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NATURAL HISTORY OF LIMACODID MOTHS (ZYGAENOIDEA) IN THE ENVIRONS OF WASHINGTON, D.C.

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ABSTRACT. The moth family Limacodidae is notable for its fascinating larval stages, but with the exception of a few important pest species, the natural history of these moths is still poorly known. The goal of this project was to investigate the natural history of moths in the family Limacodidae, as well as a species in the related family Megalopygidae, from the metropolitan Washington, D.C. area. The specific objectives of this study were to (ordered by life cycle from adult to larva): 1) summarize data on the flight times of the adult moths; 2) investigate the oviposition behavior of female moths, specifically their tendency to lay eggs in clusters; 3) document the phenology and host associations of locally-collected larvae; 4) develop an accurate means for assessing larval developmental stage; and 5) determine whether larval growth and cocoon weight predict lifetime fitness for females. In an adult flight dataset that spans ~130 years, we found significant interspecific variation in flight periods collectively encompassing a season running from April through November. Several pairs of sympatric congeners differed significantly in median flight times suggesting temporal niche separation. We found that for two of the species we studied, *Acharia stimulea* and *Euclea delphinii*, females laid eggs in clusters, but females of the other species mostly laid eggs singly. We generally found limacodid larvae from early June through October and most limacodid species were found as larvae on at least eight different host plant species, which supports the presumption that most species are generalists. For *A. stimulea* and *E. delphinii* larvae, we developed a set of equations so that we may estimate larval mass given larval body length, which allows us to estimate a larva's developmental stage in the field. Lastly, we found that for both *A. stimulea* and *E. delphinii*, there was a positive relationship between a female's cocoon mass and the number of offspring she produced the following year; thus, for these two limacodid species, cocoon mass is a predictor of lifetime fitness for females. Here we present all of the natural history observations and data that we have collected and analyzed from a variety of sources.

Additional key words: Limacodidae, Megalopygidae, oviposition behavior, flight times, larval survival, larval growth rate

Lepidoptera in the families Limacodidae and Megalopygidae have charismatic caterpillars (Figure 1). The common name for limacodids, slug caterpillar moths or simply slug moths, is derived from their unusual locomotory habit as larvae that is characterized by a high degree of ventral contact with the substrate by use of abdominal "sucker" appendages in movement and the laying down of semifluid silk ribbons; this is different from other caterpillars that typically use hooks, referred to as crochets, that cling to silk fibers (Epstein 1995). As peculiar as their locomotion is, limacodid larvae are perhaps best known for their unusual dorsal visages, which vary considerably; some species appear to be highly cryptic (e.g., Fig. 1C, G) while others possess intricate and vivid color patterning and various types of protuberances on their dorsal surfaces, some of which are thought to be aposematic (e.g., Fig. 1A, B, Wagner 2005). Megalopygid larvae also have a high degree of ventral contact, but retain rudimentary prolegs with functional crochets that are used to grasp silk strands they lay down on smooth surfaces (Epstein 1995). They are best known for

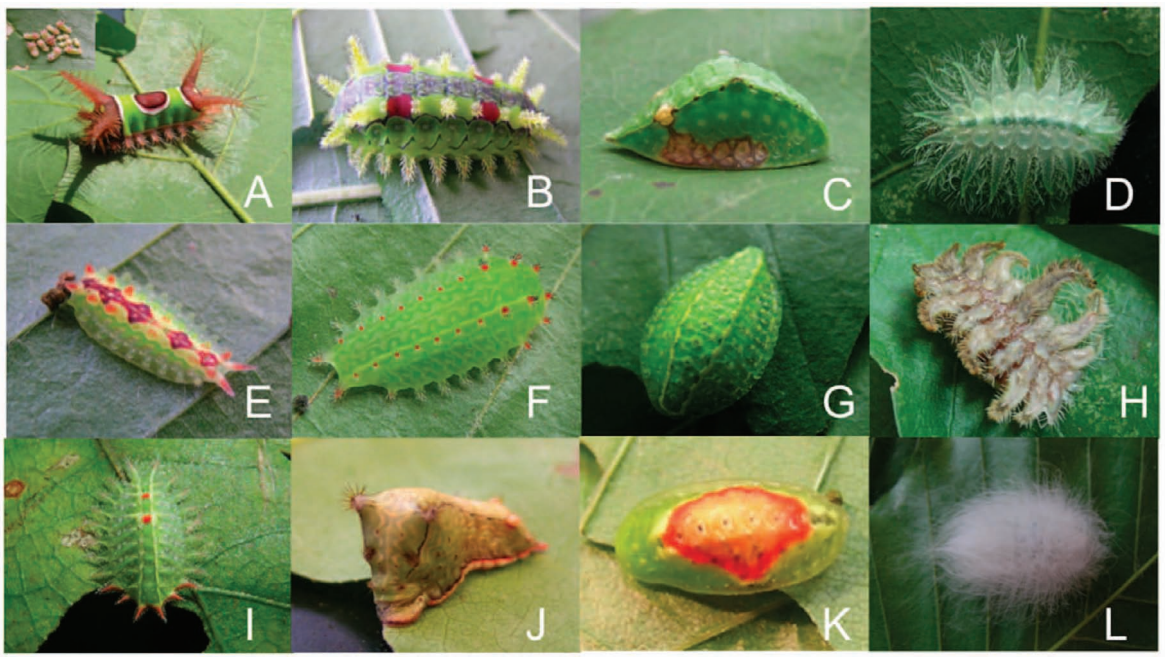

FIG. 1. Representative late-instar larvae of 11 species of Limacodidae: **A**) *Acharia stimulea*, **B**) *Euclea delphinii*, **C**) *Prolimacodes badia*, **D**) *Isochaetes beutenmuelleri*, **E**) *Adoneta spinuloides*, **F**) *Natada nasoni*, **G**) *Lithacodes fasciola*, **H**) *Phobetron pithecium*, **I**) *Isa textula*, **J**) *Parasa chloris* and **K**) *Tortricidia* sp. Representative late-instar larva of one common species of Megalopygidae: **L**) *Megalopyge crispata.*

having a woolly appearance with spines hidden beneath the silken hairs (Fig. 1L), though some have sparse hairs. Many species of both families are also remarkable for an intriguing defensive strategy: stinging setae, commonly referred to as spines. Species such as *Acharia* (=*Sibine*) *stimulea* (Clemens), *Euclea delphinii* (Boisduval) and *Megalopyge* (=*Lagoa*) *crispata* Packard (Fig. 1) possess spines for all or a portion of their larval development (Dyar 1899b) and these stinging spines are an effective defense against a variety of predators (Murphy et al. 2010). Although visually striking caterpillars from both of these families often grace the covers of field guides and other texts (e.g. Tilmon 2008), much of their basic biology remains poorly understood.

Limacodidae (~1700 species, worldwide distribution) and Megalopygidae (242 species, New World distribution) are mostly tropical groups with relatively few species currently occupying temperate climates (M. Epstein unpublished data; Epstein et al. 1998). There have been few natural history observations of North American Limacodidae since a series of detailed articles written in the late 19th and early 20th centuries by Harrison Dyar. Over a period of about five years (1895–1899), Dyar (and, at the onset, his colleague Emily Morton) described the larval stages of 18 limacodid species that live in and near New York in a series of manuscripts in the Journal of New York Entomological Society (Dyar & Morton 1895, 1896; Dyar 1896a, b, 1897a, b, c, 1898a, b, c, e, 1899b, c). During the same era, Dyar compiled a few life histories of other limacodids, including four eastern species (*Adoneta bicaudata* Dyar, *Monoleuca semifascia* (Walker), *Isochaetes beutenmuelleri* (Hy. Edwards), and *Lithacodes fiskeanus* (Dyar)), one from Florida and the Gulf Coast (*Alarodia slossoniae* (Packard)), the Florida form of *Euclea delphinii* and one introduced species from Asia (*Monema flavescens* Walker) (Dyar 1896b, 1905, 1907, 1909, 1914). Most of this work involved detailed descriptions of the caterpillars, including the morphology and number of instars, larval host plants and preferred feeding sites (above or under leaves, etc.), as well as some limited information on adult flight period, mating behavior, and oviposition behavior. Research on megalopygids from eastern North America has focused more on their role in causing allergic skin reactions in humans that get stung (Delgado Quiroz 1978; El-Mallakh et al. 1986) than on other aspects of their natural history (but see Packard 1894; Dyar 1899a). Although all of the 21 described species of limacodids from the Washington D.C. area were studied by Dyar, nearly all of his information was from localities outside of the region; thus, there is very little natural history information on limacodids from Washington, D.C. and its environs.

The overall goal of our research was to investigate the natural history of moths in the families Limacodidae and Megalopygidae from the Washington, DC area. The specific objectives of this study were as follows (ordered by life cycle from adult to larva): 1) summarize data on the flight times of adult limacodid and megalopygid moths; 2) investigate the oviposition behavior of female moths, specifically their tendency to lay eggs in clusters; 3) document the phenology and host associations of locally-collected larvae; 4) develop an accurate means for assessing larval developmental stage; and 5) determine whether larval growth and cocoon weight predict lifetime fitness for females.

MATERIALS AND METHODS

Objective 1 – Adult flight times

We compiled data for the flight times of adult limacodid and megalopygid moths from three sources: 1) our own records of moths collected at lights, 2) the Lepidoptera collections at the Smithsonian Institution's National Museum of Natural History (most of which were also light-collected) and 3) collections of D.C.-area limacodids vouchered in California at the Essig Museum (University of California, Berkeley) and the Los Angeles Co. Museum of Natural History. Together, these data sets include 987 moths collected over a span of ~130 years (1883–2010) and we know the exact collection date for 981 of the moths (several records had day and month but were missing the year or had the year, but not the day or month of collection). Over this period, moths were collected in Washington DC, 38 sites in Maryland near Washington DC or Baltimore MD (Anne Arundel County, Ashton, Baltimore County, Beltsville Agricultural Research Center, Bethesda, C&O Canal National Historic Park, Cabin John, Camp Springs, Carderock, Cheverly, Colesville, College Park, Croom, Finksburg, Forest Glen, Fort Washington Park, Frederick, Glen Echo, Greenbelt, Hickory Point, Hughes Hollow, Indian Mills, Island Creek Road, Laurel, Libertytown, Little Bennet Regional Park, Millersville, Montgomery County, Oxon Hill, Patuxent National Wildlife Research Center, Pleasant Hill, Plummers Island, Prince Georges County, Rockville, Soldiers Delight Natural Environmental Area, Southhaven, Sycamore landing, and Temple hills), 8 sites on Maryland's eastern shore (Bishopville, Elkton, Pickering Creek Audubon Center, Pocomoke City, Sharptown, Snow Hill, Wicomico State Forest, Wittman) and 18 sites in northern Virginia (Alexandria, Annandale, Arlington, Cape Henry Seashore State Park, Chesterfield County, Dismal Swamp, Fairfax County, Falls Church, Falmouth, Fort AP Hill, Franconia, Giles County, Great Falls Park, Heathsville, Konnarock, Mount Vernon, Skyland and Turkey Run Park). Moths from these collections comprise 21 species of Limacodidae including *Acharia stimulea* (Clemens), *Adoneta bicaudata* (Dyar), *Adoneta spinuloides* (H.-S.), *Apoda biguttata* (Packard), *Apoda y-inversum* (Packard), *Euclea delphinii* (Boisduval), *Heterogenea shurtleffi* Packard, *Isa textula* (H.-S.), *Isochaetes beutenmuelleri* (Hy. Edwards), *Lithacodes fasciola* (H.-S), *Monoleuca semifascia* (Walker), *Natada nasoni* (Grote), *Packardia elegans* (Packard), *Packardia geminata* (Packard), *Parasa chloris* (H.-S.), *Parasa indetermina* (Boisduval), *Phobetron pithecium* (J.E. Smith), *Prolimacodes badia* (Huebner), *Tortricidia flexuosa* (Grote), *Tortricidia pallida* (H.-S.), and *Tortricidia testacea* (Packard). In this paper two species of *Tortricidia*, *T. flexuosa* and *T. pallida*, are treated together because the species boundaries, both from a biological and a taxonomic point of view are unclear. Moths in this collection also include one species of Megalopygidae, *Megalopyge crispata* (Packard). Two other species of Megalopygidae (*Norape cretata* and *M. opercularis*) also occur in the area, but flight data for these species were sparse and the larval data were virtually nonexistent, so they are excluded forthwith. For almost all of the collection records, we know the specific date the moth was caught whereas only about half of the moths (N = 440) have been sexed.

Objective 2 – Adult female oviposition behavior

Limacodid and megalopygid females often lay more than one egg during an oviposition bout and these 'egg clusters' vary in the total number of eggs that they contain. To investigate whether females of different species vary in the number of eggs laid per cluster, we counted the number of eggs per cluster for females of six limacodid species (*Acharia stimulea*, *Adoneta spinuloides*, *Euclea delphinii*, *Isa textula*, *Natada nasoni* and *Phobetron pithecium*) and one megalopygid species (*Megalopyge crispata*). All of the moths were from our laboratory colonies and egg counts were made over two summers (2008–2009). For two species, *A. stimulea* and *E. delphinii*, we additionally recorded the time elapsed since mating for females to begin to lay eggs, how many days they laid eggs and their adult life expectancy.

Individuals in our colonies diapaused within cocoons as late-instar larvae; we housed them in individual 0.5L deli containers (Fabri-Kal, Kalamazoo, Michigan) until they pupated and emerged in early summer. As adults emerged, we placed males and females in clear, plastic mating-chambers (60 cm^3 BugDorm-2, BioQuip,

Rancho Dominguez, CA, USA) and allowed them to mate. When possible, we isolated mating pairs while *in copula* and gently placed them in clear, plastic 1L deli containers (Fabri-Kal, Kalamazoo, Michigan) to capture the entirety of a particular female's oviposition events. After mating was completed, we removed the male and left the female to lay eggs on the sides of the container, which females normally do willingly. Limacodids prefer to lay their eggs on smooth host plants (Epstein 1988; Lill et al. 2006) and the clear plastic of both mating chambers and deli containers appeared to serve as an adequate substrate. Not all mating pairs were caught *in copula* and these females laid their eggs on the interior walls of the mating chambers. Each morning during the mating season, we identified new egg clusters, circled them and individually numbered the clusters with a Vis-à-Vis pen (Sanford, Bellview, IL), which enabled us to later count the number of eggs in each cluster. For two species, *A. stimulea* and *E. delphinii*, we were able to isolate large numbers of mating pairs from the mating chambers. Thus, we were able to investigate whether the number of eggs laid by individual females differed between these two species. We counted the number of egg clusters each female laid, the number of eggs per cluster as well as the total number of eggs laid by each female during her lifetime.

We established our lab colonies in 2004 with individuals that were collected as larvae or adults from three field sites in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD) and Rock Creek Park (Washington, DC). New individuals are added yearly to maintain the genetic diversity within colonies. Adults were collected by light trapping and larvae are found by manually searching the foliage of a variety of tree species, but we focused our efforts on six focal tree species that we are studying as part of an ongoing experiment: American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.), black gum (*Nyssa sylvatica* Marsh) and pignut hickory (*Carya glabra* Mill.).

Objective 3 – Larval occurrence on host plants in the wild

Each summer and autumn (2004–2008), with the help of numerous field assistants, we manually searched for limacodid and megalopygid larvae on the foliage of native trees and shrubs. All five of our field sites are in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD), Plummers Island (Montgomery County, MD), Rock Creek Park (Washington, DC) and the United States National Arboretum (Washington, DC). Whenever we found a limacodid or megalopygid larva, we noted the species, the date of collection and the host plant on which it was found; each larva was reared in the lab to confirm identity. The seasonal pattern of larval abundance of each species was examined graphically by plotting each species' log-abundance over time, dividing the season into two-week increments.

Objective 4 – Larval growth rates in the laboratory

In 2008 we reared *A. stimulea* and *E. delphinii* larvae on six different host plants in the laboratory in order to develop standard curves relating larval length to larval mass. It is difficult to determine which instar a limacodid or megalopygid larva is in for several reasons. First, their head capsules are hidden from view, tucked under their prothorax, which makes it impossible to measure them and monitor an increase in head capsule width as larvae grow. Secondly, larvae tend to eat their molts, so in order to determine that a larva has molted, you must either observe it as it occurs or before the larva finishes eating the molt. Finally, the number of larval instars for Limacodidae is extremely high, ranging to as many as 11, with some species known to have variable numbers of instars from 8–11 (Nagamine & Epstein 2007) that could represent differences in food quality or sexual dimorphism. Thus, establishing a simple predictor of development stage (larval mass) that can be easily measured in the field is critical.

The offspring in this experiment were from two *E. delphinii* females and hatched on June 9–10, 2008. The neonate larvae were left where they hatched for ~24 hours because if neonate larvae are handled before they successfully molt from the first to second instar, they suffer high levels of mortality; all spiny larvae molt to the second instar on their second day of life and do not begin to feed until this time (Nagamine & Epstein 2007). Once the larvae molted to the second instar, they were placed on redbud (*Cercis canadensis*), which is a plant that newly-hatched larvae are often able to feed upon easily. On June 13, 60 *E. delphinii* larvae were individually placed in 0.5L deli containers (Fabri-Kal, Kalamazoo, Michigan). Each larva was assigned to one of 6 host plants, for a total of 10 larvae per host. The host plants were American beech (*Fagus grandifolia*), white oak (*Quercus alba*), northern red oak (*Quercus rubra*), black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), and pignut hickory (*Carya glabra*). Correspondingly, the offspring of two *A.*

stimulea females hatched on June 25 and the neonate larvae were similarly placed on *C. canadensis* after they successfully molted to the second instar. On July 2, 60 *A. stimulea* larvae were moved to individual 0.5L deli containers and randomly assigned one of the same 6 host plants, for a total of 10 larvae per host. These 120 larval containers were provisioned with a moistened filter paper disc (7.5 cm diameter; VWR, West Chester, Pennsylvania) and excised foliage from the focal tree species, which was replaced as needed, at least every 2–3 days. The length and mass of each larva was measured every 7 days until the larva spun a cocoon. Length measurements were made using calipers (to the nearest 0.1 mm) and included the marginal spines present in both species. Mass measurements were made using a microbalance (to the nearest 0.01 mg; Mettler-Toledo XS-105, Columbus, Ohio).

Objective 5 – Cocoon weight as a predictor of lifetime fitness

In 2009 we were able to calculate realized lifetime fitness for individual *A. stimulea* and *E. delphinii* females. These individuals were reared during the summer of 2008 on various host plants and before we put the cocoons into growth chambers for the winter (see Objective 2 for details), we weighed each cocoon using a microbalance (to the nearest 0.01 mg; Mettler-Toledo XS-105, Columbus, Ohio). The following summer (2009) we recorded the number of eggs that each successfully-mated female laid and the number of those offspring that subsequently survived (see Objective 2 for details on how females were isolated). For *E. delphinii*, we only included females that had more than 30 larvae hatch in the analyses, but for *A. stimulea* we had fewer females and thus included any female that had more than 15 larvae hatch; we left-censored the data in this way so that only females that were motivated to oviposit were included in the analyses. This approach allowed us to estimate the realized fitness for each female and determine whether cocoon mass is related to lifetime fitness as has been demonstrated for other Lepidoptera (Slansky & Scriber 1985; Murphy 2007).

Statistical Analyses

For Objective 1, we computed species-specific descriptive statistics (median, 10th, 25th, 75th, and 90th percentiles) on the collection date (using Julian dates) from all Washington, DC and evirons adult moth collection records. In addition, Mann-Whitney U Tests (Zar 1999) were used to compare the median flight dates for four pairs of congeneric species (*Adoneta spinuloides* vs. *A. bicaudata*, *Apoda biguttata* vs. *A. y-inversum*, *Parasa chloris* vs. *P. indetermina*, and *Tortricidia flexuosa/pallida* vs. *T. testacea*) to test for evidence of temporal niche separation. For Objective 2, we log-transformed egg count data and then tested for differences in the number of eggs per cluster among species with one-way ANOVA. All pairwise comparisons between means were tested with Tukey's HSD (JMP v. 6.0.3, SAS Institute Inc., Cary, NC). To test for differences between the number of eggs and clusters laid by *A. stimulea* and *E. delphinii* females, we used two-way ANOVA with species and female as the fixed effects (JMP v. 6.0.3, SAS Institute Inc., Cary, NC). For Objectives 3, 4 and 5, we performed the correlation and regression analyses as well as ANOVA with JMP v.6.0.3. For the correlation and regression analyses we fit both linear and quadratic equations and present the best fit in the results.

RESULTS

Objective 1 – Adult flight times

The data we collected and compiled demonstrate that limacodid adults in the greater DC metropolitan area may be found flying in the field from April through early November (Fig. 2, Table 1). Table 1 lists the earliest and latest recorded flight times for each species including the year in which those specimens were collected. The median collection date for most species occurs in late summer (Fig. 2) and adult flight periods span 48–74 Julian days (the number of days between the earliest recorded date and the latest recorded date for each species). Although the adult flight periods of most of our local limacodids clearly span more than a month, the community separates roughly into three cohorts of species that tend to fly together: the 'early' cohort includes *P. geminata, T. testacea*, *A. y-inversum*, and *A. biguttata*; the 'middle' cohort includes *H. shurtleffi*, *L. fasciola, E. delphinii, P. indetermina*, *A. spinuloides*, *A. stimulea*, and *N. nasoni*; and the 'late' cohort includes *P. pithecium, P. chloris, I. beutenmuelleri, P. badia*, *I. textula*, *T. flexuosa/pallida*, and *A. bicaudata*. The single megalopygid studied, *M. crispata*, would be grouped with the middle cohort. Two species, *Monoleuca semifascia* and *Packardia elegans*, are represented by only a single individual in our dataset and so little can be assessed for the flight times of the adult stage for these species other than that they do occur in the environs of Washington DC. We note that both males and females of all species with at least 10 collection records have been collected at lights; capture of females by this method allows for obtaining larvae ex ovo.

In our locally-occurring community of Limacodidae, five congeneric species pairs occur sympatrically, many of which share the same sets of host plants. For the four

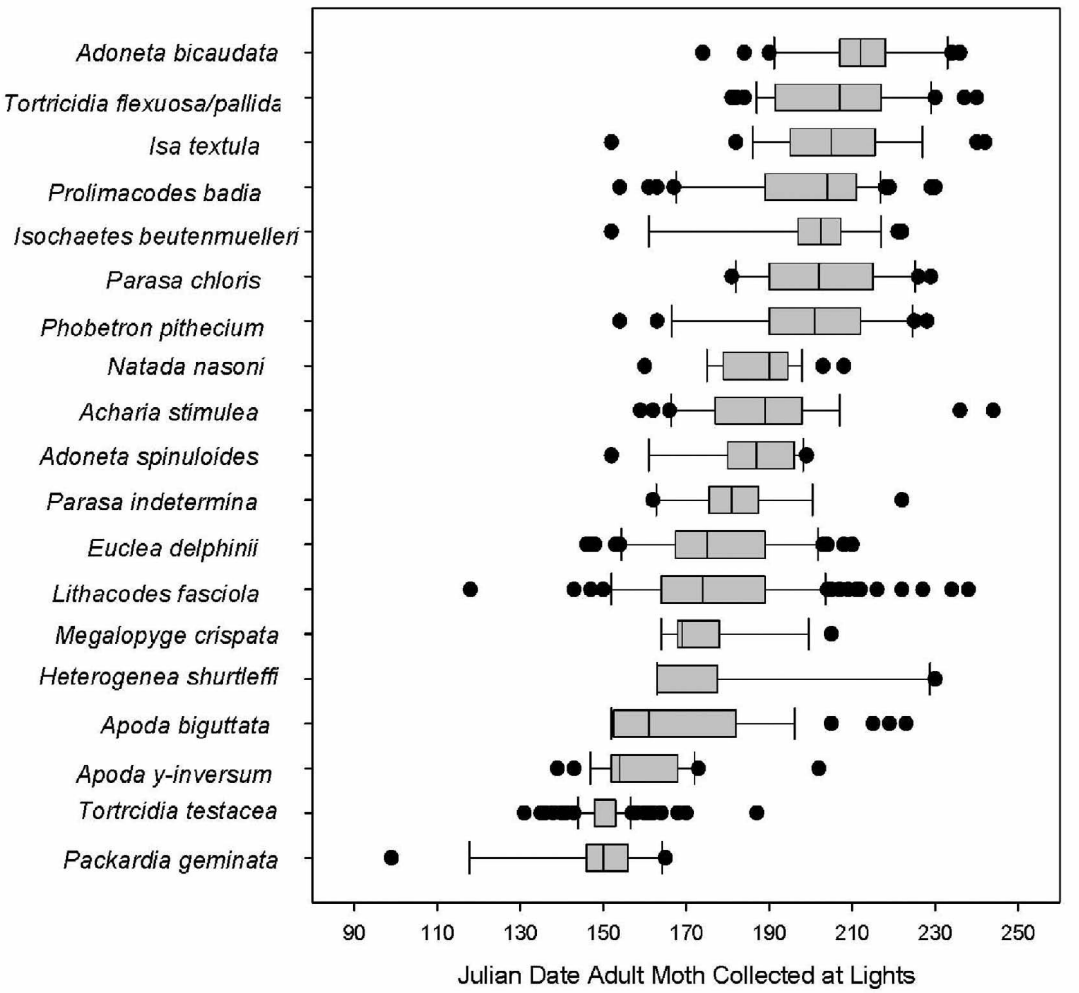

FIG 2. Seasonal occurrence of limacodid and megalopygid adults at sites in the metropolitan Washington DC area and the eastern shore of Maryland during 7 field seasons from 2004–2010 and museum collections from 1883 through 2009. From bottom to top, species are ordered by their median flight date (Julian day). Vertical lines inside of the boxes indicate the median collection date for each species, the box margins are the 25th and 75th percentiles, and error bars (whiskers) indicate the 10th and 90th percentiles. Solid circles indicate outliers. Sample sizes for each species are given in Table 1. There is one outlier data point that is not included in the figure: the latest flight date for *Adoneta bicaudata* is November 13 (Julian day 317), but it is not shown so that the other data points are more easily viewed and interpreted. There were two species that only had a single individual represented in the dataset and are thus not included in the figure: *Monoleuca semifascia* (collected on Julian day 215; 3 August 1940) and *Packardia elegans* (collected on Julian day 186, 5 July 1997).

pairs with sufficient collection data to analyze statistically, adult flight times differed significantly between each pair of congeneric taxa (*Adoneta bicaudata* vs. *A. spinuloides*, U = 756, N_1 = 30, N_2 = 27, two-tailed P < 0.0001; *Apoda biguttata* vs. *A. y-inversum*, U = 2209, N_1 = 59, N_2 = 57, P =0.003; *Parasa chloris* vs. *P. indetermina*, U = 455.5, N1 = 31, N_2 = 17, P < 0.0001; *Tortricidia flexuosa/pallida* vs. *T. testacea*, U = 13,454, N_1 = 132, N_2 = 102, P < 0.0001; compare medians of sister taxa depicted in Figure 2). Notably, most of these species pairs have very similar genitalia (both males and females; MEE, personal observation), suggesting relatively recent divergence times.

Objective 2 – Adult female oviposition behavior

For two species, *A. stimulea* and *E. delphinii*, we recorded the time elapsed since mating for females to begin to lay eggs, how many days they laid eggs and female moth life expectancy. We found that *A. stimulea* females live an average of 9.3 days (± 0.35, n=65, range=3–21 days; all variance measures are ± 1 SEM). Generally, females mate on the 2nd day after emergence (± 0.16, n=83, range=1–7 days), lay their

first egg 2.9 days after mating (± 0.32, n=72, range=0–11 days) and then lay eggs for a total of 2.9 days (± 0.26, n=72, range=1–11 days). *Euclea delphinii* females live an average of 7.6 days (± 0.36, n=37, range=4–16 days). Generally, females mate on the 2nd day after emergence (± 0.14, n=44, range=0–5 days), lay their first egg 1.6 days after mating (± 0.18, n=45, range=0–5 days) and then lay eggs for a total of 2.9 days (± 0.31, n=44, range=1–10 days).

We found that females of different species vary significantly in the number of eggs laid per cluster ($F=281.3$, df=6, $P<0.0001$; Table 2). With a mean of over 7 eggs/cluster (and as many as 85 eggs observed in a single batch), *A. stimulea* females lay significantly larger batches than any other species ($P<0.05$) and *E. delphinii* females (which average slightly more than 4 eggs/batch) lay larger batches than all of the remaining species (Table 2; $P<0.05$). The number of eggs per cluster did not differ significantly between *A. spinuloides*, *I. textula*, *N. nasoni, P. pithecium* or *M. crispata* ($P>0.05$).

There was significant variation in the number of eggs laid per cluster by individual females, even within a single species (*A. stimulea*: $F=6.7$, df=23, $P<0.0001$; *E. delphinii*: $F=33.9$, df=9, $F<0.0001$). Yet, after we controlled for this individual variation, we found that *A. stimulea* females generally laid more eggs per cluster than did *E. delphinii* females ($F=12.9$, df=1, $P=0.0003$; Table 2), similar to the results we found above when egg data were pooled across females. Although the mean number of eggs per cluster differed among females for both *A. stimulea* and *E. delphinii*, we found that neither the number of clusters ($F=1.05$, df=1, $P=0.3$) nor the total number of eggs ($F=0.06$, df=1, $P=0.8$) that were laid by individual females differed between these two species.

Finally, the incubation period (period from oviposition to larval hatching) of limacodids is approximately 7–8 days (mean = 8.74 ± 0.22 and 7.8 ± 0.37 days for *E. delphinii* and *A. stimulea*, respectively) although more detailed measures for a wider number of species under constant temperature are needed before making more general conclusions.

Objective 3 – Larval occurrence on host plants in the wild

We found limacodid and megalopygid larvae on the foliage of 19 different native plant species (Table 3). A majority of the larval species were found feeding on at least 8 different host plants; *A. stimulea*, *A. spinuloides* and *L. fasciola* larvae were each found on 10 plant species, *E. delphinii* and *N. nasoni* larvae were found on 9 plant species and *I. textula*, *M. crispata* and *P. badia* larvae were found on 8 plant species. The remaining larval species (*A. y-inversum*, *I. beutenmuelleri*, *P. chloris, P. geminata, P. pithecium* and *Tortricidia sp.*) were found on 5 or fewer plant species. We tested the possibility that host range estimates are a function of sampling effort by regressing the number of host plant species recorded per caterpillar species on the number of larval collections. We found that there was a significant, positive relationship between a caterpillar species' diet breadth and sampling effort (number of larval collections/species) ($F=10.5$, df=1, $P=0.008$).

We found limacodid and megalopygid larvae in the field from early June through early October (Fig. 3). In Figure 3, we have ranked species by abundance, which is a proxy for our confidence in the completeness of each species' records; for species with a greater number of records, the likelihood of having accurately identified their peak abundance is increased. The species for which we found larvae earliest in the year was *E. delphinii*, which was found on 13 June 2008 on *Nyssa sylvatica.* The species for which we found larvae latest in the year was *P. pithecium*, which was found on 5 October 2004 on *Quercus alba*. Larval abundances for most species peak sometime between late June and late August (Fig. 3). For the four species for which we had adequate records for both adults and larvae, we found that the larval abundances lagged behind adult abundances, typically by a few weeks (Fig. 4), as expected based on the adult life span and incubation estimates given above.

Objective 4 – Larval growth rates in the laboratory

For both *A. stimulea* and *E. delphinii* we found that larval length is a good predictor of larval mass. We found a significant correlation between the log of larval length and the log of larval mass for *A. stimulea* ($R^2=0.99$, df=1, $P<0.0001$), but significant variation could be attributed to both the host plant upon which the larva was reared ($F=7.73$, df=5, $P<0.0001$) and the interaction between host plant and log length ($F=5.97$, df=5, $P<0.001$). Despite this variation among host plants, the correlation between the log of larval length and mass remains significant and explains a large portion of the variation even when the data are pooled across host plants. From these pooled data, the following equation may be used to estimate the mass of an *A. stimulea* larva given its length:

$$(Log\ mass\ in\ mg) = -3.55 + 3.23(Log\ length\ in\ mm) \quad \text{(Eq. 1)}$$

We also found a significant correlation between the log of larval length and the log of larval mass for *E. delphinii* ($R^2=0.99$, df=1, $P<0.0001$) and neither host

TABLE 1. For each species, the earliest and latest seasonal recordings of adult flight; the year for each record is given in parentheses and the sex (M or F) is given if known; the total number of adult flight records is also given (N). These data are from sites in the metropolitan Washington DC area and the eastern shore of Maryland during 7 field seasons from 2004–2010 and museum collections from 1883 through 2009. There were two species that only had a single individual represented in the dataset and are thus not included in the table: *Monoleuca semifascia* (collected on August 3, 1940) and *Packardia elegans* (collected on July 5, 1997). Detailed statistics on flight data are given in Figure 2.

	Earliest flight date	**Latest Flight Date**	**N**
Limacodidae			
Acharia stimulea	June 8 (1900, M)	September 1 (1912)	43
Adoneta bicaudata	June 23 (1911, F)	November 13 (1987, M)	31
Adoneta spinuloides	June 1 (1975)	July 17 (2007, F)	27
Apoda biguttata	June 1 (1975)	August 11 (1993, F)	58
Apoda y-inversum	May 19 (1990, M)	July 21 (2002)	59
Euclea delphinii	May 26 (1914)	July 29 (1997 and 2005, M)	93
Heterogenea shurtleffi	June 12 (1996, F)	August 18 (2001, F)	10
Isa textula	June 1 (1930, M)	August 30 (1976)	49
Isochaetes beutenmuelleri	June 1 (2005)	August 10 (1912)	39
Lithacodes fasciola	April 28 (2002, F)	August 26 (2001)	144
Natada nasoni	June 9 (2001, F)	July 27 (2005, F)	37
Packardia geminata	April 9 (1988, F)	June 14 (1974, F)	13
Parasa chloris	June 30 (1995, M)	August 17 (1971)	31
Parasa indetermina	June 11 (1908, M)	August 10 (2003)	17
Phobetron pithecium	June 3 (1902, F)	August 16 (1912)	23
Prolimacodes badia	June 3 (1976)	August 18 (1997)	59
Tortricidia flexuosa/pallida	June 30 (1995)	August 25 (1988, F)	102
Tortricidia testacea	May 11 (2002)	July 6 (2005)	132
Megalopygidae			
Megalopyge crispata	June 13 (2009, M)	July 24 (2005, F)	12

TABLE 2. For each species, the number of eggs laid per egg cluster, the number of egg clusters laid per female and the total number of eggs laid per female are given. Data for each of these measures are presented as the mean ± SE with the range (min-max) given in parentheses. Data on eggs/cluster combine the oviposition events of a large number of lab-mated females. For a much smaller subset of two species (*A. stimulea* and *E. delphinii*), we kept track of the total oviposition events for individual females to quantify levels of intraspecific variation in both the number of cluster laid over their lifetime and total egg numbers.

Species	N Clusters (Eggs)	# Eggs/ Cluster	N Females (Clusters, Eggs)	# Clusters/ Female	# Eggs/ Female
Limacodidae					
Acharia stimulea	1423 (10,369)	7.28 ± 0.20 (1-85)	24 (946, 6,467)	39.4 ± 4.8 (1-116)	269.5 ± 27.9 (1-499)
Adoneta spinuloides	608 (1,444)	2.38 ± 0.11 (1-30)			
Euclea delphinii	1438 (5,850)	4.07 ± 0.14 (1-76)	10 (661, 3,055)	52.5 ± 9.5 (4-98)	305.5 ± 74.4 (4-618)
Isa textula	13 (13)	1.00 ± 0.00 (1-1)			
Natada nasoni	21 (21)	1.00 ± 0.00 (1-1)			
Phobetron pithecium	365 (435)	1.91 ± 0.03 (1-4)			
Megalopygidae					
Megalopyge crispata	144 (214)	1.49 ± 0.09 (1-7)			

TABLE 3. Percentage of larvae found on the foliage of various plant species at several field sites in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD), Plummers Island (Montgomery County, MD), Rock Creek Park (Washington, DC) and the United States National Arboretum (Washington, DC). Larvae were collected from 2004–2008. *=the six host plant species that were most intensively and consistently searched.

	Larval Species						
Host Plant Species	*Acharia stimulea* (N=56)	*Adoneta spinuloides* (N=89)	*Apoda y-inversum* (N=2)	*Euclea delphinii* (N=51)	*Isa textula* (N=403)	*Isochaetes beutenmuelleri* (N=50)	*Lithacodes fasciola* (N=160)
Acer negundo	4						1
Acer saccharinum	7						
Acer sacharum					1		1
Amelanchier sp.		2		4			
Asimina triloba	5	1					
Carpinus caroliniana							
*Carya glabra**	7	6	100	10	4		11
Cercis canadensis				2			1
Diospyros virginiana		1		2			
*Fagus grandifolia**	13	30		14	32	50	57
Lindera benzoin	4						
*Nyssa sylvatica**		5		8	1		3
*Prunus serotina**	4	1		23	3		8
*Quercus alba**	30	7		8	28	6	4
Quercus montana		1			10		
*Quercus rubra**	21	46		29	21	44	13
Quercus velutina							1
Robinia pseudoacacia	5						
Vaccinium sp.							

	Larval Species						
Host Plant Species	*Megalopyge crispata* (N=31)	*Natada nasoni* (N=164)	*Packardia geminata* (N=26)	*Parasa chloris* (N=39)	*Phobetron pithecium* (N=9)	*Prolimacodes badia* (N=114)	*Tortricidia sp.* (N=25)
Acer negundo							
Acer saccharinum							
Acer sacharum							
Amelanchier sp.							
Asimina triloba							
Carpinus caroliniana		2	4				
*Carya glabra**	10	8		18		7	
Cercis canadensis	16						
Diospyros virginiana	3	1				2	
*Fagus grandifolia**	10	49	77	23	78	46	24
Lindera benzoin				3			
*Nyssa sylvatica**		10	4			7	
*Prunus serotina**	7	5			11	5	4
*Quercus alba**	48	4	4		11	8	36
Quercus montana		1				2	
*Quercus rubra**	3	20	11	56		23	36
Quercus velutina							
Robinia pseudoacacia							
Vaccinium sp.	3						

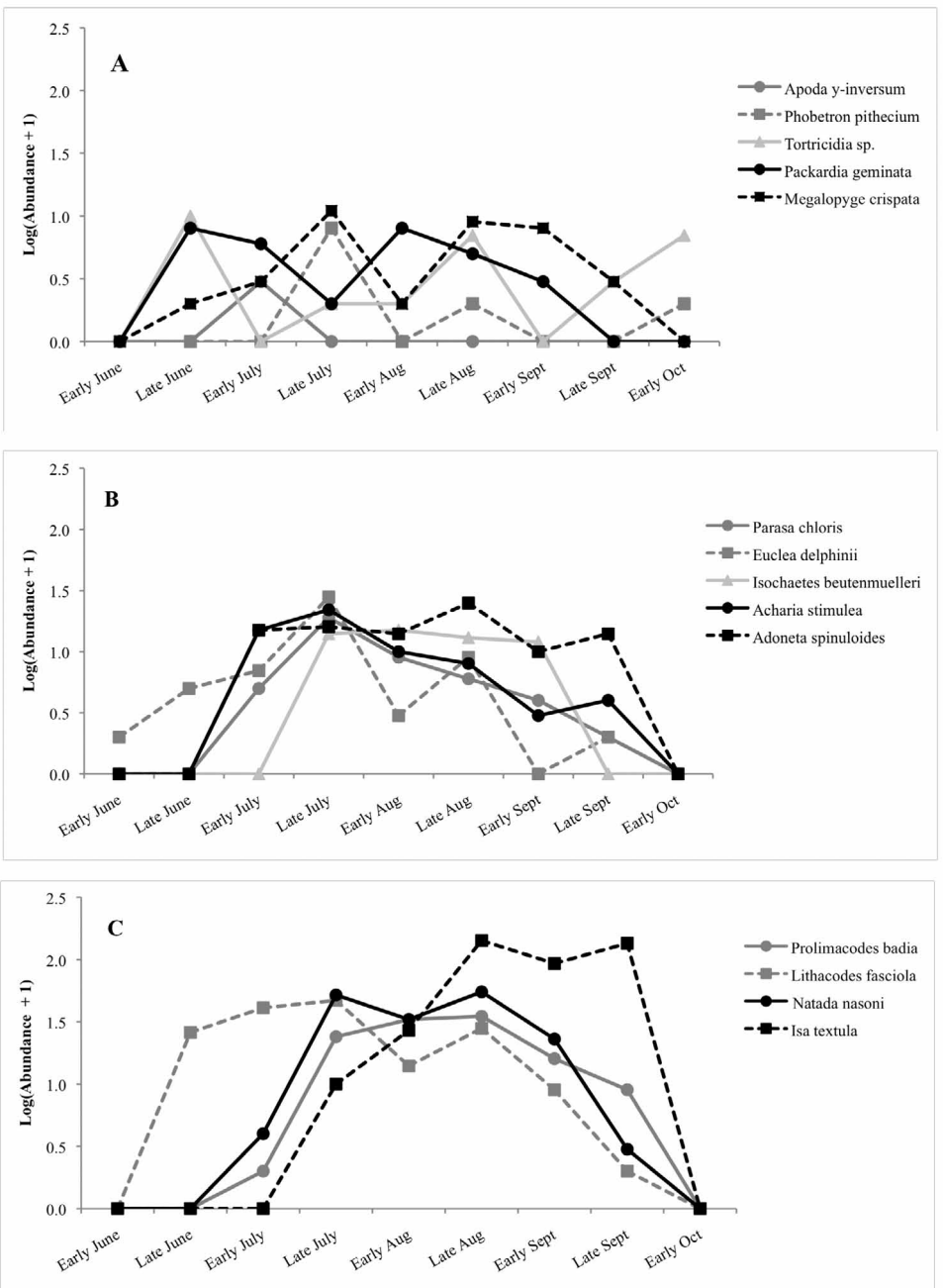

FIG. 3. Seasonal occurrence of limacodid and megalopygid larvae at sites in the metropolitan Washington DC area during 5 field seasons, from 2004–2008. Species are listed in order of abundance, which is a proxy for our confidence in the completeness of each species' records; for species with a greater number of records, we feel more confident that we have more accurately identified their peak abundance. **A**) Relatively uncommon species (*Apoda y-inversum*, N=2; *Phobetron pithecium*, N=9; Tortricidia spp., N=25; *Packardia geminata*, N=26; *Megalopyge crispata*, N=31). **B**) Moderately common species (*Parasa chloris*, N=39; *Euclea delphinii*, N=49; *Isochaetes beutenmuelleri*, N=50; *Acharia stimulea*, N=56; *Adoneta spinuloides*, N=88). **C**) Relatively common species (*Prolimacodes badia*, N=113; *Lithacodes fasciola*, N=160; *Natada nasoni*, N=164; *Isa textula*, N=402).

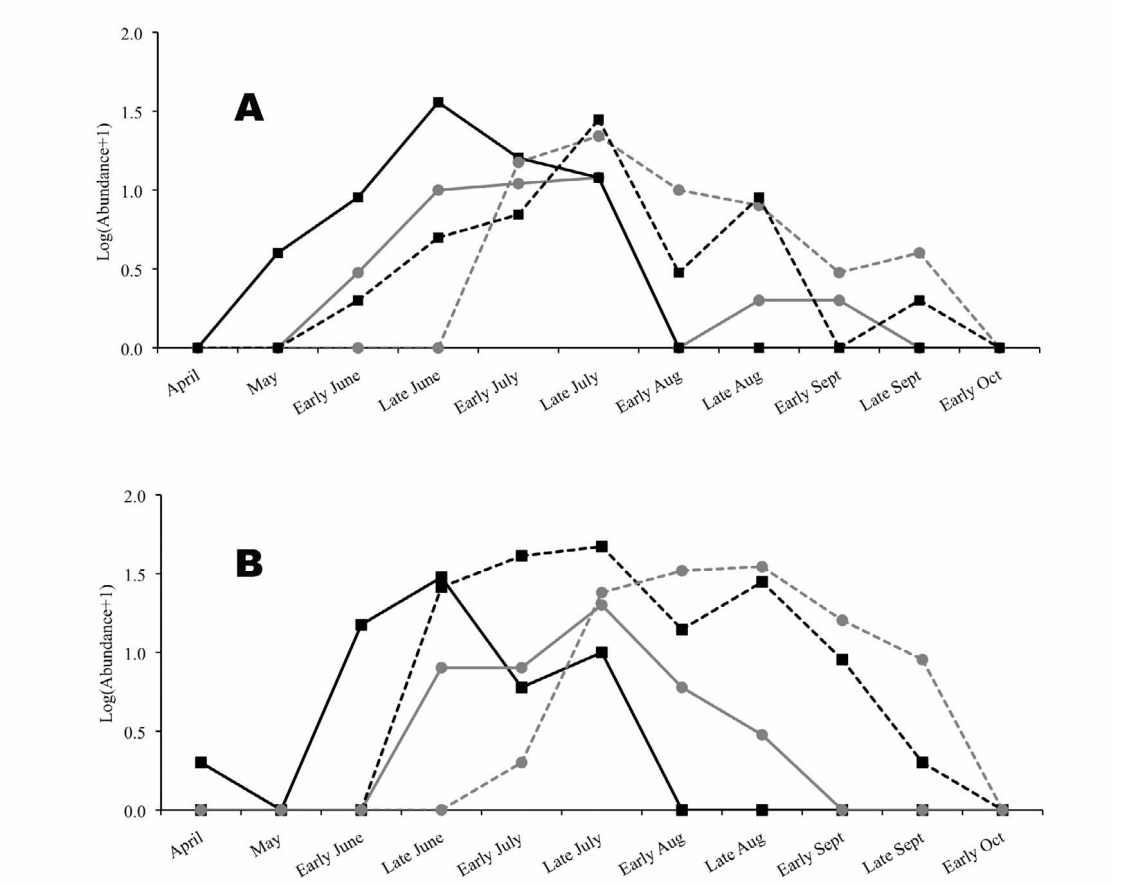

FIG. 4. Adult flight times compared to seasonal occurrence of larvae for four limacodid species. These are the same data as presented in Figures 2 and 3, but focus on the four species for which we have abundant adult and larval collection records. For all graphs, adults are solid lines and larvae are dashed lines. A) *Euclea delphinii* (black squares) and *Acharia stimulea* (gray circles). B) *Lithacodes fasciola* (black squares) and *Prolimacodes badia* (gray circles).

plant (F=0.99, df=5, P=0.42) nor the interaction between host plant and log length (F=1.28, df=5, P=0.27) were significant sources of variation in the model. Thus, given the length of an *E. delphinii* larva, we can estimate its mass with the following equation:

(Log mass in mg) = -3.01 + 2.85(Log length in mm) (Eq. 2)

Objective 5 – Cocoon weight as a predictor of lifetime fitness

We found that for both *A. stimulea* and *E. delphinii*, there was a positive relationship between a female's cocoon mass and the number of offspring she produced the following year. In other words, females that weigh more as final-instar larvae tend to have greater lifetime fitness than females that weigh less. For *A. stimulea* the relationship is nearly significant and explains 33% of the observed variation (Fig. 5; N=11 females, R^2=0.33, F=4.38, P=0.06). For *E. delphinii* the relationship between female cocoon mass and the number of viable offspring is less strong, but still positive (Fig. 5; N=23 females, R^2=0.1, F=2.27, P=0.15).

DISCUSSION

Here, for the first time in over 100 years, we compile additional information on the natural history of limacodid and megalopygid species found in eastern North America. Notably, this is the first natural history review for species found near metropolitan Washington D.C. Our findings support much of what has been commonly assumed about the biology and life histories of these species, but we have also discovered some new patterns that were not previously recognized in the literature.

Adult Life Stage

Most limacodid and megalopygid species are thought to be univoltine in temperate regions and, indeed, most of our data support this assertion. It's difficult to

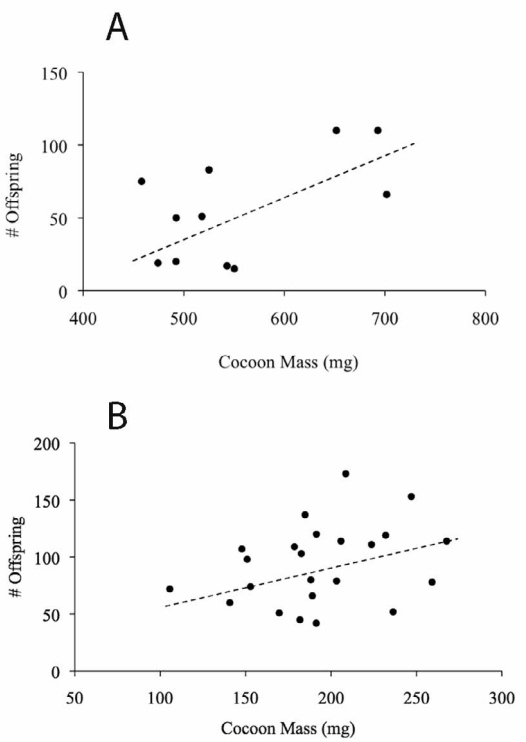

FIG. 5. Correlations between cocoon mass and the number of offspring for each female. A) *Acharia stimulea* (N=11 females, R2=0.33, F=4.38, P=0.06). B) *Euclea delphinii* (N=23 females, R2=0.1, F=2.27, P=0.15).

conclude too much from this dataset, however, because much depends on when the sampling was conducted; our records span ~130 years, but the sampling was not conducted systematically and indeed there are several decade-long gaps in the dataset (e.g., there are no records from 1918–1930 or 1945–1967) as well as spotty collecting efforts within particular years. Since 2000, collections in the DC area have been conducted more frequently and in the future it would be very helpful to devise a more systematic sampling scheme so that flight patterns could be elucidated more easily. For instance, we have anecdotal evidence that *E. delphinii* may be facultatively bivoltine, with a partial second flight in September (G. Shlichta, personal communication), but we did not include these observations in our dataset because exact dates remain unknown. As populations south of Washington, DC are reported to be multivoltine (MEE, personal observation) the partial second generation observed for *E. delphinii* may also occur in other species (e.g., *A. bicaudata*, which has a very late flight record; Table 1) and requires further investigation.

Because this community of moths is largely sympatric and the larvae occupy the same habitats (and even share many of the same host plants), there exists the potential for hybridization among closely related species (i.e., congeners or sister taxa). To our knowledge, hybridization in North American Limacodidae has not been explored, but we found it rather striking that each of the four congeneric pairs of moths in our adult dataset occupies a distinct (statistically significant) temporal window from its closest relative. Moreover, for the fifth congeneric pair, which was not compared statistically (*Packardia geminata* vs. *P. elegans*) due to a sample size of one adult collected for *P. elegans*, the median collection dates differ by more than a month (36 days), which supports the highly significant pattern of temporal niche separation in the other four congeneric pairs. Phenological separation among related taxa in sympatry has been viewed as a potentially important prezygotic reproductive isolating mechanism that either promotes or maintains species boundaries (MacArthur & Levins 1967). Most of these sister taxa also have almost indistinguishable genitalia, suggesting the observed temporal separation may serve to limit hybridization. Examination of more sympatric pairs of congeners (i.e., in the tropics where there is greater phylogenetic diversity within Limacodidae) and laboratory mating trials between congeners are necessary to test the generality of these findings.

We have found that in the lab, *A. stimulea* and *E. delphinii* females live about a week (9.3 days and 7.6 days respectively), but *A. stimulea* females in particular can live much longer as evidenced by several females who survived ~3 weeks in the lab; these data are likely upper bounds of adult lifespan in the wild, which is expected to be shorter due to predation and other stochastic events. Limacodid and megalopygid males and females mate most often at night, and the nuptial coupling normally lasts ~8–48 hours (JTL and SMM, personal observations). A notable exception is *Phobetron pithecium*, which we have found mating during daylight hours (JTL personal observation). Diurnal flight in this species is also suggested by a collection record of a male *P. pithecium* in a malaise trap (LACM: Colesville, MD, coll. Scott Miller, Aug. 1979) and an even sex ratio at light traps (both for *P. pithecium* in our study (data not shown) and for *Phobetron hipparchia* (Cramer) in Costa Rica (MEE, unpublished data)). This is the only temperate limacodid in the New World that exhibits sexual dimorphism in adult color patterning; males have clear patches in their wings and are thought to mimic wasps, which suggests daytime activity.

During mating, limacodid females prefer to hang from the substrate (leaves, twigs, branches or the mating chamber wall) by their front tarsi where they

apparently 'call' for males. Once males locate the females, the male 'climbs' down the hanging female and copulates with her while hanging from his engaged abdomen. We've found that *A. stimulea* and *E. delphinii* females typically mate on the second day after they emerge and usually begin to lay eggs a day or two later and continue to lay eggs for about 3 days. Anecdotal evidence from lab-mated *L. fasciola, P. pithecium* and *M. crispata* suggest a similar pattern and this pattern was also noted for *H. shurtleffi* in Dyar (1898d).

Female limacodids appear to be very fecund and are able to lay a considerable number of eggs over the course of their lifetime; *A. stimulea* and *E. delphinii* females averaged 270–300 eggs per female, but some females laid >500 eggs! Limacodid species vary in whether females lay eggs in batches or as singletons, as noted by Dyar & Morton (1895) in their general comments about that family. We found that some species, such as *I. textula*, *N. nasoni,* and *P. pithecium*, usually laid eggs singly, which corresponds with previous studies except that *N. nasoni* has been reported to lay eggs either singly or in small groups (Dyar 1899c). We found that *A. spinuloides* did not differ in the mean number of eggs laid per batch from these singleton species, but its variation was much greater and females sometimes laid several dozen eggs in one batch, which the other singleton species never did; Dyar (1897a) also noted that *A. spinuloides* females sometimes laid batches of 2–10 eggs. Non-quantitative, observational evidence from ovipositing females in the lab suggest that *Tortricidia* spp., *P. geminata, and P. badia* lay eggs singly, which supports earlier observations by Dyar (1896a, 1898a, b, c). Two field collections of egg clusters of *P. chloris* suggested that this species lays eggs in small clusters of 2–3 eggs, which is again consistent with Dyar (1897b) who reported that this species laid eggs singly or in small group of a few eggs. In contrast, two of the limacodid species that we studied, *A. stimulea* and *E. delphinii*, usually laid eggs in batches. In the case of *A. stimulea*, this corresponds well with field observations of the larvae (and indeed other *Acharia* species from the Neotropics), which commonly form feeding aggregations (JTL and MEE personal observation). Our observation of batch-laid eggs of *E. delphinii*, not correlated with feeding aggregations as in *A. stimulea*, does contradict the findings of Dyar (1897b), who reported eggs laid "singly, or but few together, not in … large patches of *Sibine* (=*Acharia*)." Even larger feeding aggregations of spiny, aposematic limacodid larvae have been reported in several Australian species, including *Doratifera casta* (Reader & Hochuli 2003).

These results suggest a possible causal link between clutch size and 'spiny-ness' as the species with the brightest, aposematic coloration (and often the worst stings) tend to be batch-layers while the more cryptic species tend to lay solitary eggs. Group-feeding often accompanies aposematism and is hypothesized to enhance the warning signal (Gamberale & Tullberg 1998). One locally-occurring species, *Parasa indetermina* (known as the 'stinging rose caterpillar', Wagner 2005) has highly aposematic larvae compared with its congener, *P. chloris*, whose larvae are quite cryptic. Based on this line of reasoning, we might predict that *P. indetermina* lays its eggs in batches, which is supported partially by Dyar's (1897a) report that this species lays eggs "singly or in small batches." Alternatively, it has previously been suggested that clutch size and 'spiny-ness' may also be related to whether or not larvae feed during the first instar; spiny caterpillars do not feed during the first instar while limacodids that become smooth (= gelatines) after the first instars or retain first–instar tubercles (e.g., *Phobetron*) do feed during the first instar (Nagamine & Epstein 2007). Although the adaptive significance of this is currently unclear, it is possible that the batch-laying, spiny caterpillars may avoid feeding in the first instar to prevent them from consuming the eggs containing adjacent siblings. Furthermore, these first instars can be thought of in the same way as other stadia, which cease feeding prior to molting: the only difference is that it occurs soon after eclosion. The delayed development of the plentiful sharp spines into the second instar may additionally serve to prevent the eggs, which have among the thinnest chorions in Lepidoptera (Epstein 1996; Nagamine & Epstein 2007), from rupturing. Comparative study of the oviposition behaviors of a wider sample of species within a phylogenetic framework is clearly necessary to test these hypothesized links.

Larval Life Stage

Limacodid and megalopygid larvae utilize at least 19 native plant species in the environs of Washington DC. Most species in our study fed on at least 8 different host plants. Our statistical analyses indicate that the actual host range is likely to be much greater as we found a positive linear relationship between the number of larvae found and the number of host plants utilized. Thus, our records for the number of species utilized by these generalist herbivores are likely conservative and would increase with continued sampling. Further, we have only been studying and rigorously searching native plant species for limacodid and megalopygid caterpillars, but we know from haphazard sampling that they are also found on introduced exotic species. For instance, we have found *A. stimulea* caterpillars on Mongolian oak (*Quercus mongolica*) and an ornamental

baobab houseplant that one of our colleagues placed on her porch one summer; *A. stimulea* is perhaps the most polyphagous of all of the eastern limacodids given the large number of unusual host records, including woody plants, vines (English ivy) and even corn (Forbes 1905; Wagner 2005). These anecdotal collection records on exotic species emphasize that our approximation of the number of host plant species utilized by limacodids is likely an underestimate as many species may also be using introduced plants as hosts as well.

We note, however, that one species, *Apoda y-inversum*, has only been recorded feeding on the genus *Carya* (hickories; Junglandaceae), both in our larval sampling and in Dyar's records from a century ago. While our larval sampling for this species is embarrassingly poor (N = 2 larvae collected in 6 years of sampling), finding a specialist species in this group of broadly polyphagous caterpillars would indeed be notable and worthy of further study.

Limacodid and megalopygid larvae can be found in the field near Washington D.C. from early June through early October, with peak abundances from late July through August. As such, these larvae are characterized as 'late-season' caterpillars that feed almost exclusively on the rather tough, low quality foliage characteristic of this time of year (Lill et al. 2006). *Isa textula*, in particular, is one of the most abundant larvae collected in the late fall and caterpillars are frequently found feeding on leaves in the midst of turning color in late October right up until leaf drop (JTL and MEE, personal observations). For the four species for which we have adequate sampling of both adults and larvae (*A. stimulea*, *E. delphinii*, *L. fasciola* and *P. badia*) the peak larval abundance is within a month of the peak adult abundance, but usually lags by a few weeks. The large temporal spread for larval collections likely results from environmental variation in both adult emergence time and larval development time, the latter of which is strongly related to host plant quality, which is highly variable among plant species (e.g., development time for *A. stimulea* larvae reared on red oak can be up to a month longer than larvae reared on black cherry; JTL and SMM, unpublished data). While our collection efforts for limacodid larvae are systematic and quantitative, this is not true for the adult flight data and more systematic sampling for adults in flight should be pursued in the future.

As determination of larval instar is difficult for both limacodids and megalopygids (for the specific reasons, refer to Objective 4 in the methods section), we often record body length and mass as estimates of developmental stage in laboratory experiments, instead of the more traditional measure of head capsule width. However, for field experiments, larval mass is not feasible to measure and so we wished to learn whether we could use larval length to approximate larval mass. Indeed, we found that we could estimate larval mass quite accurately given a measure of the larva's body length for both *A. stimulea* and *E. delphinii* (Equations 1 and 2, respectively). These equations facilitate the measurement of relative growth rate in field situations where obtaining accurate measurements of mass can be a challenge.

Limacodid larvae are known for their interesting morphologies and behavior. Species that possess stinging spines are well defended against a variety of predators (Murphy et al. 2010), but the effectiveness of the spines against predators appears to be increased by larval behavior. For example, when *A. stimulea* larvae are attacked by predatory paper wasps, they tend to rock back and forth in order to 'aim' their spines directly towards the offending predator and prevent access to the more vulnerable central portion of their dorsum (JTL and SMM, personal observations), but this behavior has not yet been fully studied. The biochemistry of the caterpillar's venom is not well understood, but the toxin is thought to be a protein (Foot 1922). Even some of the 'cryptic' species, which do not possess stinging spines, appear to still be chemically defended. Larvae of *Prolimacodes badia* are rather cryptic, but when disturbed they secrete droplets of fluid from pores on the dorsum (Patton 1891; Epstein 1996); however, both the effectiveness and the chemistry of this putative defense remains to be tested. Other species that are purported to have stinging spines (e.g., *Phobetron pithecium* and *Isochaetes beutenmuelleri*) have failed to yield a response in limited lab trials (JTL personal observation; Dyar 1896a; Wagner 2005). Incidentally, both of these species possess spines on deciduous tubercles that can be removed without noticeably harming the caterpillars and are regenerated when lost in early instars; in *P. pithecium* these tubercles are incorporated into their cocoons (Epstein 1996).

At the end of the larval stage, limacodid and megalopygid larvae spin cocoons in which they diapause as prepupae (Epstein 1996). They generally pupate within their cocoon the following spring and then emerge as adults shortly thereafter. Assessing the evolutionary fitness of larvae reared in the lab or in the field is a time consuming prospect because one must wait until the following year when the moths emerge, allow the adults to mate, allow females to lay eggs and then care for the eggs until they hatch and the surviving larvae may be counted. Often, however, pupal or cocoon mass is used as a predictor of lifetime fitness (the

number of surviving offspring from a single individual female) for other species of Lepidoptera (Slansky & Scriber 1985), but this relationship has not been studied in limacodids. We found that for both *A. stimulea* and *E. delphinii*, there is a positive relationship between a female's cocoon mass and the number of offspring she produces the following year. In other words, it appears that a female's realized fitness is a function of her cocoon mass. Although this relationship was only marginally significant for *A. stimulea*, it explained a large portion of the variance. One likely explanation for the lack of significance so far is our limited sample size; collecting these types of data is difficult and time consuming and we plan to continue with these efforts this year to see if the patterns hold.

Here we have documented the current state of the natural histories of North American Limacodidae and Megalopygidae for the first time since Dyar's series of papers in the 1890s. While we have a fairly detailed understanding of the phenologies of adults and larvae for multiple species, the oviposition behaviors of a few species, and the larval growth rates for an even smaller set, there is still quite a bit that we do not currently know about these charismatic species. For instance, a modern, species-level phylogeny is lacking for the group, which makes it difficult to perform research that requires a phylogenetic context. Such a phylogeny could be used to examine the evolution of the variety of defensive traits employed by different limacodid species that range from crypsis to aposematism. Because it appears that limacodid species that are physically defended with stinging spines are also the species in which females tend to lay eggs in clusters (Nagamine & Epstein 2007), it would be very interesting to study the relationship between larval defense mechanism and oviposition behavior of adult females. We are also interested in mapping key ecological associations (e.g., host-plant and host-parasitoid associations) onto such a phylogeny to investigate whether these ecological factors may have played a role in patterns of herbivore diversification. Finally, studying the chemical basis of the sting bestowed by stinging spines is yet another area of research about which almost nothing is known for these species. In sum, while we have added significantly to our understanding of limacodid and megalopygid natural history, there is still much more to be learned.

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