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Dexter R. Sowell II

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A COMPARATIVE STUDY OF THE REPRODUCTIVE  
BIOLOGY OF SYMPATRIC MORNING GLORIES  
(IPOMOEA-CONVOLVULACEAE)

Dexter R. Sowell, II



Georgia Southern University  
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**A COMPARATIVE STUDY OF THE REPRODUCTIVE  
BIOLOGY OF SYMPATRIC MORNING GLORIES  
(*IPOMOEA-CONVOLVULACEAE*)**

A Thesis

Presented to

the College of Graduate Studies of

Georgia Southern University

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In Partial Fulfillment  
of the Requirements for the Degree  
Master's of Science  
In the Department of Biology

---

by

Dexter R. Sowell, II

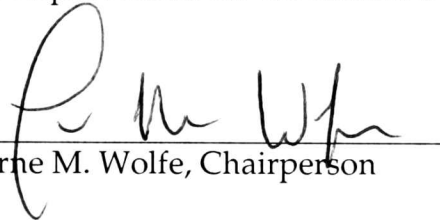
August 2001



July 3, 2001

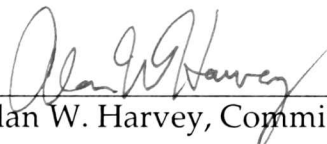
To the Graduate School:

This thesis, entitled "A Comparative Study of the Reproductive Biology of Sympatric Morning Glories (*Ipomoea*-Convolvulaceae)," and written by Dexter R. Sowell is presented to the College of Graduate Studies of Georgia Southern University. I recommend that it be accepted in partial fulfillment of the requirements for the Master's Degree in Biology.

  
Lorne M. Wolfe, Chairperson


We have reviewed this thesis and recommend its acceptance:

  
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Sowell, D. R. April 2001. Do pollination syndromes exist?: a comparative approach. Departmental Seminar, Department of Biology, Georgia Southern University, Statesboro, Georgia.

Wolfe, L. M., and D. R. Sowell. June 2001. A test of the pollination syndrome concept: what do the birds and bees say? The Society for the Study of Evolution: University of Tennessee, Knoxville, Tennessee.

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## ABSTRACT

A COMPARATIVE STUDY OF THE REPRODUCTIVE BIOLOGY OF  
SYMPATRIC MORNING GLORIES (*IPOMOEA-CONVOLVULACEAE*)

August 2001

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Directed by: Dr. Lorne M. Wolfe

Despite the astounding diversity of flowering plants and of mobile organisms that serve as pollinators, sympatric co-flowering plants can potentially share pollinators with each other. This places two selection pressures on plants. First, plants compete for pollinators to visit their flowers and secondly, entice pollinators to be faithful (specialized) and visit only other members of their species. I tested whether sympatric co-flowering plants reduced their selection pressures via temporal partitioning or differential attraction of pollinators using six closely related, sympatric co-flowering morning glories (*Ipomoea-Convolvulaceae*).

Diurnal flower phenology tightly overlapped, which did not facilitate temporal partitioning of pollinators. However, the differences in corolla color

and shape allowed for predictions of differential attraction of pollinators among the six *Ipomoea* flowers examined based on the pollination syndrome concept. Despite the recent caveats raised about the lack of rigorous fit between floral traits and pollinator fauna over large floras, the pollination syndrome concept adequately explained pollinator preferences in *Ipomoea*. As predicted, bees visited bee flowers (*I. hederacea*, *I. imperati*, *I. pandurata*, and *I. trichocarpa*), and hummingbirds and butterflies visited their respective flowers (*I. hederifolia* and *I. quamoclit*). Nectar, as predicted by the pollination syndrome concept, was of smaller volume and more concentrated in the bee flowers compared to bird flowers. Overall, bee flowers also receive much of their stigmatic pollen loads from pollen deposition by bees, whereas bird flowers received most of their stigmatic pollen loads through autogamy. Fruit and seed set were larger in bird flowers, and generally, all species had higher fruit and seed sets in 2000.

Although pollination syndromes may not adequately predict the pollinator fauna of all plants, within the *Ipomoea* model examined here pollination syndromes accurately explained pollinator preferences.



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## CHAPTER I

### INTRODUCTION

Ever since Darwin's pioneering studies with plants (1862, 1876, 1877), plants have served as model systems to study the process of evolution. The sessile lifestyle of plants, though, places a constraint on reproduction. Most angiosperms require pollinators for reproduction, so pollinators must be enticed to visit a flower for dissemination and receipt of gametes. The diversity of plants and the astonishing array of floral forms are associated with the numerous reproductive strategies and mating systems within the angiosperms. If pollinators are limiting, plants must compete for them (Waser 1978a, Rathcke 1983, Campbell et al. 1997). Competition for pollinators should lead to selection on the size or number of attractive structures or rewards offered by flowers. For example, pollinators are known to prefer larger flowers or larger displays of flowers (Galen and Newport 1987, Inoue et al. 1995, Schemske and Ågren 1995, Conner and Rush 1996, Dafni and Kevan 1997, Schemske and Bradshaw 1999) or flowers with greater rewards (Duffield et al. 1993, Cresswell and Robertson 1994, Schemske and Bradshaw 1999).

Successful attraction of pollinators is not the final determinant of reproductive success. Floral visitors vary in their effectiveness as pollinators (Ramsey 1988, Wolfe and Barrett 1989, Fenster 1991, Andersson 1994, Fishbein and Venable 1996, Olsen 1997, Lange et al. 2000), and when more than one

species is in flower, interspecific pollen deposited on stigmas can reduce reproductive success via unfertilized or aborted ovules (Feinsinger 1978, Waser 1978b, Stucky 1985). Plants, therefore, are not only under selection pressure to attract pollinators, but to encourage pollinators to be faithful in order to maximize intraspecific pollen movement.

There are several ways that co-flowering plants may increase the probability of receiving reliable and faithful pollination service. First, plants can stagger flowering time and reward offering so pollinators are partitioned (Stone et al. 1998). This temporal character displacement can occur diurnally or seasonally. Another way plants have partitioned pollinators is through differential attraction. Floral characteristics such as color (Ennos and Clegg 1983, Chittka and Waser 1997, Johnson and Dafni 1998), shape (Dafni and Kevan 1997), size (Galen and Newport 1987, Duffield et al. 1993, Inoue et al. 1995, Schemske and Ågren 1995, Conner and Rush 1996, Johnson and Dafni 1998,) and reward (e.g. nectar, pollen, oils) type (Pyke and Waser 1981, Wolfe and Barrett 1989, Duffield et al. 1993, Cresswell and Robertson 1994, Stone et al. 1998) play key roles in attracting pollinators. Selection to reduce competition for pollinators and minimize interspecific pollen movement can result in highly specialized pollination systems, in which only one or two pollinator species are used (Johnson and Steiner 1997). Plants that use the same type of pollinator (e.g. bee, hummingbird, fly, etc.) typically have flowers that have the same suite of floral characteristics, or a pollination syndrome (Faegri and van der Pijl 1979). Examples of pollination syndromes

include red, tubular flowers for hummingbird pollination (e.g. *Campsis radicans*, *Lobelia cardinalis*), flowers with visible or ultra-violet nectar guides, high nectar sugar concentration (e.g. *Delphinium* spp., *Campanula* spp.), and white, fragrant night-blooming flowers for moth and bat pollination (e.g. *Ipomoea alba*, *Yucca* spp., *Silene latifolia*). Pollination syndromes are often viewed as the product of coevolution between plant and pollinator (Grant and Grant 1965, Janzen 1980, Crepet 1983, Johnson and Steiner 1997).

Thus, plants exhibiting a specific pollination syndrome are expected to be visited by a discrete, or specialized, group of pollinator species. In contrast, plants with generalized pollination systems have flowers that are visited by a larger guild of pollinator species. Specialized and generalized pollination systems are each thought to have advantages and disadvantages (Faegri and van der Pijl 1979, Waser et al. 1996). A benefit of specialized pollination systems may be the efficient transfer of pollen. Specialized pollinators are faithful foragers and carry a higher proportion of intraspecific pollen (Feinsinger 1978, Waser 1978b), which should result in higher reproductive success. But pollinators can vary in relative abundance over time (Wolfe and Barrett 1989, Petersson 1991, Fishbein and Venable 1996, Lange et al. 2000), and the reproductive success of specialized plants should vary in time as the abundance of an obligate pollinator fluctuates. Plants with generalized pollination systems use multiple pollinator species, and are more likely to be resilient to fluctuations in the relative abundance of any one pollinator. The effects of the loss of a pollinator are dampened by the use of other pollinator

species for reproduction. Generalized pollinators typically visit multiple plant species, and thus carry both intraspecific and interspecific pollen. The maximum reproductive success of generalized plants may rarely be realized due to carryover of interspecific pollen (Feinsinger 1978, Waser 1978b, Stucky 1985). Specialized pollination systems are considered derived from generalized pollination systems (Stebbins 1970).

Despite the appeal of the concept of pollination syndromes, some biologists have questioned its relevance (Richards 1986, Herrera 1996, Waser et al. 1996). Richards (1986) notes that highly specialized flowers usually receive visits from one or a few pollinating species but that accidental pollination by other pollinators can occur. Herrera (1996) cited several lines of evidence where spatial and temporal variation in pollinator abundance and composition limits the ability of plants to specialize on pollinators that provide the best pollinator service. Selection pressure on floral traits to better fit pollinators may be outweighed by other selection pressures affecting reproductive success (Herrera 1996). Generalization may be more common than specialization based on surveys of large floras and associated pollinator fauna (Waser et al. 1996). Additionally, Waser et al. (1996) argued that since pollinators (individuals or colonies) may outlive the flowering period of their preferred species, they should visit more than one flowering species. The level of specificity of any plant's pollination system is dependent on the taxonomic level (order, family, genus, or species) that pollinators are examined (Waser et al. 1996) and time of year that a species flowers (Richards



1986). Petterson (1991) showed that *Silene vulgaris*, whose flowers fit the syndrome for moth pollination, is visited by over 26 species of moths. Johnson and Steiner's (2000) recent review led them to conclude that plants exhibit a continuum of pollination systems that range from generalized to specialized. They argue that pollinators should also be evaluated on a larger scale, such as the role pollinators play in population viability of plants, and not just in terms of the success of seed production in plants.

The overall purpose of my thesis was to investigate the reproductive biology of sympatric plant species, using a comparative approach with six species of closely related morning glories, (*Ipomoea*, Convolvulaceae). A specific goal was to evaluate whether pollination syndromes existed in the sympatric morning glories in southeast Georgia. My approach was to determine if there were differences in the pollinator fauna that visit the six *Ipomoea* species, and if these differences could be explained by flower color and nectar reward offered. The six species I chose have flowering periods that overlap extensively, and potentially compete for pollinators. I determined if there were any temporal differences in flowering that could facilitate pollinator partitioning over time, and thereby reduce pollinator sharing.

*Ipomoea hederacea*, *I. imperati*, *I. pandurata*, and *I. trichocarpa* have larger blue or white flowers, with a wide corolla throat. The remaining two *Ipomoea* species, *I. hederifolia* and *I. quamoclit*, have red flowers with a narrow corolla throat. Using the pollination syndrome concept, I hypothesized that these first four *Ipomoea* species are pollinated by bees, and the latter two *Ipomoea* species

are pollinated by hummingbirds and butterflies. Pollination syndromes allow investigators to make predictions about the floral rewards of flowers as well. Flowers typical of bee-pollination generally produce small volumes of concentrated nectar. Flowers typical of hummingbird and butterfly-pollination produce large volumes of dilute nectar. I hypothesized that the four *Ipomoea* species with larger, blue flowers (*I. hederacea*, *I. imperati*, *I. pandurata*, and *I. trichocarpa*) will produce less nectar with a higher sugar concentration relative to the two *Ipomoea* species with smaller, narrower flowers (*I. hederifolia* and *I. quamoclit*). I compared nectar reward offered, stigmatic pollen loads, and the reproductive success (fruit and seed set) of each of the six *Ipomoea* species, and compared groups of *Ipomoea* pooled by pollination syndrome.

*Ipomoea* provides an ideal model to test for pollination syndromes. Despite being closely related, the species differ in flower color and size. Any differences in pollinator fauna between the six *Ipomoea* species are due to recent evolutionary events.

**CHAPTER II**  
**MATERIALS AND METHODS**  
**Description of the Study Species**

*Ipomoea* (morning glory) is a diverse genus of 600-700 species that are centered in the tropics and warm temperate areas (Austin 1984, Austin and Huáman 1996). The *Ipomoea* species present in southeast Georgia, approximately 15 species, are annual or perennial, twining or trailing vines (Radford et al. 1968) that are self-compatible (Ennos 1981, Stucky 1985, Murcia 1990, Abbott 2000), excluding the self-incompatible *I. pandurata* (Stucky and Beckmann 1982). Most species are weedy and occupy frequently disturbed sites such as roadsides, fencerows, and the edge of crop fields. Several species occur sympatrically. Plants bloom from July to first frost and produce flowers that last less than one day. Fruits are dehiscent capsules with a maximum of four or six seeds, depending on the species. Table 1 lists flower color, flower shape, syndrome, maximum number of seeds per fruit, life history, and growth habit for six *Ipomoea* species.

I focused my research on four *Ipomoea* species due to their abundance in Southeast Georgia from 1998 to 2000: *I. hederacea* (L.) Jacq., *I. hederifolia* L., *I. quamoclit* L., and *I. trichocarpa* Ell (synonym *I. cordatotriloba* Dennst.). In 2000, I also collected data on *I. imperati* (Vahl) Griseb. and *I. pandurata* (L.) Mey. Taxonomy follows that of Austin and Huáman (1996) due to their separation of the native *I. coccinea* L. from the introduced *I. hederifolia* L. I have retained the name *I. trichocarpa* for *I. cordatotriloba*, though, according to Radford et al. (1968).

### Study Sites

I conducted most of the field studies in Bulloch County, Georgia. Field sites with multiple *Ipomoea* species within Bulloch County, Georgia included Hunter's Pointe, Hwy 80/25, Hwy 80 East, Hwy 67, Hwy 24, Howard's Lumber, and West Side Road (Table 2). I utilized three field sites with one *Ipomoea* species each; Tybee Island in Chatham County, Georgia (*I. imperati*), Youngblood Circle in Bulloch County, Georgia, (*I. pandurata*) and South Carolina Route 3 close to the Allendale/Barnwell County line, SC (*I. pandurata*) (Table 2). Although I chose six *Ipomoea* species for comparison, I did not monitor all six *Ipomoea* species for all three years. All sites were not used every year for reasons outside of my control (e.g. mowing, herbicide application, etc.). Table 2 lists all study sites, location by longitude/latitude, *Ipomoea* species present, and years sampled.

### Seasonal Flowering Phenology

I determined the seasonal flowering phenology of four *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*) over a four-month period. From August to November 1999, I made weekly surveys of three sites with *Ipomoea* (Hwy 24, Hwy 67, Hunter's Pointe) by counting all flowers at each site. Counting all flowers at a site proved to be time-consuming. In 2000, I sampled plots within *Ipomoea* sites to hasten flower censusing. I made weekly surveys from August to November at four sites with *Ipomoea*. At these four sites, I haphazardly placed 4-7 5m<sup>2</sup> plots (Hunter's Pointe-6 plots, Howard's Lumber-5 plots, Hwy 80 East-7 plots, and Hwy 80/25-4 plots) throughout the site in July as flowering began. All flowers in each plot were counted. The number of flowers for each *Ipomoea* species among all plots within a site were totaled and used as a measure of phenology at the site.

### Daily Flowering Phenology

On 25, 26, and 28 September 1999, I made hourly observations to monitor daily flowering phenology. The evening prior to observations, I clipped three to five vines of four *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*). Flowers on clipped vines open similarly to those in the field (personal observation). I chose vines that had three to six flower buds that would likely open the next morning. I estimated the degree of flower opening for a 22 hr period by assigning flowers to the following ranks:

0 : closed	5 : 51 - 63% expanded
1 : $\leq 5\%$ expanded	6 : 64 - 75% expanded
2 : 6 - 24% expanded	7 : 76 - 90% expanded
3 : 25 - 37% expanded	8 : 91 - 99% expanded
4 : 38 - 50% expanded	9 : 100% expanded

I also conducted one-time observations on the daily flower phenology of two additional species. I observed all the flowers (approximately 150) of *I. pandurata* at the Youngblood Circle site on 30 July 1999. I observed a small patch of flowers (approximately 100) of *I. imperati* at the Tybee Island site on 18 August 2000. I noted the time when flowers began opening and wilting for *I. pandurata* and *I. imperati* on their respective dates. Both days chosen for one-time observations on *I. imperati* and *I. pandurata* were typical hot summer days.

### Nectar Biology

I quantified nectar volume and sugar in six *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. imperati*, *I. pandurata*, *I. quamoclit*, and *I. trichocarpa*) at three sites (Hunter's Pointe, Youngblood Circle, Tybee Island) over six days in 2000. Shortly after sunrise and just before pollinator foraging, I haphazardly chose 15

flowers of each *Ipomoea* species and assigned to each flower one of three pollinator treatments: initial, unvisited, and visited.

**Initial** - I extracted nectar before pollinator foraging began in the *Ipomoea* site between 0630-0800 hrs. Flowers assigned to the initial treatment had no nectar removed by pollinators foraging.

**Unvisited** - I prevented pollinators from removing nectar on specific flowers by either placing bridal veil or screen mesh enclosures around specific flowers. I extracted nectar from the flowers after pollinator foraging had subsided in the community, between 1100-1300 hours.

**Visited** - The flowers were not manipulated and were available to pollinators for servicing. I extracted any available nectar from the flowers after pollinator foraging had subsided in the community, between 1100-1300 hours.

I extracted nectar from the base of the corolla with a 5  $\mu$ L glass capillary tube (micropipette). I measured the fraction of the micropipette that nectar occupied to determine microliters of nectar, and then placed nectar onto a refractometer to determine sugar concentration in percent sucrose equivalents. If nectar was too concentrated or of too small of volume to refract light properly, I added a known volume of water to make refraction possible. The original sugar concentration was estimated with the following formula:

$$\text{volume}_1 \times \text{concentration}_1 = \text{volume}_2 \times \text{concentration}_2$$

Nectar volumes and sugar concentrations were pooled across sites and days within species for a two-way ANOVA on ranks. Additionally, the six *Ipomoea* species were pooled into two groups by their pollination syndrome, bee flowers (*I. hederacea*, *I. imperati*, *I. pandurata*, *I. trichocarpa*), and hummingbird and butterfly flowers (*I. hederifolia*, *I. quamoclit*), hereafter called bird flowers. Nectar volumes and sugar concentrations were pooled within their syndromes and

analyzed by a two-way ANOVA on ranks of nectar volume and sugar concentration to determine if there were differences among nectar volume and concentration among these two groups, as a pollination syndrome would predict.

### **Pollination Biology**

I studied the pollinators of six *Ipomoea* species at eight sites (Brannen Street, Howard's Lumber, Hwy 24, Hwy 67, Hwy 80 East, Hwy 80/25, Hunter's Pointe, Railroad) over a three-year period (1998-2000). I was specifically interested in which pollinators visit the six *Ipomoea* species to see if the different pollinator types specialize on a different colored *Ipomoea* species. In other words, is floral selection random with respect to the *Ipomoea* species? To statistically compare the observed to the expected visitation, I performed weekly counts of the flowers available to pollinators where pollinator data was collected to obtain the relative abundance of flowers of each *Ipomoea* species present.

In 1998 I collected pollinator data from a single site, Hwy 24. I observed individual pollinators foraging in the community. I noted the type pollinator (bumblebee, sulphur butterfly, etc.) and the species of the first *Ipomoea* flower visited. Using only one flower per pollinator to test for preferences reduces the non-independence of samples (using multiple flower visits by any one pollinator). Later, I compared the number of flowers that pollinators visited to the number of flowers available. In 1999, I collected pollinator data at six sites (Brannen Street, Howard's Lumber, Hwy 24, Hwy 67, Hunter's Pointe, Railroad) from August to November. I used the same methodology as in 1998. In 2000, I collected pollinator data weekly at four sites (Howard's Lumber, Hwy 80 East, Hwy 80/25, Hunter's Pointe) from August to November. I compared the

frequency of flower visits of pollinators to the six *Ipomoea* species and then compared the pollinators to groups of *Ipomoea* pooled by flower color.

### **Stigmatic Pollen Load**

I estimated the importance of pollinators as pollen carriers by quantifying pollen deposition in 2000. I quantified the amount of pollen on the stigma, or stigmatic pollen load, for six *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. imperati*, *I. pandurata*, *I. quamoclit*, and *I. trichocarpa*) at five sites (Hwy 80 East, Howard's Lumber, Hunter's Pointe, Youngblood Circle, Tybee Island). I used three treatments to determine the amount of pollen on stigmas before and after anthesis, and the importance of pollinators for pollen import. I haphazardly chose 15 flowers from each *Ipomoea* species present shortly after sunrise (see next paragraph for methods specific for *I. pandurata*). I haphazardly assigned to each flower one of the three pollinator treatments.

**Initial** - I removed pistils before pollinator foraging began in the *Ipomoea* community between 0630-0800 hrs. Flowers assigned to the initial treatment had no pollen on their stigmas due to pollinators, and any pollen present was from autogamy.

**Unvisited** - I prevented pollinators from removing or depositing pollen on specific flowers by either placing bridal veil or screen mesh enclosures around specific flowers. I removed the pistils from the flowers after pollinator foraging had subsided in the community. Autogamy was still possible under this treatment.

**Visited** - The flowers were not manipulated and were available to pollinators for servicing. I removed the pistils from the flowers after pollinator activity had subsided in the community. The flowers assigned to the after



pollinators treatment would have pollen on their stigma due to autogamy and pollinator deposition.

*Ipomoea pandurata* has a style length that varies considerably within the species relative to the other *Ipomoea* species studied. Style length is known to effect stigmatic pollen load (Wolfe and Barrett 1989, Murcia 1990). At the Youngblood Circle site on 14 and 22 August 2000, I grouped 64 flowers of *I. pandurata* into one of four groups based on style length relative to stamen length: long, moderate, short, and reduced (Figure 1). Shortly after sunrise and before pollinator movement began at the site, I haphazardly assigned 3-7 flowers of each style length group present to each of the three pollinator treatments: initial, unvisited, and visited.

For all flowers assigned treatments, I placed stigmas individually in a small plastic vial and transported the vials back to the lab. In the lab, I placed a small cube (2×2×3 mm) of fuchsin-glycerine gel onto a microscope slide, melted the gel with a lighter, and rubbed the stigma onto the melted fuchsin-glycerine gel until all the pollen was removed from the stigma (Wolfe and Barrett 1989). I then placed a cover slip onto the gel and allowed pollen to stain for 24 hrs. I counted pollen loads under 20-30× magnification.

I calculated mean stigmatic pollen loads within each treatment for each species and within style-length groups for *I. pandurata*. I pooled species (excluding *I. pandurata* due to variable style length) into two groups by syndrome, bee flowers (*I. hederacea*, *I. imperati*, *I. trichocarpa*) and bird flowers (*I. hederifolia*, *I. quamoclit*) and calculated mean stigmatic pollen loads within each treatment for each syndrome.

### **Reproductive Success in Natural *Ipomoea* Communities**

I measured percent fruit set and percent seed set of four *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*) over two years (1999 and 2000). I tagged a total of 350 flowers on eight sampling days at seven sites in 1999 and 2000. Fruits were collected 4-6 weeks after flowers were tagged. Fruit set was defined as the percentage of flowers that develop a fruit. Seed set was the percentage of ovules that matured into seeds. I analyzed fruit set and seed set among species and year with a two-way ANOVA. Additionally, I grouped the four *Ipomoea* species into two groups by syndrome, bee flowers (*I. hederacea*, *I. trichocarpa*) and bird flowers (*I. hederifolia*, *I. quamoclit*), and analyzed fruit and seed set between syndrome and year with a two-way ANOVA. *Ipomoea imperati* and *I. pandurata* were not included in the analyses for reproductive success because fruit and seed set data was not collected in 1999. In 2000, I collected mature fruits of *I. imperati* and *I. pandurata*, to calculate seed set.

## CHAPTER III

### RESULTS

#### Seasonal Flowering Phenology

*Ipomoea* began flowering in late July in 1999 and 2000. Seasonal phenologies were similar among species and years in 1999 and 2000. In 1999, the three *Ipomoea* species surveyed (*I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*) had peak flowering, defined as the day that had the largest percentage of total flowers surveyed for the season, within a ten-day period, between 4 and 14 October (Julian dates 277-287, Figure 2) among the three sites (Hwy 67, Hwy 24, Hunter's Pointe). In 2000, the four *Ipomoea* surveyed (*I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*) exhibited a similar seasonal phenology. Peak flowering of each of the four *Ipomoea* species occurred over a 32-day period between 24 August and 26 September (Julian dates 236-269, Figure 2) among the two sites (Hwy 80 East, Hunter's Pointe). Pooling the phenology of the two sites, *I. hederacea* had the earliest peak bloom on 24 August (Julian date 236). The phenology of *I. hederifolia* was much longer and had no distinct peak. The remaining two species, *I. quamoclit* and *I. trichocarpa* had synchronous peak blooms around 26 September (Julian date 269).

#### Daily Flowering Phenology

*Ipomoea hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa* exhibited similar daily phenologies, differing mostly in the time the corolla begins to expand in the morning (Figure 3). Peak corolla expansion and corolla wilting were highly synchronous among the four species (Figure 3). By 1200 hrs, the flowers of all four species had begun to wilt. By sunset (1820 hrs), *I. hederacea*, *I.*

*quamoclit*, and *I. trichocarpa* flowers had fully closed, and *I. hederifolia* flowers were more than 75% closed. *Ipomoea hederifolia* did not fully close until 2300 hrs. I made observations on 18 August 2000 at 0630 hrs for phenology of *I. imperati* at Tybee Island beach. At 0630 hrs, approximately 40 minutes after daybreak, most of the approximately 100 flowers of *I. imperati* were untwisted but not yet open. By 0800 hrs, most flowers were fully expanded well after daybreak. Most *I. imperati* flowers were closed by 1300 hrs. On 30 July 1999, I made observations on *I. pandurata* at Youngblood Circle. At 0400 hrs, one hour and 20 minutes before daybreak, approximately half of the 150 flowers were fully expanded. At daybreak (0540 hrs), nearly all of the flowers were fully expanded. Most flowers closed between 1200 and 1300 hrs. For all six *Ipomoea* species studied, the anthers dehisced at the start of anthesis (personal observation).

### Nectar Biology

All six *Ipomoea* examined produced nectar as a reward for pollinators.

**Nectar volume** - There was a significant species-treatment effect on nectar volume (Scheirer-Roy-Hare extension of the Kruskal-Wallis test, hereafter called a two-way ANOVA of ranks;  $H_{\text{int}}=20.6$ ,  $df=10$ ,  $P<0.05$ ; Table 3). *Ipomoea imperati*, *I. pandurata*, and *I. quamoclit* contain the largest nectar volumes in flowers excluded from pollinators at the end of anthesis (unvisited). *Ipomoea hederacea*, *I. hederifolia*, and *I. trichocarpa* have the largest nectar volumes in flowers at the beginning of anthesis before pollinators begin foraging, usually between 0630-0800 hrs. Irrespective of flower treatments, there were differences in nectar production between the species ( $H_{\text{spp}}=39.1$ ,  $df=5$ ,  $P<0.001$ ; Table 3). *Ipomoea hederifolia*, *I. quamoclit*, and *I. pandurata* produced more nectar than *I. hederacea*, *I. imperati*, and *I. trichocarpa* (Table 4). Irrespective of species, flower treatments did not effect nectar volume ( $H_{\text{trt}}=20.2$ ,  $df=2$ ,  $P>0.50$ ; Table 3). Flowers available to

effect nectar volume ( $H_{\text{trt}}=20.2$ ,  $df=2$ ,  $P>0.50$ ; Table 3). Flowers available to pollinators (visited) contained the least amount of nectar. Table 4 lists mean nectar volumes for each *Ipomoea* species-flower treatment.

There was no significant syndrome-treatment interaction on nectar volume ( $H_{\text{int}}=1.8$ ,  $df=2$ ,  $P<0.001$ ; Table 3). Bird flowers have slightly less nectar in bagged (unvisited) flowers compared to open (visited) flowers, whereas bee flowers contained significantly more nectar in unvisited flowers (Figure 4). There were significant differences between syndromes ( $H_{\text{syn}}=23.4$ ,  $df=1$ ,  $P<0.001$ ), irrespective of flower treatments, for nectar volume (Table 3). Bird flowers produced significantly more nectar (Figure 4) than bee flowers. Flower treatment did have a significant effect on nectar volume ( $H_{\text{trt}}=65.2$ ,  $df=1$ ,  $P<0.001$ ), with bagged flowers generally having larger volumes of nectar exclusive of species.

**Sugar concentration** - There was a significant species-treatment interaction effect on sugar concentration (two-way ANOVA of ranks,  $H_{\text{int}}=86.2$ ,  $df=5$ ,  $P<0.001$ ; Table 3). *Ipomoea hederifolia* sugar concentrations are nearly equal in all three flower treatments (Table 5). *Ipomoea imperati* had high sugar concentrations before pollinator foraging began (initial) as well as in flowers excluded from pollinators at the end of anthesis (unvisited), with lowest sugar concentrations in flowers available to pollinators at the end of anthesis (visited). *Ipomoea hederacea*, *I. pandurata*, *I. quamoclit*, and *I. trichocarpa* had the highest sugar concentrations in open flowers available to pollinators (visited).

Flower treatment had a significant effect ( $H_{\text{trt}}=27.1$ ,  $df=1$ ,  $P<0.001$ ) on nectar sugar concentration (Table 3). Flowers excluded from pollinators (unvisited) had the highest sugar concentrations in four of the six *Ipomoea* species. Irrespective of the flower treatments, there were differences in sugar

concentration ( $H_{\text{spp}}=22.9$ ,  $df=5$ ,  $P<0.001$ ; Table 3). Nectar concentrations vary from 47.3-5.7% sucrose equivalents (Table 5).

Pooling the six *Ipomoea* species into their syndromes (bee vs. bird), there was a significant two-way interaction between syndrome and treatments ( $H_{\text{int}}=12.5$ ,  $df=2$ ,  $P<0.01$ , Table 3). This interaction was due to the high nectar sugar concentration in flowers of *I. hederifolia* visited by pollinators (Table 5). The other five species show reduced nectar sugar concentration in flowers visited by pollinators (visited) relative to flowers excluded from pollinators (unvisited).

### Pollination Biology

A total of twelve pollinator species was observed visiting the six *Ipomoea* species over a three-year period (Table 6). Using pooled data, bumblebees preferred the blue-flowered *I. hederacea* (50 of 191 visits) and *I. trichocarpa* (125 of 191 visits). Together, 92% bumblebee visits (175/191) were to the two blue-flowered *Ipomoea* species. Solitary bees preferred the white-flowered *I. imperati* (39 of 68 visits) and *I. pandurata* (26 of 68 visits). Together, 96% solitary bee visits (65/68) were to the two white-flowered *Ipomoea* species. Sulphurs preferred the red flowered *I. hederifolia* (66 of 255 visits) and *I. quamoclit* (162 of 255 visits). Together, 89% visits (228/255) were to the two red-flowered *Ipomoea* species.

The other pollinator taxa (fritillary, hummingbirds, skippers, swallowtails) were much less common and rarely serviced *Ipomoea* flowers.

Grouping the twelve pollinator species into seven taxa (bumblebee, solitary bee, fritillary, skipper, sulphur, swallowtail, and hummingbird), six of the seven pollinator taxa did not forage randomly for flowers; pollinators have preferences for specific flower types (Table 7). Pooling the six *Ipomoea* species into three groups based on flower color: blues (*I. hederacea*, *I. trichocarpa*), whites (*I. imperati*, *I. pandurata*), and reds (*I. hederifolia*, *I. quamoclit*), all seven pollinator

taxa foraged differently from random (Table 8). Clear preferences for one flower color group were apparent for all pollinators excluding skippers. Bumblebees and swallowtails preferred blue flowers (*I. hederacea*, *I. trichocarpa*); fritillaries, sulphurs, and hummingbirds preferred red flowers (*I. hederifolia*, *I. quamoclit*); and solitary bees preferred the white flowers (*I. imperati*, *I. pandurata*). Skippers preferred both blue (*I. trichocarpa*) and white flowers (*I. pandurata*). Figure 5 shows the proportion of visits to *Ipomoea* flowers by bumblebees, solitary bees, skippers, swallowtails, gulf fritillaries, sulphurs, and hummingbirds, respectively.

### Stigmatic Pollen Load

Pollinator visits increased the stigmatic pollen load in two of the five *Ipomoea* species, thus, there was a significant species-treatment interaction effect on stigmatic pollen load (two-way ANOVA of ranks,  $H_{int}=22.0$ ,  $df=8$ ,  $P<0.01$ ; Table 9). *Ipomoea imperati* and *I. trichocarpa* had substantially larger stigmatic pollen loads in visited flowers,  $240 \pm 18$  and  $181 \pm 14$  (mean pollen grains  $\pm 1$  SE), respectively, compared to unvisited flowers,  $138 \pm 18$  and  $71 \pm 13$ , respectively (Table 10). The other three *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. quamoclit*) had marginally increased stigmatic pollen loads due to pollen import (Table 10). There was little difference in stigmatic pollen loads between initial and unvisited flower treatments (Tables 10-12). Many *Ipomoea* flowers had pollen present on the stigma before pollinators began foraging.

Pooling the *Ipomoea* species into two groups by syndrome, excluding *I. pandurata* (see next paragraph), bird flowers had stigmatic pollen loads that were approximately one-third larger in visited flowers than unvisited flowers (Table 11). Bee flowers had stigmatic pollen loads that were approximately four times larger in visited flowers than unvisited flowers.

*Ipomoea pandurata* was analyzed separately for stigmatic pollen load (Table 12) because style length varies within the species (Figure 1). Differences in style length did affect the stigmatic pollen load ( $F_{\text{style}}=105.9$ ,  $df=3,52$ ,  $P<0.0001$ , Table 9). Pollination treatment (initial, unvisited, visited) also affected stigmatic pollen load ( $F_{\text{trt}}=21.47$ ,  $df=2,52$ ,  $P<0.0001$ ). Stigmas of long-styled flowers had the highest stigmatic pollen loads, both from autogamy (unvisited) and in flowers open to pollination (visited). However, there was a net loss of pollen when visited by pollinators (Table 12). The other three style length groups (moderate, short, reduced) received a net gain of pollen when visited by pollinators. This caused a significant interaction between style length and pollination treatment ( $F_{\text{int}}=3.06$ ,  $df=6,52$ ,  $P<0.01$ ). Stigmas of reduced-style flowers are isolated below the hairy bases of stamens and received almost no pollen from autogamy or pollination. Stigmas of moderate and short-styled flowers received a net gain of pollen when visited by pollinators compared to autogamy.

### **Reproductive Success in Natural *Ipomoea* Communities**

**Fruit set** - There were significant differences for fruit set ( $F_{\text{sp}}=5.59$ ,  $df=3,344$ ,  $P<0.0009$ ) among the four species (Table 13). Year added a marginally significant effect on fruit set ( $F_{\text{yr}}=3.78$ ,  $df=1, 344$ ,  $P<0.053$ ). In 1999, 80% of *I. quamoclit* flowers produced fruit. Fruit set was much lower in the other three species. *Ipomoea hederacea*, *I. hederifolia*, and *I. trichocarpa* had fruit sets of 42%, 35%, and 25%, respectively (Table 14). In 2000, *I. hederacea* had a fruit set of 47%, similar to 1999. The other three *Ipomoea* species had fruit sets nearly equal to each other, but different from their fruit sets from the previous year. *Ipomoea hederifolia*, *I. quamoclit*, and *I. trichocarpa* had fruit sets of 65%, 63%, and 65%, respectively (Table 14). From 1999 to 2000, *I. quamoclit* had a reduction in fruit set, *I. hederacea* had almost no change, and *I. hederifolia* and *I. trichocarpa* had



substantial gains in fruit set. Thus, there was a significant two-way interaction between species and year for fruit set ( $F_{\text{int}}=4.08$ ,  $df=3,344$ ,  $P<0.0073$ ) among the four *Ipomoea* species (Table 13).

Pooling the four *Ipomoea* species into two groups based on their syndromes (bee vs. bird flowers), there was a significant difference between the two groups for fruit set ( $F_{\text{syn}}=4.70$ ,  $df=1, 344$ ,  $P<0.03$ ; Table 13). Year also had a significant effect on fruit set ( $F_{\text{yr}}=4.38$ ,  $df=1,344$ ,  $P<0.04$ ). More flowers produced fruits in 2000 ( $F_{\text{yr}}=4.38$ ,  $df=1, 344$ ,  $P<0.04$ ). The interaction between syndrome and year was not significant ( $F_{\text{int}}=0.67$ ,  $df=1,344$ ,  $P<0.41$ ).

Pooling 1999 and 2000, *I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa* had fruit sets of 44%, 50%, 72%, and 45%, respectively. Pooling species by syndrome (bee and bird) and year, bee flowers had mean fruit sets of 45%, whereas bird flowers had mean fruit sets of 61%.

*Ipomoea imperati* and *I. pandurata* were surveyed for fruit set in 2000. Fruit set was high for *I. imperati* at 93%. Fruit set could not be determined for *I. pandurata*. Only two *I. pandurata* populations surveyed yielded fruiting plants, and much less than 1% of flowers probably produced fruit.

**Seed set** - Of the four *Ipomoea* species examined for reproductive success, three species can have a maximum number of four seeds per fruit. The remaining species, *I. hederacea*, can produce a maximum of six seeds per fruit. There were significant differences for seed set ( $F_{\text{spp}}=3.84$ ,  $df=3,180$ ,  $P<0.01$ ) among the four *Ipomoea* species (Table 13). *Ipomoea hederacea* and *I. hederifolia* had higher seed sets, and *I. quamoclit* and *I. trichocarpa* had lower seed sets in 2000, relative to 1999. The increases and decreases in seed sets between the four species result in no net change in seed set between years ( $F_{\text{yr}}=0.14$ ,  $df=1,180$ ,  $P<0.91$ ). There were no species-year interaction ( $F_{\text{int}}=0.23$ ,  $df=3,180$ ,  $P<0.88$ )

effects on seed set either. *Ipomoea hederacea* had lower seed sets compared to the other three species. In 1999, the percentage of fruits with full seed sets in *I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa* were 24%, 33%, 40%, and 0% (only one of four tagged flowers matured to a three-seeded fruit), respectively. In 2000, the percentage of fruits with full seed sets in *I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa* were 8%, 62%, 42%, and 23%, respectively.

Pooling the four *Ipomoea* species into two groups by syndrome, bee flowers (*I. hederacea*, *I. trichocarpa*) and bird flowers (*I. hederifolia*, *I. quamoclit*), there was a significant difference (Table 13) between the two groups for seed set ( $F_{pt}=10.50$ ,  $df=1, 180$ ,  $P<0.001$ ). Bird flowers had larger seed sets in both years. Neither year ( $F_{yr}=0.80$ ,  $df=1,180$ ,  $P<0.37$ ) nor syndrome-year interaction ( $F_{int}=0.80$ ,  $df=1.180$ ,  $P<0.37$ ) had a significant effect on seed set (Table 13). Pooling syndromes among years, bee flowers had mean seed sets of 63%, whereas bird flowers had mean seed sets of 75%.

*Ipomoea imperati* and *I. pandurata* were surveyed for seed set in 2000. Seed set in *I. imperati* was similar to other bee flowers at 57%, and only 14% of fruits have a full seed set. *Ipomoea pandurata* had seed set similar to bird flowers at 76%, and 33% of fruits have a full seed set.

## CHAPTER IV

### DISCUSSION

In general, there was a high degree of concordance between theory and reality for the *Ipomoea* model examined. There was strong agreement between nectar constitution, flower color, and pollinator fauna as predicted by pollination syndromes. Each of the six *Ipomoea* species was visited predominately by the predicted pollinator type. Numerous studies report that hummingbirds and butterflies forage on species whose flowers have nectar with less concentrated sugar (Baker 1975, Bolten and Feinsinger 1978, Corbet and Wilmer 1981, Pyke and Waser 1981, Feinsinger et al. 1986, Bernardello et al. 2000), compared to bee-pollinated species with less nectar but more concentrated sugar (Pedersen 1953, Gut et al. 1977, Brink and deWet 1980, Durkee et al. 1981, Southwick and Southwick 1983, Cresswell and Robertson 1994). In general, as pollinator body mass increases, nectar production rates increase and sugar concentrations decrease (Pyke 1981). These consistent differences in nectar preferences of pollinators could be argued as evidence supporting the role of nectar in shaping pollination syndromes.

There is some disagreement in the scientific literature, however, between rewards and pollinators in light of pollination syndromes. There are studies that reveal that hummingbirds prefer foraging on flowers with much higher nectar concentrations. Gut et al. (1977) never observed hummingbirds visit the 'typical' hummingbird flowers of *Ipomopsis aggregata* and *Aquilegia*

*formosa*, both of which have nectar concentrations of 25% sucrose at their study site. Hummingbirds instead heavily visited on two species of *Cirsium* that had nectar concentrations of 54 and 59% sucrose. Watt et al. (1974) showed that the flowers visited by hummingbirds had nectars with the highest mean sugar concentration at 36.9% sucrose equivalents. Flowers visited by bees had nectars with a mean sugar concentration of 30.5% sucrose equivalents. Selection pressure is theorized to maximize a pollinator's rate of reward intake (Schoener 1971, Charnov 1976, Pyke et al. 1977). Consequently, pollinators should visit plants or species that offer them the most energetic rewards in one visit, with minimal flight time to the next flower. Plants should be under a selection pressure to offer highly energetic rewards, via large nectar volumes or highly concentrated nectars, yet not to the extent that a pollinator becomes satiated or remains at the plant and does not disseminate pollen.

Some *Ipomoea* species are known to be self-compatible and apparently produce fruit from selfing consistently (Ennos 1981, Murcia 1990, Abbott 2000). If plants are self-compatible, then one question that arises is why produce large flowers or offer large rewards? Some *Ipomoea* can self-pollinate in the absence of pollinators, such as *I. hederacea*, which has its stigma fixed level with the anthers (Ennos 1981). Other *Ipomoea* species, such as *I. purpurea* and *I. trichocarpa*, have stigmas exerted beyond the anthers, thereby reducing opportunities for selfing, can still set fruits from self pollen in the absence of pollinators due to wind or gravity dispersal of pollen. Pollinator abundance

likely varies over time for *Ipomoea*. The flowers may provide *Ipomoea* ample outcrossing opportunities in years when pollinators are abundant.

The outcrossing rates of the morning glories I studied are not known, save for *I. hederacea*, which has been shown to have a low outcrossing rate of 4-7% (Ennos 1981). My data indirectly support low outcrossing in *I. hederacea*, for there was little difference in stigmatic pollen loads of visited and unvisited flowers (Table 10). In southeast Georgia, *Ipomoea trichocarpa* has its stigma exerted above the anthers in its flowers, unlike *I. hederacea*, and most likely need pollinators for sufficient pollination. Stigmatic pollen loads in *I. trichocarpa* were five times higher in flowers available to pollinators, compared to unvisited flowers excluded from pollinators. *Ipomoea trichocarpa*, predominately visited by bumblebees, is likely to be the most outcrossed *Ipomoea*. Bees do groom themselves periodically to remove pollen on their body, and some pollen most likely never reaches a conspecific stigma. But high fidelity and their hairy bodies make bumblebees quite adept at carrying pollen.

The styles of the two bird-pollinated species, *I. hederifolia* and *I. quamoclit*, elongate during anthesis (personal observation). The stigmas pass by the anthers, which have already dehisced their pollen. *Ipomoea hederifolia* and *I. quamoclit* appear to receive autogamous pollen in the morning. If so, the lower stigmatic pollen loads in these two species could be explained by higher selfing rates. The *Ipomoea* flowers visited by bees produce more pollen than flowers visited by hummingbirds and butterflies, which suggests that the bird

flowers are utilizing autogamous pollen for pollination more than the bee flowers. The ability of *I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa* to produce fruits in the absence of pollinators, as well as anther dehiscence occurring before or at anthesis, indicates that autogamy probably plays a part in their reproductive success of all four species. *Ipomoea pandurata* is known to be self-incompatible and rarely produces fruit (Stucky and Beckmann 1982), and therefore, requires outcrossing in the strictest sense for reproduction. Both *I. imperati* and *I. pandurata* produce copious amounts of pollen, which may be linked with their predominate pollinator, pollen-collecting solitary bees.

Pollinators foraging on multiple plant species could cause plants to compete with each other for pollination service (Waser 1978a, Rathcke 1983, Campbell et al. 1997). Interspecific pollen movement is thought to be a stronger selective force than competition for pollinators, though, in determining fitness (Waser 1982, Rathcke 1983). Pollen movement between species reduces reproductive success by way of unfertilized ovules (Feinsinger 1978, Waser 1978b). Plants should, therefore, be under selection pressure to maximize reproductive success by promoting pollinator faithfulness to improve the dissemination and receipt of pollen. Consequently, pollination syndromes are a way of explaining why flowers are of certain shape, color, and reward to entice specific pollinating agents to be faithful to its species.

Sympatric plants with overlapping flowering periods can push their flowering phenologies apart from each other to reduce competition for

pollinators or to minimize interspecific pollen transfer (Stone et al. 1998). This is probably rarely an option though given the short time period pollinators may be available (Herrera 1996, Waser et al. 1996). In populations where the closely related *Ipomoea purpurea* and *I. hederacea* are sympatric, two previous studies both found that the more attractive *I. purpurea* (Stucky 1984) had higher outcrossing rates (Ennos 1981, Stucky 1985). Ennos (1981) concluded that interspecific pollen flow from *I. purpurea* to *I. hederacea* may have selected to fix stigma-anther separation to zero in *I. hederacea*, so that autogamous pollen, which lands on the stigma before anthesis begins, could block *I. purpurea* pollen from clogging the stigma on *I. hederacea* flowers and prevent the subsequent loss of reproductive success (Guries 1978). Fruit and seed sets were higher in autogamous pollination of *I. hederacea* compared to autogamous and outcross pollination (Stucky 1985). *Ipomoea hederacea* seems adapted for selfing, which would allow it to coexist sympatrically with species with similar flowers.

The lack of substantial differences in flowering phenologies among *Ipomoea* gives merit to pollination syndromes as a way of segregating pollinators in sympatric communities with multiple species in bloom. The two white-flower *Ipomoea* species, *I. imperati* and *I. pandurata*, begin blooming two months earlier than the other four *Ipomoea* species examined (personal observation). These two species are also predominately visited by solitary bees, unlike the other four *Ipomoea* species, and may be confined to an earlier flowering phenology when solitary bees are available. The other four *Ipomoea*

species, *I. hederacea*, *I. hederifolia*, *I. quamoclit*, and *I. trichocarpa*, have strongly overlapping flowering phenologies, both diurnally and seasonally. Although their pollinators are available earlier in the season, other factors may constrain when the *Ipomoea* species can grow or flower (daylight length, competition, etc).

Pollination syndromes are generally thought to be the products of coevolution between pollinators and plants (Stebbins 1970, Faegri and van der Pijl 1979, Crepet 1983). Changes in one species instigate a reciprocal change in the other species so that the benefit each receives (plant's reproductive success, the pollinator's foraging efficiency) is maintained. Species with pollination syndromes in this light are, accordingly, evolutionarily more advanced within a phylogenetic group than those that utilize many different pollinators and show no adaptation to any one pollinator (Stebbins 1970, Faegri and van der Pijl 1979, Crepet 1983). This seems intuitive when specialized pollinators are most efficient in terms of pollen movement and subsequent reproductive success is maximized. Some authors have argued, though, that selection pressures for plants to specialize on one pollinator species can be confounded by other selection pressures and thus retard or negate the ability of coevolution (Herrera 1996, Waser et al. 1996). If the plants and the pollinators are not in complete sympatry, then there should exist a set of individuals of both plants and pollinators that do not interact with each other. Waser et al. (1996) points out that specialization is often defined above the species level. Solitary bees, which are often thought of as specialized pollinators, are so only



when foraging for pollen. Solitary bees show less specialization in flower visitation when foraging for nectar, and they can effectively pollinate those flowers for which they are not specialized. Waser et al. (1996) argues that specialization should only occur when one pollinator is consistently the most efficient pollinator or is the most abundant. A counterpoint they add, though, is there is usually heterogeneity in pollinator diversity, efficiency, or composition that thwarts the ability of a plant to specialize on one pollinator (Schemske and Horvitz 1984, Wolfe and Barrett 1989, Fishbein and Venable 1996, Herrera 1996).

Richards (1986) points out that most of the known pollination syndromes have exceptions. He gives an example where bees can come in contact with the much exerted stamens and pistils of some 'bird' flowers and cause pollination, though the nectar is far removed from the bee's reach. Richards also acknowledges that increasing complexity in flower shape reduces the number and kinds of pollinators that can visit the flower. Zygomorphic flowers are, therefore, more likely to be visited by specialized pollinators (Wolfe and Krstolilc 1999). Another exception of pollination syndromes was the discovery that bees see red flowers (Chittka and Waser 1997). The red-flowered *Asclepias tuberosa* (butterfly weed) is in fact most effectively pollinated by *Bombus* and *Apis* bees (Fishbein and Venable 1996), which defies the normal color preferences for bees. Johnson and Steiner (2000) make two important statements in their review of pollination studies. First, plants occupy all points between specialization and generalization in their

pollination systems. This implies the dichotomous labeling of a plant's pollination system as either generalized or specialized is not appropriate. Secondly, there is much we do not know in way of pollination systems in species-rich developing countries of the world. The claims made that most pollination systems are generalized or specialized seem premature.

In conclusion, the six *Ipomoea* species I studied have simple flower shapes, are self-compatible, and are in fact visited by more than one pollinator species/type. However, there are definite associations between pollinators and floral displays that fit the classic pollination syndromes. Pollinators do not forage randomly and are apparently cueing in on rewards, flower color, or shape when choosing flowers to visit. The importance of these separate floral traits in contributing to the overall floral display should be determined. This could be done through the use of color mutants, nectar manipulation, and alteration of flower size and shape and observing any changes in pollinator composition and visitation frequency.

Table 1. Flower color and shape, pollination syndrome, maximum number of seeds per fruit, life history, and growth habit of the six *Ipomoea* species examined in this study.

<i>Ipomoea</i> species	flower color	flower shape	syndrome	max # seeds/fruit	life history	growth habit
hederacea	blue	funnelform	bee	6	annual	twining
hederifolia	red	tubular	hummingbird- butterfly	4	annual	twining
imperati	white	funnelform	bee	4	perennial	trailing
pandurata	white	funnelform	bee	4	perennial	trailing
quamoclit	red	tubular	hummingbird- butterfly	4	annual	twining
trichocarpa	blue	funnelform	bee	4	perennial	twining

Table 2. List of study sites, longitude/latitude of study sites, *Ipomoea* species present, and years sampled.  
 NR=no longitude/latitude readings made.

<i>Ipomoea</i>									
SITE	LONGITUDE/ LATITUDE	hederacea	hederifolia	imperati	pandurata	quamoclit	trichocarpa	YEAR SAMPLED	
Hwy 24	32° 27' 21.262" N 81° 44' 04.811" W	√	√			√	√	1998, 1999	
Hwy 67	32° 21' 33.255" N 81° 44' 36.589" W		√			√	√	1999	
Hwy 80 East	32° 25' 28.709" N 81° 43' 54.436" W	√	√			√	√	2000	
Hwy 80/25	32° 31' 10.583" N 81° 50' 41.969" W	√	√			√	√	1999, 2000	
Howard's Lumber	32° 25' 52.710" N 81° 46' 14.622" W	√	√			√	√	1999, 2000	
Hunter's Pointe	32° 29' 34.749" N 81° 48' 49.810" W	√	√			√	√	1999, 2000	
Railroad	32° 26' 18.697" N 81° 46' 50.832" W		√			√		1999	
Brannen Street	32° 26' 21.913" N 81° 46' 50.832" W		√			√	√	1999	
Youngblood Circle	32° 25' 42.307" N 81° 43' 09.925" W				√			1999, 2000	
Tybee Island	NR			√				2000	
Route 3-SC	NR				√			2000	

Table 3. Results of a two-way nonparametric test (Scheirer-Roy-Hare extension of the Kruskal-Wallis test) for the effect of species, treatment, and species-treatment interaction on nectar volume and sugar concentration for six *Ipomoea* species. Flower treatments included nectar volume and sugar concentrations in flowers at the beginning of anthesis (initial), as well as after anthesis in flowers excluded from pollinators (unvisited), and flowers available to pollinators (visited).

<b>nectar</b>	<b>source of variation</b>	<b>df</b>	<b>H</b>	<b>P</b>	
<b>volume</b>	species	5	39.1	***	
	treatment	2	20.2	***	
	species × treatment	10	20.6	*	
	species pooled-bee vs. bird syndrome	1	24.1	***	
	treatment	2	19.4	***	
	syndrome × treatment	2	1.8	NS	
	<b>% sugar</b>	species	5	22.9	***
		treatment	2	10.8	**
		species × treatment	10	19.9	*
species pooled-bee vs. bird syndrome		1	21.4	***	
treatment		2	17.0	***	
syndrome × treatment		2	12.5	**	

\* P<0.05; \*\* P<0.01; \*\*\* P<0.001; NS P>0.05

Table 4. Nectar volume (mean microliters  $\pm$  1 SE) of six *Ipomoea* species.

Sample size for each mean ranged from 5-25 flowers. Nectar was extracted before pollinator foraging began in the community (initial), as well as flowers excluded from pollinators (unvisited) and flowers open to pollinators (visited).

<i>Ipomoea</i> species	flower color	NECTAR VOLUME		
		initial	unvisited	visited
hederacea	blue	0.80 $\pm$ 0.24	0.36 $\pm$ 0.15	0.02 $\pm$ 0.02
hederifolia	red	2.60 $\pm$ 0.44	1.45 $\pm$ 0.59	1.58 $\pm$ 0.48
imperati	white	0.34 $\pm$ 0.08	0.46 $\pm$ 0.18	0.28 $\pm$ 0.07
pandurata	white	0.42 $\pm$ 0.07	1.35 $\pm$ 0.21	0.50 $\pm$ 0.14
quamoclit	red	0.80 $\pm$ 0.13	1.44 $\pm$ 0.27	0.33 $\pm$ 0.19
trichocarpa	blue	0.52 $\pm$ 0.15	0.30 $\pm$ 0.13	0.02 $\pm$ 0.01

Table 5. Nectar sugar concentration (mean % sucrose equivalents  $\pm$  1 SE) of six *Ipomoea* species. Sample size for each mean ranged from 2-21 flowers, except for three values without standard errors, for which only one flower each had a determinable sugar concentration. The three flower treatments are as in Table legend 4.

<i>Ipomoea</i> species	flower color	SUGAR CONCENTRATION		
		initial	unvisited	visited
hederacea	blue	13.8 $\pm$ 2.5	27.3 $\pm$ 1.9	13.0
hederifolia	red	29.8 $\pm$ 0.5	29.7 $\pm$ 9.2	32.7 $\pm$ 0.5
imperati	white	19.5 $\pm$ 3.4	16.0	5.7 $\pm$ 1.5
pandurata	white	14.0 $\pm$ 1.8	47.3 $\pm$ 7.6	14.9 $\pm$ 3.9
quamoclit	red	22.7 $\pm$ 1.3	34.4 $\pm$ 5.0	24.5 $\pm$ 7.5
trichocarpa	blue	14.7 $\pm$ 7.2	41.8 $\pm$ 13.9	8.0

Table 6. List of pollinator taxa observed visiting *Ipomoea* among eleven sites over a three-year period. Bumblebees, solitary bees, and sulphurs were the most common pollinators over three years.

	POLLINATOR TYPE	COMMON NAME
hymenoptera	<b>bumblebee</b>	
	<i>Bombus</i> sp. 1	bumblebee
	<i>Bombus</i> sp. 2	bumblebee
	<b>solitary bee</b>	
	solitary bee sp. 1 solitary bee sp. 2	
lepidoptera	<b>fritillary</b>	
	<i>Dione vanillae</i>	gulf fritillary
	<b>skipper</b>	
	<i>Epargyreus clarus</i>	silver-spotted skipper
	<i>Lerema accius</i>	clouded skipper
	<i>Hylephila phyleus</i>	fiery skipper
	<b>sulphur</b>	
	<i>Phoebis sennae</i>	cloudless sulphur
	<b>swallowtail</b>	
	<i>Pterourus glaucus</i>	eastern tiger swallowtail
<i>Pterourus palamedes</i>	palamedes swallowtail	
	<b>hummingbird</b>	
	<i>Archilochus colubris</i>	ruby-throated hummingbird

Note: bumblebees are likely *Bombus pennsylvanicus* and *B. impatiens*



Table 7. Frequency of seven pollinator taxa observed visiting flowers of six *Ipomoea* species. Data were pooled from nine *Ipomoea* communities over a three-year sampling period. Bold numbers indicate when the observed number of visits to a flower type significantly exceeded the expected number of visits.

pollinator	<i>Ipomoea</i>						$\chi^2$	P
	hederacea	hederifolia	imperati	pandurata	quamoclit	trichocarpa		
bumblebee	<b>50</b>	0	0	16	0	<b>125</b>	224.6	***
gulf fritillary	<b>3</b>	4	0	0	7	1	7.7	NS
hummingbird	0	<b>6</b>	0	0	0	0	37.2	***
solitary bee	3	0	<b>39</b>	<b>26</b>	0	0	354.1	***
skipper	0	1	0	<b>6</b>	0	<b>13</b>	31.3	***
sulphur	7	<b>66</b>	2	3	<b>162</b>	15	217.5	***
swallowtail	<b>9</b>	<b>2</b>	0	0	1	2	34.9	***

\* P<0.05; \*\* P<0.01; \*\*\*P<0.001; NS P>0.05

Table 8. Frequency of seven pollinator taxa observed visiting three flower-color groups of six *Ipomoea* species. Bold numbers indicate when the observed number of visits to a flower color type exceeded expected visits. Blue (*I. hederacea* and *I. trichocarpa*) and white (*I. imperati* and *I. pandurata*) flowers have bee syndrome characteristics. Red (*I. hederifolia* and *I. quamoclit*) flowers have hummingbird-butterfly syndrome traits.

<i>Ipomoea</i>						
pollinator	blue	white	red	X <sup>2</sup>	P	
bumblebee	<b>175</b>	16	0	217.2	***	
gulf fritillary	4	0	<b>11</b>	6.1	*	
hummingbird	0	0	<b>6</b>	7.7	*	
solitary bee	3	<b>65</b>	0	318.3	***	
skipper	<b>13</b>	<b>6</b>	1	12.4	**	
sulphur	22	5	<b>228</b>	215.8	***	
swallowtail	<b>11</b>	0	3	9.0	*	

\* P<0.05; \*\* P<0.01; \*\*\*P<0.001

Table 9. Results of a two-way nonparametric test (Scheirer-Roy-Hare extension of the Kruskal-Wallis test) for the effect of species, treatment, and interaction on stigmatic pollen load for five *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. imperati*, *I. quamoclit*, and *I. trichocarpa*). Treatments included collecting stigmas before pollinator foraging began in the community (initial), as well as after pollinator foraging subsided in the community from flowers protected from pollinators (unvisited) and flowers open to pollinators (visited). *Ipomoea pandurata* was analyzed separately due to variable style length within the species. Style length, treatment (same as above), and interaction were tested with a parametric two-way ANOVA.

SPL	source of variation	df	H	P
	species	4	31.0	***
	treatment	2	38.1	***
	species × treatment	8	22.0	**
	species pooled-bee vs. bird syndrome	1	17.3	***
	treatment	2	33.7	***
	syndrome × treatment	2	6.6	*
		<b>df</b>	<b>F</b>	<b>P</b>
<b>pandurata</b>	style length (L, M, S, R)	3,52	105.9	****
	treatment	2,52	21.5	****
	style length × treatment	6,52	3.1	**

\* P<0.05; \*\* P<0.01; \*\*\* P<0.001; \*\*\*\* P<0.00001

Table 10. Stigmatic pollen load (mean  $\pm$  1 SE) for five *Ipomoea* species. Sample size for each mean ranged from 10-20 flowers. Flower treatments for stigmatic pollen load were initial, unvisited, and visited. Net gain of pollen via pollination = mean visited – mean unvisited stigmatic pollen load.

<i>Ipomoea</i> species	flower color	STIGMATIC POLLEN LOAD			net gain of pollen via pollination
		initial	unvisited	visited	
hederacea	blue	30.5 $\pm$ 5.2	33.3 $\pm$ 4.3	40.2 $\pm$ 5.8	+ 6.9
trichocarpa	blue	10.3 $\pm$ 3.1	11.8 $\pm$ 3.6	56.6 $\pm$ 9.6	+ 44.8
quamoclit	red	11.6 $\pm$ 2.3	14.5 $\pm$ 3.6	15.4 $\pm$ 2.1	+ 0.9
hederifolia	red	11.4 $\pm$ 2.1	14.7 $\pm$ 3.2	24.9 $\pm$ 3.9	+ 10.2
imperati	white	20.3 $\pm$ 9.0	32.0 $\pm$ 8.5	216.6 $\pm$ 28.0	+ 184.6

Table 11. Stigmatic pollen load (mean  $\pm$  1 SE) for *Ipomoea* pooled by expected syndrome (bee vs. hummingbird-butterfly). Sample sizes for each mean ranged from 20-40 flowers. Flower treatments for stigmatic pollen load were initial, unvisited, and visited (see Table 9 for treatment descriptions). Net gain of pollen via pollination = mean visited – mean unvisited stigmatic pollen load.

<i>Ipomoea</i> species pooled by syndrome	STIGMATIC POLLEN LOAD			net gain of pollen via pollination
	initial	unvisited	visited	
bee	20.3 $\pm$ 5.7	25.7 $\pm$ 5.5	104.5 $\pm$ 14.5	+ 78.8
bird	11.5 $\pm$ 2.2	14.6 $\pm$ 3.4	20.2 $\pm$ 3.0	+ 5.6

Table 12. Stigmatic pollen load (mean  $\pm$  1 SE) for *Ipomoea pandurata*. Sample size for each mean ranged from 4-7 flowers. Flowers were grouped into one of four categories (long, moderate, short, reduced) based on style length relative to the stamens (see Figure 1 for explanation). Flower treatments for stigmatic pollen loads were initial, unvisited, and visited (see Table 9 for treatment descriptions). Net gain of pollen via pollination = mean visited – mean unvisited stigmatic pollen load.

<i>Ipomoea pandurata</i> style category	STIGMATIC POLLEN LOAD			net gain of pollen via pollination
	initial	unvisited	visited	
long	229.7 $\pm$ 71.4	312.0 $\pm$ 51.9	203.6 $\pm$ 21.3	- 108.4
medium	5.4 $\pm$ 2.3	39.7 $\pm$ 16.8	155.0 $\pm$ 22.1	+ 115.3
short	5.3 $\pm$ 3.5	5.0 $\pm$ 1.9	56.8 $\pm$ 13.8	+ 51.8
reduced	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	1.0 $\pm$ 0.4	+ 0.9

Table 13. Two-way ANOVA for the effect of species, year, and interaction on fruit set and seed set in four *Ipomoea* species.

reproductive measure	source of variation	df	F	P	
% fruit set	species	3	5.59	***	
	year	1	3.78	†	
	species × year	3	4.08	**	
	error	344			
	species pooled-bee vs. bird syndrome	1	4.70	*	
	year	1	4.38	*	
	syndrome × year	1	0.67	NS	
	error	344			
	% seed set	species	3	3.84	**
		year	1	0.01	NS
species × year		3	0.22	NS	
error		180			
species pooled-bee vs. bird syndrome		1	10.50	***	
year		1	0.80	NS	
syndrome × year		1	0.80	NS	
error		180			

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; †  $0.05 < P < 0.06$ ; NS  $P > 0.05$

Table 14. Reproductive success measured via percent fruit set (% of flowers that developed fruit, mean  $\pm$  1 SE) and percent seed set (% of maximum number of seeds possible, mean  $\pm$  1 SE) for six *Ipomoea* species. Sample size for each mean ranged from 2-60 flowers, except values where no standard error are given, for which only one fruit is represented.

<i>Ipomoea</i> species	flower color	syndrome	year	% fruit set (mean $\pm$ 1 SE)	% seed set (mean $\pm$ 1 SE)
hederacea	blue	bee	1999	41.5 $\pm$ 7.5	53.9 $\pm$ 6.7
			2000	47.3 $\pm$ 6.5	56.4 $\pm$ 5.4
hederifolia	red	bird	1999	35.1 $\pm$ 7.9	75.0 $\pm$ 16.0
			2000	65.0 $\pm$ 6.2	80.1 $\pm$ 4.4
imperati	white	bee	1999	X	X
			2000	91.0 $\pm$ 24.6	56.6 $\pm$ 2.9
pandurata	white	bee	1999	X	X
			2000	<< 1%	76.2 $\pm$ 5.0
quamoclit	red	bird	1999	80.0 $\pm$ 8.1	75.0 $\pm$ 5.5
			2000	63.3 $\pm$ 6.2	69.7 $\pm$ 4.5
trichocarpa	blue	bee	1999	25.0	75.0
			2000	65.0 $\pm$ 6.2	68.6 $\pm$ 4.4
<b>*<i>Ipomoea</i> pooled by syndrome</b>		bee	1999	40.0 $\pm$ 7.4	55.1 $\pm$ 8.0
			2000	56.5 $\pm$ 4.6	63.7 $\pm$ 3.0
		bird	1999	56.9 $\pm$ 5.9	75.0 $\pm$ 4.5
			2000	64.2 $\pm$ 4.4	75.0 $\pm$ 3.5
<b>*<i>Ipomoea</i> pooled by syndrome and years</b>	bee-pooled across years			44.7 $\pm$ 6.0	63.5 $\pm$ 5.5
	bird-pooled across years			60.9 $\pm$ 5.2	75.0 $\pm$ 4.0

\*Note: *I. imperati* and *I. pandurata* were excluded from the pooled means because data was collected only in 2000.



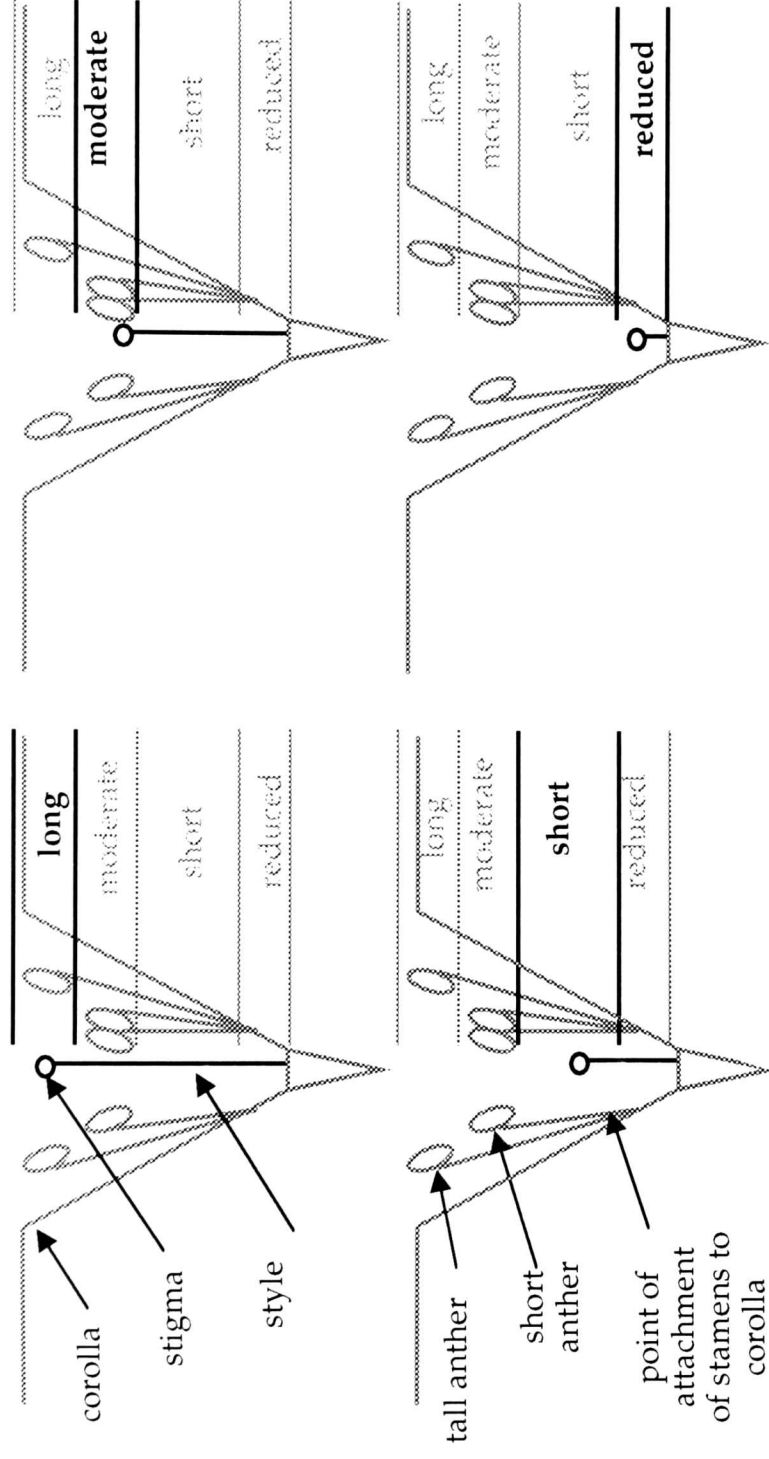


Figure 1. Longitudinal sections of (clockwise from top left) long (L), moderate (M), reduced (R), and short-styled (S) *I. pandurata* flowers. Style length was categorized by position of stigma. L - stigmas level with tall anthers; M - stigmas level with short anthers; S - stigmas below short anthers but above the point of stamen attachment to corolla; R - stigmas below the point of stamen attachment to corolla.

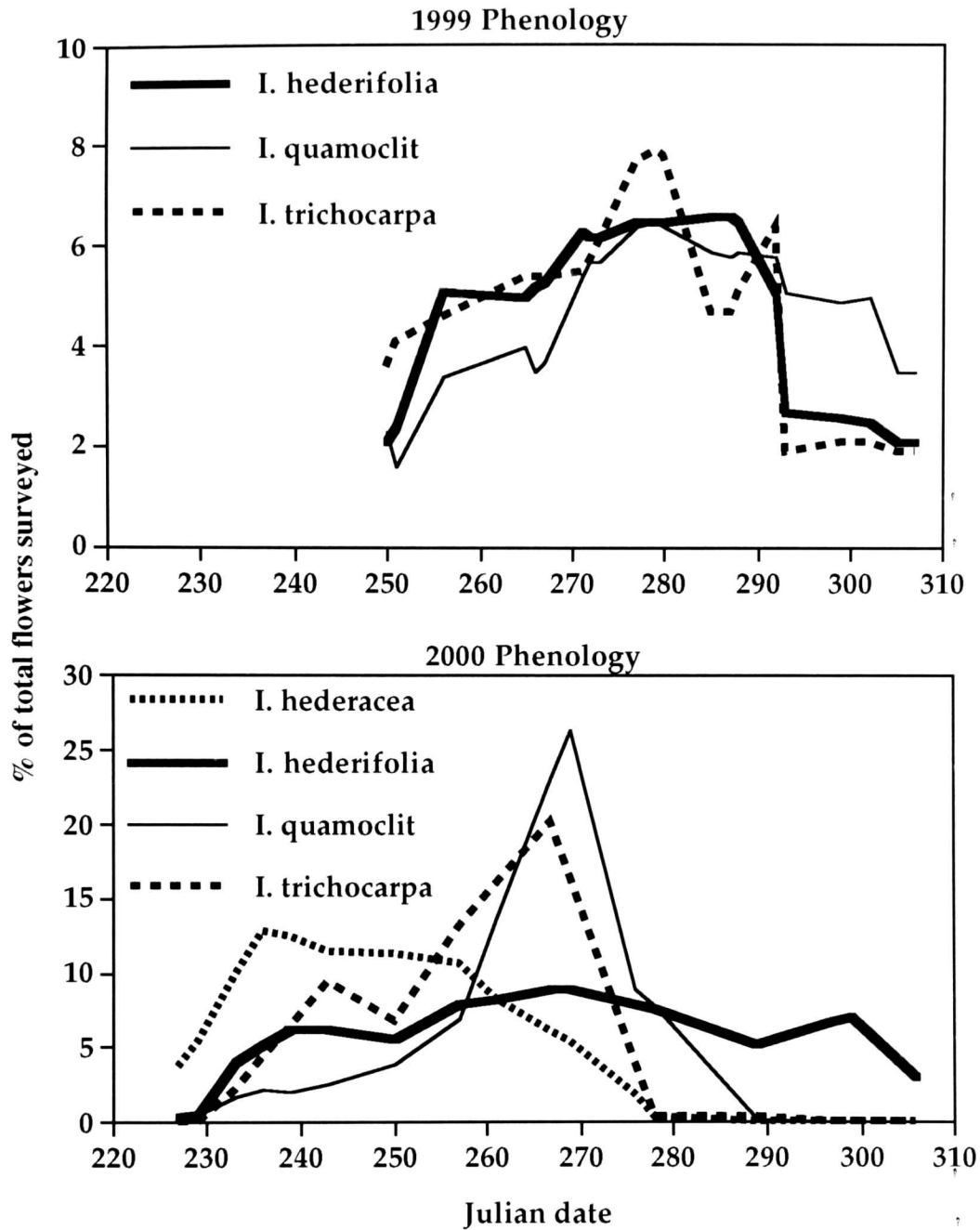


Figure 2. Phenology curves for four *Ipomoea* species for 1999, excluding *I. hederacea*, and 2000.

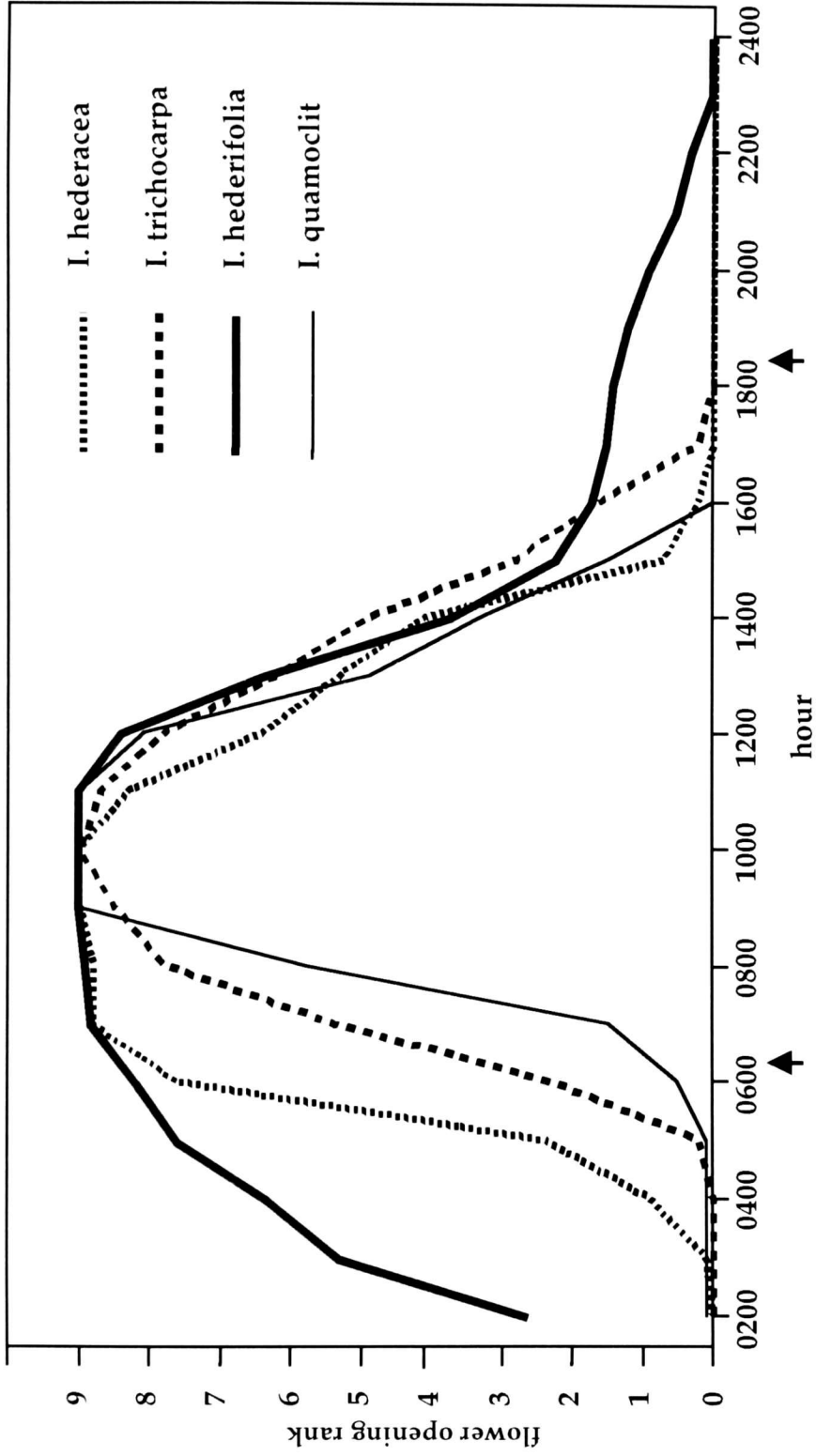


Figure 3. Daily phenology curves for four *Ipomoea* species (*I. hederacea*, *I. hederifolia*, *I. quamoclit*, *I.*

*trichocarpa*). Flowers were scored for flower opening hourly over a 22 hr period. Flowers were scored on a rank from 0 (closed) to 9 (fully expanded). Arrows mark sunrise and sunset, respectively.

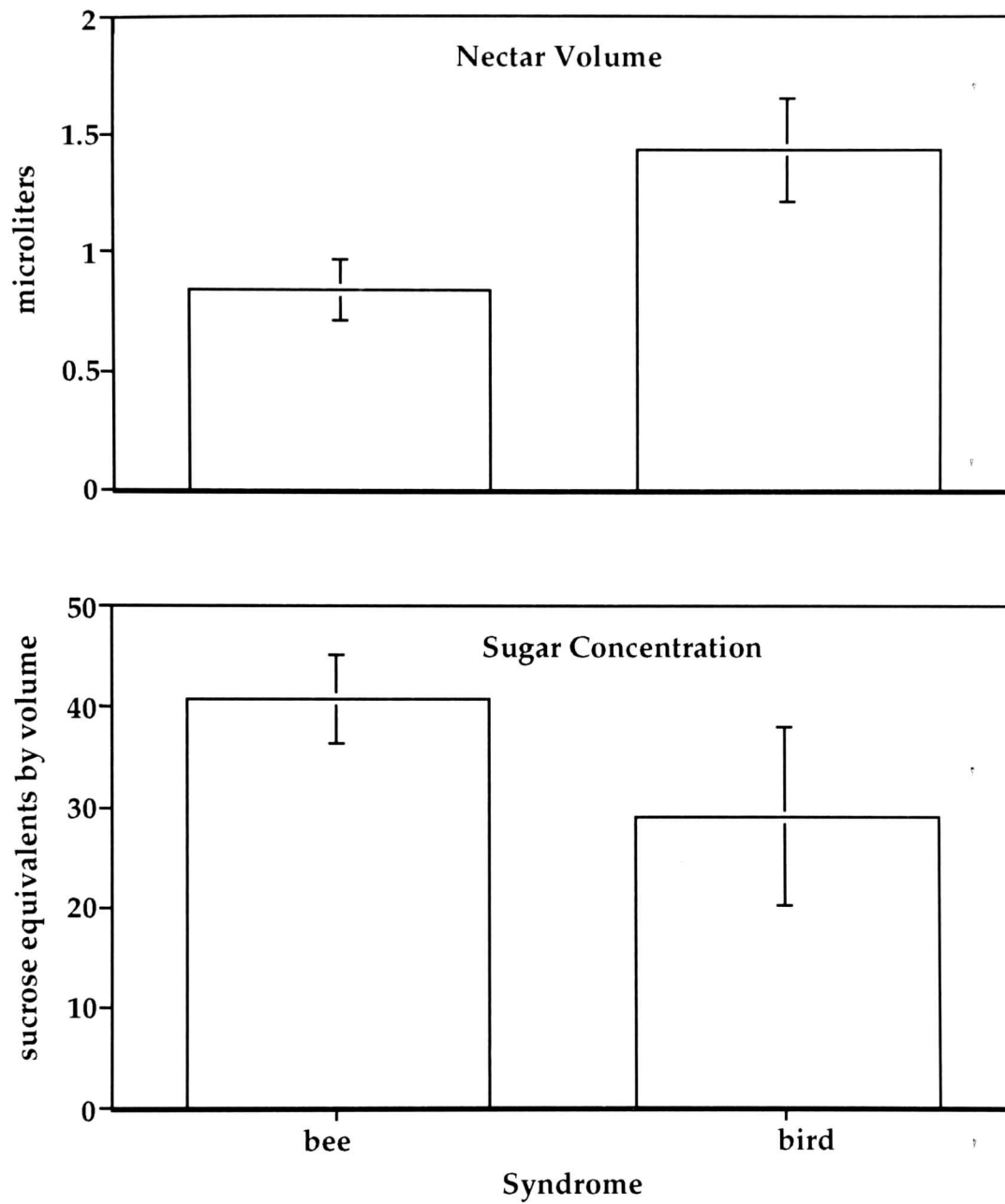


Figure 4. Nectar volume and sugar concentration of *Ipomoea* nectar by syndrome in flowers excluded from pollinators.

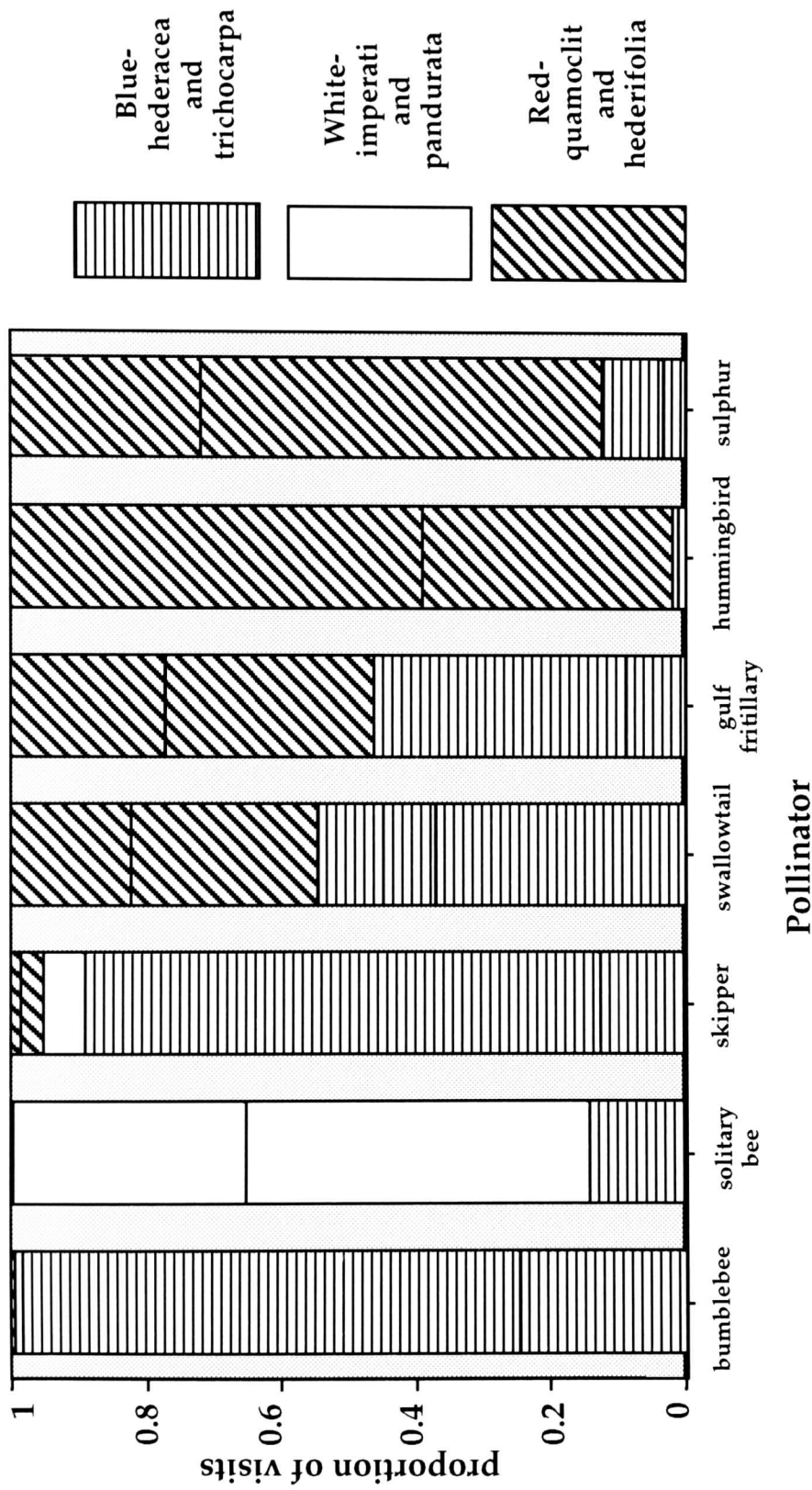


Figure 5. Proportion of all visits by seven pollinators to six *Ipomoea* species pooled by flower color. Data set represents all pollinators visits, and is more inclusive than data used for statistical analyses in Tables 7 and 8.

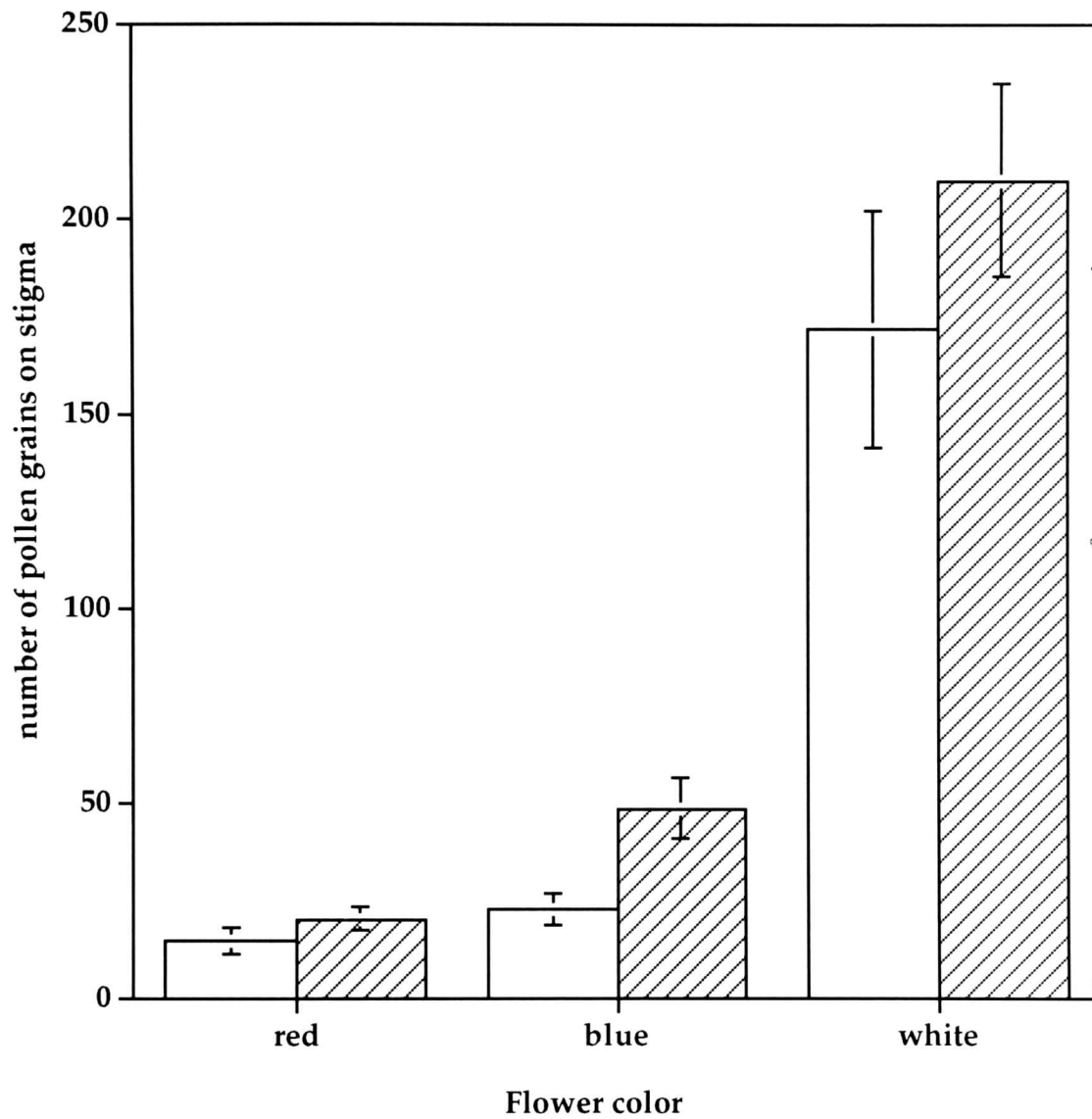


Figure 6. Stigmatic pollen loads (mean  $\pm$  1 SE) of six *Ipomoea* species pooled by flower color. Clear columns represent flowers excluded from pollinators, hatched columns represent flowers open to pollinators. Red (*I. hederifolia* and *I. quamoclit*), blue (*I. hederacea* and *I. trichocarpa*), and white (*I. imperati* and long-styled *I. pandurata*).

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## APPENDICES

## APPENDIX A

Floral Measurements of Six *Ipomoea* Species

Measurements of flower traits and results for ANOVA on corolla length and width for six *Ipomoea* species. Flower color, syndrome, mean corolla length and width in millimeters (mean  $\pm$  1 SE), and coefficient of variation (CV) for corolla width and length. Sample size for each mean ranged from 20-90 flowers. CVs determined from less than 26 flowers were corrected with Williams correction. Means followed by the same letter in a column are not significantly different from each other (Tukey-Kramer test).

<i>Ipomoea</i> species	flower color	syndrome	corolla length	corolla width	CV length	CV width
hederacea	blue	bee	32.8 $\pm$ 0.7 c	32.9 $\pm$ 1.0 c	10.9	14.8
hederifolia	red	bird	32.2 $\pm$ 0.3 c	16.3 $\pm$ 0.3 d	8.4	13.0
imperata	white	bee	43.7 $\pm$ 1.2 b	63.3 $\pm$ 1.6 b	12.3	11.6
pandurata	white	bee	61.0 $\pm$ 0.8 a	74.8 $\pm$ 0.9 a	12.1	11.6
quamoclit	red	bird	31.6 $\pm$ 0.3 c	18.5 $\pm$ 0.3 d	6.4	9.3
trichocarpa	blue	bee	30.3 $\pm$ 1.2 c	30.5 $\pm$ 0.9 c	6.8	14.2
			<b>F</b>	331.6	978.3	
			<b>df</b>	5,268	5,268	
			<b>P</b>	<0.0001	<0.0001	



## APPENDIX B

### Floral Measurements of Six *Ipomoea* Species Pooled by Syndrome

Measurements of flower traits and results for one-way ANOVA on corolla length and width for two groups of six *Ipomoea* species pooled by syndromes. Syndrome, mean corolla length and width in millimeters (mean  $\pm$  1 SE), and the coefficient of variation (CV) for corolla width and length. Sample size for each mean ranged from 59-110 flowers. T-tests results are from bee (all) vs. bird syndrome for corolla length and width.

<i>Ipomoea</i> pooled by syndrome	corolla length	corolla width	CV length	CV width
bee (blue)	31.4 $\pm$ 0.8	31.5 $\pm$ 0.7	19.3	16.9
bee (white)	57.9 $\pm$ 0.9	72.8 $\pm$ 0.9	16.8	13.1
bee (all)	48.6 $\pm$ 1.2	58.4 $\pm$ 1.6	31.5	36.7
bird	32.0 $\pm$ 0.2	17.1 $\pm$ 2.3	7.7	13.2
<b>t</b>	11.06	19.65		
<b>df</b>	272	272		
<b>P</b>	<0.0001	<0.0001		

## APPENDIX C

Frequency of Floral Herbivory in *Ipomoea*

Surveys were made 2-3 times a week from August to October to quantify the frequency of damage to *Ipomoea* flowers by floral herbivores, predominately larval *Spodoptera* sp., a noctuid moth. Mean percent of flowers damaged by floral herbivores is a mean of weekly means. Statistics of a two-way ANOVA on *Ipomoea* pooled by syndrome, year, and interaction are given below. The syndrome-interaction term is significant because bee flowers saw an increase in frequency of floral herbivory damage, while bird flowers saw a decrease in frequency of damage.

<i>Ipomoea</i> species	flower color	syndrome	year	total # flowers surveyed	# flowers damaged by floral herbivores	mean $\pm$ 1 SE percent flowers damaged by floral herbivores
hederacea	blue	bee	1999	2493	47	2.2 $\pm$ 0.5
			2000	794	23	5.3 $\pm$ 2.2
hederifolia	red	bird	1999	17,718	94	0.7 $\pm$ 0.1
			2000	3065	23	0.5 $\pm$ 0.3
quamoclit	red	bird	1999	12,439	154	1.4 $\pm$ 0.1
			2000	2817	23	0.5 $\pm$ 0.4
trichocarpa	blue	bee	1999	6143	197	4.6 $\pm$ 0.8
			2000	4103	595	10.1 $\pm$ 2.0

	F	df	P
syndrome	39.5	1,235	****
year	2.6	1,235	NS
interaction	5.9	1,235	*

\*  $P < 0.05$ , \*\*\*\*  $P < 0.0001$ , NS  $P > 0.05$

## APPENDIX D

## Effect of Floral Herbivory on Fruit and Seed Set

Flowers damaged by larval noctuid moths, *Spodoptera* sp., and adjacent undamaged flowers were tagged and fruits collected in subsequent weeks in 1999. A G-test was used to compare the number of flowers in each treatment for each *Ipomoea* species that developed a fruit (fruit set), as well as the number of seeds in a fruit (seed set). The percentage of flowers that developed a fruit, and mean number of seeds per fruit are given below.

FRUIT SET				
<i>Ipomoea</i> species	G	P	treatment	% of flowers developing fruit
hederacea	0.47	NS	control	41.5
			damage	34.2
hederifolia	1.04	NS	control	35.1
			damage	24.3
quamoclit	7.73	<0.01	control	80.0
			damage	48.6
trichocarpa	1.53	NS	control	25.0
			damage	0.0
SEED SET				
<i>Ipomoea</i> species	G	P	treatment	mean number of seeds/fruit
hederacea	2.92	NS	control	3.2
			damage	2.6
hederifolia	3.88	NS	control	3.0
			damage	3.2
quamoclit	15.77	<0.01	control	3.0
			damage	0.8
trichocarpa	1.53	NS	control	0.8
			damage	0.0

NS  $P > 0.05$