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Visitors to Southeastern Hawkmoth Flowers

Sean P. Graham*

Abstract - Despite global concern for the status of animal pollinators, studies on pollination systems in the southeastern United States are disproportionately low compared to the diversity of this region. For example, sphingophilous, or hawkmoth-attracting plants, occur in the southeastern US, but confirmation is lacking for the large, long-tongued hawkmoths predicted to visit these flowers by previous researchers. *Hymenocallis coronaria* (Shoals Spider Lily, or Cahaba Lily), *H. occidentalis* (Woodland Spider Lily), *Oenothera biennis* (Common Evening Primrose), and *O. grandiflora* (Large-flowered Evening Primrose) were studied to confirm this prediction. *Manduca rustica* (Rustic Sphinx) was confirmed as a frequent visitor to all four plant species studied. *M. sexta* (Carolina Sphinx) was confirmed for three of the four plants. To determine the range of animal visitors to these plants, three of the plant species were observed during day- and night-observation periods, and total visitation was compared between these times. For *H. coronaria,* flower-visitation rates did not differ between day and night periods. *H. occidentalis* and *O. biennis* were visited significantly more during night hours than during the day. Although hawkmoths are frequent visitors to *H. occidentalis* and *O. biennis*, and are probably their most efficient pollinators, *Archilochus colubris* (Ruby-throated Hummingbird) may also play a role in the pollination of *H. coronaria*.

Introduction

Recent concern for the loss or decline of animal pollinators and this phenomenon's possible impact on plant populations, environmental integrity, and human welfare, make descriptive studies of pollination biology necessary (Cane and Tepedino 2001, Kremen and Ricketts 2000, National Research Council 2007, Watanabe 1994). Even faunal lists of visitors and pollinators have the potential to advance our understanding of this globally important mutualism by providing baseline information for more theoretical or long-term studies (National Research Council 2007). Unfortunately, especially considering the exceptional biodiversity of this species-rich region of North America (Odum 2002), studies on southeastern US species are few (for exceptions see Fenster and Dudash 2001, Irwin and Adler 2006, Motten 1986).

Studies of pollination biology lead to the recognition of consistent trends among floral traits, including those referred to as pollination syndromes. Pollination syndromes are suites of floral characteristics which are apparently adapted to attract specific pollinators, and are classically thought to represent cases of recurring co-evolution between plants and pollinators with specific behavioral and morphological proclivities (Proctor et al. 1996). The pollination-syndrome concept has been criticized

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based on the repeated finding that many plants with apparently specialized morphologies corresponding to syndromes are actually generalized in their attractiveness to diverse visitors (Waser et al. 1996). However, whether due to specialized or generalized attraction patterns, pollination syndromes do outline predictions and are therefore testable hypotheses. A famous example of one of these hypotheses is Darwin's (1862) prediction that the spectacularly long-spurred *Angraecum sesquipedale* Thouares (Madagascar Orchid) co-evolved with an equally incredible long-tongued hawkmoth (Kritsky 1991). Modern studies revealed several species of long-tongued hawkmoths pollinate the long-spurred orchid guild in Madagascar (Nilsson et al. 1987, Wasserthal 1997).

A review of North American hawkmoth flowers listed plants in the southwestern and southeastern US with characteristics consistent with hawkmoth pollination, listed known moth visitors and pollinators for numerous species, and provided a similar, and currently untested prediction (Grant 1983b). These sphingophilous, or hawkmoth-attracting, plants share a suite of characters which define a well-known pollination syndrome. This syndrome is characterized by 1) pale-colored flowers with nocturnal anthesis; 2) heavy, sweet, nocturnal perfume; and 3) long nectar tubes or spurs (Grant 1983b, Proctor et al. 1996). Sphingophily is common in the tropics and southwestern US, and interactions between *Manduca* moths and *Datura* species from this area are well studied (Grant 1983a, b; Raguso and Willis 2005; Raguso et al. 2003). However, Grant (1983b) concluded this review by highlighting our lack of information of species in the southeastern US which conform to this syndrome. Several plant genera of the Southeast, including *Hymenocallis* (Amaryllidaceae), *Zephyranthes* (Amaryllidaceae), *Oenothera* (Onagraceae), and *Crinum* (Amaryllidaceae), have night-blooming, large, pale flowers with long nectar tubes (>4 cm) and heavy nocturnal perfume. Thus, he predicted that several long-tongued hawkmoth species native to the Southeast (e.g., *Manduca sexta* L. [Carolina Sphinx], *Manduca rustica* Fabricius [Rustic Sphinx], *Agrius cingulatus* Fabricius [Pink-spotted Hawkmoth], and *Cocytius antaeus* Drury [Giant Sphinx]) visit these species and transfer their pollen (Grant 1983b).

Here, I test Grant's (1983b) hypothesis that southeastern hawkmoth plants are visited by these predicted species of long-tongued hawkmoths. *Hymenocallis coronaria* (Le Conte) Kunth (Shoals Spider Lily, or Cahaba Lily), *H. occidentalis* (Le Conte) Kunth (Woodland Spider Lily), *Oenothera biennis* L. (Common Evening Primrose), and *O. grandiflora* L'Hér. (Large-flowered Evening Primrose) were studied because they are among those genera predicted to conform to the hawkmoth plant syndrome, and are locally abundant, facilitating flower-visitor observations. One of these species, *H. coronaria*, is also a source for conservation concern, and therefore flower-visitation information is important from a management perspective. Finally, I compared the range of diurnal and nocturnal visitors to three of the plant species to estimate the relative importance of hawkmoths as potential pollinators.

Methods

Study Areas

Hymenocallis coronaria visitor observations were conducted at Yellowjacket Shoals (32.87521°N, 84.410031°W) and Hightower Shoals (32.810056°N, 84.401047°W) on the Flint River in west-central Georgia. These shoals contain hundreds of *H. coronaria* individuals, and during peak bloom (see below), thousands of flowers can be observed. Observations of *H. occidentalis* took place in the floodplain forest of Choctafaula Creek in Tuskegee National Forest, Macon County, AL (32.490048°N, 85.603969°W). *Oenothera biennis* were observed along County Road 53 in Macon County, AL (32.514118°N, 85.610238°W), which is <2 km from the Choctafaula Creek site. *Oenothera grandiflora* were observed at three localities: along Florida State Road 85, Okaloosa County, FL (30.742161°N; 86.564364°W), along Byrne Lake Landing Road, Baldwin County, AL (30.794004°N, 87.891685°W), and along Alabama State Road 225, Baldwin County, AL (30.893665°N, 87.855374°W). Both *Oenothera* species are found sympatrically in south Alabama, and *O. biennis* and *O. grandiflora* are syntopic at the Byrne Lake Landing Road site.

Studied plants

Hymenocallis coronaria is one of 15 recognized spider lily species in the southeastern US (Smith and Garland 2003), and is unique in its habitat preference for large lotic streams (Fig. 1a; Davenport 1996). The flowers of *H. coronaria* have a large corona (a membranous staminal cup; Smith and Garland 2003), with projecting strap-like perianth elements, long (4–6 cm) stamens, and a 6–8 cm pistil. The corona has a long nectar tube (mean = 5.51 cm, range = 3–7.5 cm, n = 10). It blooms from mid-May through early June. Individual plants have six to ten flowers, and new flowers open in mid- to late afternoon (Patrick et al. 1995, Davenport 1996). These wither the next morning (Patrick et al. 1995) and continue to produce scent intermittently throughout blooming (S.P. Graham, pers. observ.). A previous study documented only two visitors to this species (*Battus philenor* L.

Figure 1. Growth habit and habitat of the plant species observed in this study. a) *Hymenocallis coronaria*, Yellowjacket Shoals on the Flint River, Talbot County, GA. b) *H. occidentalis*, Tuskegee National Forest, Macon County, AL. c) *Oenothera biennis*, Macon County, AL. Inset: close-up of *O. biennis* at night. d) *O. grandiflora*, Okaloosa County, FL. Scale bars = approximately 4 cm.

[Pipevine Swallowtail] and *Paratrea plebeja* Fabricius [Plebian Sphinx]), and concluded that animal pollination and clonal propagation (apomixis) are probably equally important to this species' breeding system since animal visitation is rare (Davenport 1996).

Hymenocallis occidentalis has similar flower morphology (Smith and Garland 2003; Fig. 1b); however, this species occurs in much lower population densities at a given site, and each plant can be separated from its nearest neighbor by as much as 50–100 m. It prefers sites in floodplains or wet woods (Davenport 1996, Smith and Garland 2003). It has a more widespread geographic distribution throughout southeastern floodplain forests than *H. coronaria* (Smith and Garland 2003). Anthesis was observed for three flowers on two different plants, each occurring approximately 1 h before sunset. One to three new flowers open each night, resulting in one to six flowers per plant. These flowers can remain open for at least 48 h before withering (S.P. Graham, pers. observ.). The nectar tube is longer than that of *H. coronaria* (mean = 8.6 cm; range = 4.9–11.2 cm; n = 9). This species blooms in late July to early August at the Alabama study area, and flowers remain open throughout the day and produce a heavy, pleasant odor that can be detected from up to 10 m away from a single plant. Scent could also be detected during daylight hours (S.P. Graham, pers. observ.). No data on animal visitors to this plant are currently available.

The genus *Oenothera* contains the highest proportion of sphingophilous species in North America (Grant 1983b, 1985). *Oenothera biennis* is the most widespread and common member of its genus in the eastern US (Cleland 1972). The tall (2 m) plants live in highly disturbed habitats and in August–October, produce four to 25 new flowers each night (Fig. 1c), which start blooming approximately 1.5 h after dark and continue opening one at a time every four to ten minutes. These flowers are closed by 0800 h the next morning. The 1–2 cm long petals are pale yellow, and the stamens and pistil protrude only one cm from the corolla. The hypanthium tube averages 4.17 cm long (range = 3.9–4.6 cm, n = 11). Ten hymenopterans, one moth, and one dipteran have been recorded as visitors to this species' flowers at a New Jersey study site (Dickerson and Weiss 1920).

Oenothera grandiflora lives in similar habitats and blooms during the same time period as *O. biennis*, but is more locally distributed in the southeastern United States. Earlier authors considered it endemic to the Mobile Bay area (Schumacher and Steiner 1993), but it is now found in surrounding areas as well (Steiner and Stubbe 1984). It has much larger flowers than *O. biennis* (up to 10 cm in diameter) and often has a stigma that protrudes approximately 1.5 cm further than the stamens (Fig. 1d). The hypanthium tube is longer than in *O. biennis*, averaging 5.72 cm (range = 5.4–6.3 cm, n = 10). The flowers of *O. grandiflora* are closed by mid-morning; however, the exact timing of their closing was not observed. A similarly sized population of *O. grandiflora* seems to produce a much heavier scent than *O. biennis* (S.P. Graham, pers. observ.). This species outcrosses extensively, although genetic analyses have demonstrated that self-pollination and hybridization with local members of the *O. biennis* complex is taking place within its historical range (Schumacher and Steiner 1993). Currently, no information regarding visitors to this species is available.

Hymenocallis coronaria, *H. occidentalis*, and *Oenothera grandiflora* were specifically predicted to be sphingophilous in Grant's review of North American hawkmoth flowers (1983b). *Oenothera biennis* was omitted from the review, probably because it is considered to be primarily self-pollinated (Cleland 1972).

Observations and collections

Observations of *H. coronaria* were conducted to determine the range of visitors during 2006–2009 for a total of 28 h (day and night). Each observation ranged from one to several hours. Daytime observations were conducted using binoculars and video camera at a distance of 20 m from one to three patches of approximately five to 20 *H. coronaria* plants (≈50–250 flowers). Night surveys in 2006–2008 were conducted using headlamps, and a red light was used during 2009. Night surveys were conducted by standing immediately alongside a patch of spider lilies, scanning the patch slowly with the head lamp with red light filter. Visitors were defined as species observed to enter the flower and feed or attempt to feed from the corona tube's opening.

For *H. occidentalis*, 50 observation hours were conducted at individual plants (day and night) in July–August 2009. Observations took place with the observer standing 10 m away from the plant, or by viewing video footage taped remotely using night-shot function. Observations of *Oenothera biennis* were conducted from August–September 2009 for a total of 45 h. These plants were initially checked at all times of the day, night, and morning to determine flowering phenology at this locality. Cameras were placed for night and morning observations (flowers are completely closed during the afternoon). Due to the distance of natural populations of *Oenothera grandiflora* from my base of operations, this species was observed for five person-hours on three nights in September 2009. Comparisons between day and night visitation were not conducted for this plant.

Attempts were made during observation hours to collect and identify at least one individual of each insect species observed to visit the above flowers using a butterfly net, and photographs were taken of subsequent visitors captured of the same species. Care was taken not to disturb the plants while capturing visitors. Animal visitors were placed into the following categories to facilitate analysis: birds, bumblebees, other hymenopterans (e.g., wasps or hornets), flies, butterflies, hawkmoths (family Sphingidae), and other moths. Contacts with stamens and/or stigma were noted for all categories of visitors and many species, and additional notes were also taken (e.g., direction of visitor travel). For certain visitor species, attempts were made to determine individual flower visitation rates by recording the number of seconds spent feeding at individual flowers. Pollen was noted when grossly apparent on moths or moth organs; however, no attempt was made to quantify or identify pollen. Moths were identified by consulting Hodges (1971) and Covell (1984). All insects collected were prepared and deposited in the Auburn University entomology collection.

Data analysis

Mean number of visitors to plant patches (*H. coronaria*) or individual plants (*H. occidentalis, O. biennis*) per hour per observation period for all visitor categories were compared between day observations (dawn to dusk) and night observations (dusk and night) using an independent-samples *t*-test (i.e., the same plants were not observed on consecutive nights in most cases). Data were normalized by increasing each mean visitation rate/observation period by a factor of one, followed by log transformation . However, to assist in interpretation, untransformed means are presented in the figures. Mean number of visits per hr/observation period for each visitor category were also calculated for each plant species, but these data were not compared statistically. Statistical analyses were performed using SPSS, with $\alpha = 0.05$.

Results

Flower Visitors

Visitor rates for the plant species observed during night and day periods are summarized in Table 1. For *Hymenocallis coronaria*, visitation rates did not differ significantly between day (from dawn up to dusk) and night (dusk and night) observations ($t_{1,\ 15} = 0.599$; $P > 0.05$; Fig. 2a). Daytime visitors were small *Bombus* sp. (bumblebees), *Archilochus colubris* L. (Ruby-throated Hummingbird), and various unidentified butterflies. Most butterflies visited too briefly to be identified or collected. Hawkmoths were common nighttime visitors; other moth species visited occasionally. Significantly more nighttime visits occurred at *H. occidentalis* ($t_{1,\ 14} = 3.857$, $P = 0.002$; Fig. 2b). One fly attempted to feed on the nectar of *H. occidentalis* on one occasion during the day, whereas hawkmoths and other moths were common visitors to this species at night. *Oenothera biennis* was also visited significantly more often at night ($t_{1,17} = 5.808$, $P < 0.0001$; Fig. 2c). Small

Table 1. Summary of diurnal vs. nocturnal visitation patterns for visitors to the studied plants. Total number of visits recorded indicated, and mean number of visits/hour/observation period indicated in parentheses. For *H. coronaria*, mean number of visits to plant patches are presented; for *H. occidentalis* and *O. biennis*, means are for individual plants. Day = dawn until dusk; Night = dusk until dawn.

	Hymenocallis coronaria		*Hymenocallis occidentalis*		*Oenothera biennis*	
Visitor categories	Day	Night	Day	Night	Day	Night
Bumblebees	36 (3.43)	3 (0.18)	0	0	4 (0.28)	0
Other Hymeopeterans	2 (0.19)	0	0	0	0	0
Fly	0	0	1 (0.07)	0	0	0
Ruby-throated Hummingbird	22 (2.1)	2 (0.11)	0	0	1 (0.07)	0
Butterflies	5 (0.48)	1 (0.05)	0	0	1 (0.07)	0
Moths	0	21 (1.24)	0	11 (0.37)	0	5 (0.16)
Hawkmoth	2 (0.19)	79 (4.65)	0	22 (0.74)	4 (0.29)	132 (4.24)

hawkmoths (possibly *Dolba hyloeus* Drury [Pawpaw Sphinx]) were day (dawn) visitors to *O. biennis*, and three bumblebees, one hummingbird, and one butterfly were also observed visiting this plant during the day. Hawkmoths were abundant visitors to *O. biennis* at night, while other moths were occasional visitors.

Bumblebees, Ruby-throated Hummingbirds (Fig. 3a–b), hawkmoths (Fig. 3c–d), and other moths (Fig. 3e) were observed to contact the anthers and stigma of *H. coronaria*, and hawkmoths and other moths frequently contacted the anthers and stigma of *H. occidentalis*, *O. biennis*, and *O. grandiflora* (Table 2). However, the rapid wing beats and large wingspan and body of Ruby-throated Hummingbirds and hawkmoths resulted in more frequent contact with these floral organs compared to other visitors.

There appeared to be interesting trends in the timing of visitation and behavior of the various hawkmoth species (Table 1). The diurnal *Hemaris thysbe* Fabricius (Hummingbird Clearwing) was observed in the evening and also during midday visiting *H. coronaria*. *Dolba hyloeus* visited both *H. coronaria* and *H. occidentalis* at dusk, consistent with previous observations that this moth is a dusk flier (Hodges 1971). *Paratrea plebeja* and *Manduca rustica* visits began ≈1 h after dark at *H. coronaria* patches and continued as late as 0100 h the following morning. *Manduca rustica* usually visited *H. occidentalis* 1–2 h after dark, and no visits were recorded by any moths after this time at these plants. Large hawkmoths (*M. rustica* and *M. sexta*) arrived at *O. biennis* as soon as the first flowers opened (≈2100 h), and *P. plebeja* begin visiting shortly thereafter. *Paratrea plebeja* and *M. sexta* were also captured visiting *O. biennis* shortly before sunrise, suggesting that visitation occurs intermittently throughout the night in this species. Hawkmoths tended to visit *H. coronaria* plants from downstream to upstream ($n \geq 20$ observations).

Two of the large, long-tongued hawkmoth species predicted by Grant (1983b) as possible visitors to southeastern hawkmoth flowers were confirmed as visitors to the study plants (Table 2). *Manduca rustica* were captured twice visiting *H. coronaria*, twice visiting *H. occidentalis*, once visiting *O. biennis*, and once visiting *O. grandiflora*; large hawkmoths with morphology consistent with this species and presumed to be *M. rustica* were also observed numerous additional times visiting each of these species.

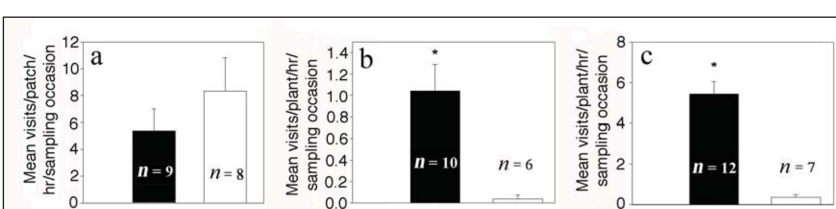

Figure 2. Mean visitation rates between night (dusk through dawn; black bars) and day (dawn up to dusk; white bars) for all visitors to *Hymenocallis coronaria* patches (a), *Hymenocallis occidentalis* plants (b), and *Oenothera biennis* plants (c). *n* = number of observation periods.

Manduca sexta was captured twice visiting *O. biennis* and once visiting *O. grandiflora*, and a hawkmoth with morphology consistent with this species was videotaped visiting *H. coronaria* (Fig. 3c).

Pollination mechanisms

The far-exerted stigma and widely-spaced anthers of *Hymenocallis* contacted the larger visitors (hummingbirds and hawkmoths) on the wings and abdomen as they oriented into the flower to feed (Fig. 3b–c; Table 2). Hawkmoths often hovered at the flowers while feeding, and during this time, their wings thoroughly agitated the stamens and stigma. Occasionally these insects simply landed at the flowers to feed. Pollen was not grossly apparent

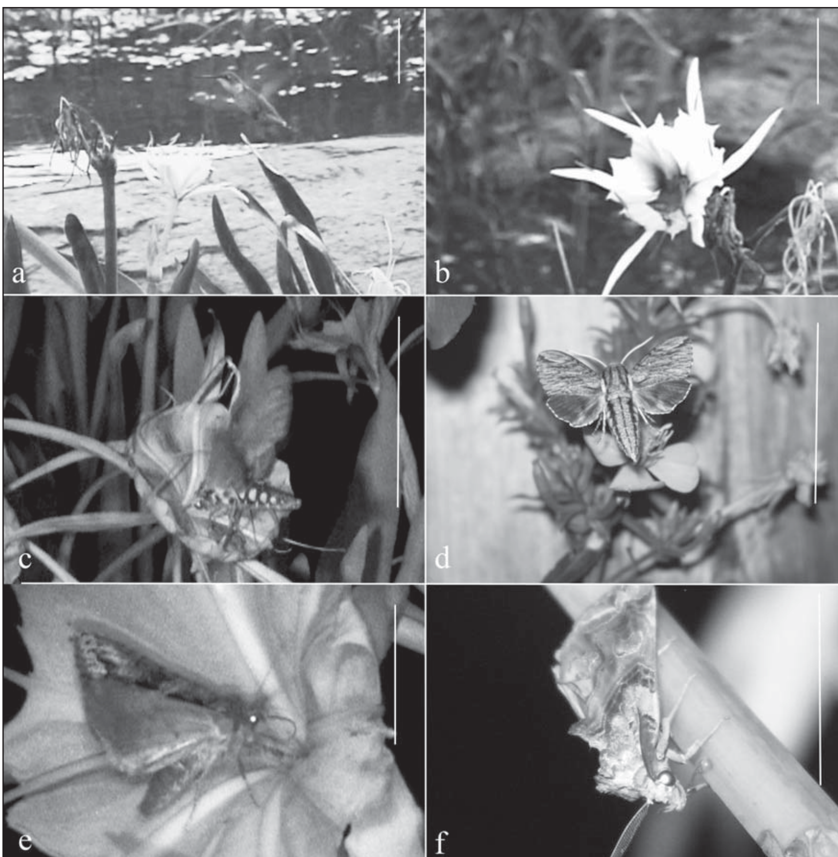

Figure 3. Visitors to southeastern hawkmoth flowers. a) Ruby-throated Hummingbird hovering over *H. coronaria*. b) Ruby-throated Hummingbird feeding from *H. coronaria*. c) Large hawkmoth (probably *M. sexta*) visiting *H. coronaria*. d) *Paratrea plebeja* visiting *Oenothera biennis*. e) Unidentified moth visiting *H. coronaria.* f) *Plusiodonta compressipalpis* (Moonseed Moth) robbing nectar from *H. occidentalis*. Images a, b, c, and e recorded at Hightower Shoals, Talbot County, GA, and d and f taken in Macon County, AL. Scale bars for a–d are approximately 4 cm; scale bars for e–f are approximately 2.5 cm.

Table 2. Summary of animal visitors to southeastern hawkmoth flowers, presented in ascending order of presumed pollination effectiveness; large species which contacted stamens and stigma most often, visited most often, and visited each flower longest are presumed the most efficient pollinators.* indicates pollinator species predicted by Grant (1983b). *H.c.* = *Hymenocallis coronaria, H.o.* = *Hymenocallis occidentalis, O.b.* = *Oenothera biennis, and O.g.* = *Oenothera grandiflora.*Day = dawn until dusk; Dusk = period between sunset and total darkness; Night = total darkness until dawn.

Common name	Latin name	Day	Dusk	Night	*H.c.*	*H.o.*	*O.b.*	*O.g.*	Stigma contact	Anther contact	Mean visit time per flower
Rustic Sphinx*	*Manduca rustica*			x	x	x	x	x	x	x	2 sec.; n = 4 plant visits
Carolina Sphinx*	*M. sexta*			x	x		x	x	x	x	
Banded Sphinx	*Eumorpha fasciatus*			x				x	x	x	
Pandorus Sphinx	*E. pandorus*			x				x	x	x	
Ruby-throated Hummingbird	*Archilochus colubris*	x	x		x		x		x	x	2.39 sec.; n = 4 patch visits
Plebian Sphinx	*Paratrea plebeja*			x	x		x	x	x	x	1.18 sec.; n = 1 patch visit
Pawpaw Sphinx	*Dolba hyloeus*		x		x	x			x	x	
Hummingbird Clearwing	*Hemaris thysbe*	x	x		x				x	x	2.42 sec.; n = 2 patch visits
Banded Tussock Moth[A]	*Halysidota tessalaris*			x		x					
Bilobed Looper Moth[A]	*Autographa biloba*			x	x						
Common Looper Moth[A]	*A. precationis*			x				x			
Tobacco Budworm Moth[A]	*Heliothis virescens*			x	x			x			
Sharp-stigma Looper Moth[A]	*Agrapha oxygramma*			x		x		x			
Bumblebees[B]	*Bombus spp.*	x	x		x		x				
Butterflies		x	x		x						
Gulf Fritillary	*Agraulis vanillae*	x					x				
Other Hymenopterans		x			x						
Flies		x				x					

[A]Moths occasionally observed to contact stigma and anther.
[B]Bumblebees rarely observed to contact stigma and anther.

on the body of most visitors to either *Hymenocallis* species. *Oenothera biennis*' stamens and pistil are equally exerted from the corolla, protrude only about one cm, and are less widely spaced than in *Hymenocallis*. The proboscides of *Manduca rustica*, *M. sexta,* and *P. plebeja* were sufficiently long for individuals to hover and feed from flowers without contacting the stamens or stigma with the wings, head, or body in many cases. However, the sticky pollen threads of newly-opened flowers adhered to the visiting moth's proboscis, and individuals of these species were observed moving between plants with large accumulations of pollen attached to this organ (see photos in Gregory 1963–1964). Hawkmoths contacted the anthers and stigma of *O. grandiflora* with their proboscis, head, abdomen, wings, and legs, and pollen accumulations were noted on these areas on the insects.

Other interactions

A few moths were observed to rob nectar from *H. coronaria* by probing their proboscis between the perianth elements from underneath the corona. *Plusiodonta compressipalpis* (Noctuidae) Guenée (Moonseed Moth) were observed robbing nectar from *H. occidentalis* on several occasions by inserting their proboscis into holes in the corolla tube near its base (Fig. 3f). Several other flowers were found with the characteristic bore holes used by this moth. *Oenothera grandiflora'*s stamens and pistil are exerted further than in *O. biennis*, and prevented small noctuid moths from contacting them; no stigma contact was observed from moths other than hawkmoths in this species. However, small moths were frequent visitors to the nectar tube opening, where they probably rob nectar.

Discussion

In this study, I confirmed Grant's prediction that southeastern plant genera which exhibit characteristics consistent with the hawkmoth pollination syndrome are primarily visited by sphingid moths. One of Grant's predicted hawkmoth species (*Manduca rustica*; Fig. 6) was observed to frequently visit *Hymenocallis coronaria, H. occidentalis*, *Oenothera biennis*, and *O. grandiflora*. Another predicted species, *M. sexta*, was confirmed as a visitor to *O. biennis* and *O. grandiflora*, and *H. coronaria* (Fig. 3c). Unfortunately, although videotaping plants was extremely useful for documenting visitation rates of different visitor categories, positive species identification was impossible for many recorded visits (e.g., color and morphology useful in identification was not discernable). I am confident that I have not determined the total number of visiting hawkmoth species to these plants.

Several other animal groups with a corresponding pollination syndrome were also observed to frequently visit *H. coronaria*. Although it could be argued that they are unable to transfer the pollen of these plants, at least one (the Ruby-throated Hummingbird) is probably an important pollinator of this species. There was no difference in day vs. nighttime visitation in *H. coronaria*, and hummingbirds frequently fed at this species and probably transfer pollen between individual plants and possibly even different populations. Hummingbirds visited during the evening, and since the flowers open before dark, it is possible that they often transfer pollen before moths do. This observation supports the view that pollination syndromes are often less predictive due to the generalized pollination patterns of most plant species (e.g., Waser et al. 1996).

For *H. occidentalis* and *O. biennis*, hawkmoths visited most frequently and contacted the stigma and anthers of these species far more frequently than any other visitor. This result is probably also true for *O. grandiflora*, whose flowers also close during the day. Despite the potential for alternative visitors in one of the hawkmoth plants studied, the syndrome is highly predictive for the species taken together. Many of the same hawkmoth species visited these plants despite large differences in blooming period, geography, habitat, density, and phylogeny (Table 1). This pattern is similar to findings from the western US, where a guild of hawkmoths visit plants from diverse phylogenetic ancestry and convergent flower morphology (e.g., Grant 1983b). Additional experiments are needed to determine the relative importance of these visitors to southeastern hawkmoth plants, and to confirm whether any of them actually transfer pollen between individuals of these plants.

The transfer of pollen by large hawkmoths (*Manduca rustica*, *M. sexta*, and *Paratrea plebeja*) and hummingbirds might explain published patterns of gene flow in *H. coronaria*. Markwith and Scanlon (2007) hypothesized downstream gene flow in *H. coronaria*, predicting stream current generally carries seeds and genetic material downstream. However, they found no evidence of this, and could not exclude zoochory or animal pollination as a possible explanation for their results, despite lack of evidence for frequent animal visitation. This paper provides evidence for frequent animal visitation in *Hymenocallis* and the potential for frequent pollen transfer among plants. Most hawkmoths visited patches of *H. coronaria* moving upstream, probably following scent trails in air currents carried downstream. This direction of pollen transfer possibly counteracts downstream movement of gene flow by hydrochory. The migrations of either hawkmoths or hummingbirds are capable of long-range pollen transfer (Raguso and Willis 2003, Williamson 2001). It is likely that hawkmoths—particularly *M. rustica*—are responsible for movement of genetic material among shoals or even among drainages, since hummingbirds have largely completed migration when *H. coronaria* is blooming (Williamson 2001).

The different visitor types between the two *Hymenocallis* species are likely linked to their habitat preferences and density. *H. coronaria* can attain very high population densities and cover an entire shoal of a large river. In this respect, they are essentially a meadow of flowers that can elicit visitation from large numbers of generalist visitors that are feeding among other plants in the area. *H. occidentalis* are less numerous, and individual plants are scattered and are therefore only visited by more specialized visitors. It is also interesting to note that the longer nectar tube length of *H. occidentalis* may exclude visitation from short-tongued bees and lepidopterans. However, this feature does not explain the lack of visitation by hummingbirds in this species, which were present in the area when they bloom. Interestingly, *H. coronaria* is one of the only North American *Hymenocallis* with a yellow spot on the staminal cup (Smith and Garland 2003), which may be a derived feature to attract visually oriented diurnal feeders. Perhaps these and other features (e.g., shorter nectar tube, earlier diel bloom time) became adaptive during the evolutionary shift to the more open shoal habitat of *H. coronaria*. Clearly, southeastern *Hymenocallis* offer an excellent opportunity for comparative research in pollination biology.

Oenothera biennis exhibits many features consistent with hawkmoth pollination, and is visited frequently by hawkmoths, yet Grant (1983b) omitted this plant from his list of sphingophilous North American species. This omission was presumably due to genetic work that determined this species as being primarily self-pollinating and producing clonal seeds (Cleland 1972, Gregory 1964). If this is indeed the case, the results of this study are surprising and suggest that a plant with a highly specialized, self-pollination breeding system has dispensed with the benefits of outcrossing via frequent hawkmoth visitation. Despite exhibiting derived features associated with self-pollination (smaller flowers, equal stamen and style lengths, clonal seed lines), the flowers of *O. biennis* still produce nectar, perfume, and viscid pollen threads similar to their sphingophilous relatives which encourage hawkmoth visitation (S.P. Graham, pers. observ.). This discrepancy begs one of two possible explanations: either *O. biennis* achieves more cross-pollination than previously assumed (e.g., Cleland 1972), or that in this area, clonal plants are robbed by insect visitors which do the plant no pollination service yet take the rewards. The abundant visitation this plant receives suggests that the plant receives some benefit, as do many other facultative self-pollinators (Proctor et al. 1996). Cleland (1972) suggested the possibility that *O. biennis* occasionally outcrosses, and that the rampant hybridization between true-breeding clonal lines in this complex is probably brought about by pollinators.

Oenothera grandiflora has many apparently ancestral features consistent with cross-pollination (larger flowers, longer hypanthium tube, and larger, unequally exerted stamens and pistil), and is also visited frequently by hawkmoths. Visits from these insects probably provide the hybridization mechanism between *O. biennis* and *O. grandiflora* reported by researchers interested in the genetics of this group (Schumacher and Steiner 1993). Both plants are common near the Baldwin County, AL study sites, and the same species of hawkmoths visit both plants. The *O. biennis* complex and *O. grandiflora* provide yet another comparative opportunity for pollination studies, and future research on these plants would benefit from an extensive amount of genetic information already available (e.g., Cleland 1972, Schumacher and Steiner 1993, Steiner and Stubbe 1984).

Further studies on these and other sphingophilous species in the southeastern US (e.g ., *Crinum*, *Zephyranthes,* and *Ipomoea* spp.) are encouraged and will likely uncover similar fascinating interactions. The results of this study provide evidence that hawkmoths are probably important pollinators for plants in the southeast which exhibit the hawkmoth plant syndrome, although other visiting species are possibly important in some cases. Similar studies are recommended by naturalists interested in our southeastern flora, and attempts should be made to determine pollination patterns of additional understudied species, which will simultaneously provide information about the plants and their visitors.

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