooms and stigmatic slits and actively mouthing floral stems, recurved sepals, and uppermost leaves, lasting from 9–175+ minutes. Milkweed pollinia were noted on three of the four species. Maximum firefly presence was observed the first two survey days, 7 and 8 July, falling to low but persistent numbers the remainder of the survey. These firefly behaviors were observed primarily in the four hours before sunset and after sunrise. Twelve *Photuris* larvae were observed feeding on milkweed rhizomes in captivity. Reports of milkweed-firefly associations involving at least four additional firefly species in two additional genera, *Lucidota atra* (Olivier), *Photinus indictus* (LeConte), *Pyropyga decipiens* (Harris) and a species of *Pyractomena* Melsheimer spanning 90 years across the eastern US are presented along with recent reports of similar behaviors witnessed from Texas to Canada.

Key Words: defensive chemicals, firefly, pollinia, cardenolide, lucibufagin, lightning bug

Most North American fireflies, aposematic by day with warning colors and by night with bioluminescence (Lloyd 1973; Underwood *et al*. 1997; De Cock and Mattheysen 1999; Vencl *et al*. 2012) are chemically protected. Eisner *et al*. (1978) first discovered that many species of fireflies of both sexes have a number of defensive chemicals including steroidal pyrones collectively called lucibufagins (LBGs) (Meinwald *et al*. 1979; Goetz *et al*. 1981; Eisner *et al*. 1997; Gonzales *et al*. 1999a, b; Gronquist *et al*. 2005). The cardio-toxic properties and chemical structure of LBGs are similar to the cardiac glycosides, bufadienolides, and cardenolides found in milkweeds, other plants, and animals. Uncertainty remains on just how and where most firefly genera obtain or manufacture these steroid-based defensive chemicals.

With the exception of the voracious female aggressive mimic, *femme fatale* fireflies of the genus *Photuris* Dejean (Lloyd 1965, 1975; Faust *et al*. 2012a; Lewis *et al*. 2012), which devour and obtain defensive chemicals from other firefly genera (Eisner 1997; Gonzalez *et al*. 1999a, b; Gronquist *et al*. 2006), little is known about the complete nutritional habits of adult and larval North American fireflies. Hess (1920) wrote that though adult fireflies have mouthparts, it is uncertain whether if or what fireflies eat as adults. Eighty years later, Lloyd (2004) uses the term "adult fasting rule" to describe the apparent lack of eating seen in adult fireflies (*Photuris* the exception). Rooney and Lewis (2000) observed *Ellychnia corrusca* (L.) feeding on floral nectaries of Norway maples, *Acer plantanoides* L.(Aceraceae), in spring and positioned near winter sap flows of sugar maples, *Acer saccharum* Marshall. Lloyd (1998) gives the most detailed account with accompanying photographs of wild Jamaican *Photinus pallens* (F.) gathering in swarms on non-native, invasive ginger lilies, *Hedychium* sp. (Zingiberaceae) and native "jointer trees" *Piper* sp. (Piperaceae) for both apparent feeding and mating. Today, most firefly researchers agree that, though possible and

occasionally observed, nutritional intake does not appear necessary for the short-lived adult fireflies, whose focus appears to be survival and successful mating. It has been generally assumed the poorly understood 1–2 year larval stage may be the most likely time fireflies obtain their energy and chemicals for life.

Interactions between insects and chemically laden milkweed have been long studied (Brower and Brower 1964; Rothschild *et al*. 1966; Agrawal *et al*. 2012). All parts of the milkweed plant, including nectar, flowers, latex, and rhizomes, contain cardenolides in varying levels (Malcolm 1995; Rasmann *et al*. 2009; Manson *et al*. 2012). Milkweed nectarivores must have strategies for encountering these toxins (Isman *et al*. 1977; Dobler 2012).

Milkweed-associated Coleoptera are discussed in Betz *et al*. (1994, 1997), Malcolm (1995), Fordyce and Malcolm (2000), Matter (2001), and others. Weiss and Dickerson (1921) list *Pyropyga decipiens* (Harris) and *Lucidota atra* (Olivier) as visitors to milkweed in New Jersey. The work by Daily *et al*. (1978) surveying all the Coleoptera on the common milkweed, *Asclepias syriaca* L. (Apocynaceae), over a 90-day period during June-August in Ohio found 132 beetle species represented. Two of the 18 most common species were fireflies, *Photinus pyralis* (L.) and *P. decipiens,* with lower numbers of *Photinus indictus* (LeConte) and *Photuris* sp. Similar observations as made by Rea *et al*. (2010) in their field guide *Milkweed, Monarchs and More* illustrated with a photograph of a species of *Pyractomena* Melsheimer on a bloom of *Asclepias curassavica* L. (Quinn 2008; M. Quinn, *in litt.* 2013) in south Texas. Rea *et al*. (2010) write, "It is believed that some adults (fireflies) don't eat but some (like Quinn's photo) seem attracted to nectar." On Ottawa, Canada's Fletcher Wildlife Garden and Monarch Way Station Project's photo page (Fletcher Wildlife Garden 2013), nature photographer Christine Hanrahan's Marlborough Forest photograph shows a *Photuris* sp., pollinia attached to the left front tarsi, appearing to nectar. She writes (*in litt.* 2013), "I have seen fireflies of various species nectaring on milkweeds…I see this often enough that I do not always photograph them." A short video by entomologist Dr. Robert Klips (2010) of Ohio State University shows a *P. pyralis* investigating blooms of another milkweed, *Asclepias sullivantii* Engelm. ex Gray, though he writes he has observed this phenomenon only once (*in litt*. 2013). Despite these observations and findings over the past 92 years, no specific studies have been conducted to more fully understand the depth and cause of utilization of milkweed or other plants by certain firefly species.

This study details the results of a field survey where adult fireflies were initially, unexpectedly found in large numbers nectaring and actively mouthing (mouthparts extended, firefly actively working) the coronal blooms, nectar glands, recurved sepals and petals of the corolla, flower stems, and tender leaves of common milkweed. Specific behaviors were noted, as was the presence of attached pollinia to the fireflies, the maturational state of the preferred blooms and plants, the times of day/night most likely for this behavior to be observed, and the general seasonality and growing degree-day ranges for peak utilization of these milkweeds by fireflies. Results of captive larval feeding responses to milkweed rhizomes and leaves are also provided. The purpose of this paper is not to prove or disprove cardenolide or other chemical sequestration by adult or larval fireflies, but simply to report this feeding behavior, so that researchers can be aware of and further investigate the ecological and chemical implications of these firefly-milkweed associations.

Material and Methods

From 7 July to 7 September 2013, milkweed patches were surveyed by the authors for fireflies nectaring and actively mouthing at four primary locations, with three additional subsites 1–8 km from the main sites, in the hill and valley region of four East Tennessee counties: Knox (N35°53′54.76″ W84°13′50.10″), Grainger (N36°6′45.48″ W83°37′38.71″), Jefferson (N36°6′24.76″ W83°37′23.01″), and Cocke (N35°49′07.11″ W83°8′42.36″). These diverse sites included former pastureland adjoining a new large suburban high school, protective boundary lands surrounding an active limestone quarry, a 101.2-hectare river island with ongoing native grassland restoration and sunflower cultivation, uncultivated farm fields and fence rows, and an interstate exit. Elevations ranged 277–382 m. These sites formed a triangle with legs of 99 km, 58 km, and 54 km, covering 1,295 km^2. Preliminary late season, more northern, higher elevation studies, 959 m and 1,027 m respectively, were conducted 23–25 August by LF at two sites in and near the Jefferson National Forest in Tazewell Co., VA (N37°7′13.10′ W81°16′51.76″ and N37°7′41.91″ W81°14′45.15″) to compare firefly/milkweed interaction behaviors.

Nineteen days of surveys, averaging two hours/day (range 1–4 hours) were conducted at all hours night and day, until the most productive times for finding fireflies on milkweed were determined. Each bloom of individual flowers within the umbel, leaf, stem, and pod was visually inspected for firefly activity; then, if none was seen, each milkweed umbel was carefully shaken (while remaining attached to its plant) into an insect net and the contents further inspected and recorded. Approximately 405 flowering milkweed stems

with blooms (Bookman 1981) and 330+ non-flowering, yet suitable appearing (fresh leaves) stems were inspected for firefly activity until the milkweed blooming season ended. Multiple sites were inspected some days and sites were occasionally visited twice in a given day. Sites were visited 3–5 times a week in July until the end of the primary milkweed bloom and at least once a week thereafter (Grainger Co. site only) where summer mowing of a colony of milkweed caused a delayed bloom. Studies were halted 7 September 2013 after four consecutive surveys at the two largest sites produced no firefly activity on milkweed and <5% of fireflies displaying or evident in prime habitats, when all milkweed blooms were gone and dried pods were beginning to burst.

In order to establish whether these fireflies were exhibiting similar behaviors on the nearby neighboring flowers of other abundant species, inspections were made each survey day on Queen Anne's lace (*Daucus carota* L.; Apiaceae), fleabane (*Erigeron pulchellus* Michaux; Asteraceae), black-eyed Susan (*Rudbeckia hirta* L.; Asteraceae), trumpet vine (*Campsis radicans* (L.) Bureau; Bignoniaceae), wild potato vine (*Ipomoea pandurata* (L.) G. Meyer; Convolvulaceae), common mullein (*Verbascum thapsus* L.; Scrophulariaceae), jimsonweed (*Datura stramonium* L.; Solanaceae), and horse nettle (*Solanum carolinensis* L.; Solanaceae). Later in the season, passion flower (*Passiflora incarnata* L.; Passifloraceae), golden rod (*Solidago nemoralis* Aiton; Asteraceae), and latex-containing flowering spurge (*Euphorbia corollata* L.; Euphorbiaceae) were included. The two common, closely related Apocynaceae, *Asclepias tuberosa* L. and Indian hemp dogbane, *Apocynum cannabinum* L., were likewise carefully inspected each survey.

Common shared behaviors and presence of attached pollinia were noted, feedings timed when possible, photographed, and videotaped with an ancient LG flip phone (first surprising day), Sony Cybershot T20, Olympus 770 SW, and Nikon D7000. Milkweed phenological data were obtained from Dailey *et al*. (1978), Kephart (1987), and Bartholomew and Yeargan (2001). Firefly phenological data and degree-days (Faust and Weston 2009) were determined using the closest station, Newport, TN # 406534 (Northeast Regional Climate Center 2013). Combined with personal observations, the point in the season of both the maximum flowering of the milkweed and the maximum peak population dates/degree-day values of the targeted firefly species was estimated to more accurately interpret the 2013 results and to better predict observations of this phenomenon in future years. Modified corn-growing degree-days (or 86/50) are presented as published by the Northeast Regional Climate Center (2013) in Fahrenheit (mGDDF), with centigrade values provided in parentheses (mGDDC). All photographs were taken by the authors, except Fig. 3 which was taken in June 2008 at Marlborough Forest in Ottawa, Canada by Canadian naturalist photographer Christine Hanrahan.

Description of milkweed parts and explanation of the complex mechanisms of insect vectored pollination via pollinia were taken from Bookman (1981), Ollerton and Liede (1997) and Johnston (2005).

On 24 September 2013, 12 captive late instar *Photuris* (probably *quadrifulgens* Barber) (length 14.5–16.2 mm, pronotal width 4.7–5.1 mm) and one *L. atra* larva (length 14 mm, pronotal width 1.8 mm) were kept in natural photoperiod housed in 90 mm dia × 60 mm containers (four *Photuris* larvae per container to minimize cannibalism) with moistened crumpled coffee filter paper for moisture and cover. The larvae were offered small pieces of freshly dug milkweed rhizomes (cut to 20 mm long) and tender milkweed leaves, along with other foods (cat food, apple, stinkbug, grasshopper, worm, basil, and lettuce) over an 84-hour period to check for reaction. Foods were kept fresh by periodic replacement. Larvae were kept for another week to check for adverse reactions, and then reoffered fresh milkweed rhizomes and cat food.

Results

Firefly Behaviors. From 7 July to 17 August 2013, 56 fireflies of four species were observed both separately and together by the two authors at the East Tennessee sites. These beetles appeared to collect nectar on blooms or actively mouth new leaves, petals, and floral stems of common milkweed (Fig. 1). Active mouthing would be described as the firefly rapidly crisscrossing the upper (rarely and briefly lower) surface of still

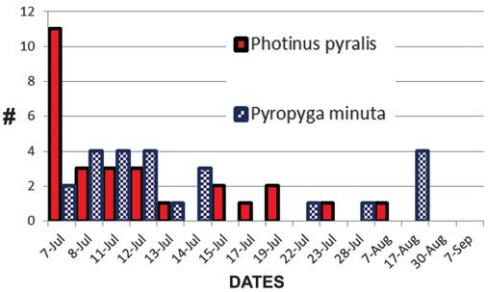


Fig. 1. Seasonal presence of *Photinus pyralis* and *Pyropyga minuta* exhibiting nectaring behaviors and active mouthing on milkweed. Two *Photuris* sp. and one *Photinus cooki* were observed on milkweed 7 and 8 July only.

tender, mature leaves (top one-third of the plant or uppermost 8–12 leaves) or open blooms with mouthparts extended and in contact with the plant parts. The brief stops often near a leaf vein or stigmatic slit resumed in usually in less than <5 seconds. The firefly appeared to draw its dorsum up slightly when stopped to actively mouth. Actual chewing of the plant structures or sipping latex exudation was not seen. This active behavior was opposed to the stationary resting on vegetation commonly seen in concealed fireflies during the day or the prolonged stationary stance assumed by fireflies sipping dew, apple slices, or honey-soaked paper in captivity.

All species of fireflies (*P. pyralis, P. cooki, Pyropyga minuta* LeConte and *Photuris* sp.) exhibited seven similar behaviors on *A. syriaca*. No pollinia were observed on *P. cooki*. *Pyropyga minuta* displayed an eighth and *P. pyralis* a ninth behavior.

1. Fireflies appeared to nectar or mouth the individual multiple flowers on each umbel by thrusting their heads into the hoods of each five-sectioned corona (Fig. 2) as did many other nectarivores.

2. Fireflies frequently appeared to sip nectar or mouth the base of the stigmatic slits between each of the five coronal hoods located on the corollar tube (Fig. 3) as did many other nectarivores.

3. Fireflies actively mouthed the top one-third leaves or uppermost 8–12 leaves of *A. syriaca* (Fig. 4).

4. Fireflies chose only the freshest aromatic blooming umbels, avoiding any wilted or immature blooms and all lower two-thirds past-prime leaves. They also appeared to avoid over-mature milkweed stems or their clones which had begun to set pods.

5. Fireflies were often out of sight while foraging inside the recurved petals, sepals, and the small floral stems within the umbels.

6. Pollinia (milkweed pollen packets) were attached to the leg and tarsi of three of the firefly species (Fig. 5).

7. These behaviors were not observed on two other common Apocynaceae species or the abundant neighboring plants and flowers inspected during the surveys.

8. Only *P. minuta* was observed feeding among the aphid (*Aphis nerii* Boyer de Fonscolombe)-infested umbels, with possible ingesting or obtaining liquid from the aphids as an additional strategy. In late season, two *P. minuta*, male and female not in copula, were found on a small, 4.8 cm long, young green pod, but the activity was uncertain.

9. Individuals of *P. pyralis,* along with many other milkweed insect visitors, were occasionally found in a death-like state lying on their backs on the leaf just under the milkweed umbel. Some eventually recovered, others did not.

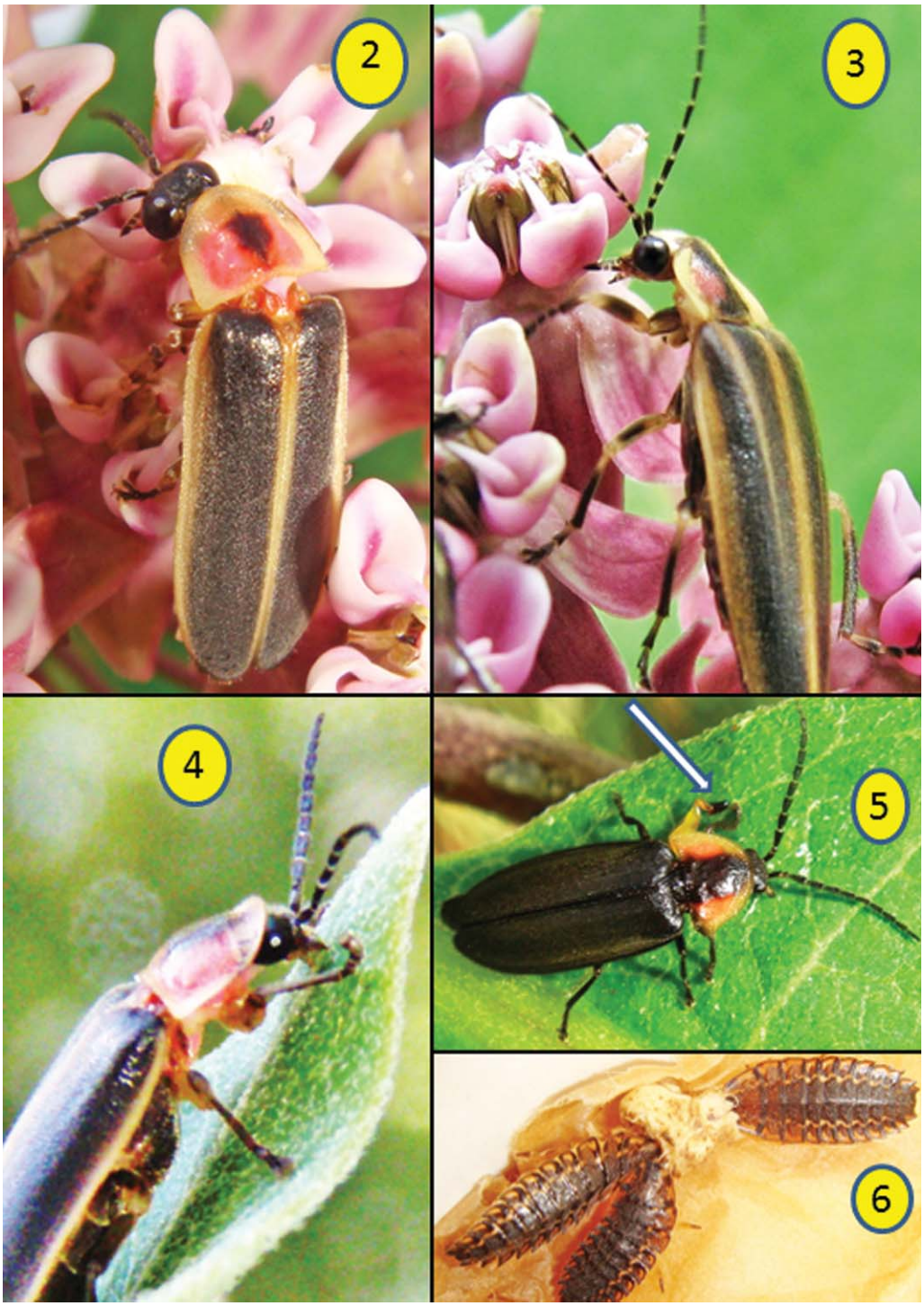
On the peak days of 7–8 July (Fig. 1), males and females, predator and prey species, were found feeding together on the blooms with no apparent mating or predatory interest in one another. Two species, both sexes alate, *P. pyralis* (crepuscular, 11–14 mm) and *P. minuta (*diurnal, 4–6 mm) accounted for 53 of the 56 records. One *P. cooki* (diurnal, 7 mm) and two individuals in the *Photuris versicolor* complex (nocturnal, 14–16 mm) were also found on and just under the blooms, respectively, showing the same behaviors. No fireflies were found on the 30 August – 7 September 2013 surveys when observed milkweed blooms and firefly numbers were <5%, relative to the peak.

Photinus pyralis males and females were found active on *A. syriaca* in generally equal ratios. Because of the small size (5–7 mm) and similarity of both sexes of *P. minuta*, field sexing was impossible. Of 11 *P. minuta* examined under the microscope, all were female with the exception of one male found alongside a female on a milkweed pod. It is possible that *P. decipiens* was also represented on the milkweed, but since all collected specimens were female and all nearby males caught by sweep net were determined as *P. minuta* by dissection, we must assume for now that all the *Pyropyga* were *P. minuta.* The fireflies, especially *P. minuta*, were rarely easy to spot because of their small size, camouflaged coloration, and tendency to work deep within each milkweed umbel or disappear inside the recurved petals of the individual flowers. The *Photuris* sp., both females, were most likely *Photuris lucicrescens* Barber as this was the primary *Photuris* species displaying nightly at this site during the study.

Feeding times obtained for five *P. pyralis* on umbels were nine, 14, 25, 43, and 47 minutes. Another female *P. pyralis*, snaring a pollinia midway through this timing, was observed methodically nectaring from most of the 106 flowers of an umbel for 175+ minutes. During this time, she moved to the leaf just under the umbel four brief times, but returned to the flowers each time. One *P. minuta* actively mouthed a leaf for 45 minutes, another for 22 minutes. Beginning or ending times were not always known for many of the other observed fireflies. Along with a number of other milkweed feeding insects observed having similar fates, three fireflies were found dead or apparently paralyzed, lying on their backs motionless, legs in the air, on the leaves right below fresh blooms. When collected, two recovered over a period of hours, while the third firefly did not.

Pollinia were observed on one *P. pyralis* (tarsi of hind leg), one *P. minuta* (femur of foreleg) (Fig. 5) and one *Photuris* sp. (tarsi of foreleg).

A cut (by author) milkweed leaf spilling milky, sticky latex was actively avoided by a *P. minuta*



Figs. 2–6. Fireflies on common milkweed. **2)** Female *Photinus pyralis* nectaring bloom; **3)** *Photuris* sp. sipping from stigmatic slit. Photograph by C. Hanrahan; **4)** *Photinus pyralis* actively mouthing leaf; **5)** Milkweed pollinia (arrow) on front left femur of *Pyropyga minuta*; **6)** *Photuris quadrifulgens* larvae hollowing out center of milkweed rhizome.

who nevertheless remained actively mouthing the same leaf for another 20 minutes. A *P. pyralis* who likewise avoided the latex, remained actively mouthing the leaf away from the spilled latex for 15 minutes. Many insect species including a firefly were seen dead or dying with legs entrapped in the stigmatic slits or stuck in latex.

Twelve *P. quadrifulgens* late instars ignored the milkweed leaves but showed interest in the cut pieces of fresh milkweed rhizome by appearing to eat the cut ends repeatedly (Fig. 6), singly and in groups, and dragging pieces a distance of 50 mm across their 90-mm diameter containers to cover to continue feeding. Individuals were not marked, but groups of 2, 3, and 4 feeding simultaneously in the three containers, respectively, showed at least 75% of the larvae fed on the rhizomes during this 84-hour test. One or more larvae were in contact with the rhizomes at any given time. When investigated after removal, the rhizomes showed partially hollowed out interiors and masticated clumps of rhizomal matter. Instead of seeking cover as they rested during the day, many larvae chose to curl around and beside the milkweed placed in the center. Larvae were kept an additional week to check for adverse reactions, of which none were observed. They were offered fresh rhizomes and leaves after one week, yet showed no interest in either, though they did eat more cat food. The *L. atra* larva, housed separately, showed no interest in the rhizomes yet readily ate a worm. It should be noted that these larvae appeared more attracted to the known preferred foods of moistened dried cat food, apple slices, and scavenged insects, but after satiation, retreated to cover or moved to the milkweed rhizomes.

Timing and Seasonality. With the exception of the first two evenings (7 and 8 July) when firefly numbers were very high on *A. syriaca* (23 individuals found in less than 1.5 hour on 15 stems) (Fig. 1), finding fireflies was difficult and not evenly spaced in time. It was soon discovered that the 4 hours before sunset (4:30–8:30 EDST) were the most productive, followed by the 4 hours after sunrise (7–11 AM EDST), for finding *P. pyralis*. Only one *P. pyralis* was found foraging during the midday hours of 11 AM–4:30 PM, when temperatures ranged 26–32 °C in 2013. *Pyropyga minuta* was not as temporally constrained, with four of 26 individuals found from noon - 3 PM on a cloudy, overcast, relatively cool (22 °C) August day. The nighttime hours (10 PM–6 AM) yielded only two fireflies, both *P. pyralis*. The rough average of finding one firefly per hour of searching reflects the effort required for success in finding the inconspicuous nectaring and actively mouthing fireflies on non-peak days.

The relative peak abundance of both the fireflies and *A. syriaca* blooms in 2013 was similar, occurring the last week of June and first week of July. The two days of maximum observed firefly-milkweed association, 7 and 8 July, when almost half the fireflies were found, had an accumulated corn-growing degree-day (mGDDF) value of about 1,800 mGDDF (990 mGDDC). *Photinus pyralis* was found in lower numbers until 7 August or 2,574 mGDDF (1,416 mGDDC), and *P. minuta* was found until 17 August 17 or 2,818 mGDDF (1,550 mGDDC). Our impression was that we missed the beginning days of the peak visitation because of the unanticipated discovery of this phenomenon.

Other Sites. The studies in Tazewell County, VA showed that two released female *P. pyralis* (collected on site, both in flight at dusk, not counted in firefly totals) exhibited the same behaviors on milkweed as seen in the Tennessee fireflies. Despite the trauma of being captured and released, neither attempted flight once placed on the milkweed. One fed on seven of the 10 freshest flowers in the 40-flower umbel for 22 minutes before moving to actively mouth the two uppermost leaves (Fig. 4). The other female fed on seven flowers of a 10-flower umbel for 19 minutes before moving to an uppermost leaf and becoming motionless. Nighttime observations on 23–24 August detected very few active male *P. pyralis* (three total on a 0.8-hectare site) and sweep netting yielded no fireflies. Local peak for *P. pyralis* at this more northern site was estimated to be six weeks earlier, around 4–11 July 2013, when "100s were flashing at dusk" (personal communication, Johnsie Beck, landowner).

Photographic surveys conducted by naturalist/photographer Christine Hanrahan at Ottawa, Canada's Fletcher Wildlife Garden and nearby Marlborough Forest in June and July 2008–2013 revealed similar firefly behaviors by *Photuris* sp. on *A. syriaca* (Fig. 3) and *P. decipiens* or *Pyropyga nigricans* (Say), including nectaring, active mouthing, attached pollinia, and occasional fireflies caught by their legs in the stigmatic slits (Fletcher Wildlife Garden 2013; personal communication, Christine Hanrahan).

Discussion

This paper documents the first targeted look at milkweed-firefly associations, including the identification of seven common (plus two preliminary) behaviors that fireflies exhibited on *A. syriaca*, the presence of pollinia on three of four observed species of fireflies, seasonality, peak occurrence, and diurnal timing of this phenomena. Combined with previous studies and photographic records,

we offer that at least eight North American firefly species, *L. atra*, *P. pyralis, P. indictus, P. cooki, P. decipiens* (and/or *P. nigricans*), *P. minuta, Photuris* sp. (possibly representing >1–3 species), and a *Pyractomena* sp. have been reported or documented over the past century (Weiss 1921; Dailey *et al.* 1978; Klips 2010; Fletcher Wildlife Garden 2013) on milkweed ranging over 1,400 km from Tennessee to Ottawa, Canada and west to Texas. This still- to-be-understood milkweed-firefly association appears to be often overlooked and unrecognized but relatively common and widespread.

Why is this just being discovered? In addition to the cited published studies, milkweed-firefly interactions have been observed often, especially by monarch butterfly watchers and naturalist photographers (personal communication, Christine Hanrahan, Wanda Dewaard, 2013). Because the significance of these associations was not fully understood and the commonly held, preconceived belief that adult fireflies do not eat prevailed, these associations were not seriously considered and therefore assumed to be chance encounters. Common milkweed is widespread across eastern North America from Texas to the eastern coast and up to Ontario, Canada. The distributions of *P. pyralis* (Lloyd 1966) and the eastern *Pyropyga, Lucidota* and *Photuris* species are similar to that of common milkweed. In East Tennessee, common milkweed nears the southern edge of its range (Woodson 1954; Wyatt *et al.* 1993), yet 283 km miles northeast in Tazewell County, VA, it becomes a common roadside and fencerow weed, as it is even farther north in Pennsylvania (Faust *et al.* 2012b). It is possible that in East Tennessee, because of the lower density of milkweed but the high densities of *P. pyralis* and *P. minuta*, fireflies are simply easier to find than in areas where milkweed is much more abundant and fireflies more relatively dispersed. The times the fireflies were most likely to be found (four hours before sunset and four hours after sunrise) are not usual times many surveys, for flowers, monarchs, or fireflies, are conducted. In spite of the conclusion by Daily *et al.* (1978) that two species of fireflies are some of the most common Coleoptera on milkweed in Ohio, their survey times (noon - 6 PM) were not the most ideal for finding fireflies. The inconspicuousness of these small insects as they forage within the umbels is an added factor. Had the authors not accidentally stumbled upon the large numbers of fireflies nectaring the first two peak-like days of this survey, 7 and 8 July 2013 (1,800 mGDDF, 990 mGDDC) (Faust and Weston 2009), this phenomena would have most likely gone unnoticed, as only very dedicated searching revealed fireflies nectaring and mouthing milkweed after this peak time. As suggested by the dramatic decrease in *P. pyralis* numbers on milkweed after 8 July, milkweed visitation may be a brief and possibly one-time phenomenon for newly eclosed *P. pyralis* and others with short season habits. *Pyropyga minuta*, which has a more extended season (Faust and Weston 2009) lacked this dramatic peak in milkweed visitation. It is hoped that future firefly-milkweed associations will be more generally recognized as potentially significant.

Lewis *et al.* (2012) found that predatory *femme fatale Photuris* sp.were reluctant to eat *P. pyralis* fireflies, yet readily ate most other offered *Photinus* species and genera. It is possible that different species of fireflies use a combination of strategies to obtain or manufacture the needed defensive chemicals via larval predation and underground plant feeding, adult predation (*Photuris* sp. only), and above ground plant feeding when available.

Better understanding of the relationship that fireflies have with milkweed and other plants will advance the wider field of chemical ecology which continues to decipher the incredibly complex endogenous and exogenous chemical interactions constantly occurring between and within plants and animals.

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References Cited

Agrawal, A., G. Petschenka, R. Bingham, M. Weber, and S. Rasmann. 2012. Toxic cardenolides: Chemical ecology and coevolution of specialized plant–herbivore interactions. Tansley review. New Phytologist 194: 28–45.

Bartholomew, K., and K. Yeargan. 2001. Phenology of milkweed (Asclepiadaceae) growth and monarch (Lepidoptera: Nymphalidae) reproduction in Kentucky and ovipositional preference between common and honey vine milkweed. Journal of the Kansas Entomological Society 74(4): 211–220.

Betz, R., W. Romnel, and J. Dichtl. 1997. Insect herbivores of 12 milkweed (*Asclepias*) species [pp. 7–19]. *In*: Proceedings of the Fifteenth North American Prairie Conference (C. Warwick. editor). The Natural Areas Association, Bend, OR.

Betz, R., and R. Struven, J. Wall, and F. Heitler. 1994. Insect pollinators of 12 milkweed species [pp. 45–60]. *In*: Proceedings of the Thirteenth North American Prairie Conference: Spirit of the Land, Our Prairie Legacy (R. G. Wickett, P. D. Lewis, A. Woodliffe, and P. Pratt,

editors). Department of Parks and Recreation, Windsor, ON, Canada.

Bookman, S. S. 1981. Floral morphology of *Asclepias speciosa* (Asclepiadaceae) in relation to pollination and a clarification in terminology for the genus. American Journal of Botany 68: 675–679.

Brower, L. P., and J. V. Z. Brower. 1964. Birds, butterflies and plant poisons: a study in ecological chemistry. Zoologica (New York) 49: 137–159.

Dailey, P., R. Graves, and J. Kingsolver. 1978. Survey of the Coleoptera collected on the common milkweed, *Asclepias syriaca*, at one site in Ohio. The Coleopterists Bulletin 32: 223–229.

De Cock, R., and E. Matthysen. 1999. Aposamatism and bioluminescence: Experimental evidence from glow-worm larvae (Coleoptera: Lampyridae). Evolutionary Ecology 13: 619–638.

Dobler, S., S. Dalla, V. Wagschal, and A. Agrawal. 2012. Community-wide convergent evolution in insect adaptation to toxic cardenolides by substitutions in the NA,K-ATPase. Proceedings of the National Academy of Sciences 109(32): 13040–13045.

Eisner, T., M. A. Goetz, D. Hill, S. Smedley, and J. Meinwald. 1997. Firefly "femmes fatales" acquire defensive steroids (lucibufagins) from their firefly prey. Proceedings of the National Academy of Sciences 94: 9723–9728.

Eisner, T., D. Wiemer, L. Haynes, and J. Meinwald. 1978. Lucibufagins: defensive steroids from the fireflies *Photinus ignitus* and *P. marginellus* (Coleoptera: Lampyridae). Proceedings of the National Academy of Sciences 75: 905–908.

Faust, L., R. De Cock, and S. Lewis. 2012a. Thieves in the night: Kleptoparasitism by fireflies in the genus *Photuris* Dejean (Coleoptera: Lampyridae). The Coleopterists Bulletin 66(1): 1–6.

Faust, L., R. De Cock, K. Stanger-Hall, Z. Marion, and S. Sander. 2012b. Allegheny National Forest Firefly Survey of Forest and Warren Counties, PA. USDA, Forest Service Agreement 12-DG-11091900-011. Available from: firefly.genetics.uga.edu/KSH/Publications.html (Accessed 15 April 2014).

Faust, L., and P. Weston. 2009. Degree-day prediction of adult emergence of the firefly *Photinus carolinus*. Environmental Entomology 38(5): 1505–1512.

Fletcher Wildlife Garden. 2013. Monarch Waystation. Available from: www.ofnc.ca/fletcher/index.php, www.pbase.com/fwg/monarch_waystation (Accessed 6 October 2013).

Fordyce, J., and S. Malcolm. 2000. Specialist weevil *Rhyssomatus lineaticollis* does not spacially avoid cardenolides defenses of common milkweed by oviposition in pith tissue. Journal of Chemical Ecology 26: 2857–2874.

Goetz, M., J. Meinwald, and T. Eisner. 1981. Lucibufagins IV, New defensive steroids and a pterin from the firefly *Photinus pyralis* (Coleoptera: Lampyridae) Experientia 37: 679–690.

Gonzales A., J. Hare, and T. Eisner. 1999a. Chemical egg defense in *Photuris* firefly *femme fatales*, Chemoecology 9: 177–185.

Gonzalez A., F. Schoeder, and A. Attygalle. 1999b. Metabolic transformations of acquired lucibufagins by firefly *femme fatales*. Chemoecology 9: 105–112.

Gronquist M., J. Meinwald, T. Eisner, and F. Schroeder. 2005. Exploring uncharted terrain in nature's structure space using capillary NMR spectroscopy: 13 steroids from 50 fireflies. Journal of American Chemical Society 127(31): 10810–10811.

Gronquist, M., F. Schoeder, H. Ghiradella, and D. Hill. 2006. Shunning the night to elude the hunter: Diurnal fireflies and the "femmes fatales" Chemoecology 16(1): 39–43.

Hess, W. 1920. Notes on the biology of some common Lampyridae. Biological Bulletin 38: 39–76.

Isman, M., S. Duffey, and G. Scudder. 1977. Cardenolide content of some leaf- and stem-feeding insects on temperate North American milkweeds (*Asclepias* spp.). Canadian Journal of Zoology 55(6): 1024–1028.

Johnston, B. 2005. A close-up view of the unusual wildflower *Asclepias syriaca* (Canada). Available from: www.microscopy-k.org.uk/mag/indexmag.html?, www.microscopy-uk.org.uk/mag/artfeb05/bjmilkweed.html (Accessed 6 October 2013).

Kephart, S. 1987. Phenological variation in flowering and fruiting of *Asclepias*. American Midland Naturalist 118(1): 64–76.

Klips, R. 2010. Firefly wanders on milkweed flowers July 10, 2010. Available from: www.youtube.com/watch?v=5grO6jmwj-8. (Accessed 6 October 2013).

Lewis, S., L. Faust, and R. De Cock. 2012. The Dark Side of the Light Show. Predators of Fireflies in the Great Smoky Mountains. Psyche. doi:10.1155/2012/634027. Accompanying video, Lewis lab, vimeo.com/28816083.

Lloyd, J. E. 1965. Aggressive mimicry in *Photuris*: firefly *femmes fatales*. Science 149: 653–654.

Lloyd, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. Miscellaneous Publications Museum of Zoology, University of Michigan 130: 1–95.

Lloyd, J. E. 1973. Firefly parasites and predators. The Coleopterists Bulletin 27: 91–106.

Lloyd, J. E. 1975. Aggressive mimicry in *Photuris*: signal repertoires by *femmes fatales*. Science 187: 453–453.

Lloyd, J. E. 1998. On research and entomological education II: A conditional mating strategy and resource sustained lek(?) in a classroom firefly (Coleoptera: Lampyridae; *Photinus*). Florida Entomologist 81(3): 261–272.

Lloyd, J. 2004. Fireflies (Coleoptera: Lampyridae) [pp.841–862]. *In*: Encyclopedia of Entomology. Vol. 2. (J. Capinera, editor). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Malcolm, S. 1995. Milkweeds, monarch butterflies and the ecological significance of cardenolides. Chemoecology 5–6: 101–117.

Manson, J., S. Rasmann, R. Halitschke, J. Thomson, and A. Agrawal. 2012. Cardenolides in nectar may be more than a consequence of allocation to other plant parts: A phylogenetic study of *Asclepias*. Functional Ecology 26(5): 1100–1110.

Matter, S. 2001. Effects of above and below ground herbivory by *Tetraopes tetraophthalmus* (Coleoptera: Cerambycidae) on the Growth and Reproduction of *Asclepias syriaca* (Asclepidacae). Environmental Entomology 30(2): 333–338.

Meinwald, J., D. Wiemer, and T. Eisner. 1979. Lucibufagins. 2. Esters of 12-Oxo-2B,11A-trihydroxybufalin, the major defensive steroids of the firefly *Photinus pyralis*. J. American Chemical Society 101: 3055–3059.

Northeast Regional Climate Center. 2013. CLIMOD. Available from: climod.srcc.lsu.edu/climod/dd/ (Accessed 6 October 2013).

Ollerton, J., and S. Liede, 1997. Pollination systems in the Asclepiadaceae: A survey and preliminary analysis. Biological Journal of the Linnean Society 62(4): 593–610.

Quinn, M. 2008. Texas Beetle Information Firefly - *Pyractomena* sp. www.texasento.net/Pyractomena.htm (Accessed 15 October 2013).

Rasmann, S., A. Agrawal, A. Erwin, and S. Cook. 2009. Cardenolides, induced responses, and interactions between above and belowground herbivores in the milkweeds (*Asclepias* spp.). Ecology 90: 2393–2404.

Rea, B., K. Oberhauser, and M. Quinn. 2010. Milkweed, Monarchs and More. A Field Guide to the Invertebrate Community in the Milkweed Patch. Expanded 2nd Edition. Bas Relief Publishing Group, Union, WV.

Rooney, J., and S. Lewis. 2000. Notes on the life history and mating behavior of *Ellychnia corrusca* (Coleoptera: Lamypridae). Florida Entomologist 83: 324–334.

Rothschild, M., T. Reichstein, J. Parsons, and R. Aplin. 1966. Poisons in aposematic insects. Royal Society Conversazione 12 May 1966: 10.

Underwood, T. J., D. W. Tallamy, and J. D. Pesek. 1997. Bioluminescence in firefly larvae: A test of the aposematic display hypothesis. Journal of Insect Behavior 10: 365–370.

Vencl, F. V., S. Shah, A. Gerber, and A. D. Carlson. 2012. Octopamine and DUM neurons orchestrate the larval firefly aposematic defence: A "Key Innovation"? Lampyrid 2: 99–112.

Weiss, H., and E. Dickerson. 1921. Notes on milkweed insect in New Jersey. Journal of the New York Entomological Society 29: 123–145.

Woodson, R. 1954. The North American species of *Asclepias* L. Annals of the Missouri Botanical Garden 41: 1–211.

Wyatt R., A. Stoneburner, S. Broyles, and J. Allison. 1993. Range extension southward in common milkweed, *Asclepias syriaca* L. Bulletin of the Torrey Botanical Club 120(2): 177–179.

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