

Final Report

Determining Population Status Of Newly-Discovered Bee Species
and Single-Floral Host, *Balduina angustifolia* on NW Florida
Barrier Islands

Gulf Coast Cooperative Ecosystem Studies Unit (GC-CESU)

Task Agreement

between

The United States Department of the Interior

National Park Service

Gulf Islands National Seashore

and

University of Florida

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Project Overview and Key Results

Hesperapis oraria is a solitary ground nesting bee endemic to barrier islands and the immediate coast (within 0.5 km) of the Northern Gulf of Mexico. It is significant not only for its restricted geographic distribution but also for its specialization to a sole floral host, *Balduina angustifolia*. The objectives of this project were to:

1. Compare the distribution of *Hesperapis oraria*'s between surveys completed in 1993/1994 and 2011 along the Florida panhandle,
2. Characterize the foraging habitat of *H. oraria*'s and habitat of its floral host, *B. angustifolia*,
3. Estimate the density of *H. oraria* and *B. angustifolia* on the Perdido Key, Fort Pickens and Santa Rosa Units of Gulf Island National Seashore in 2011 and 2012,
4. Determine probability of patch occupancy and detectability, and
5. Characterize relative density changes from 2012 to 2014 for state parks and Perdido Key and Fort Pickens.

The limited information known about the bee and its key habitat makes these objectives important. The research questions are summarized below along with key findings. Chapters 1-4 are presented in detail within the attached thesis. Chapter 5 is presented within the executive summary and summary figures with tables presented in an accompanying attached file. Tables and figures referenced in the Executive Summary may be found within the following accompanying files:

[Final Report HANNAH HUNSBERGER \(2013\) Master's Thesis ReportDM.docx](#)
[Chapter 5 final report bee-balduina graphs.docx](#)
[Hesperapis oraria burrowing video.wmv](#)

Overview of Methods

1. To confirm *H. oraria*'s specialization on *B. angustifolia* and determine *H. oraria*'s and *B. angustifolia*'s distribution in coastal and non-coastal areas, 10 of the same locations visited in the fall of 1993 and 1994 by entomologists from Auburn University were resampled within *H. oraria*'s documented range in Florida (Cane et al. 1996). Using belt transect sampling, 24 large-scale plots were sampled for *H. oraria* density and *B. angustifolia* density. These plots were placed through a variety of landscape features and possible habitat types. Overall, approximately

4000m² were sampled at each site which encompasses more than the estimated maximum foraging distance of *H. oraria* based on behavior and body size (Gathmann and Tscharntke 2002, Zurbuchen et al. 2010c). Density of the bee was compared between island and coastal mainland sites. Sampling took place October 4-22, 2012.

2. Using data collected from the same 24 large-scale plots further analyses was conducted to understand habitat use of *H. oraria* and *B. angustifolia*. Habitat use was quantified at two spatial scales by running four analyses in Salford System's program CART (Salford System's CART software, SPM Modeler 7.0; 2013). Two analyses were run using the presence or absence of *H. oraria* as the dependent variable, the first analysis determined habitat patch use at a regional scale and the second tree quantified habitat patch use on a landscape scale. Similarly two analyses were run using the presence or absence of *B. angustifolia* as the target variable on a regional and landscape scale.
3. A subset of *H. oraria* foraging habitat patches were re-sampled in 2013 to determine probability of patch occupancy and detectability and to provide information on density changes from 2012 to 2013. In total 102 independent patches were visited 5-7 times and sampled using a belt transect method. The presence or absence of the bee was recorded at each visit. A single season occupancy analysis (2013) was run using the program Presence.
4. A concentrated effort to determine population density of *H. oraria* through time on the Perdido Key and Fort Pickens Units of GINS was conducted using the perpendicular distance transect method and belt transect method. Data was collected October 7-15, 2011 and October 3-20, 2012 from plots randomly placed in *B. angustifolia* patches on Perdido Key and Fort Pickens Units of GINS. Due to the government shutdown, patches on Fort Pickens and Perdido Key could not be revisited until October 19-20, 2013. Unfortunately, the host plant was already past peak bloom on Perdido Key and therefore the density of *H. oraria* was not sampled. The Santa Rosa Unit was sampled but not used in analysis after the bees were determined to be absent from the entire unit. The number of *B. angustifolia* was also recorded in one m² quadrats placed systematically along the transect. Additionally, the total number of flowers in the bottom right quarter of the quadrat was recorded. In December, *B. angustifolia* seedheads were collected from each patch. For the 2012 collection, the number of seeds per seedhead was counted after the plants were dry. Plant height (cm), width (cm), number of seed heads per plant, and width of each seed head collected (cm) were recorded. Lastly, the percent cover of all vegetation in these quadrats was recorded. Precipitation data for 2011 and 2012 was collected from the Naval Air

Station's (NAS) National Oceanic Atmospheric Administration (NOAA) weather station (Retrieved from wunderground.com).

5. Additional sampling was completed in 2013 and 2014 using the same patches on Perdido Key and Fort Pickens Units of GINS and using the methods described for 2011 and 2012. In addition, similar methods were used to assess *H. oraria* density and *B. angustifolia* plant and flower density on selected state parks from Big Lagoon to St. Andrews in 2012 and Henderson Beach to Deer Lake in 2013 and 2014.

Key Results

1. *What is the nature of H. oraria's specialization on B. angustifolia and has the broad geographical distribution of H. oraria in Florida changed since 1994?*

Observations in 2012 support original conclusions that *H. oraria* is only found in coastal habitats (less than 500 m from the gulf) where *B. angustifolia* is abundant. The range and overall regional distribution of *H. oraria* did not change from the 1993-1994 field seasons to the 2012 field season. That is, *H. oraria* can be found on Perdido Key, Fort Pickens, and Santa Rosa Units of GINS as well as the following state parks: Perdido Key, Big Lagoon, Henderson Beach, Topsail Hill, Grayton Beach, Deer Lake, and St. Andrews. Additionally, *H. oraria* was found on Santa Rosa Island in the areas owned by University of West Florida and Eglin Air Force Base. *B. angustifolia* was present on 0.16 ha or 10% of the non-coastal mainland sites where *H. oraria* was absent. Also, *H. oraria* was absent from all sites where *B. angustifolia* was absent; 6.57 ha or 82% of barrier island and coastal mainland (coastal) sites surveyed did not have *B. angustifolia* (Table 2-2; for chapters 1-4 see tables found in attached file *Final Report HANNAH HUNSBERGER (2013) Master's Thesis ReportDM.docx*). Although present outside of sampled transects, *H. oraria* were not found within transects established on either barrier island (Santa Rosa and Perdido Key) within GINS and University of West Florida sties, and only three bees were found in Eglin Air Force Base sites on Santa Rosa Island. In contrast, a total of 44 *H. oraria* were counted within transects on coastal-mainland sites (within 500 m of the Gulf), and only at Big Lagoon State Park was the bee absent during the surveys (Table 2-3). Coastal-mainland sites had more *B. angustifolia* patches, the patches covered more area, and the host plant and flower density were higher than on barrier island sites. The estimated density of *H. oraria* in sampled *B. angustifolia* patches situated in coastal sites was 39 bees/ha contrasting with an average of 2 bees/ha in sampled *B. angustifolia* patches located on barrier islands (Table 2-3).

In summary, *H. oraria* is dependent on *B. angustifolia* in coastal areas for their foraging needs. *H. oraria* density estimates suggest the bees are influenced by variability in *B. angustifolia* characteristics among coastal sites and *B. angustifolia* characteristics vary with occurrence on or off barrier islands and with the dominant plant communities on site. Coastal mainland habitat supported higher bee densities than barrier island foraging habitat and had more *B. angustifolia* patches, the patches covered more area and the host plant and flower density were higher than in barrier island sites. The average number of patches on a barrier island site was 10 compared to 36 patches per 120,000 m² on the coastal mainland. There was also variability in plant and bee quantity among coastal mainland sites in response to the increase of habitats unsuitable to *B. angustifolia* such as dense scrub and flatwoods with dense midstory of shrubs. These scrub habitats are densely wooded except for small openings between shrubs and *B. angustifolia* only grows in the small openings in the woody vegetation. Total area of *B. angustifolia* within a state park was not always the highest where abundance of *H. oraria* was the greatest. In summary, for coastal mainland sites the density of *B. angustifolia* was more descriptive of a site supporting a higher abundance of *H. oraria* than total patch area. *H. oraria* does not occupy forested habitats or non-coastal mainland areas even if its host plant is plentiful. It can be concluded that *H. oraria*, as a specialist bee, is restricted to foraging in open coastal and barrier island habitats where *B. angustifolia* is abundant with no major changes to their range in Florida occurring in the last 18 years.

2. What is the habitat use for *H. oraria* and *B. angustifolia* at the landscape and regional scales?

***H. oraria* Regional scale:**

The analysis of *H. oraria* habitat use on a regional scale yielded a classification tree that identified the number of *B. angustifolia* patches per site as the most important variable predicting *H. oraria* presence. The distance between patches of *B. angustifolia* (m), total area covered by *B. angustifolia* patches (m²), maximum distance to the bay (m), cover of group 3 plant communities (% cover), and the minimum distance to the bay (m) were also identified as important variables in that order (Table 2-5). The classification tree predicts that *H. oraria* will be present when there are at least 12 patches of *B. angustifolia* at a site, which was correct 85% of the time. The tree also predicts that an area is not used by *H. oraria* if there are less than 12 patches at a site; this prediction was correct 67% of the time (Table 2-4).

***H. oraria* Landscape scale:**

The analysis of *H. oraria* habitat use of *B. angustifolia* patches at a landscape scale identifies *B. angustifolia* patch size (m^2), *B. angustifolia* density within the patch (plants/m^2), the landscape in which the *B. angustifolia* patch was located, the presence of a swale in the surrounding environment, distance to the Gulf of Mexico (m), and the density of *B. angustifolia* flowers ($\text{flowers}/\text{m}^2$) as important variables in that order. The classification tree predicts that *B. angustifolia* patches less than or equal to 111.5 m^2 were not used as foraging habitat by *H. oraria*, this prediction was correct 100% of the time. If the patch size was greater than 111.5 m^2 and there was a swale found within 10 meters of the patch, the patch was unused by foraging *H. oraria*; again, this prediction was correct 100% of the time. The model predicts *H. oraria* used foraging habitat if the patch was greater than 111.5 m^2 , had no swale within 10 m, was no further than 475.37 m from the Gulf of Mexico, and had a *B. angustifolia* density of more than 2.5 plants per m^2 . This prediction was correct 74% of the time.

***B. angustifolia* Regional scale:**

The analysis of habitat use by *B. angustifolia* at a regional scale yielded a tree that identified minimum distance of the site to the bay as the most important variable. The maximum elevation (m), cover of group 4 plant communities (%), the maximum distance to the bay (m), the area covered by washover sand flats, and the cover of group 2 plant communities were also identified as important variables in that order (Table 2-9). The optimal classification tree predicts *B. angustifolia* was present when the site was greater than 25 meters from the bay at its closest point and absent if the site was 25 meters or nearer to the bay, these predictions are correct 100% of the time.

***B. angustifolia* Landscape scale:**

The analysis of habitat use by *B. angustifolia* at a landscape scale identifies (in order of importance) landscape feature, washover sand flat presence in the surrounding 10 m, *B. angustifolia* patch size (m^2), distance of the patch from the gulf (m), presence of a swale in the surrounding 10 m, presence of a herbaceous interdunal area and presence of a mixed grassy/woody dune in the surrounding 10 m as important variables determining habitat suitability. The chosen classification tree predicted a habitat patch situated within an herbaceous interdunal area, swale, or washover sand flat would be unsuitable for *B. angustifolia* and this prediction was correct 88% of time. The model indicated that a habitat patch located in a bowl, flatwoods, grassy dune, grassy dune field, mixed grassy/woody dune, scrub dune, scrub opening, or swale ridge, without a washover sand flat in the surrounding 10 meters was suitable for *B. angustifolia*. If the patch was further than 110 m inland

from the Gulf of Mexico the habitat was suitable, but if the patch is located less than or equal to 110 m inland from the gulf then it was predicted to be unsuitable for *B. angustifolia*. Branch five predicted a habitat patch located in a bowl, grassy dune, grassy dune field, scrub dune, or scrub opening situated further than 10 meters from the nearest washover sand flat with no swale present is unsuitable for *B. angustifolia*. This prediction was correct 83% of the time. Lastly, the model predicted a patch found in a bowl, flatwoods, mixed grassy/woody dune, or swale ridge can still be suitable for *B. angustifolia* even with a washover sand flat in the surrounding area (69% of the cases in this branch classified correctly).

3. *What is the probability of detecting H. oraria in a patch of B. angustifolia when the bee is present, and what is the probability of H. oraria occupying a patch of B. angustifolia?*

Overall, the single season occupancy model determined that at 23% of patches sampled, *H. oraria* was detected at least once. Also, the probability of a bee being present at a patch is 44%. The detection probability is 14%. This means that in a survey of a patch where *H. oraria* is present it will only be detected 14% of the time in a single survey. However, because the probability of occupancy is not very high the conditional psi is 27%. The conditional psi means that if a patch is surveyed 5 times and the bee is not detected, there is still a 27% chance that the bee is present because the probability of detection is only 14%.

Management Implications:

The results from this analysis show that the efficacy of any sampling technique used to detect this bee need to be carefully considered. The belt transect method will work but sampling effort needs to be considered. If a patch can be visited 5 times and there is still a 27% chance that the bee is incorrectly recorded as absent then these uncertainties should be acknowledged if not addressed directly.

4. *How did B. angustifolia patch size, cover of all vegetation and B. angustifolia plant density, flower density, plant height, plant width, number of seedheads per plant, and seedhead width change from 2011 to 2012 for Fort Pickens and Perdido key? How did H.oraria density in foraging habitat change from 2011 to 2012? What characteristics of foraging habitat influence H. oraria density?*

B. angustifolia patch size, flower density, and *H. oraria* density decreased from 2011 to 2012. Seed head width (cm) increased from 2011 to 2012. The remaining explanatory variables did not change significantly between years (Table 3-1).

Median patch size decreased significantly from 2011 (13.5m) to 2012 (3.0m) ($Z=-2.11$, 1 df, $P< 0.0326$) (Table 3-2). Median *B. angustifolia* flower density decreased three fold from 2011 ($12/m^2$) to 2012 ($3/m^2$) ($Z=-2.11$, 1 df, $P< 0.0336$) (Table 3-2). Seed head width (cm) significantly increased from 2011 (0.9 cm) to 2012 (1.0 cm) ($Z=2.82$, 1 df, $P< 0.0038$) (Table 3-2). Mean *H. oraria* density decreased from 2011 (74 bees/ha) to 2012 (34 bees/ha). Change in *H. oraria* density cannot be further analyzed because bees were found in 5 of the 51 patches surveyed in 2011 and 2 of the 51 patches surveyed in 2012 in the three units of GINS. This resulted in too many zeros in the dataset to determine any pattern through time. Data collected from across the range of *H. oraria* in 2012 better predicted the foraging habitat characteristics for the bee. Models using presence/absence data predicted *B. angustifolia* density, and patch size positively correlated with *H. oraria* use of the habitat (Chapter 2). The mean number of seeds per *B. angustifolia* seedhead was 32. On average there were 29 seeds per seedhead at both Santa Rosa Island and Perdido Key Units and 38 seeds per seedhead at Fort Pickens Unit. Correlations of higher than average precipitation with smaller *B. angustifolia* patches and lower flower density and therefore fewer bees indicates that the heavy rainfall events of 2012 flooded some landscape features containing *B. angustifolia*. Swales flood periodically and were observed to have flooded significantly and often in 2012. *B. angustifolia* was observed to have established early in the season in swales but died where flooded before reaching maturity and producing flowers (personal observation). Furthermore, models from chapter 2 show that although *B. angustifolia* was commonly found on the periphery of swales *H. oraria* was rarely found within 10 meters of a swale. All these findings indicate that swales were unreliable habitat for *B. angustifolia* growth and *H. oraria* foraging. *H. oraria* might use patches of *B. angustifolia* on the periphery of swales as a foraging resource in a dry year but not in a wet year. Lack of interannual reliability indicates that long term trends could show *H. oraria* favoring drier landscape features.

5. What changes in *H. oraria* density in foraging habitat were found from 2011-2014 throughout the Florida range?

H. oraria density varied along the coast and through time (see supplemental Figures with Tables found in attached file [Chapter 5 final report bee-balduina graphs.docx](#)). Not all sites were sampled in all years and patch size was not constant. As a result sampling effort was not consistent. Therefore, the magnitude of changes in bee density may not be accurate but the trends provide opportunities to develop hypothesis about the causes of these dynamics. Longer time frames will be needed to determine the significance and cause of these changes. In addition, both the line distance method and belt transect method were used to determine density. The line

distance method is preferred for sparse populations, but samples must include at least 40 individuals for the estimates to be accurate. Therefore, estimates that combine multiple sites are more accurate than estimates made for individual sites. The methods give different estimates but the relative values and trends from year to year and among sites are similar.

Management Implications:

1. The dependency of *H. oraria* on *B. angustifolia* for foraging is clear. The focus of conserving foraging habitat for *H. oraria* should be on conservation of *B. angustifolia*. Furthermore, the lack of *H. oraria* in non-coastal mainland areas implies that management should concentrate efforts to known coastal habitat.
2. *H. oraria* shows a preference for sites with more *B. angustifolia* patches and patches of a substantial size indicating the bees are attracted to a site by pollen and nectar rewards (Potts et al. 2004, Larsson and Franzen 2007). It is therefore valuable to identify the habitat needs for this plant in order to understand comprehensive conservation needs for *H. oraria*. The bee's host plant grows in open sandy soils, not subjected to prolonged flooding and sand movement. In other words *B. angustifolia* requires moderate disturbance to create openings in vegetation where the aster can grow. Moderate precipitation is also important for plant recruitment and survival. However, too much disturbance shapes features such as washover sand flats and too much precipitation floods swales; both of which are unsuitable landscape features for *B. angustifolia* to flower with the reliability from year to year necessary for *H. oraria* foraging. Furthermore, *B. angustifolia* was predicted to use the more stable features of the coast when there was a washover sand flat nearby indicating limited disturbance is preferable to no disturbance. Therefore, identifying, protecting, and possibly even creating these features of moderate disturbance could be important for managing for this bee.

An idea first proposed by Cane (1994) suggests an experimental introduction of *H. oraria* at a new location as a possible management technique to protect the species from extinction. The populations of *H. oraria* are so isolated that any major disturbance in one area could wipe out a local population with no hope of re-colonization. This experiment could be taken a step further with introduction of the bee to non-coastal areas where *B. angustifolia* is present. If the bee can survive in well managed relict dune communities away from the coast, the threat of sea level rise could be vastly mitigated.

3. Patches of *B. angustifolia* decreased in size and flower density and *H. oraria* density also decreased from 2011 to 2012. Therefore, the most general conclusion to be drawn is that smaller patches and fewer flowers of *B. angustifolia* result in fewer *H. oraria*. It is therefore important to manage for larger patches of *B. angustifolia* and ensure a density of flowers necessary to sustain *H. oraria* foraging needs. The correlations of higher than average precipitation with smaller *B. angustifolia* patches and lower flower density and therefore fewer bees indicates the unreliability of the host plant in or near swales from year to year. Therefore, critical habitat should exclude even large dense patches of *B. angustifolia* on the periphery of swales and concentrate on more reliable habitat patches.

Future Work:

Only with multiple years of data can an accurate population estimate of *H. oraria* be established. Understanding the population dynamics of solitary bees is important, because if large population fluctuations exist, a long term data set is required for any conclusion to be drawn about the population status of the bee as well as the pollination services provided by the bee (Franzen and Nilsson 2013). Without these long-term studies, the population size could be consistently under or overestimated (Franzen and Nilsson 2013). A long-term metapopulation study looking at colonization/extinction dynamics as well as reproduction could shed some light on the population dynamics of *H. oraria*. Furthermore, a long term project could create a more complete picture of the rare bee's distribution and project its future survival accounting for changing climatic conditions. *H. oraria* is under threat of both climatic and environmental change. As a dynamic environment, coastal landscapes are under constant pressures of change from wind and water punctuated by significant change from storm events. Additionally, climate change models predict future change including an increase in storm frequency and intensity as well as significant sea level rise. All of these current and future changes should be included in plans to successfully protect these ecosystems.

In order to determine characteristics of foraging habitat which influence *H. oraria* density, the plots sampled in 2011 and 2012 should continue to be visited for several more years. Resulting time series data could be used to quantify changes in *H. oraria* density per foraging patch as well as characteristics of dynamic of patch size and plant density. Ultimately, this data could point to important relationships between precipitation and *B. angustifolia* density as well as floral reliability and *H. oraria* population dynamics. For instance, it would be interesting to determine patches of *B. angustifolia* that offer a reliable food source for the bee and how the presence of a reliable food source influences *H. oraria* patch selection.

Another possible explanation for *H. oraria*'s patchy distribution and selectivity of patches could be the bee's ecology. Flower morphology is the result of natural selection enacted by pollinators (Nattero et al. 2010). Pollinators select flowers based on their perceived pollen amount and quality. Because *H. oraria* is restricted to *B. angustifolia* it is likely a main driver in the local-scale evolution of the plant. The bee is likely selecting for certain floral traits and floral cues among and between patches. A study looking at the visitation rate of individual flowers along with more information on the floral cues of *B. angustifolia* is necessary to determine what traits *H. oraria* is selecting for.

During this project *H. oraria* was observed resting on and gathering resources from *Chrysopsis* spp. There are three species of *Chrysopsis* (goldenaster) found in these habitats. Previously, Cane 1994 documented males on a yellow-flowered composite that was not *B. angustifolia* but later identifies all species of *Chrysopsis* as coastal plants not visited by *Hesperapis* bees (Cane, 1994). Therefore, this is the first known documentation of *H. oraria* visiting this plant. There are a few reasons a monolectic bee might visit another host plant. Bees use olfactory and visual cues to locate their host plants (Filella et al. 2011) and pollination is guided by both innate and learned behaviors (Riffell et al. 2008; Praz et al. 2008). For specialist pollinators precise host recognition is key (Filella et al. 2011). Therefore, this could indicate that the bee is not monolectic as previously thought, but is oligolectic (Cane 1994), meaning they specialize in few select species of host plants. Cane mentions this possibility in a research report (1994) but named the bee as a monolectic species in publications. The timing of bee emergence coinciding exactly with *B. angustifolia* flower indicates it as the strongly preferred host plant at the very least. Possibly the individuals observed on *Chrysopsis* were stretched for resources (Aizen and Harder 2007; Potts et al. 2003). The area where this behavior was observed contained *B. angustifolia* in great number but the competition among and between species was also high. Lastly, perhaps the bees observed on *Chrysopsis* were only collecting nectar and not pollen. Most bee species collect nectar from a wide variety of plants even if they are selective in choosing their pollen source (Filella et al. 2011). All of these reasons are speculative and it is not clear if *Chrysopsis* is in any way important to *H. oraria*. More research into this relationship could be key for management and restoration of the bee.

Pesticides and invasive fire ants might also threaten the survival of *H. oraria* (Cane, 1994). All counties in Florida where the bee is found regularly spray pesticides for mosquito and other pest control. Most applications are to ponds and standing water and targeted at mosquito larvae. However, there is a considerable effort toward pest control in the form of aerial and road side aerosol applications. The bee populations on protected land should be shielded from these chemicals however many of the parks are so small that they do not offer much of a buffer from public roads where applications occur. There are also many doubts as to the precision of aerial applications. Fire ants

(*Solenopsis spp*) are also a threat to many ground dwelling animals and prefer deep sandy soils characteristic of coastal locations where *H. oraria* may nest. An invasion of fire ants to these coastal habitats may be devastating to nest survival; therefore, this situation should be monitored.

Lastly, the most important next step in conservation efforts for *H. oraria* is to determine the nesting habitat needs for the bee. Samplers in 1993-1994 and 2011-2012 were not able to locate the nests even after a concentrated effort (Cane et al. 1996). Females with full pollen loads were commonly observed leaving foraging areas, indicating they do not nest among the host plants. Furthermore, males were observed seeking females at host flowers and not searching the ground under host plants as most solitary bee species do to find emerging virgin females (Cane 1994). This behavior was also observed in the course of this study which supports the hypothesis that the nesting habitat is not the same as foraging habitat. However, in the fall of 2014 a single *H. oraria* was observed actively digging on Fort Pickens within the largest patch of *B. angustifolia* found in our study area. A short video of this activity is attached to the report ([*Hesperapis oraria burrowing video.wmv*](#)). The bee was seen actively moving sand at approximately noon Sept. 11, 2014. Understanding the bee's foraging habitat can at best provide an incomplete picture of the habitat requirements of *H. oraria*. It is important for nests to be located and nesting habitat quantified to develop comprehensive conservation plans for this rare, endemic species.

Final Report HANNAH HUNSBERGER (2013) Master's Thesis ReportDM.docx follows:

DISTRIBUTION AND HABITAT USE OF FLORIDA ENDEMIC SOLITARY BEE
HESPERAPIS ORARIA AND HOST PLANT *BALDUINA ANGUSTIFOLIA*

By

HANNAH K HUNSBERGER

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To EPD and ISH

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The analysis and maps for this paper was generated using ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute

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Abstract of Thesis Presented to the Graduate School
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DISTRIBUTION AND HABITAT USE OF FLORIDA ENDEMIC SOLITARY BEE
HESPERAPIS ORARIA AND HOST PLANT BALDUINA ANGUSTIFOLIA

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The solitary ground nesting bee *Hesperapis oraria* is endemic to the barrier islands and immediate, coastal mainland of the Northern Gulf of Mexico. Significant not only for its restricted geographic distribution but also for its specialization to a sole floral host, *Balduina angustifolia*, this rare bee warrants further investigation into its habitat needs. *H. oraria* density decreased overall from 2011 to 2012 and was lower on barrier island sites when compared with coastal mainland sites. No *H. oraria* were found on non-coastal mainland sites (0.5 km from the Gulf of Mexico). Results from Wilcoxon rank-sum tests indicate that *B. angustifolia* patch size (m) and flower density (no/m²) decreased from 2011 to 2012. This study also quantified the habitat use of *H. oraria* and *B. angustifolia* at two spatial scales using a classification tree species distribution modeling approach. Analyses determined the regional distribution of *H. oraria* was driven by the number of *B. angustifolia* patches, while at the landscape scale *H. oraria* presence or absence was predicted most strongly by *B. angustifolia* patch area and plant density as well as proximity to ephemeral wetlands. *H. oraria* was absent from *B. angustifolia* patches when these patches were in close proximity to ephemeral wetlands. The regional distribution of *B. angustifolia* was influenced by the proximity to

the bay and within a landscape *B. angustifolia* distribution was strongly influenced by the stability of the landscape feature in which it is found. Within a landscape *H. oraria* was predicted to use foraging patches less than 475 meters from the gulf and *B. angustifolia* occupied areas greater than 110 meters from the gulf. These two models can be combined to predict that land between 110- 475 meters from the Gulf of Mexico is suitable habitat for *H. oraria* as well as *B. angustifolia* making this area critical foraging habitat for *H. oraria*. Establishing a long term monitoring program to determine the population status of this rare bee is vital to its conservation. It is also important to protect *B. angustifolia* habitat by maintaining the stability of these coastal ecosystems.

CHAPTER 1 INTRODUCTION

Threats to Specialized Solitary Bees

Biological conservation traditionally focuses on conserving charismatic vertebrates, plants, and communities and, therefore, there has been a distinct lack of effort towards the conservation of insect species (Gullan and Cranston 2010). The conservation of rare insects is often threatened simply because insects are frequently overlooked due to low detection (Brust et al. 2008; Hill and O'Malley 2010). Much of the effort in insect conservation has been focused on charismatic insects which can act as flagship species. However, even the plight of flagship species can prove hard to detect. For example, a threat to the narrow food source (*Myrmica* ant societies) of the globally threatened *Maculinea arion* or Large Blue Butterfly went unnoticed until the butterfly came close to extinction (Thomas et al. 2009). The conservation of insects is important for many reasons. Insects can act as keystone species, meaning their loss would collapse the wider ecosystem of which they are a part, or indicator species, species whose population health can be used to gauge the health of the ecosystem at large. Knowledge of the importance of insects has grown and there are numerous examples of successful insect conservation endeavors. For example, the El Segundo blue, *Euphilotes battoides* spp. *allyni*, lives primarily in sand dunes near the Los Angeles airport. Urban sprawl threatened this habitat but with education and negotiations 80 hectares of their prime habitat was set aside as a reserve and surrounding golf courses agreed to preserve their larval food plant *Erigeron parvifolium*. This reserve not only protects the El Segundo blue but also an endangered habitat and other threatened insects (Gullan and Cranston 2010). General solutions to mitigate threats to rare and

threatened insects include increasing knowledge about the existence of these species, determining where they are found, and quantifying their habitat needs. In recognition of the importance of even the smallest members of an ecosystem, there is a recent increase in research efforts to gather precise information about insects' resource requirements and determine habitats that do and could support endangered insects (Hill and O'Malley 2010; Thomas et al. 2009; Snep et al. 2011; Horak 2011).

About 87% of angiosperms are pollinated by animals (Ollerton et al. 2011) and insects make up an important portion of the world's pollinators. Insect-plant interactions in the form of pollination is a mutualistic relationship, the insect gathers resources from the plant and in turn aids that plant in sexual reproduction. Threats to pollinators include loss and fragmentation of habitat, climate change, and the introduction of exotic species (Rathcke and Jules 1993; Allen-Wardell et al. 1998; Debinsky and Holt 2000). Understanding the plant-pollinator community structure is vital to conservation efforts focusing on pollinator and host-plant populations (Aizen 2007; Pemberton 2010; Potts et al. 2003). Bees are considered the most important group of pollinator insects because they pollinate the majority of the world's wild plant species and are economically vital for their pollination services to crops (Klein et al. 2007; Potts et al. 2010). There has been a recent rise in concern over increasing reports on the loss of bee diversity worldwide (Brown and Paxton 2009; Brown 2011; National Research Council of the National Academies 2006). Despite a general consensus of their importance and imperiled status, bee population dynamics and conservation knowledge is grossly inadequate; especially when compared with similar taxa (Biesmeijer et al. 2006, Kremen et al. 2007, Potts et al. 2010). Therefore, more research on bee ecology, population genetics,

population dynamics and behavior is critical to make informed decisions and effective conservation efforts (Cerna et al. 2013; Franzen and Nilson 2013).

Insects display a variety of social behavior ranging from eusocial, or “true social”, to solitary. Eusocial insects co-operate for the common good of their colony; they are defined by (1) a division of labor with a rigid caste system which includes non-reproductive individuals, (2) co-operation in caring for the young and (3) an overlap in generations where all work simultaneously for a common goal of the persistence and success of the colony. Solitary insects exhibit none of these co-operative behaviors. Solitary insects care for their brood on their own, in fact, nearly all solitary insects are parasitoids where adults immobilize arthropod prey for their offspring to feed on. Non-social insects in the Hymenoptera order are restricted to a few aculeate (ovipositor is modified as a sting) in the Apocrita suborder within the superfamilies Chrysidoidea, Vespoidea, and Apoidea (Gullan and Cranston 2010). Solitary bees (Apoidea) use pollen to provision their nest and feed their larvae, instead of arthropod prey. Every solitary female bee is fertile and inhabits the nest she built alone. Eusocial bees have some advantages over solitary bees since foraging, feeding the queen, caring for offspring, and nest maintenance are all performed simultaneously by different castes where solitary bees must perform all these tasks in sequence. As a result individual errors for eusocial bees have little or no consequence compared with solitary bees where one mistake could be fatal to an individual female and therefore all her potential offspring. Furthermore, solitary bees lack the ability to defend against more formidable predators that eusocial bees could cooperatively thwart. Despite their disadvantages

solitary bees make up a significant portion of the world's pollinators and can play key roles in the functioning of their ecosystem.

Solitary bees provide important pollination services. These bees can be especially important for outcrossing plant species, even when they are not the only pollinators visiting the plant (Bischoff et al. 2013). A rare solitary bee, *Hylaeus matamoko*, was found to be responsible for 90% and 95% of the pollination of two outcrossing plant species in the New Zealand alpine which were visited just as often by a fly species (Bischoff et al. 2013). Zych and Stpiczyska (2012) studied the pollination effectiveness of various pollinators on *Fritillaria meleagris* (Liliaceae) and concluded that while *Bombus* queens are the most frequent visitors, the small-bodied solitary bees (genera *Andrena* and *Lasioglossum*) carried almost three times larger pollen loads. The researchers concluded that small solitary bees could therefore be more effective pollinators in terms of quality of pollination (Zych and Stpiczyska 2012). These studies also point to the importance of understanding the effectiveness of each visit by a pollinator in addition to the rate of visitation to identify the importance of each pollinator species for a plant or community (Bischoff et al. 2013; Zych and Stpiczyska 2012). Solitary bees might not be the most frequent visitors but, possibly because they are doing all the work by themselves, they can still be more effective and are therefore more important than casual observation might indicate.

In most pollination systems insects broadly pollinate all or most flowering plants without discrimination. However some insects are faithful pollinators toward one or a few select plants. For example, fig wasp species are known to be specific pollinators of specific fig species and some moth proboscis lengths match exactly to the flower depth

of only certain species (ie *Angaecum sesquipedale* and *Xanthopaa morgana paraedicta*). Specialist bees use olfactory receptors on their antennae to detect flower odorants and can distinguish plant species as well as differentiate between rewarding and non-rewarding flowers within species (Dobson and Bergström 2000; Raguso 2008). Examples of specialist bees include *Heriades truncorum* which are restricted to heaths (Praz et al. 2008), *Hoplitis adunca* which solely collects pollen from plants in the *Echium* genus (Boraginaceae) (Burger et al. 2010), and *Andrena vaga* (Andrenidae) which specializes on the genus *Salix* (willow) as a host plant (Cerna et al. 2013). Specialist bees may be restricted to their host by physiological adaptations for pollen digestion and/or neurological adaptations to identify floral features (Sedivy et al. 2008) but they find their host plant using taxon-specific olfactory cues (Dötterl and Vereecken 2010). Older bees can also use learned features of host plants to locate them (Dobson and Bergström 2000; Dötterl and Vereecken 2010; Milet-Pinheiro et al. 2012). While many solitary bees are oligolectic, or specialist pollinators to a few related plant species. True monoleptic bees, bees which only pollinate one species of flower, are extremely rare.

Bee populations worldwide are threatened and the ecology of specialist bees makes them particularly imperiled. Habitat degradation and fragmentation from landscape changes are major threats to bee populations (e.g. Klein et al. 2007; Kremen et al. 2007). Rare and endangered species are often threatened because of their specialized food and habitat requirements; this is especially true of many rare insects (Brust et al. 2008; Hill and O'Malley 2010; Thomas et al. 2009; Snep et al. 2011; Horak 2011). Specialist bees seem to be especially sensitive to negative effects of habitat fragmentation compared with generalists species (Biesmeijer et al. 2006; Cane et al.

2006). For bees that pollinate more than one flower species there is opportunity to optimize the best balance of water and sugar by varying the foraging patterns appropriately. However, monolectic bees that rely on a single floral host usually specialize in the most abundant and reliable host species, often one with simple flowers that can be pollinated by many species (Dötterl and Vreecken 2010). The availability of one reward over another can be limiting to the bee species that specialize in this way (Pemberton 2010, Willmer 1986). Pemberton (2010) documented a correlation between the reductions in the abundance of a specialist bee to the decline of the only oil-reward plant in an area. Monolectic bees also do not have the luxury of choosing their foraging time to optimize water-sugar ratios in flower nectar because this would reduce overall inputs and add to cell stocking time thereby, increasing the nest's susceptibility to nest-robbing and parasitism (Willmer 1986). Often, the only remaining option for specialist bees to optimize foraging is the choice between floral patches of the same species. Resource inputs are controlled by the number of flowers visited in a given trip (Willmer 1986). Because of the lack of control over energy-water ratios, monolectic solitary bees are thought to forage primarily to fulfill their own physiological water needs and, assuming the monolectic relationship occurs because of co-evolution, it is likely that sugar needs are met by default (Willmer 1986). For example, a study of a monolectic solitary bee, *Chalicodoma sicula*, concludes that it chooses its foraging strategy in relation to optimal water, rather than caloric rewards in arid environments (Willmer 1986). Pollen specialization can also affect the reproductive success of the host-plant as both the quality and quantity of pollination available to them can be limited (Aizen 2007). Since specialists rely on specific habitats and narrow food sources,

anthropogenic disturbance of either is a significant threat (Brust et al. 2008; Hill and O'Malley 2010; Thomas et al. 2009; Snep et al. 2011). Pollinator specialist are thus vulnerable to food loss due to habitat fragmentation, and monolecty further increases this sensitivity as the reliance on one host plant increases the chances that landscape change can likely affect the species' entire food source (Bommarco et al. 2010).

Physiological factors influence the distance an individual bee can travel from nest to foraging patch. Therefore, the density of small-bodied specialized species is more likely to decrease over time in small habitat patches than larger habitat patches (Bommarco et al. 2010). Bommarco et al. (2010) concludes that a high proportion of small specialist bees are extinct because of habitat fragmentation; demonstrated by low species richness found in small habitat patches (Bommarco et al. 2010).

Solitary bees are also highly vulnerable to habitat change. Solitary bees rely on flowers for both energy and water needs as well as brood provisions; this is unlike many social bees that often take breaks from pollen foraging to meet their water needs from a different source (Pemberton 2010; Willmer 1986). Solitary bees must return to their nests multiple times throughout a day to supply their brood cells with pollen and nectar (Zurbuchen et al. 2010b). Therefore, habitat fragmentation and landscape barriers can limit the resources available to a population (Zurbuchen et al. 2010c). Furthermore, solitary bees are susceptible to negative impacts from landscape fragmentation or any change that might increase the distance between their nests and floral host patches because they have a higher frequency of trips from nesting sites to foraging sites than social bees (Zurbuchen et al. 2010b). A study by Peterson and Roitberg (2006) demonstrated that the reproduction success of some solitary bee species suffered when

the foraging distance was increased. Understanding the distance a bee is capable of covering between the nest and host plant patch is therefore critical in the preservation of endangered bee species populations (Zurbuchen et al. 2010b). However, the maximum foraging distance is not always representative of the actual distances females will travel, as some species are shown to often stop short of their maximum (Zurbuchen et al. 2010a; Zurbuchen et al. 2010c). Overall, solitary bees have less flexibility and are therefore more vulnerable to landscape change and habitat fragmentation than their social counterparts.

The vulnerability of a host plant species to habitat fragmentation depends on the extent of their mutualism with a pollinator (Aizen et al. 2002b). Research in pollinator and host plant interaction indicates that habitat fragmentation reduces the abundance of pollinators and is therefore responsible for a decline in pollination rates that results in a decrease in fruit and/or seed production of host plants (Steffan-Dewenter and Tscharntk 1999; Cunningham 2000). For example, Cunningham (2000) found flowers of *Acacia brachybotrya* and *Eremophila glabra* decreased fruit production when growing in fragmented habitats because they are pollen limited.

Hesperapis oraria* and *Balduina angustifolia

Hesperapis oraria is a ground-nesting solitary bee endemic to coastal areas on northern Gulf of Mexico. Recently described, this bee is a species of interest for its limited geographic range and its dependence on a single floral host plant, *Balduina angustifolia*, for all its nectar and pollen needs (Cane et al. 1996). There is limited information on the habitat needs of the bee and much of what is known is inferred from its closest relative, *Hesperapis carinata*, found in mid and north-western United States. Preliminary studies indicate that *H. oraria* is rare and likely endangered as a result of

habitat loss and fragmentation from both natural and anthropogenic disturbances (Cane et al. 1996). In order to protect this rare species it is important to determine and characterize its geographic distribution. Their apparent reliance on a single host plant species makes the characteristics of *B. angustifolia* habitat important as well. The host plant is dependent on pollination for seed production and, therefore, *H. oraria* may be important for its reproductive success in these coastal habitats. However, *B. angustifolia* can be found in locations where *H. oraria* is not present indicating that the plant's distribution is not completely driven by the bee but is influenced by other environmental factors and is pollinated by other insects.

CHAPTER 2 HABITAT SUITABILITY OF BALDUINA ANGUSTIFOLIA AND HESPERAPIS ORARIA AT TWO SPATIAL SCALES

Background

Described in 1996 *Hesperapis oraria*, an endemic species with a range from eastern Mississippi barrier islands to the eastern coast of the Florida panhandle, is the only known species of the Dasypodaidae family to occur east of the Mississippi River (Cane et al. 1996). In 1993 and 1994 entomologists from Auburn University and the U.S. Department of Agriculture determined *H. oraria*'s endemism to select coastal locations on the northern Gulf of Mexico. They also presented it as a rare monolectic species, meaning the female bees gather all their pollen for brood provision from only one species of plant, *Balduina angustifolia* (Cane et al. 1996). Monolecy is extremely rare; in fact, many species initially documented as monolectic have since been documented collecting pollen on a substitute host when their preferred host plant is unavailable (Dötterl and Vreecken 2010; Muller and Kuhlmann 2008; Westrich 2008). The nests of *H. oraria* have not been located but information on their lifecycle can be inferred from foraging behavior and general knowledge of other ground-nesting solitary species. *H. oraria* emerges for about three weeks from the end of September to the middle of October to reproduce, females likely mate shortly after emergence and spend the rest of their time provisioning their nests (Cane 1994). *H. oraria* is therefore a species of interest because of its limited geographic range, the threatened state of its limited habitat, and its monolecy. Beyond the study conducted in 1993 and 1994, there is no information on the distribution or habitat needs for *H. oraria*.

The genus *Balduina* is composed of three species found in southeastern United States and is characterized by "unique receptacular bractlets connected into

honeycomb-like structures surrounding the achene” (Small 1933; Parker 1975). *Balduina angustifolia* or coastal plain honeycomb head is a self-incompatible annual. It grows in dry soils of deep sand ridges along rivers and on shallow dunes of the Atlantic and Gulf Coast beaches and can be found throughout Florida and into southern Georgia and Alabama (Parker 1975). The plant is the sole known host plant for *H. oraria*, however, it is regularly visited by a broad variety of pollinators. In coastal areas, coastal plain honeycomb head has a patchy distribution and only flowers for a short period coinciding with foraging activity of *H. oraria*. The coastal areas of the Gulf of Mexico are under the pressure of constant change from wind, waves, sedimentations, sea-level rise punctuated by storms and hurricanes that cause sporadic changes in geomorphic features (Lucas and Carter 2010). The limited flowering period coupled with the dynamic landscape of the gulf coast habitats contributes to the patchy distribution of the plant in these environments. Human development and habitat degradation threaten many species that live entirely in these dynamic habitats making these species especially sensitive to further disruption from alterations of vegetation (Lucas and Carter 2010; Pries et al. 2009). Therefore, it is important to understand what drives the distribution of this host plant if we aim to understand the distribution of *H. oraria*.

In order to understand the agents driving the distribution of *H. oraria* and *B. angustifolia* it is necessary to examine their interactions with each other and abiotic and biotic factors at different scales (Urban et al. 1987). The complexity of the interactions between these factors and how spatial scale affects them can be overwhelming. Therefore, this study attempts to simplify the system into basic components operating at different scales. By designing analyses at two different scales (Simon 1962) it is

possible to predict how spatial scale influences the interactions between *H. oraria*, *B. angustifolia*, and their environment.

Study Area

Barrier islands, coastal mainland areas, and non-coastal mainland areas were surveyed for *H. oraria* and *B. angustifolia* throughout most of the known range of *H. oraria* in Florida (Figure 2-1). Sites were located on lands managed by state and federal agencies and included: Gulf Islands National Seashore (GINS), Eglin Air Force Base (EAFB), Florida Park Service land, and Florida State Forest land (Figure 2-2). Three units of GINS were included: Perdido Key, Fort Pickens, and Santa Rosa Island. Both non-coastal mainland and Santa Rosa Island sites were sampled on EAFB. Florida State lands included Big Lagoon State Park, Henderson Beach State Park, Topsail Hill State Park, Grayton Beach State Park, Deer Lake State Park, St. Andrews State Park, and Point Washington State Forest. An area owned by the University of West Florida on Santa Rosa Island was also included.

Gulf of Mexico barrier islands are narrow strips of sand running parallel to the mainland. Barrier islands included in the study were Perdido Key and Santa Rosa Island, Florida. Together they stretch from approximately two miles west of the Alabama border (30.2767°N, -87.5519°W) to Destin Florida (30.3886°N, -86.5180°W). Santa Rosa Island is about 60 km long and 0.5 km wide. The island has foredunes near the Gulf of Mexico that run intermittently the length of the island parallel to the shoreline. Secondary dunes are found behind foredunes closer to the bay. The area between these dunes consists of sand flats and rolling grasslands with ephemeral wetlands, called swales, found scattered throughout. Dominant species of the foredunes include sea oats (*Uniola paniculata*), cakile (*Cakile spp.*), beach morning glory (*Ipomoea*

imperati), and seashore elder (*Iva imbricata*). The secondary dunes are dominated by woody species such as Florida rosemary (*Ceratiola ericoides*), woody goldenrod (*Chrysoma pauciflosculosa*), sand live oak (*Quercus geminata*), and sand pine (*Pinus clausa*) (Pries et al. 2008). Perdido Key is about 24 km long and 0.5 km wide, has fewer well developed dunes and generally lacks the woody secondary dunes compared to Santa Rosa Island (Looney et al. 1993). However, the species composition of the islands is comparable. Perdido Key also features a wider section of the island where the secondary dunes develop into a scrubby flatwood forest with a slash pine (*Pinus elliotii*) overstory (FNAI 2010).

Coastal mainland sites included all the Florida State Parks (Fig 2-2) and were defined as the first 0.5 km of mainland closest to the Gulf of Mexico. These sites are composed of foredunes close to the gulf, behind which are secondary woody dunes similar in composition to those found on the barrier islands. However, behind the woody scrub dunes is denser woody vegetation composed of evergreen shrubs and, in some cases, a pine canopy (scrub and scrubby flatwoods). Dominant species include Florida rosemary (*Ceratiola ericoides*), sand pine (*Pinus clausa*), myrtle oak (*Quercus myrtifolia*), sand live oak (*Quercus geminata*), Chapman's oak (*Quercus chapmanii*), and saw palmetto (*Serenoa repens*). Interspersed through the woody species are openings consisting of bare ground and sparse herbaceous species (FNAI 2010).

The non-coastal mainland sites included in this study consist of Mesic and Scrubby Flatwoods and Sandhill communities located further than 0.5 km from the Gulf of Mexico. Mesic and Scrubby flatwoods have an open canopy of longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliotii*). These communities consist of low shrubs

including saw palmetto (*Serenoa repens*), inkberry (*Ilex glabra*), and fetterbush (*Lyonia lucida*). Dominant understory species are dwarf live oak (*Quercus minima*), runner oak (*Q. elliotii*), shiny blueberry (*Vaccinium myrsinites*), Darrow's blueberry (*V. darrowii*), dwarf huckleberry (*Gaylussacia dumosa*), wiregrass (*Aristida stricta* var. *beyrichiana*), pineywoods dropseed (*Sporobolus junceus*), panicgrasses (*Dichanthelium* spp.), and broomsedges (*Andropogon* spp.). Sandhill communities are composed of a longleaf pine (*Pinus palustris*) overstory and a midstory dominated by turkey oak (*Quercus laevis*), bluejack oak (*Q. incana*), sand live oak (*Q. geminata*), sand post oak (*Q. margaletta*), saw palmetto (*Serenoa repens*), and sparkleberry (*Vaccinium arboreum*). The understory is composed of a diversity of grasses and forbs, the dominant of these are wiregrass (*Aristida stricta* var. *beyrichiana*), dwarf huckleberry (*Gaylussacia dumosa*), pricklypear (*Opuntia humifusa*), gopher apple (*Licania michauxii*), pineywoods dropseed (*Sporobolus junceus*), lopsided indiagrass (*Sorghastrum secundum*), several species of bluestems (*Andropogon* spp.), and little bluestem (*Schizachyrium scoparium*) (FNAI 2010).

Methods

To confirm *H. oraria*'s specialization on *B. angustifolia* and determine *H. oraria* and *B. angustifolia* distribution in coastal and non-coastal areas, locations visited in previous years were re-surveyed. In the fall of 1993 and 1994 entomologists from Auburn University searched for *H. oraria* on barrier islands, coastal mainland areas, and non-coastal mainland areas from Mississippi to the eastern Florida panhandle (Cane et al. 1996). The researchers searched for the bee in areas with abundant *B. angustifolia* and areas with little or no *B. angustifolia*, collecting voucher specimens for species verification. They did not have GPS/GIS technology to accurately document the

location of their search areas, so this study relied on resulting publications and reports along with correspondences between Cane and land managers to locate sampling areas. Ten of the same locations initially sampled in 1993-1994 were resampled within *H. oraria*'s documented range in Florida.

To determine the spatial distribution of *H. oraria* and *B. angustifolia* 24 large-scale grids were established at each site. Each site was sampled using belt transects orientated to fit within the boundaries of the undeveloped sections of the state and federal lands. (Figure 2-3). Using 2006 Digital Orthophoto Quarter Quads (DOQQs) from the United State Geological Survey (USGS), transects were placed through a variety of landscape features and possible habitat types. Length and configuration of transects was confined by the Gulf of Mexico, bays (Choctawhatchee Bay, Santa Rosa Sound, Pensacola Bay, and Big Lagoon), highways, parking lots, housing developments, and other anthropogenic features. As a result, transect length varied in two ways. At 18 sites four two meter wide and 400 meters long belt transects were established, the transects were all 50 meters apart and ran perpendicular to the Gulf of Mexico within undeveloped areas. Every 100 meters along the transects a circular point count area of 28 meters was established. At six sites, 10 two meter wide and 200 meters long belt transects were established. These transects were all 50 meters apart and ran perpendicular to the Gulf of Mexico also exclusively within undeveloped areas. There was a point count covering 28 meters every 100 meters along the length of these transects. Overall, approximately 4000m² were sampled at each site which encompasses more than the estimated maximum foraging distance of *H. oraria* based on behavior and body size (Gathmann and Tscharntke 2002, Zurbuchen et al. 2010c).

Data Collection

To determine *H. oraria*'s habitat use in 2011 and 2012 observations occurred within large scale sampling site transects. However, for descriptive purposes only, observations outside sampling transects were included to denote the presence of the bee when it was not always detected during formal sampling. Furthermore, Camp Helen State Park and Perdido Key State Park were visited without establishing sampling transects. These locations were informally searched for two hours or until the bee was found. No revisits were possible within the time of the bee's activity.

Sampling for *H. oraria* took place from October 4th through October 22nd 2012. To eliminate bias, two samplers were randomly assigned a site, sampling time, starting location and the role of recorder or surveyor. At the beginning of the survey, a temperature reading (C°) was recorded in the shade using an "Enviro-Safe© Easy Read", non-digital thermometer. At all point count locations, a hand held Kestral© wind meter was used to determine average wind speed (mph), and maximum wind gusts (mph). *H. oraria* and other pollinators were searched for at each point count by both samplers who stood back to back for two minutes and recorded all pollinators spotted within a three meter radius from the center of the point count. Four pictures were also taken at each point count, in the four cardinal directions. Between the point count locations transects were surveyed in a consistent manner. Transects were sampled at a steady pace and all *H. oraria* and other pollinators up to a meter on either side of the transect line were counted. When an *H. oraria* bee was found, the location was marked with a flag and geographic coordinates and the landscape feature in which the bee was found were recorded. A photo of the location was taken where any *H. oraria* bee was found.

In order to quantify the landscape in which *H. oraria* and *B. angustifolia* were found, landscape features and dominate vegetation were surveyed and quantified at both a regional and landscape scale. Nine landscape features were identified: washover sand flat (an area eroded by storm surge or wind, very flat, sparse or no recovering vegetation), grassy dune field (expanses of dunes dominated by *U.paniculata*, *P.amarum*, *S.patens*, or *S.maritimum*), grassy dune (well-developed dune dominated by grass cover of primarily *U.paniculata*, *P.amarum*, *S.patens*, or *S.maritimum*), mixed grassy/woody dune (well-developed dunes with a mix of grass and woody species), woody scrub dune (well developed dunes dominated by woody species), herbaceous interdune (areas between dunes vegetated by herbaceous species), bowl without swale (depression/ blowout between dunes without swale vegetation), swale ridge (mostly low lying dunes with irregular and undulating margins that snake along the edges of swales), and swale (densely vegetated ephemeral wetlands) (Branch et al. 2011). The length of each landscape feature along the transect was recorded along with the dominant plant species and total percent cover. Also, the location and length along the transect of each patch of *B. angustifolia* was measured. The width of the entire patch and distance to the next patch including patches outside the transect was determined to the nearest meter using paces and a measuring tape. *B. angustifolia* plants and flower density in each patch was determined using meter square quadrats placed randomly within each patch; the number of quadrats used was in proportion to the area covered by the patch.

Using a digital elevation model from USGS Lidar data the average elevation of a site and each *B. angustifolia* patch was calculated. The presence or absence of

foredunes and the average and maximum foredune height (m) at a site were also determined. ArcMap was used to calculate the maximum and minimum distances of each site to the Gulf of Mexico and the bay. Also, the distance from the center of each *B. angustifolia* patch to the Gulf of Mexico and the bay, if present, was calculated. Using historic hurricane tracks from 1990 to 2012 from the National Oceanic and Atmospheric Administration (NOAA) the distance of each site and *B. angustifolia* patch to the nearest storm landfall location, category of storm, and the distance to the nearest category three hurricane landfall locations were recorded.

Statistical Analyses

The area sampled was calculated separately for all coastal sites (barrier islands and coastal mainland) with *B. angustifolia* present and all coastal sites where *B. angustifolia* was absent. The area sampled of non-coastal mainland was also calculated. Additionally, the ecological density of *H. oraria* was calculated using the number of bees counted per area of *B. angustifolia* sampled. The means of each of the following *B. angustifolia* characterization variables was calculated: nearest patch distance, flower density, plant density, patch area, and number of patches per site. These values were calculated per site, per location (barrier island, coastal mainland, and non-coastal mainland), and overall across all study sites.

To determine dominant community types the sampling sites were grouped by similar characteristics via hierarchical clustering using Sorensen (Bray-Curtis) for the distance measure and Flexible Beta for the linkage method in PC-ORD (Figure 2-4). This combination was recommended by McCune and Grace (2002) for ecological data. Sorensen (Bray-Curtis) was used because it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune and Grace 2002). Indicator species

analysis was performed to decide where to prune the dendrogram or how many clusters are optimal. Four community types were selected as the best level of classification. Each group was formed by environmental variables and can be identified by species composition (Table 2-1). These groups were then used to represent dominant community types in regional scale species distribution models.

A classification tree is a non-parametric species distribution model that is often used to handle complex relationships inherent in ecological data (De'ath and Fabricius 2000). Classification trees split the data into two groups that are mutually exclusive in terms of each predictive variable (as measured by the Gini impurity index). The goal is a set of homogenous groups in terms of the response variable (De'ath and Fabricius 2000). Often this goal is unrealistic and a tree is built until the data cannot be divided any further. Four analyses were run in Salford System's program CART (Salford System's CART software, SPM Modeler 7.0; 2013). Two analyses were run using the presence or absence of *H. oraria* as the dependent variable, the first analysis determined habitat use at a regional scale and the second tree quantified habitat patch use on a landscape scale. Similarly two analyses were run using the presence or absence of *B. angustifolia* as the target variable on a regional and landscape scale.

H. Oraria Habitat Use

Regional scale: To develop a model for predicting *H. oraria* habitat use on a regional scale a classification tree analysis was run in CART (Salford System's CART software, SPM Modeler 7.0; 2013) with *H. oraria* presence or absence at a sampling site as the dependent variable. Sixteen sites determined to be habitat (i.e. coastal sites which had *B. angustifolia* present) were included. The 30 predictor variables used

were: location of the site (mainland coastal, or barrier island), the presence/absence of a foredune for at least 5% of the coastline of site (a foredune is defined as any dune feature at least two meters tall situated closer than 100 meters from the gulf), the category of the storm with the closest landfall since the 1990s (Tropical depression:SD, Tropical storm:TS, Category 1 hurricane:H1, Category 2 hurricane:H2, Category 3 hurricane:H3), density of all other pollinators (insects/ m²) excluding *H. oraria*), average density of *B. angustifolia* (plants/m²), average density of *B. angustifolia* flowers (flowers/m²), the total number of *B. angustifolia* patches in a site, average size of *B. angustifolia* patches (m²), total area covered by all *B. angustifolia* patches (m²), average distance between *B. angustifolia* patches (m), average percent cover of *B. angustifolia* in a patch, minimum and maximum distance to the bay and the gulf (m), temperature during sampling (C°), average height of foredunes (m), maximum foredune height (m), average elevation (m), maximum elevation (m), minimum elevation (m), wind speed during sampling (mph), average gusts during sampling (mph), total cover of washover features (% cover), distance from the center of the site to the nearest named storm event since 1990 (km), distance to the nearest category 3 hurricane landfall since 1990, percent cover of group 1 community type, percent cover of group 2 community type, percent cover of group 3 community type, and percent cover of group 4 community type (Table 2-1). A V-fold cross validation method was used on this model because the sample size was too small to withdraw an independent test sample. Using 100% of the data a maximal, exploratory tree was grown and no pruning was performed. Then (by setting V=10) 10 cross-validation sub-trees were grown on a random 90% of the data, and tested against the remaining 10%. The error rates of the sub-trees were combined

and mapped to the exploratory tree. The maximal tree was then pruned using the error estimates from each node. The percent of sites correctly classified was used as an overall measure of predictive success. The receiver operating characteristic (ROC) curve was also recorded to measure the accuracy of the model, or how well they separate the data into groups with and without *H. oraria* or *B. angustifolia*. An ROC score of 1 indicates perfect predictive accuracy where a score of 0.5 is the predictive accuracy of random guess.

Landscape scale: The second analysis was run to quantify *H. oraria* foraging habitat use on a landscape scale. The differences between *B. angustifolia* patches where the bee was present and the patches where bee was absent were analyzed to determine foraging habitat. For this analysis there were eight predictor variables: the landscape feature in which the patch was found, percent cover of *B. angustifolia*, distance to the nearest patch (m), distance to the gulf (m), density of *B. angustifolia* (plants/m²), density of *B. angustifolia* flowers (flowers/m²), elevation (m), and the presence/absence of each feature within 10 meters of the patch (features = washover, grassy dune field, grassy dune, scrub dune, swale, scrub, flatwoods, road, mixed grassy/woody dune, herbaceous interdune, swale ridge, opening in scrub, and bowl). A series of classification models were run on 2/3 of the original data (learn data) and cross-validated with the remaining 1/3 (test data) to determine the misclassification rate for each tree. The trees were pruned by minimizing misclassification rate. The percent correctly classified was used as an overall measure of predictive success. The receiver operating characteristic (ROC) curve was also recorded to measure the accuracy of the model.

B. angustifolia Habitat Use

Regional scale: To develop a model for predicting *B. angustifolia* habitat use on a regional scale a classification tree analysis was run in CART with *B. angustifolia* presence or absence at a sampling site as the dependent variable. The predictor variables for the landscape scale analyses are the same as for site suitability of *H. oraria* excluding the *B. angustifolia* plant and patch characteristics leaving 23 explanatory variables: location of the site (mainland inland, mainland coastal, barrier island), the presence/absence of a foredune for at least 5% of the coastline of site (a foredune is defined as any dune feature at least 2 meters tall situated closer than 100 meters from the gulf), the category of the storm with the closest landfall since the 1990s (SD, TS, H1, H2, H3), density of all pollinators (insects/m² excluding *H. oraria*), minimum and maximum distance to the bay and the gulf (m) (or the distance to each body of water to the closest and furthest edge of each site), temperature during sampling (C°), average height of foredunes (m), maximum foredune height (m), average elevation (m), maximum elevation (m), minimum elevation (m), wind speed during sampling (mph), average gusts during sampling (mph), total cover of washover features (%), distance from the center of the site to the nearest named storm event since 1990 (km), distance to the nearest category 3 hurricane landfall since 1990, total cover of group 1(%), total cover of group 2(%), total cover of group 3 (%), and total cover of group 4(%). Again, a V-fold cross validation method was used on this model with 10 cross-validated sub-trees. The percent of patches correctly classified was used as an overall measure of predictive success. The receiver operating characteristic (ROC) curve was also recorded.

Landscape scale: The second analysis was run to quantify *B. angustifolia* habitat use on a landscape scale. Patches of *B. angustifolia* documented along each transect were used as habitat patches and using ArcMap, a total of 450 random points were generated across all transects excluding known *B. angustifolia* patches to represent non-habitat units. For this analysis there were five predictor variables: the landscape feature in which the patch was found, distance to the gulf (m), distance to the bay (m), elevation (m), and the presence/absence of each feature within 10 meters of the patch (features = washover, grassy dune field, grassy dune, scrub dune, swale, scrub, flatwoods, road, mixed grassy/woody dune, herbaceous interdune, swale ridge, opening in scrub, and bowl). A classification tree was run to examine habitat preference of *Balduina angustifolia*. Again, the model was run on 2/3 of the original data and cross-validated with the remaining 1/3 to determine the misclassification rate for each tree. The percent correctly classified was used as an overall measure of predictive success. The receiver operating characteristic (ROC) curve was noted to determine model accuracy.

Results

Comparing sites searched in the 1993-1994 field seasons to sites searched in the 2012 field season resulted in no differences in the range or overall regional distribution of *H. oraria*. In both studies *H. oraria* was only found in coastal areas where *B. angustifolia* was present. In the 2012 field season *H. oraria* was absent from Camp Helen State Park but was found during the survey of Perdido Key State Park. *H. oraria* was also absent at all point count surveys. *B. angustifolia* was present on 0.16 ha or 10% of the non-coastal mainland sites where *H. oraria* was absent. Also, *H. oraria* was absent on the 6.57 ha or 82% of barrier island and coastal mainland (coastal) sites

surveyed without *B. angustifolia*. (Table 2-2). Although present outside of sampled transects, *H. oraria* were not found within transects established on either barrier island within GINS and UWF sties, and only three bees were found in EAFB sites on Santa Rosa barrier island. In contrast, a total of 44 *H. oraria* were counted within transects on coastal- mainland sites, and the bee was absent only at the site on Big Lagoon State Park (Table 2-3). Coastal mainland sites had more *B. angustifolia* patches, the patches covered more area, and the host plant and flower density were higher than on barrier island sites. The estimated density of *H. oraria* in sampled *B. angustifolia* patches situated in coastal sites was 39 bees/ha contrasting with an average of 2 bees/ha in sampled *B. angustifolia* patches located on barrier islands (Table 2-3).

H. Oraria Habitat Use

Regional scale: The analysis of *H. oraria* habitat use on a regional scale yielded a tree with two branches (Figure 2-5) which fits the data well while minimizing the misclassification error rate. (Table 2-4). The number of *B. angustifolia* patches per site was identified as the most important variable predicting *H. oraria* presence. The distance between patches of *B. angustifolia* (m), total area covered by *B. angustifolia* patches (m²), maximum distance to the bay (m), plant community group 3 (% cover), and the minimum distance to the bay (m) were also identified as important variables in that order (Table 2-5). These variables are important but do not show up as a splitter in the classification tree, indicating they are surrogate splitters, or back-up splitters that could be used when the primary splitter is missing. The classification tree predicts that *H. oraria* will be present when there are at least 12 patches of *B. angustifolia* at a site, which was correct 85% of the time. The tree also predicts that if there are less than 12 patches at a site then the area is not used by *H. oraria*, this prediction was correct 67%

of the time (Table 2-4). No other variables offered further explanation of *H. oraria* presence or absence at a site. The entire tree correctly classified 75% of cases. The relative cost, which measures the performance of the test sample scaled with 1.00 being random and 0 a perfect scenario, is 0.49 which is more than would be expected by chance. However, the ROC is only 0.5 which indicates a predictive performance no better than chance. This discrepancy occurs because classification rates are dependent on the distribution of observations in the classification tree. Therefore, the uneven number of sites with *H. oraria* absent versus sites with *H. oraria* present can cause some inaccuracies in measuring the predictive success of the model. An ROC curve calculates the sensitivity and specificity for each cutoff value and can therefore account for inequalities in observations. In conclusion, this is not a strongly predictive model but the relationships laid out in this tree are notable and warrant further investigation.

Landscape scale: The analysis of *H. oraria* habitat use of *B. angustifolia* patches at a landscape scale yielded nine classification trees. The tree with five branches was (Figure 2-6) optimal because it fit the data well with the lowest misclassification rate (Table 2-6). This tree identifies *B. angustifolia* patch size (m^2), *B. angustifolia* density within the patch (plants/ m^2), the landscape in which the *B. angustifolia* patch was located, the presence of a swale in the surrounding environment, distance to the Gulf of Mexico (m), and the density of *B. angustifolia* flowers (flowers/ m^2) as important variables in that order. The landscape feature and *B. angustifolia* flower density were important but were not splitters in the classification tree (Table 2-7). The classification tree predicts that *B. angustifolia* patches less than or equal to $111.5m^2$ were not used as foraging habitat by *H. oraria*, this prediction was correct 100% of the

time. If the patch size was greater than 111.5 m² and there was a swale found within 10 meters of the patch, the patch was unused by foraging *H. oraria*; again, this prediction was correct 100% of the time. The model predicts *H. oraria* used foraging habitat if the patch was greater than 111.5m², had no swale within 10 meters, was no further than 475.37 meters from the Gulf of Mexico, and had a density of more than 2.5 *B. angustifolia* plants per m². This prediction was correct 74% of the time. Overall, the tree correctly classified 75.5% of the cases at the relative cost of 0.447, which is more than would be expected by chance (Table 2-6). The ROC value is 0.78 which indicates a good predictive accuracy.

B. Angustifolia Habitat Use

Regional scale: The analysis of habitat use by *B. angustifolia* at a regional scale yielded two possible classification trees. A tree with two branches (Figure 2-7) is optimal because it minimized the misclassification error rate and fit the data well (Table 2-8). This tree identified minimum distance of the site to the bay as the most important variable. The maximum elevation (m), cover of group 4 communities (%), the maximum distance to the bay (m), the area covered by washover sand flats, and the cover of group 2 communities were also identified as important variables in that order (Table 2-9). The optimal classification tree predicts *B. angustifolia* was present when the site was greater than 25 meters from the bay at its closest point and absent if the site was 25 meters or nearer to the bay, these predictions are correct 100% of the time. No other variable offered further explanation of *H. oraria* presence or absence at a site. The entire tree correctly classified 75% of cases. (Table 2-8) The relative cost measuring the model performance was 0.49 which is more than would be expected by chance. The ROC of 0.92 provides further evidence to accurate model performance.

Landscape scale: The analysis of habitat use by *B. angustifolia* at a landscape scale yielded 28 possible classification trees. A tree with six branches was chosen (Figure 2-8). This tree did not have the lowest misclassification error rate (Table 2-10) but still fit the data well and had a low misclassification rate; the optimal tree was overly complicated for practical predictive purposes. Furthermore, it contained end nodes created from a limited number of cases leading to uncertainty of its predictions. The six branch tree chosen for this model identified landscape feature, washover sand flat presence in the surrounding 10 m (negative), *B. angustifolia* patch size (m^2) (positive), distance of the patch from the gulf (m), presence of a swale in the surrounding 10 m (negative), presence of a herbaceous interdunal area and presence of a mixed grassy/woody dune in the surrounding 10 m as important variables in that order. The chosen tree did not include patch size, presence of a herbaceous interdunal area, and presence of a mixed grassy/woody dune in the surrounding 10 m but all could serve as surrogate splitters in the place of primary splitters (Table 2-11). The chosen classification tree predicted a habitat patch situated within an herbaceous interdunal area, swale, or washover sand flat would not be used by *B. angustifolia* and this prediction was correct 88% of time. The model indicated that a habitat patch located in a bowl, flatwoods, grassy dune, grassy dune field, mixed grassy/woody dune, scrub dune, scrub opening, or swale ridge, without a washover sand flat in the surrounding 10 meters was used by *B. angustifolia*. If the patch was further than 110 m inland from the Gulf of Mexico the habitat was suitable, but if the patch is located less than or equal to 110 m inland from the gulf then it was predicted to be unsuitable for *B. angustifolia*. The first prediction was correct 70% of the time and the second prediction was correct 65%

of the time. Branch five predicted the habitat patch located in a bowl, grassy dune, grassy dune field, scrub dune, or scrub opening situated further than 10 meters from the nearest washover sand flat with no swale present is unsuitable for *B. angustifolia*. This prediction was correct 83% of the time. Lastly, the model predicted a patch found in a bowl, flatwoods, mixed grassy/woody dune, or swale ridge can still be suitable for *B. angustifolia* even with a washover sand flat in the surrounding area (69% of the cases in this branch classified correctly). Overall, the tree correctly classified 70.9% of the cases at the relative cost of 0.528 which is more than would be expected by chance (Table 2-10). The ROC indicates an accurate model performance with a value of 0.77.

Discussion

The original survey determined the range of *H. oraria* to extend from Horn Island, Mississippi east to Saint Andrews State Park in Panama City, Florida (Cane et al. 1996). Entomologists searched for *H. oraria* both inland and along the immediate coast along the northern Gulf Coast (Cane et al. 1996). The bee was not detected at any non-coastal sites even when *B. angustifolia* was abundant, nor was it observed anywhere without *B. angustifolia*. **Compared to the 1993-94 survey, our survey included a greater area of non-coastal (inland) sites and included all coastal and non-coastal habitat types. With this more extensive survey we were able to confirm the absence of the bees from non-coastal sites even when *B. angustifolia* was abundant and the lack of bees when *B. angustifolia* was absent. Although there have been 2 inundation events (Hurricanes Opal and Ivan), Impact level 4 (Sallenger 2000) the greatest potential coastal hazard identified by the USGS storm-impact scale and many less damaging swash and collision (Impact level 1,2) and overwash events (impact level 3) between 1994 and 2012, we found no**

change in the range or overall distribution of the bee between surveys. However, the density of the bees in our study was markedly lower on the barrier islands compared to the coastal mainland. This reduced bee density may reflect the more severe coastal impact associated with barrier island inundation and loss of both foredunes and back-barrier dunes (Pries 2008). This also suggest the barrier island habitat for this endemic bee is more vulnerable to impacts associated with global climate change than coastal-mainland habitat.

H. oraria density estimates suggest the bees are influenced by variability in *B. angustifolia* characteristics among coastal sites. Also, *B. angustifolia* characteristics vary with occurrence on or off barrier islands and with the dominant plant communities on site. Coastal mainland habitat supported higher bee densities than barrier island foraging habitat and had more *B. angustifolia* patches, the patches covered more area and the host plant and flower density were higher than in barrier island sites. The average number of patches on a barrier island site was 10 where the average number of patches on a coastal mainland site was 36 patches per 120,000 m². There was also variability in plant and bee quantity among coastal mainland sites in response to the increase of habitats unsuitable to *B. angustifolia* such as dense scrub and flatwoods with dense midstory of shrubs. These scrub habitats are densely wooded except for small openings between shrubs and *B. angustifolia* only grows in the small openings in the woody vegetation. Big Lagoon and St. Andrews State Parks both had high numbers of *B. angustifolia* patches but low patch areas compared to the other state parks sampled because Big Lagoon and St. Andrews consisted primarily of rosemary scrub

and scrub dunes. Coastal sites in other state parks contained more washover sand flats and grassy dunes and less scrub than Big Lagoon and St. Andrews State Parks. However, *B. angustifolia* plant and flower density was comparable among sites. Furthermore, the total area of *B. angustifolia* within a state park was not always the highest where abundance of *H. oraria* was the greatest. Topsail Hill had the most *H. oraria* but the smallest total area of the host plant. This resulted in a significantly higher ecological density (bees/*B. angustifolia* area) of *H. oraria* than at other similar sites. In summary, the *B. angustifolia* average patch number and area and the density of host plants was more descriptive of a site supporting a higher abundance of *H. oraria* than total patch area.

Observations in 2012 support original conclusions that *H. oraria* is only found in coastal habitats where *B. angustifolia* is abundant and it appears the bee does not occupy non-coastal mainland areas even if its host plant is plentiful (Cane et al. 1996). A recent study on pollinator distribution reported about 11% of bee species found in open sites and 2% of forest bee species were specialists and concluded open habitat bee species have narrower diets than forest bee species (Grundel et al. 2010). *H. oraria* appears to uphold these findings and does not occupy forested habitats. Further work would be needed to determine if non-coastal mainland sites are suitable but bees presence is limited by barriers that stop dispersal inland from coastal sites.

Most coastal sites are separated from inland open pine forest communities supporting *B. angustifolia* by dense scrubby vegetation and/or roads and buildings. The surrounding plant communities have a history of fire; however, with increased development and fragmentation, fire has long been excluded from these areas allowing

a thick mid-story to develop (Jokela et al. 2006). Fire is also a positive predictor for specialist bee abundance (Grundel et al. 2010). Recent acquisitions by Florida State land agencies land that includes coastal to forested habitats uninterrupted by major development offers hope that better land management including the return of fire or shrub removal will increase connectivity between coastal and non-coastal sites. For now, it can be concluded that *H. oraria*, as a specialist bee, is restricted to foraging in open coastal and barrier island habitats where *B. angustifolia* is abundant with no major changes to their range in Florida occurring in the last 18 years.

Disturbance has been shown to greatly influence the spatial distribution of populations of many species of bee (Potts et al. 2003a, Williams and Kremen 2007, Russell et al. 2005, Winfree et al. 2007) and *H. oraria* distribution and habitat use appears to be driven by a moderate amount of disturbance. *H. oraria* showed a preference for sites with more *B. angustifolia* patches and patches of a substantial size indicating the bees are attracted to a site by pollen and nectar rewards (Potts et al. 2004, Larsson and Franzen 2007). It is therefore valuable to identify the habitat needs for this plant in order to understand comprehensive conservation needs for *H. oraria*. Bee species that specialize are more likely to use foraging habitat that consists of open areas rather than forests (Grundel et al. 2010). This association is linked to the presence of disturbance dependent plants, often of the family Asteraceae, preferred by specialists and found in disturbed sandy soils (Swink and Wilhelm 1994). *H. oraria*'s host plant *B. angustifolia* fits this description. The bee's host plant grows in open sandy soils, not subjected to prolonged flooding and sand movement. For example, the bees and the plant were predicted to be absent from certain landscape features such as

swales, which are subject to periodic flooding, and any feature with sparse vegetation, such as interdunal areas, or washover sand flats, which experience constant sand movement as windy conditions dominate and inadequate vegetative roots provide little to hold the sand particles in place. Both environments may be inhospitable for annual plants. However, *B. angustifolia* was predicted to use the more stable features of the coast when there was a washover sand flat nearby indicating limited disturbance is preferable to no disturbance. Hurricanes may cause the most drastic disturbance throughout the range of the *H. oraria*, but this analysis did not indicate that the proximity to and strength of recent storms directly impacted *H. oraria* or *B. angustifolia* distribution. However, the undeniable impact of these storms on the vegetation and geomorphology of these landscapes, especially with respect to dune development, points out an indirect relationship between storm activity and *H. oraria* and *B. angustifolia* (Pries et al. 2008). For example, bee density on barrier islands was much reduced when compared to coastal mainland, this may be a result of increased storm activity and/or susceptibility of the barrier islands within this study. In conclusion, some disturbance such as low intensity fires and moderate openings in vegetation, create useable habitat for *B. angustifolia* and *H. oraria*.

Distance to the Gulf of Mexico and to the bay (if present) was an important predictor for habitat suitability of both species at both regional and landscape scales. For barrier islands, this distance was important as it indicates the overall stability of the landscape. Generally, a wider portion of a barrier island is less susceptible to storm overwash and contain larger dunes and more established vegetation. For coastal sites attached to the mainland, the distance to the gulf was an important indicator of

increased woody vegetation from scrub dunes transitioning into scrub or flatwoods forest communities. . Within a landscape *H. oraria* was predicted to use foraging patches less than 475 meters from the gulf and *B. angustifolia* used habitat greater than 110 meters from the gulf. These two models can be combined to predict that land between 110- 475 meters from the Gulf of Mexico is the interception of suitable habitat for *H. oraria* as well as *B. angustifolia* making this area critical foraging habitat for *H. oraria*.

Table 2-1. Indicator species of the 4 optimal clusters from the cluster analysis performed based on environmental variables.

Cluster	Species*
Group1	HYPSP, ILEGLA, POLGRA, POLPOL, SCHMAR
Group2	CERERI, CHRPAU, CHRSP, LICMIC, MAGGRA, QUEGEM, QUEMYR
Group3	ILEVOM, MAGVIR, PINELL, PINPAL, QUEINC, QUELAE, TAXASC
Group4	IVAIMB, PANAME, UNIPAN

*CERERI = *Ceratiola ericoides*
 CHRPAU = *Chrysoma pauciflosculosa*
 CHRSP = *Chrysopsis species*
 HYPSP = *Hypericum species*
 ILEGLA = *Ilex glabra*
 ILEVOM = *Ilex vomitoria*
 IVAIMB = *Iva imbricata*
 LICMIC = *Licania michauxii*
 MAGGRA = *Magnolia grandiflora*
 MAGVIR = *Magnolia virginiana*
 PANAME = *Panicum amarum*

PINELL = *Pinus Elliotii*
 PINPAL = *Pinus palustris*
 POLGRA = *Polygonella gracilis*
 POLPOL = *Polygonella polygama*
 QUEGEM = *Quercus geminata*
 QUEINC = *Quercus incana*
 QUELAE = *Quercus laevis*
 QUEMYR = *Quercus myrtifolia*
 SCHMAR = *Schizachyrium maritimum*
 TAXASC = *Taxodium ascendens*
 UNIPAN = *Uniola paniculata*

Table 2-2. Total sampling effort for *H.oraria* in coastal and non-coastal mainland areas with and without host plant *B.angustifolia*.

		Coastal Area Sampled in 2012 Field Season (ha)		Non-coastal Mainland Area Sampled in 2012 Field Season (ha)	
		<i>B. angustifolia</i> present	<i>B. angustifolia</i> absent	<i>B. angustifolia</i> present	<i>B. angustifolia</i> absent
Hectares Sampled		1.432	6.567	0.1586	1.441
Percent of Total Area (%)		18	82	10	90
H. oraria	Count (no.)	47	Not Found	Not Found	Not Found
	Density (no./ha)	7.88	Not Found	Not Found	Not Found

Table 2-3. Summary of *H. oraria* count data and *B. angustifolia* characteristics by location, unit and site. Gulf of Mexico barrier islands are narrow strips of sand running parallel to the mainland. Coastal non-island areas consist of the first 500 meters of mainland closest to the Gulf of Mexico. The non-coastal mainland sites included in this study consist of Mesic and Scrubby Flatwoods and Sandhill communities located further than 0.5 km from the Gulf of Mexico. Park units include Gulf Islands National Seashore (GINS), University of West Florida (UWF), Eglin Air Force Base (EAFB), Florida State Parks, and Florida State Forests.

Location	Park Unit	Site (120,000m ²)	<i>H. oraria</i> count (no.)	<i>B.</i> <i>angustifolia</i> patch count (no.)	<i>H. oraria</i> ecological density (no./ha)	Total <i>B.</i> <i>angustifolia</i> patch size (m ²)	<i>B.</i> <i>angustifolia</i> density (no./m ²)	Flower density (no./m ²)	Average distance between <i>B.angustifolia</i> patches (m)
Barrier Island	Perdido Key (GINS)	1	0	17	0	69	14	33	23
		2	0	0	0	0	0	0	0
		3	0	7	0	929	2	28	52
	Fort Pickens (GINS)	1	0	10	0	496	14	45	28
		2	0	15	0	2281	10	39	26
		3	0	0	0	0	0	0	0
	Santa Rosa Island (UWF)	1	0	30	0	908	5	34	21
		Santa Rosa Island (GINS)	1	0	10	0	1144	9	51
	2		0	0	0	0	0	0	0
	Santa Rosa Island (EAFB)	1	0	5	0	485	10	54	20
		2	1	24	16	602	8	36	22
		3	2	20	14	1219	6	24	27
		4	0	5	0	398	11	24	29
		5	0	0	0	0	0	0	0
		Sum	3	143	30	8530	89	366	270
Barrier Island Total		Average	0	10	2	609	6	26	19

Table 2-3. cont.

Location	Park Unit	Site (120,000m ²)	<i>H.</i> <i>oraria</i> count (no.)	<i>B.</i> <i>angustifolia</i> patch count (no.)	<i>H. oraria</i> ecological density (no./ha)	Total <i>B.</i> <i>angustifolia</i> patch size (m ²)	<i>B.</i> <i>angustifolia</i> density (no./m ²)	Flower density (no./m ²)	Average distance between <i>B.angustifolia</i> patches (m)
Coastal Mainland	Big Lagoon State Park	1	0	50	0	185	6	28	21
	Henderson Beach State Park	1	14	13	42	6448	9	18	18
	Topsail Hill State Park	1	15	35	114	529	9	32	12
	Grayton Beach State Park	1	12	15	43	3825	13	39	20
	Deer Lake State Park	1	1	23	10	2840	13	48	19
	St. Andrews State Park	1	2	81	25	189	8	37	6
Coastal Mainland Total		Sum	44	217	234	14016	59	202	96
		Average	7	36	39	2336	10	34	16
Non- coastal Mainland	Eglin Air Force Base	6	0	2	0	1806	10	23	15
	Grayton Beach State Park	2	0	10	0	34	3	14	27
	Deer Lake State Park	2	0	4	0	13	2	13	7
	Point Washington State Forest	1	0	29	0	1806	8	42	21
		Sum	0	45	0	3659	23	91	70
Non-coastal Mainland		Average	0	11	0	915	6	23	17
Total		Sum	47	405	264	26205	171	660	437
		Average	2	17	11	1092	7	27	18

Table 2-4. Prediction success (of the test data) for the classification tree in predicting site habitat use by *H.oraria* at a regional scale. *Class 0* indicates sites where *H.oraria* was not detected, *class 1* indicates sites where *H.oraria* was present. The error (%) is the percent of sites misclassified, and the cost of each misclassification is of equal weight.

Actual Class	Sites within each class	Sites classified correctly (%)	Sites misclassified (%)	Class 0 (n=4)	Class 1 (n=12)
0	3	66.67	33.33	2	1
1	13	84.62	15.38	2	11
Average*	-	75.64	-	-	-
Overall Correct**	-	81.25	-	-	-

*Average = average model prediction success for the test sample, or the average percent of sites classified correctly.

**Overall correct = overall model prediction success for the test sample, or the total percent of sites classified correctly regardless of class.

Table 2-5. Variables important for predicting the site habitat use of *H.oraria* at a regional scale. The relative importance values are specific for the given model from 0-100.

Variable	Relative Importance Score
Total number of <i>B.angustifolia</i> patches	100
Average distance (m) between <i>B.angustifolia</i> patches	72
Total area (m ²) covered by <i>B.angustifolia</i> patches.	72
Maximum distance (m) of the site to the bay	68
Community group 3 (% cover)*	60
Minimum distance (m) of the site to the bay	56

*Community group 3: *Ilex vomitoria*, *Magnolia virginiana*, *Pinus Elliotii*, *Pinus palustris*, *Quercus incana*, *Quercus laevis*, *Taxodium ascendens*

Table 2-6. Prediction success (of the test data) for the classification tree in predicting habitat patch use by *H.oraria* at a landscape scale. *Class 0* indicates patches where *H.oraria* was not detected, *class 1* indicates patches where *H.oraria* was present. The error (%) is the percent of patches misclassified, and the cost of each misclassification is of equal weight.

Actual Class	Patches within each class (n)	Patches classified correctly (%)	Patches misclassified (%)	Class 0 (n=71)	Class 1 (n=27)
0	93	75.27%	23.73	70	23
1	5	80.00%	20.00	1	4
Average*	-	77.63%	-	-	-
Overall correct*	-	75.51%	-	-	-

*Average = average model prediction success for the test sample, or the average percent of patches classified correctly.

**Overall correct = overall model prediction success for the test sample, or the total percent of sites classified correctly regardless of class.

Table 2-7. Variables important for predicting the habitat patch use of *H.oraria* at a landscape scale. The relative importance scores are specific for the given model from 0-100.

Variable	Relative Importance Score
<i>B.angustifolia</i> patch size (m ²)	100
<i>B.angustifolia</i> density (no./m ²)	63
Landscape feature	46
Presence of a swale in the surrounding 10 meters	39
Distance of the patch to the Gulf of Mexico (m)	36
Density of <i>B.angustifolia</i> flowers (no./m ²)	34
Cover of <i>B.angustifolia</i> (%)	8

Table 2-8. Prediction success (of the test data) for the classification tree in predicting site habitat use by *B. angustifolia* at a regional scale. *Class 0* indicates sites where *B. angustifolia* was not detected, *class 1* indicates sites where *B. angustifolia* was present. The error (%) is the percent of sites misclassified, and the cost of each misclassification is of equal weight.

Actual Class	Sites within each class (n)	Sites classified correctly (%)	Sites misclassified (%)	Class 0 (n=71)	Class 1 (n=27)
0	4	100.00	0.00	4	0
1	20	95.00	5.00	1	19
Average*	-	97.50	-	-	-
Overall correct**	-	95.83	-	-	-

*Average = average model prediction success for the test sample, or the average percent of sites classified correctly.

**Overall correct = overall model prediction success for the test sample, or the total percent of sites classified correctly regardless of class.

Table 2-9. Variables important for predicting the site habitat use of *B.angustifolia* at a regional scale. The relative importance scores are specific for the given model from 0-100.

Variable ^z	Relative Importance Score
Minimum distance to the bay (m)	100
Maximum elevation (m)	90
Community Group 4	82
Maximum distance to the bay	79
Presence of a washover sand flat in the surrounding 10 m.	74
Community Group 2	67

^zVariable

Community Group 4: *Iva imbricata*, *Panicum amarum*, *Uniola paniculata*

Community Group 2: *Ceratiola ericoides*, *Chrysoma pauciflosculosa*, *Chrysopsis spp.*,
Licania michauxii, *Magnolia grandiflora*, *Quercus geminata*, *Quercus myrtifolia*

Table 2-10. Prediction success (of the test data) for the classification tree in predicting *B. angustifolia* habitat patch use at a landscape scale. *Class 0* indicates patches where *B. angustifolia* was not detected, *class 1* indicates patches where *B. angustifolia* was present. The error (%) is the percent of patches misclassified, and the cost of each misclassification is of equal weight.

Actual Class	Patches within each class	Patches classified correctly (%)	Patches misclassified (%)	Class 0 (n=71)	Class 1 (n=27)
0	160	62.50	37.50	100	60
1	98	84.69	15.31	15	83
Average*	-	73.60	-	-	-
Overall correct*	-	70.93	-	-	-

*Average = average model prediction success for the test sample, or the average percent of patches classified correctly.

**Overall correct = overall model prediction success for the test sample, or the total percent of patches classified correctly regardless of class.

Table 2-11. Variables important for predicting the habitat patch use of *B.angustifolia* at a landscape scale. The relative important scores are specific for the given model from 0-100.

Variable	Relative Importance Score
Presence of a washover sand flat in the surrounding 10 m.	100
<i>B.angustifolia</i> patch size (m ²)	84
Distance of patch to the Gulf of Mexico (m)	26
Presence of a swale in the surrounding 10 m.	8
Presence of a herbaceous interdune in the surrounding 10 m.	4

Table 2-12. Site surveyed for *H.oraria*, including the 1993-1994 field seasons (Cane et al. 1996) and 2011- 2012 field seasons.

State	County	Location	H.oraria present in 1993-1994?	B.angustifolia present 1993-1994?	H.oraria present in 2011-2012?	B.angustifolia present 2011-2012?
Mississippi	Jackson	Petit Bois Island, Gulf Island National Seashore	No	Yes	Area Not Searched	Area Not Searched
Mississippi	Jackson	West & central Horn Island, Gulf Island National Seashore	Yes	Yes	Area Not Searched	Area Not Searched
Alabama	Mobile	Dauphin Island	No	No	Area Not Searched	Area Not Searched
Alabama	Baldwin	Gulf Shores State Park	No	Yes	Area Not Searched	Area Not Searched
Alabama	Baldwin	Ft. Morgan National Monument	Yes	Yes	Area Not Searched	Area Not Searched
Alabama	Baldwin	Bon Secour National Wildlife Ref., west shore Long Lagoon, south Gator Lake	Yes	Yes	Area Not Searched	Area Not Searched
Alabama	Baldwin	Romar Beach (Ala. 182, mile 11)	Yes	Yes	Area Not Searched	Area Not Searched
Florida	Escambia	Perdido Key State Park	Area Not Searched	Area Not Searched	Yes	Yes
Florida	Escambia	Gulf Island National Seashore, Perdido Key Unit	Yes	Yes	Yes	Yes
Florida	Escambia	Big Lagoon Sate Rec. Area, entrance	Yes	Yes	Yes	Yes
Florida	Escambia	Gulf Island National Seashore, Ft. Pickens, Battery 224, 234 and Cooper on Santa Rosa Island	Yes	Yes	Yes	Yes
Florida	Escambia	Santa Rosa Island, 1 mi east of Pensacola Beach	Yes	Yes	Yes	Yes
Florida	Okaloosa	Santa Rosa Island, east gate Eglin Air Force Base and site A-7	Yes	Yes	Yes	Yes
Florida	Okaloosa	Eglin Air Force Base approx. 6 miles inland	Area Not Searched	Area Not Searched	No	Yes
Florida	Walton	Henderson Beach State Rec. Area	Yes	Yes	Yes	Yes
Florida	Walton	Blue Mountain Beach	Yes	Yes	Area Not Searched	Area Not Searched
Florida	Walton	Grayton Beach State Park	Yes	Yes	Yes	Yes
Florida	Walton	Topsail Hill, near coast	Yes	Yes	Yes	Yes

Table 2-12 continued

State	County	Location	H.oraria present in 1993-1994?	B.angustifolia present 1993- 1994?	H.oraria present in 2011-2012?	B.angustifolia present 2011- 2012?
Florida	Walton	1.3 mi inland from Grayton Beach State Park	No	Yes	Yes	Yes
Florida	Walton	Point Washington State Forest (approx. 1.6 miles inland)	Area Not Searched	Area Not Searched	No	Yes
Florida	Walton	Deer Lake State Park coastal	Area Not Search	Area Not Searched	Yes	Yes
Florida	Walton	Deer Lake State Park (approx. 1 mile inland)	Area Not Searched	Area Not Searched	No	Yes
Florida	Walton	West Inlet Beach nr. Seaside	No	Yes	Area Not Searched	Area not Searched
Florida	Walton	Camp Helen State Park	Area Not Searched	Area Not Searched	No	Yes
Florida	Walton	North Freeport	No	Yes	Area Not Searched	Area Not Searched
Florida	Bay	West Laguna Beach	No	Yes	Area Not Searched	Area Not Searched
Florida	Bay	North Fla. 395 (2 mi from coast)	No	Yes	Area Not Searched	Area Not Searched
Florida	Bay	Tyndall Air Force Base, east & west ends of Crooked Island, Shell Island	No	No	Area Not Searched	Area Not Searched
Florida	Bay	St. Andrews State Park, ¼ m from entrance	Yes	Yes	Yes	Yes
Florida	Gulf	Mexico Beach	No	No	Area Not Searched	Area Not Searched
Florida	Franklin	St. Joseph Peninsula State Park and Cape San Blas	No	No	Area Not Searched	Area Not Searched
Florida	Calhoun	St. George Island State Park	No	No	Area Not Searched	Area Not Searched
Florida	Walton	North Freeport (north Choctawhatchee Bay)	No	Yes	Area Not Searched	Area Not Searched
Florida	Calhoun	Clarksville	No	Yes	Area Not Searched	Area Not Searched

FIGURES

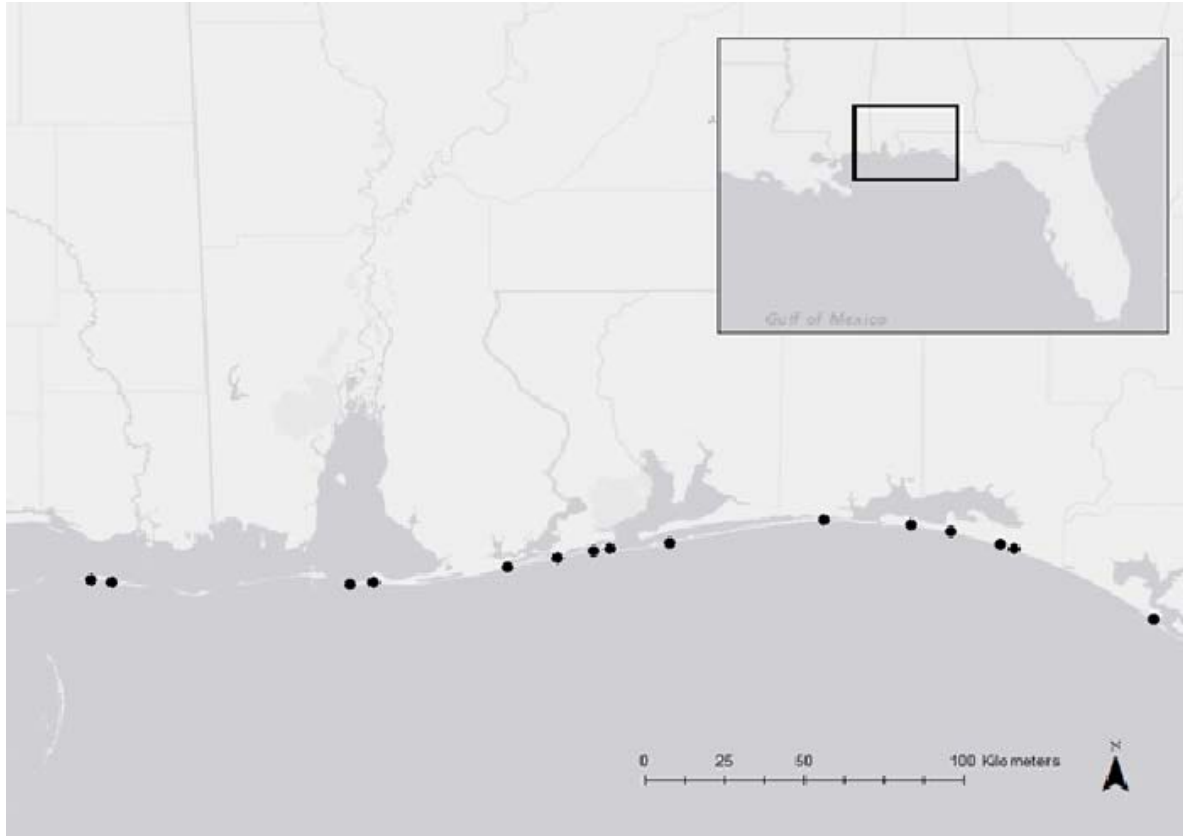


Figure 2-1. The geographical range of *Hesperapis oraria* documented in 1993-1994 field seasons (Cane et al. 1996).



Figure 2-2. Sites visited, fall 2012, where *B.angustifolia* was present and *H.oraria* was either present or absent.



Figure 2-3. Sites sampled (with transects), fall 2012, where *B. angustifolia* and *H. oraria* were present.

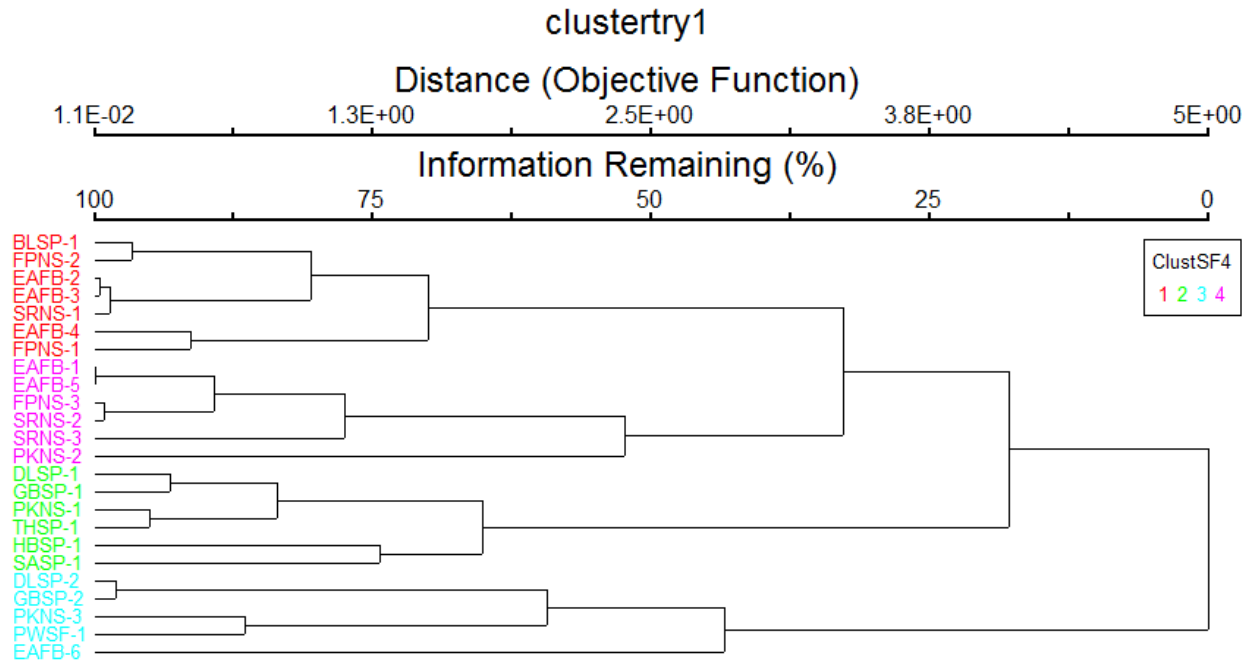


Figure 2-4. Sites grouped into dominant community types via hierarchical clustering using Sorensen (Bray-Curtis) for the distance measure and Flexible Beta for the linkage method in PC-ORD. The optimal number of clusters was determined to be four after an indicator species analysis yielded the smallest average p-value ($p = 0.334$) and the most number of species with significant p-values (13 species).

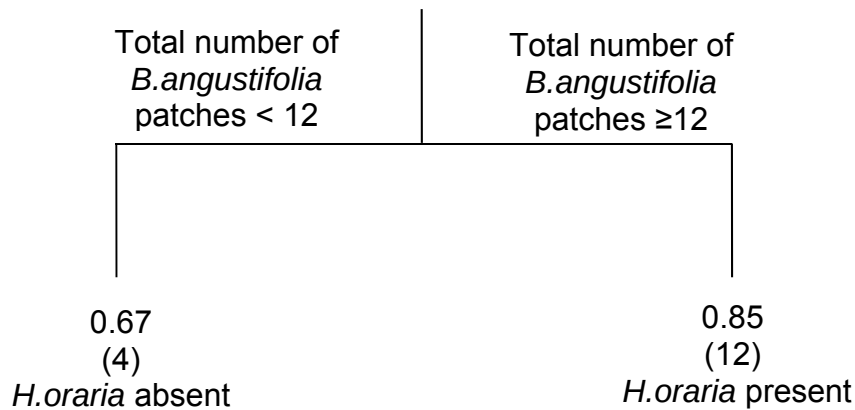


Figure 2-5. Classification tree relating probability of site use by *H.oraria* to landscape features over a regional scale. *Categories or numbers* on top of each branch indicate the value of the explanatory variable that, when used to split the response variable, leads to maximum homogeneity of resulting groups. The end of each branch is labeled according to whether *H.oraria* was present or absent. *Numbers* at the end of each branch indicate the proportion of observations in that group correctly classified. The total number of observations in each group is listed within *parentheses*.

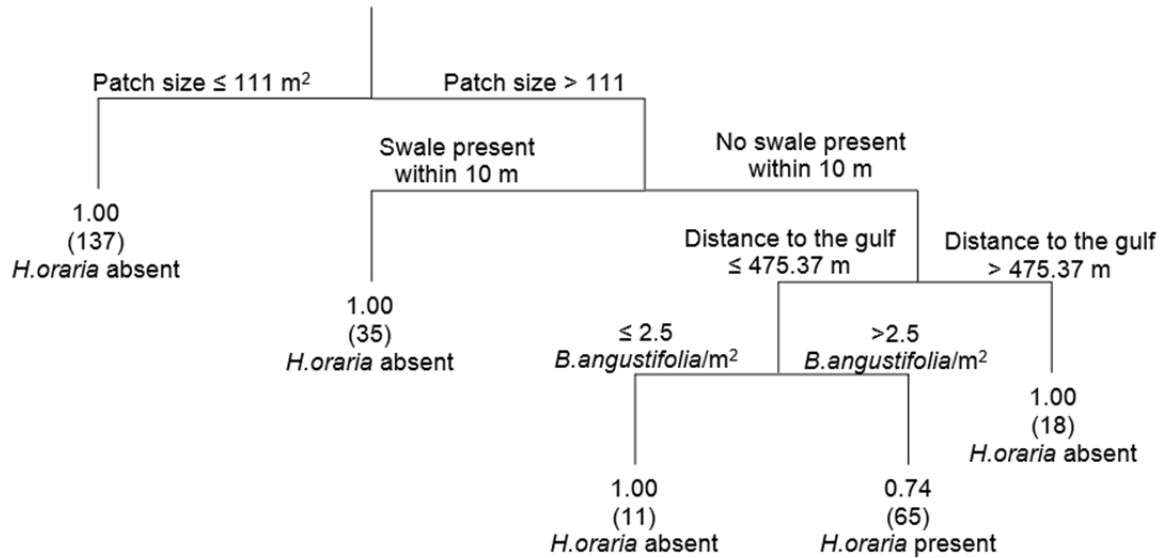


Figure 2-6. Classification tree relating probability of patch use by *H. oraria* to landscape features over a landscape scale. *Categories or numbers* on top of each branch indicate the value of the explanatory variable that, when used to split the response variable, leads to maximum homogeneity of resulting groups. The end of each branch is labeled according to whether *H. oraria* was present or absent. *Numbers* at the end of each branch indicate the proportion of observations in that group correctly classified. The total number of observations in each group is listed within *parentheses*.

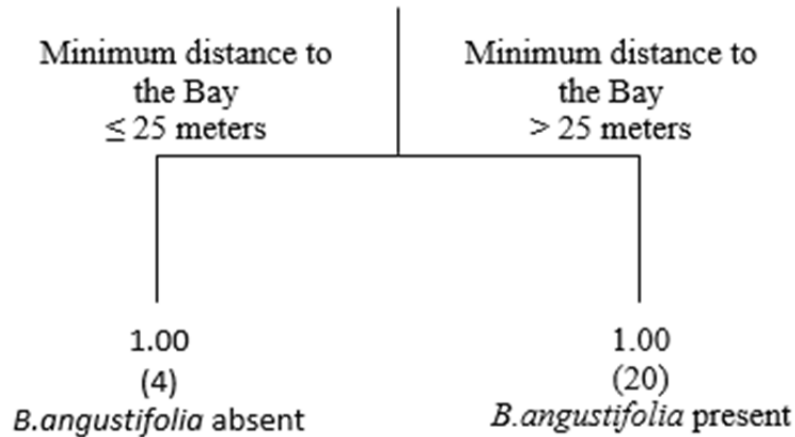


Figure 2-7. Classification tree relating probability of occupancy of *B. angustifolia* to landscape features over a large scale. *Categories or numbers* on top of each branch indicate the value of the explanatory variable that, when used to split the response variable, leads to maximum homogeneity of resulting groups. The end of each branch is labeled according to whether *B. angustifolia* was present or absent. *Numbers* at the end of each branch indicate the proportion of observations in that group correctly classified. The total number of observations in each group is listed within *parentheses*.

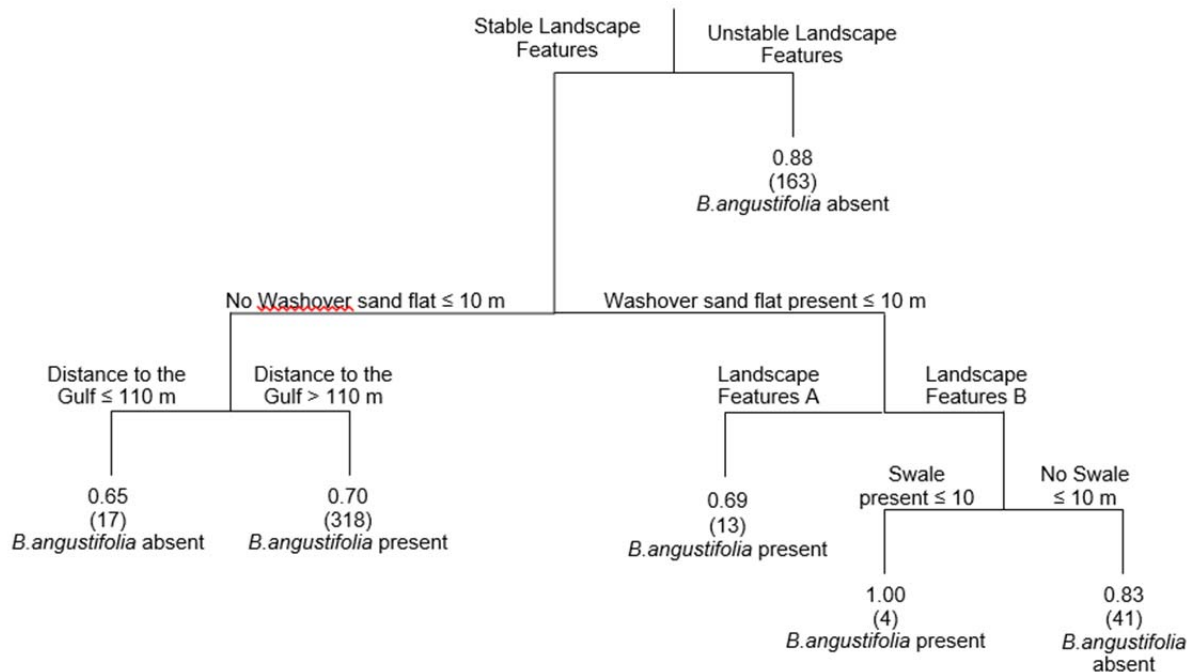


Figure 2-8. Classification tree relating probability of habitat patch occupancy of *B. angustifolia* to landscape features. *Categories or numbers* on top of each branch indicate the value of the explanatory variable that, when used to split the response variable, leads to maximum homogeneity of resulting groups. The end of each branch is labeled according to whether *B. angustifolia* was present or absent. *Numbers* at the end of each branch indicate the proportion of observations in that group correctly classified. The total number of observations in each group is listed within *parentheses*. Stable Landscape Features: bowl, flatwoods, grassy dune, grassy dune field, mixed grassy/woody dune, scrub dune, scrub opening, swale ridge. Unstable Landscape Features: herbaceous interdunal area, swale, washover. Landscape Features A: bowl, flatwoods, mixed grassy/woody dune, swale ridge. Landscape Features B: grassy dune, grassy dune field, scrub dune, scrub open.

CHAPTER 3 CHANGES IN BALDUINA ANGUSTIFOLIA AND HESPERAPIS ORARIA DENSITY OVER TIME

Background

In the practice of conservation it is important to identify habitat critical to target species and to understand how changes to habitat impact target species survival. Understanding this relationship can be especially important for species occupying dynamic landscapes (Pries et al. 2009) as the availability and quality of habitat can change quickly with stochastic events (Carlsson and Kindval 2001; van Horne et al. 1997). Therefore, it is important to examine not only key features that determine spatial distribution or population density, but also how they might change and how those changes might affect the species of interest (Pries et al. 2009). Sufficient foraging habitat is critical for the survival of any species.

H. oraria foraging habitat is defined as any area where its preferred host plant *B. angustifolia* can be found. Threats to *H. oraria* foraging habitat such as inadvertent damage from visitor use and overwash associated with hurricanes could affect the density of *B. angustifolia* and, therefore, *H. oraria*. By monitoring *B. angustifolia* patch characteristics and density of both species over time an understanding of the relationships between host and bee can be gained to protect and restore critical habitat to better inform population management. The objectives of this chapter are (1) to quantify the changes in *B. angustifolia* patch size, cover of all vegetation and *B. angustifolia* plant density, flower density, plant height, plant width, number of seedheads per plant, and seedhead width from 2011 to 2012 and (2) to quantify changes in *H. oraria* density in foraging habitat from 2011 to 2012 and (3) to ultimately determine characteristics of foraging habitat which influence *H. oraria* density.

Density of *H. oraria* in foraging habitat was determined for three units of the Gulf Islands National Seashore (GINS): Santa Rosa, Fort Pickens and Perdido Key (Figure 3-1). The Perdido Key unit is located on Perdido Key, a barrier island located just southwest of Pensacola Florida. Santa Rosa and Fort Pickens units are located on Santa Rosa Island southeast of Pensacola Florida. Sampling was conducted in relatively undeveloped areas but occasionally in close proximity to roads and, in the Fort Pickens unit, on manmade earthworks or embattlements.

Perdido Key, is about 24 km long and 0.5 km wide. The GINS Perdido Key unit is located at the eastern most end of Perdido Key (Figure 3-1). Perdido Key has a few well developed foredunes but generally lacks substantial woody secondary dunes. Sampling was conducted close to the park entrance where Perdido Key is wider and where the secondary scrub dunes transition into a scrubby flatwoods with a slash pine (*Pinus elliotii*) overstory. Sampling was also conducted at the eastern end of the island where grassy dune fields surround the remnant military fortifications of Fort McRee. Areas sampled here were located on the sound side of the island behind wet flatwoods communities.

The Fort Pickens unit, on the western end of Santa Rosa Island (Figure 3-1), had the most manmade structures of the units included in this study. Surrounded by remnants of these structures the host plants are located in grassy dune fields and swales (ephemeral wetlands) on the gulf side of the island and in flatter, patchy rosemary scrub on the bay side of the island.

The Santa Rosa unit (Figure 3-1) is located about 1.5 miles east of Pensacola Beach. This portion of the island has fragmented foredunes near the Gulf of Mexico

and remnant scrub dunes on the sound side of the island but is dominated by undulating grassy dune fields with sandy and herbaceous interdunal areas. On the Santa Rosa unit the host plants are located on and around the back dunes as well as in some interdunal areas. The dominant species on these study sites are sea oats (*Uniola paniculata*), bitter panicgrass (*Panicum amarum*), gulf bluestem (*Schizachyrium maritimum*), beach elder (*Iva imbricata*), goldenaster species (*Chrysopsis spp.*), coastal honeycomb head (*Balduina angustifolia*), and woody goldenrod (*Chrysoma pauciflosculosa*).

Transects varying in length from 3-84 m, located in 51 *B. angustifolia* patches were sampled for *H. oraria*. The patches sampled were randomly selected from a near complete survey of all *B. angustifolia* patches in the GINS units. The number of transects sampled within each unit is proportionate to the number and size of host plant patches within each unit. Within each patch the width, or the baseline, was measured to determine the number of transects needed to sample approximately 20% of the area covered by the patch. This resulted in a total of 58 transects throughout the entire study area.

Methods

Data Collection

The population density of *H. oraria* was estimated using the perpendicular distance transect method. Data was collected from the 7th to the 15th of October in 2011 and 3rd to the 20th of October in 2012. This sampling technique required samplers to walk transects at a constant pace and mark the location of each bee to the transect. The perpendicular distance (m) of each observed individual bee from the line was measured. The number of *B. angustifolia*, was recorded in one m² quadrats placed

systematically (on alternating sides of the line) every three meters along each transect. Additionally, the total number of flowers in the bottom right quarter of the quadrat was recorded.

In December, *B. angustifolia* seedheads were collected from each patch. A 0.5m² quadrat was placed every five meters along the transect within which seeds were collected from randomly selected plants. For the 2012 collection, the number of seeds per seedhead was counted after the plants were dry. Plant height (cm), width (cm), number of seed heads per plant, and width of each seed head collected (cm) were recorded. Lastly, the percent cover of all vegetation in these quadrats was recorded.

Precipitation data for 2011 and 2012 was collected from the Naval Air Station's (NAS) National Oceanic Atmospheric Administration (NOAA) weather station.

(Retrieved from wunderground.com)

Statistical Analyses

The significance of the change in value of individual predictor variables and bee density between 2011 and 2012 was evaluated with non-parametric Wilcoxon rank-sum tests (SAS[®] software, Version 9.2; 2008). Because there were no bees found on the Santa Rosa unit in either 2011 or 2012, analysis was restricted to results from Perdido Key and Fort Pickens units. Regression analysis (PROC REG) was used to determine the relationship between the response variable (*H. oraria*/ha) and predictor variables: transect length (m)- as a proxy for patch size, cover of all vegetation (%), *B. angustifolia* plant density (plants/m²), flower density (flowers/m²), plant height (cm), plant width (cm), number of seedheads per plant, and seedhead width (cm). Pearson's correlation procedure was performed to determine correlation among predictor variables. The

number of seeds in each seedhead counted for the 2012 season was used to calculate the mean number of seeds per seedhead overall and per GINS unit.

Precipitation throughout *B. angustifolia*'s germination and growing period (March-October) was calculated using average daily precipitation, maximum daily precipitation, and total average precipitation. The 30-year mean for March through October (1983-2012) for daily precipitation, maximum daily average precipitation, and total average precipitation was calculated.

Results

B. angustifolia patch size, flower density, and *H. oraria* density decreased from 2011 to 2012. Seed head width (cm) increased from 2011 to 2012. The remaining explanatory variables did not change significantly between years (Table 3-1). Median patch size decreased significantly from 2011 (13.5m) to 2012 (3.0m) ($Z=-2.11$, 1 d.f., $P<0.0326$) (Table 3-2). Median *B. angustifolia* flower density decreased three fold from 2011 ($12/\text{m}^2$) to 2012 ($3/\text{m}^2$) ($Z=-2.11$, 1 d.f., $P<0.0336$) (Table 3-2). Seed head width (cm) significantly increased from 2011 (0.9 cm) to 2012 (1.0 cm) ($Z=2.82$, 1 d.f., $P\leq 0.0038$) (Table 3-2). Mean *H. oraria* density decreased from 2011 (74/ha) to 2012 (34/ha). Change in *H. oraria* density cannot be further analyzed because bees were found in 5 of the 51 patches surveyed in 2011 and 2 of the 51 patches surveyed in 2012 in the three units of GINS. This resulted in too many zeros in the dataset to determine any pattern through time.

The regression analysis determined characteristics of foraging habitat which influenced *H. oraria* density. However, none of the characteristics were shown to predict *H. oraria* density with an acceptable probability in this model (Table 3-3). The overall power of this model was too low to make any predictions on bee density F-value

= 0.44, $P = 0.8944$. Pearson's correlation procedure ruled out any multicollinearity that could have confounded these results. Data collected from across the range of *H. oraria* in 2012 better predicted the foraging habitat characteristics for the bee. Models using presence/absence data predicted *B. angustifolia* density, and patch size positively correlated with *H. oraria* use of the habitat (Chapter 2). The mean number of seeds per *B. angustifolia* seedhead was 32. On average there were 29 seeds per seedhead at both Santa Rosa Island and Perdido Key units and 38 seeds per seedhead at Fort Pickens unit.

The amount of precipitation between the two years was markedly different (Figure 3-4). Precipitation in 2011 was below average and precipitation in 2012 was above average. Most of the rain in 2012 occurred in events such as tropical storm Debby in June, hurricane Isaac in August, and an unnamed storm in June. In 2011, the average daily precipitation from March through October (during germination and growth of *B. angustifolia*) was 0.33 cm, the maximum precipitation experienced in one day was 11.30 cm (July 17th), and the total precipitation was 71.30 cm. In 2012, the average daily precipitation during germination and growth from March through October doubled to 0.61 cm and the maximum daily precipitation was 33.35 cm, occurring on June 9th, and the total precipitation was 141.55 cm. The 30 year mean for March through October (1983-2012) for daily precipitation was 0.46 cm, maximum daily average was 12.60 cm, and the total average precipitation was 112.29 cm.

Discussion

Specialist bee species have been shown to vary in their population size from year to year correlating positively with variation in their host plant (Minckley et al. 1994). The results from this study show patches of *B. angustifolia* decreased in size and flower

density while *H. oraria* density also decreased from 2011 to 2012. Therefore, the most general conclusion to be drawn is that smaller patches and fewer flowers of *B. angustifolia* correlate with fewer *H. oraria*.

The first year of sampling was drier than average followed by a wetter than average year. Therefore, a year with above average precipitation correlates with smaller *B. angustifolia* patches and lower flower density as well as fewer bees. This relationship indicates that the heavy rainfall events of 2012 flooded some landscape features containing *B. angustifolia*. These findings are supplemented by regional scale analyses of chapter 2. In the coastal landscapes where *H. oraria* was found, the distribution and reliability of *B. angustifolia* varied with landscape features. *B. angustifolia* was found in bowls, flatwoods, grassy dunes, grassy dune fields, mixed grassy and woody dunes, scrub dunes, openings in scrub, and on the periphery of swales (Chapter 2). Swales flood periodically and were observed to have flooded significantly and often in 2012. *B. angustifolia* was observed to have established early in the season in swales but died where flooded before reaching maturity and producing flowers (personal observation). Models from chapter 2 show *B. angustifolia* rarely grew in swales but was often found on the periphery of swales. The models from chapter 2 were run on data collected during bee foraging and therefore, model *B. angustifolia* distribution after reaching maturity and in full flower. Furthermore, these models show that although *B. angustifolia* was commonly found on the periphery of swales *H. oraria* was rarely found within 10 meters of a swale. All these finding indicate that swales were unreliable habitat for *B. angustifolia* growth and *H. oraria* foraging.

H. oraria might use patches of *B. angustifolia* on the periphery of swales as a foraging resource in a dry year but not in a wet year. Lack of interannual reliability indicates that long term trends could show *H. oraria* favoring drier landscape features. Studies into the spatial distribution of bees have found their populations to be patchily distributed in the landscape even when resources are broadly distributed (Minckley et al. 1999). This has been attributed to the interannual reliability of flowers, as bees prefer to forage in areas with dependable resources from year to year (Minckley et al. 1999). Previous studies indicate that pollinators occur more frequently at sites where host plants flower more predictably from year to year (Herrera 1998; Minckley et al. 1999). By tracking *B. angustifolia* patches over time some patches might be determined as consistently better for *H. oraria* foraging than others. Changes in patch characteristics indicate the reliability of flowering of *B. angustifolia* varies between years. The decrease in patch size points to the uncertainty of a patch persisting over time.

Classical metapopulation theory explains occupancy as a function of patch area and connectivity (Hanski 1999; Franzen and Nilson 2013). Therefore, Bee populations can also change over time for reasons unrelated to variable weather patterns. A study on population dynamics of orchid bees (*Euglossini*) found great variability in population size over two decades; bee abundance varied up to 14-fold with no clear trend or ecological explanation (Roubik 2001). Another study by Franzen and Nilsson (2013) examined the population dynamics of solitary bee *Andrena humilis* and concluded that pollen resources are critical for population persistence and that weather played no role in the population fluctuations. They observed such dramatic population fluctuations that

they could not attribute the change to any direct or indirect effect of either resources or weather. They also ruled out the possibility that the fluctuations were a result of the previous year's reproduction. An earlier study by Franzen and Nilsson (2010) drew similar conclusions looking at the solitary bee *Andrena hattorfiana* at a landscape scale. Again, they found local population persistence was related to pollen availability and the local population size of a habitat patch but not to connectivity or weather. The variability in *H. oraria* population from 2011 to 2012 might be a part of an overall longer temporal trend. Understanding the population dynamics of solitary bees is important because if large population fluctuations exist a long term data set is required for any conclusion to be drawn about the population status of the bee as well as the pollination services provided by the bee (Franzen and Nilsson 2013). Without these long-term studies, the population size could be consistently under or overestimated (Franzen and Nilsson 2013). In conclusion, a long-term metapopulation study looking at colonization/ extinction dynamics as well as reproduction could shed some light on the population dynamics of *H. oraria*.

Another possible explanation for *H. oraria*'s patchy distribution and selectivity of patches could be the bee's ecology. Flower morphology is the result of natural selection enacted by pollinators (Nattero et al. 2010). Pollinators select flowers based on their perceived pollen amount and quality. For example, pollinators have been shown to visit large flowers over small ones as flower size is usually correlated with nectar and pollen reward (Campbell 1991; Vaughton and Ramsey 1998; Galen 2000; Fenster et al. 2006). Many studies have also shown floral shape, specifically corolla shape, to be a factor in flower selection as well (Herrera 2001; Galen and Cuba 2001;

Nattero et al. 2010). Because *H. oraria* is restricted to *B. angustifolia* it is likely a main driver in the local-scale evolution of the plant. The bee is likely selecting for certain floral traits and floral cues among and between patches. A study looking at the visitation rate of individual flowers along with more information on the floral cues of *B. angustifolia* is necessary to determine what traits *H. oraria* is selecting for.

Table 3-1. Summary statistics of *B.angustifolia* patch characteristics that showed significant changes between 2011 and 2012.

Variable	n		Median		Minimum		Maximum	
	2011	2012	2011	2012	2011	2012	2011	2012
<i>B.angustifolia</i> seed head width (cm)	16	14	0.9	1.0	0.6	0.9	1.1	1.1
Length of transects (m)	16	14	13.5	3.0	3.0	3.0	64.0	63.0
<i>B.angustifolia</i> flower density (no./m ²)	16	14	12	4	0.4	0.4	36	16

Table 3-2. Wilcoxon rank-sum test results showing *H.oraria* density and *B.angustifolia* patch characteristics that changed significantly between 2011 and 2012.

Variable	Units	n		Sum of Scores		Expected Under H0		St. Dev Under H0		Mean Score		Two-sided Pr >= S-Mean	z statistic
		2011	2012	2011	2012	2011	2012	2011	2012	2011	2012		
<i>B.angustifolia</i> density	no./m ²	16	14	264	201	248	217	23.46	23.46	16.5	14.4	0.5075	-0.66
<i>B.angustifolia</i> flower density	no./m ²	16	14	298	167	248	217	23.5	23.5	18.6	11.9	0.0336	-2.11
Length of transects	m	16	14	297	167	248	217	23.21	23.21	18.6	12.0	0.0326	-2.11
<i>B.angustifolia</i> plant height	cm	16	14	247	218	248	217	24.05	24.05	15.4	15.6	0.9755	0.02
<i>B.angustifolia</i> plant width	cm	16	14	236	229	248	217	24.04	24.04	14.8	16.4	0.6300	0.48
<i>B.angustifolia</i> seedheads	no./plant	16	14	264	200	248	217	23.96	23.96	16.5	14.3	0.5033	-0.67
<i>B.angustifolia</i> seedhead width	cm	16	14	185	279	248	217	22.02	22.02	11.6	20.0	0.0038	2.82
Cover of vegetation	%	16	14	228	237	248	217	23.86	23.86	14.3	16.9	0.4254	0.80
<i>H.oraria</i> density	no./ha	16	14	270	195	248	217	15.62	16.62	16.9	13.9	0.1928	-1.38

Table 3-3. Parameter estimates for the full regression model comparing characteristics of foraging habitat (*B.angustifolia* patches) against *H.oraria* density.

Variable	Units	DF	Estimate	Error	t-value	Pr > t
Intercept	-	1	-231.698	543.9175	-0.43	0.6747
Year	-	1	-152.347	154.5879	-0.99	0.3362
<i>B.angustifolia</i> plant density	no./m ²	1	2.82441	16.03312	0.18	0.8619
<i>B.angustifolia</i> flowers	no./m ²	1	13.10636	45.83814	0.29	0.7779
Length of transects	m	1	-1.77355	3.87008	-0.46	0.6517
<i>B.angustifolia</i> plant height	cm	1	-10.2455	14.19522	-0.72	0.4788
<i>B.angustifolia</i> plant width	cm	1	10.8039	25.83907	0.42	0.6803
<i>B. angustifolia</i> seedheads	no./plant	1	0.56133	12.70219	0.04	0.9652
<i>B.angustifolia</i> seed head width	cm	1	495.5865	587.2568	0.84	0.4087
Cover of vegetation	%	1	-3.84571	5.30935	-0.72	0.4773

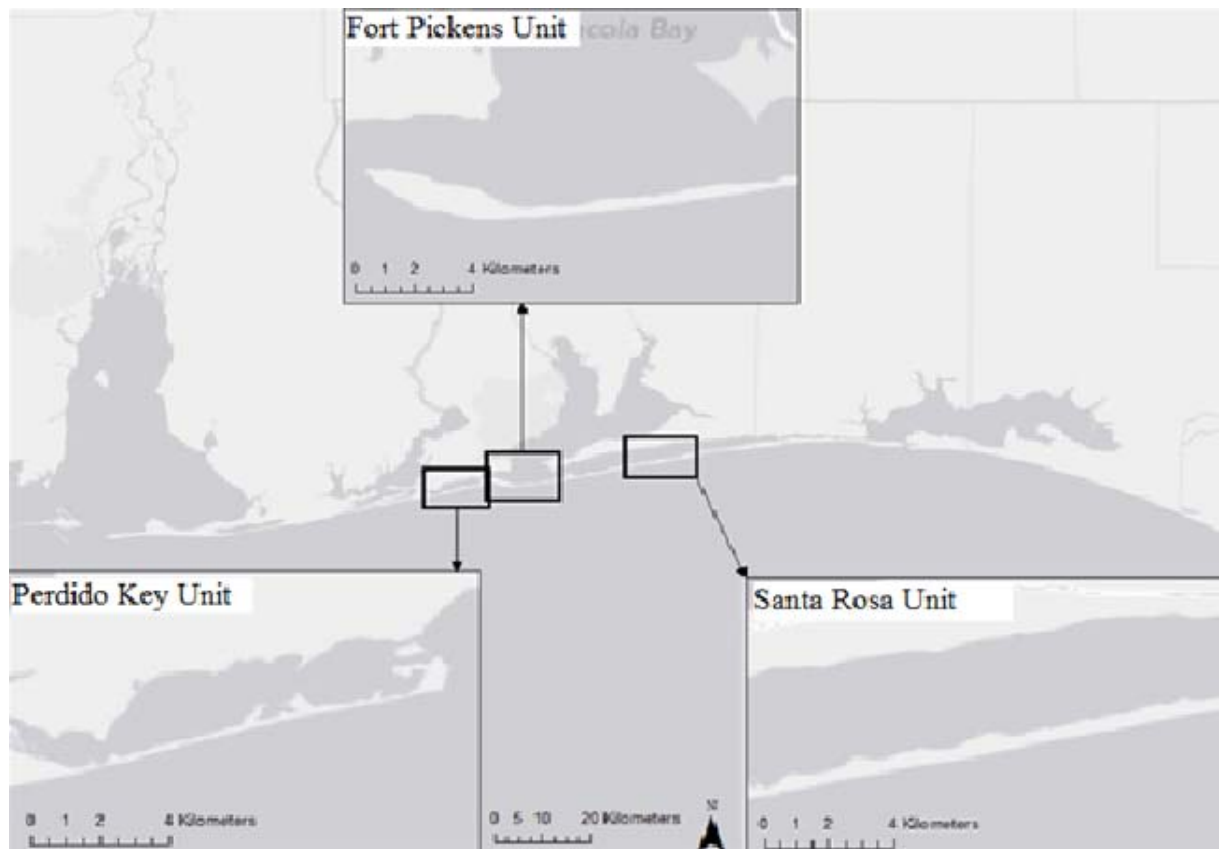


Figure 3-1. Gulf Islands National Seashore units Perdido Key, Fort Pickens, and Santa Rosa.

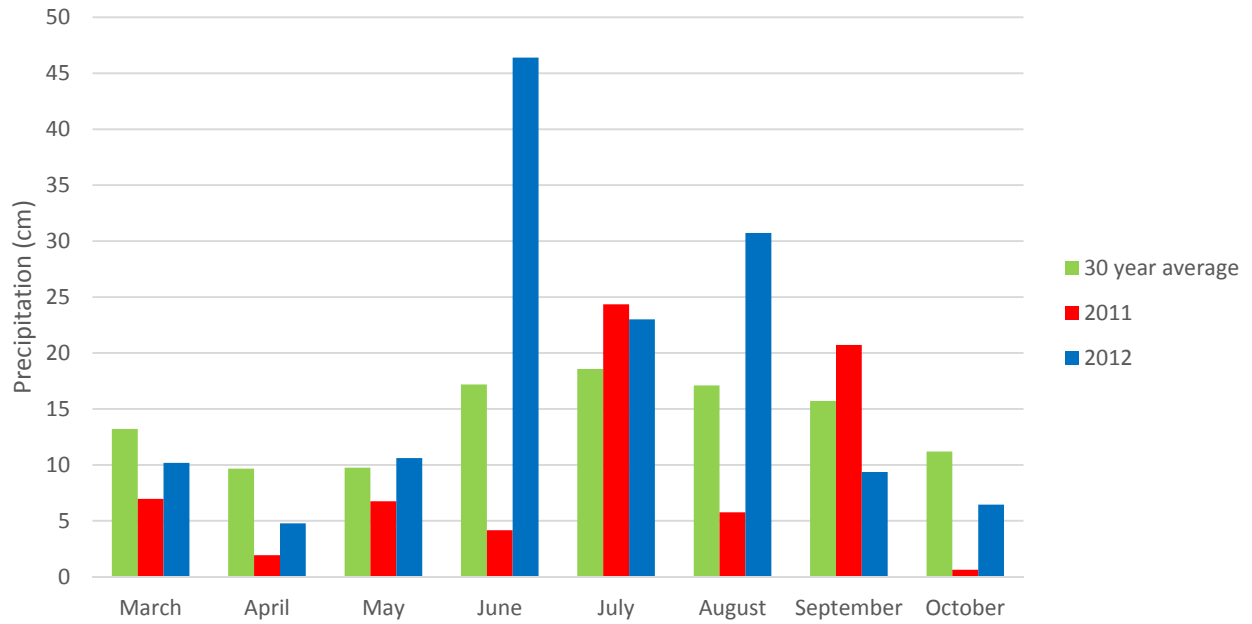


Figure 3-2. Total monthly precipitation for months preceding and for the duration of *H.oraria* foraging and *B.angustifolia* flowering. Data compares the average monthly precipitation from 1983-2012 with 2011 and 2012 sampling season precipitation.

CHAPTER 4

FUTURE DIRECTIONS AND MANAGEMENT IMPLICATIONS

The results of this study produced useful conclusions about the habitat needs of *Hesperapis oraria* and *Balduina angustifolia*. The dependency of *H. oraria* on *B. angustifolia* for foraging is clear. At a regional scale *H. oraria* is only present if the host plant is present and within a landscape the bee primarily uses larger patches with a higher density of the host plant. The habitat needs of *B. angustifolia* are therefore important for the specialist bee's survival. *B. angustifolia* requires moderate disturbance too create openings in vegetation where the aster can grow and precipitation is important for plant recruitment and survival. However, too much disturbance shapes features such as washover sand flats and too much precipitation flooded swales; both of which are unsuitable landscape features for *B. angustifolia* to flower with the reliability from year to year necessary for *H. oraria* foraging.

The questions addressed in this thesis have potential for becoming a long-term project; only with multiple years of data can an accurate population estimate of *H. oraria* be established. Furthermore, a long term project could create a more complete picture of the rare bee's distribution and project its future survival accounting for changing climatic conditions. Species distribution models have become popular as useful tools to understand species occurrence patterns and forecast effects of environmental change at different spatial scales (Bakkenes et al. 2002; Peterson et al. 2002). Species distribution models have been used to predict global species extinction risk, exposing the potentially substantial impact of climate change on extinction (Thomas et al. 2004). The species distribution models in this study could be combined into a habitat suitability map of the distribution of *H. oraria* and *B. angustifolia*. The entire documented range of

H. oraria is under threat of both climatic and environmental change. As a dynamic environment coastal landscapes are under constant pressures of change from wind and water punctuated by significant change from storm events. Additionally, climate change models predict future change including an increase in storm frequency and intensity as well as significant sea level rise. All of these current and future changes should be included in plans to successfully protect these ecosystems. Therefore, combining the current habitat suitability map with climate change models would produce a powerful predictive tool for extrapolating future distribution of *H. oraria* and potential threats to the survival of the species and its habitat.

In order to determine characteristics of foraging habitat which influence *H. oraria* density, the plots sampled in 2011 and 2012 should continue to be visited for several more years. Resulting time series data could be used to quantify changes in *H. oraria* density per foraging patch as well as characteristics of dynamic of patch size and plant density. Ultimately, this data could point to important relationships between precipitation and *B. angustifolia* density as well as floral reliability and *H. oraria* population dynamics. For instance, it would be interesting to determine patches of *B. angustifolia* that offer a reliable food source for the bee and how the presence of a reliable food source influences *H. oraria* patch selection.

During this project *H. oraria* was observed resting on and gathering resources from *Chrysopsis* spp. There are three species of *Chrysopsis* (goldenaster) found in these habitats. Previously, Cane 1994 documented males on a yellow-flowered composite that was not *B. angustifolia* but later identifies all species of *Chrysopsis* as coastal plants not visited by *Hesperapis* bees (Cane, 1994). Therefore, this is the first

known documentation of *H. oraria* visiting this plant. There are a few reasons a monolectic bee might visit another host plant. Bees use olfactory and visual cues to locate their host plants (Filella et al. 2011) and pollination is guided by both innate and learned behaviors (Riffell et al. 2008; Praz et al. 2008). For specialist pollinators precise host recognition is key (Filella et al. 2011). Therefore, this could indicate that the bee is not monolectic as previously thought, but is oligolectic (Cane 1994), meaning they specialize in few select species of host plants. Cane mentions this possibility in a research report (1994) but named the bee as a monolectic species in publications. The timing of bee emergence coinciding exactly with *B. angustifolia* flower indicates it as the strongly preferred host plant at the very least. Possibly the individuals observed on *Chrysopsis* were stretched for resources (Aizen and Harder 2007; Potts et al. 2003). The area where this behavior was observed contained *B. angustifolia* in great number but the competition among and between species was also high. Lastly, perhaps the bees observed on *Chrysopsis* were only collecting nectar and not pollen. Most bee species collect nectar from a wide variety of plants even if they are selective in choosing their pollen source (Filella et al. 2011). All of these reasons are speculative and it is not clear if *Chrysopsis* is in any way important to *H. oraria*. More research into this relationship could be key for management and restoration of the bee.

An idea first proposed by Cane (1994) suggests an experimental introduction of *H. oraria* at a new location as a possible management technique to protect the species from extinction. The populations of *H. oraria* are so isolated that any major disturbance in one area could wipe out a local population with no hope of re-colonization. This experiment could be taken a step further with introduction of the bee to non-coastal

areas where *B. angustifolia* is present. If the bee can survive in well managed relict dune communities away from the coast, the threat of sea level rise could be vastly mitigated.

Pesticides and invasive fire ants might also threaten the survival of *H. oraria* (Cane, 1994). All counties in Florida where the bee is found regularly spray pesticides for mosquito and other pest control. Most applications are to ponds and standing water and targeted at mosquito larvae. However, there is a considerable effort toward pest control in the form of aerial and road side aerosol applications. The bee populations on protected land should be shielded from these chemicals however many of the parks are so small that they do not offer much of a buffer from public roads where applications occur. There are also many doubts as to the precision of aerial applications. Fire ants (*Solenopsis spp*) are also a threat to many ground dwelling animals and prefer deep sandy soils characteristic of coastal locations where *H. oraria* may nest. An invasion of fire ants to these coastal habitats may be devastating to nest survival; therefore, this situation should be monitored.

Lastly, the most important next step in conservation efforts for *H. oraria* is to determine the nesting habitat needs for the bee. Samplers in 1993-1994 and 2011-2012 were not able to locate the nests even after a concentrated effort (Cane et al. 1996). Females with full pollen loads were commonly observed leaving foraging areas, indicating they do not nest among the host plants. Furthermore, males were observed seeking females at host flowers and not searching the ground under host plants as most solitary bee species do to find emerging virgin females (Cane 1994). This behavior was also observed in the course of this study which supports the hypothesis that the nesting

habitat is not the same as foraging habitat. Understanding the bee's foraging habitat can at best provide an incomplete picture of the habitat requirements of *H. oraria*. It is important for nests to be located and nesting habitat quantified to develop comprehensive conservation plans for this rare, endemic species.

LIST OF REFERENCES

- Aizen MA, Harder LD (2007) Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *The Ecol Soc Am* 88:271-281
- Aizen MA, Ashworth L, Galetto L (2002) Reproductive Success in Fragmented Habitats: do compatibility systems and pollination specialization matter? *J Veg Sci* 13:885-892
- Allen–Wardell G, Bernhardt P, Bitner R et al. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12:8–17
- Bakkenes M, Alkemade JRM (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob Change Biol* 8: 390-407
- Biesmeijer JC, Roberts SP, Reemer M et al. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354
- Bischoff M, Campbell DR, Lord JM et al. (2013) The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. *Austral Ecol* 38:169-176
- Bommarco R, Biesmeijer JC, Meyer B et al. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *P Roy Soc B-Biol Sci* 277: 2075-2082
- Branch LC, Miller DM, Wilkinson EB (2011) Habitat restoration for beach mice: landscape-level population studies and dune restoration, Final Report to the U.S. Fish and Wildlife Service, Panama City
- Brown MJF, Paxton RJ (2009) The conservation of bees: a global perspective. *Apidologie* 40:410–416
- Brown MJF (2011) Conservation: the trouble with bumblebees. *Nature* 469:169–170
- Brust ML, Hoback WW, Wright RJ (2008) A synopsis of Nebraska Grasshopper Distributions. *J Kansas Entomol Soc* 81:208-255
- Burger H, Ayasse M, Haberlein CM et al. (2010) Echium and Pontechium specific floral cues for host-plant recognition by the oligolectic bee *Hoplitis adunca*. *S Afr J Bot* 76:788–795

- Burger H, Ayasse M, Dötterl S et al. (2013) Perception of floral volatiles involved in host-plant finding behavior: comparison of a bee specialists and generalist. *J Comp Physiol A* 199:751-761
- Cane JH (1994) Range, taxonomy and ecology of a newly discovered Gulf Coast solitary bee, *Hesperapis oraria*, belonging to a Southwestern desert genus. Dept. of Entomology, Auburn University, Auburn AL
- Cane JH, Snelling RR, Kervin LJ (1996) A New Monolectic Coastal Bee, *Hesperapis oraria* Snelling and Stage (Hymenoptera: Melittidae), with a Review of Desert and Neotropical Disjunctives in the Southeastern US. *J Kansas Entomol Soc* 69:238-247
- Cane JH, Minckley RL, Kervin LJ, et al. (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol Appl* 16:632-644
- Cane JH, Sampson BJ, Miller SA (2011) Pollination Value of Male Bees: The specialist bee *Peponapis pruinosa* (Apidae) at Summer Squash (*Cucurbita pepo*). *Environ Entomol* 40:614-620
- Carlsson A, Kindvall O (2001) Spatial dynamics in a metapopulation network: recovery of a rare grasshopper (*Stauroderus scalaris*) from population refuges. *Ecography* 24:452-460
- Cerna K, Straka J, Munclinger P (2013) Population structure of pioneer specialist solitary bee *Andrena vaga* (Hymenoptera: Andrenidae) in central Europe: the effect of habitat fragmentation or evolutionary history? *Conserv Genet* 14:875-883
- Cunningham S (2000) Depressed Pollination in Habitat Fragments Causes Low Fruit Set. *P Roy Soc B-Biol* 267:1149-1152
- De'ath G, Frabricsius KE (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-3192.
- Debinsky DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv. Biol* 14:342-55
- Dobson HEM, Bergström G (2000) The ecology and evolution of pollen odors. *Plant Syst Evol* 222:63-87
- Dötterl S, Vereecken NJ (2010) The chemical ecology and evolution of bee-flower interactions: a review and perspectives. *Ca J Zool* 88:668-697

- Filella I, Bosch J, Llusia J et al. (2011) Chemical cues involved in the attraction of the oligolectic bee *Hoplitis adunca* to its host plant *Echium vulgare*. *Biochem Syst Ecol* 39:498-508
- Florida Natural Areas Inventory (FNAI) (2010) Guide to the natural communities of Florida: 2010 edition. Florida Natural Areas Inventory, Tallahassee, FL. (FNAI 2010).
- Franzen M, Larsson M (2007) Pollen harvesting and reproductive rates in specialized solitary bees. *Ann Zool Fenn* 44:405-414
- Franzen M, Nilsson SG (2013) High population variability and source-sink dynamics in a solitary bee species. *Ecology* 94:1400-1408
- Gathmann A, Tschardt T (2002) Foraging ranges of Solitary bees. *Journal of Animal Ecology* 71: 757-764
- Grundel R, Jean RP, Frohnapple KJ (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecol Appl* 20:1678-1692
- Gullan P, Cranston P (2010) *The insects: An Outline of Entomology*. (4 ed.). Chichester, West Sussex: Wiley-Blackwell A John Wiley & Sons, Ltd.
- Herrera C (1998) Population-level estimates of interannual variability in seed production: what do they actually tell us? *Oikos* 82:612-616
- Hill KE, O'Malley R (2010) A picky palate? The host plant selection of an endangered June beetle. *J Insect Conserv* 14:277-287
- Horak J, Chobot K, Gabris R, et al. (2011) Uphill distributional shift of an endangered habitat specialist. *J Insect Conserv* 15:743-746
- Jose S, Jokela EJ, and Miller DL (2006) *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. Springer Science+Business Media, LLC
- Klein AM, Vaissiere BE, Cane JH, et al. (2007) Importance of pollinators in changing landscapes for world crops. *P Roy Soc B-Biol Sci* 274:303-313
- Kremen C, Williams NM, Aizen MA et al. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change. *Ecol Lett* 10:299-314
- Lucas KL, Carter GA (2010) Decadal Changes in Habitat-Type Coverage on Horn Island, Mississippi, U.S.A. *J Coastal Res* 26: 1142-1148

- McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software, Gleneden Beach, Oregon, USA (www.pcord.com) 304 pages. With a contribution by Dean L. Urban
- McCune B, Mefford MJ (2005) PC-ORD, Multivariate analysis of ecological data, Version 5 for Windows edition. MjM Software Design, Gleneden Beach, Oregon USA
- McCune B, Mefford MJ (2011) PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, U.S.A
- Milet-Pinheiro P, Ayasse M, Schindwein C, et al. (2012) Host location by visual and olfactory floral cues in an oligolectic bee: innate and learned behavior. *Behav Ecol* 23:531–538
- Minckley RL, Cane JH, Kervin L, Roulston TH (1999) Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biol J Linn Soc* 67:119-147
- Minckley RL, Wcislo WT, Yanega D. et al. (1994) Behavior and phenology of a specialist bee (*dieunomia*) and sunflower (*helianthus*) pollen availability. *Ecology* 75:1406-1419
- National Research Council of the National Academies (2006) Status of pollinators in North America. National Academy Press, Washington, DC
- Ollerton J, Winfree T, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–26
- Parker ES, Jones SB (1975) Systematic study of genus *balduina* (Compositae, Heliantheae). *Brittonia* 27: 355-361
- Pemberton RW (2010) Biotic Resource Needs of Specialist Orchid Pollinators. *Bot Rev* 76:275-292
- Peterson AT, Ortega-Huerta MA, Bartley J et al. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 416: 626-629
- Peterson JH, Roitberg BD (2006) Impact of resource level sex ratio and resource allocation in Solitary bee, *Megachile rotundata*. *Environ Entomol* 35: 1404-1410
- Potts SG, Biesmeijer JC, Kremen C, et al. (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345-353

- Potts SG, Vulliamy B, Dafni A et al. (2003) (a) Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101:103-112
- Potts SG, Vulliamy B, Dafni A et al. (2003) (b) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84: 2628-2642
- Potts SG, Vulliamy B, Roberts S (2004) Nectar resource diversity organizes flower-visitor community structure. *Entomol Exp Appl* 113:103-107
- Praz CJ, Mueller A, Dorn S (2008) Host recognition in a pollen-specialist bee: evidence for a genetic basis. *Apidologie* 39:547-557
- Pries, A. (2006). *Hurricane impacts on coastal dunes and spatial distribution of santa rosa beach mice (peromyscus polionotus leucocephalus) in dune habitats.* (Master's thesis) Retrieved from <http://uf.catalog.fcla.edu/>
- Pries AJ, Miller DL, Branch LC (2008) Identification of structural and spatial features that influence storm-related dune erosion along a barrier-island ecosystem in the Gulf of Mexico. *J Coastal Res* 24:168-175
- Pries AJ, Branch LC, Miller DL (2009) Impact of Hurricanes on Habitat Occupancy and Spatial Distribution of Beach Mice. *J Mammal* 90:841-850
- Rathcke BJ, Jules E S (1993) Habitat fragmentation and plant–pollinator interactions. *Curr Sci* 65:273–277
- Riffell JA, Alarcon R, Abrell L et al. (2008) Behavioral consequences of innate preferences and olfactory learning in hawkmoth-flower interactions. *Proceedings of the national academy of sciences of the United States of America* 105:3404-3409
- Raguso RA (2008) Start making scents: the challenge of integrating chemistry into pollination ecology. *Entomol Exp Appl* 128:196–207
- Russell KN, Ikerd H, Doege S (2005) The potential conservation value of unmowed powerline strips for native bees. *Biol conserv* 124:133-148
- Sallenger, A.H. (2000). Storm Impact Scale for Barrier Islands. *Journal of Coastal Geology*. 16(3): 890-895.
- Simon HA (1962) The architecture of complexity. *Proc Am Philos Soc* 106:467-482
- Small JK (1933) *Manual of the Southeastern flora*. New York.

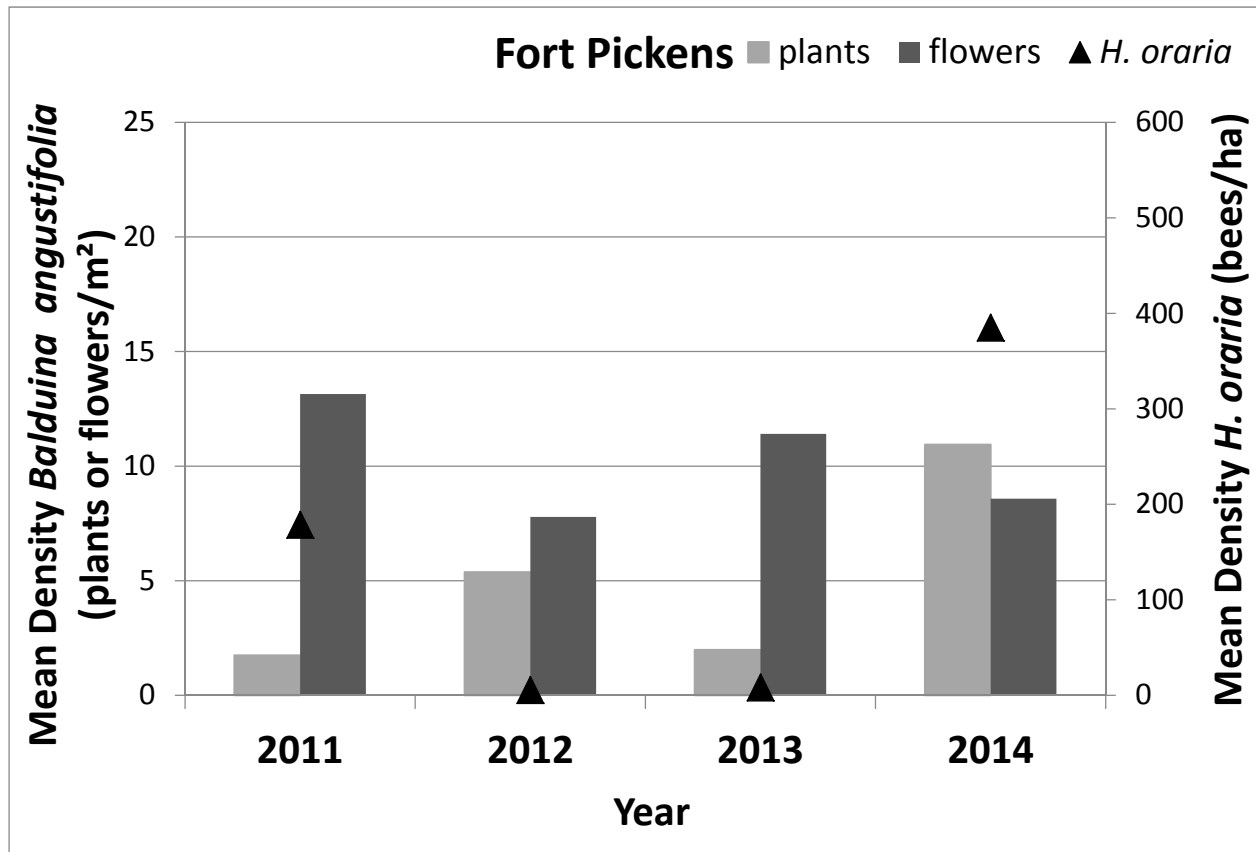
- Snep RPH, WallisDeVries MF, Opdam P (2011) Conservation where people work: A role for business districts and industrial areas in enhancing endangered butterfly populations? *Landscape Urban Plan* 103:94-101
- SPM Salford Predictive Modeler ® Software Suite © 1984-2013 Salford Systems, CART © 1984-2013 California Statistical Software, Inc.
- Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432-440
- Swink F, Wilhem G (1994) *Plants of the Chicago region* Fourth Edition. Indiana Academy of Sciences, Indianapolis, Indiana, USA.
- Thomas CD, Cameron A, Green RE et al. (2004) Extinction risk from climate change. *Nature* 427:145-148.
- Thomas JA, Simcox DJ, Clarke RT (2009) Successful Conservation of a Threatened *Maculinea* Butterfly. *Science* 325:80-83
- Urban DL, Oneill RV, Shugart HH (1987) Landscape Ecology. *Bioscience* 37:119-127
- Van Horne B, Olson G.S, Schooley RL, Corn JG, Burnham KP (1997) Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. *Ecol Monogr* 67:295-315
- Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol Appl* 17:910-921
- Willmer PG (1986) Foraging Patterns and Water Balance: Problems of Optimization for a Xerophilic Bee, *Chalicodoma sicula*. *J Anim Ecol* 55:941-962
- Winfrey R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conserv Biol* 21:213-223
- Zurbuchen A, Bachofen C, Mueller A (2010) (a) Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species. *Apidologie* 41:497-508
- Zurbuchen A, Cheesman S, Klaiber J et al. (2010) (b) Long foraging distances impose high costs on offspring production in solitary bees. *J Anim Ecol* 79:674-681
- Zurbuchen A, Landert L, Klaiber J et al. (2010) (c) Maximum foraging ranges in solitary bees: only few individuals have capability to cover long foraging distances. *Biol Conserv* 143:669-676

Zych M, Stpiczynska M (2012) Neither protogynous nor obligatory out-crossed: pollination biology and breeding system of the European Red List *Fritillaria meleagris* L. (Liliaceae). *Plant Biol* 14:285–294.

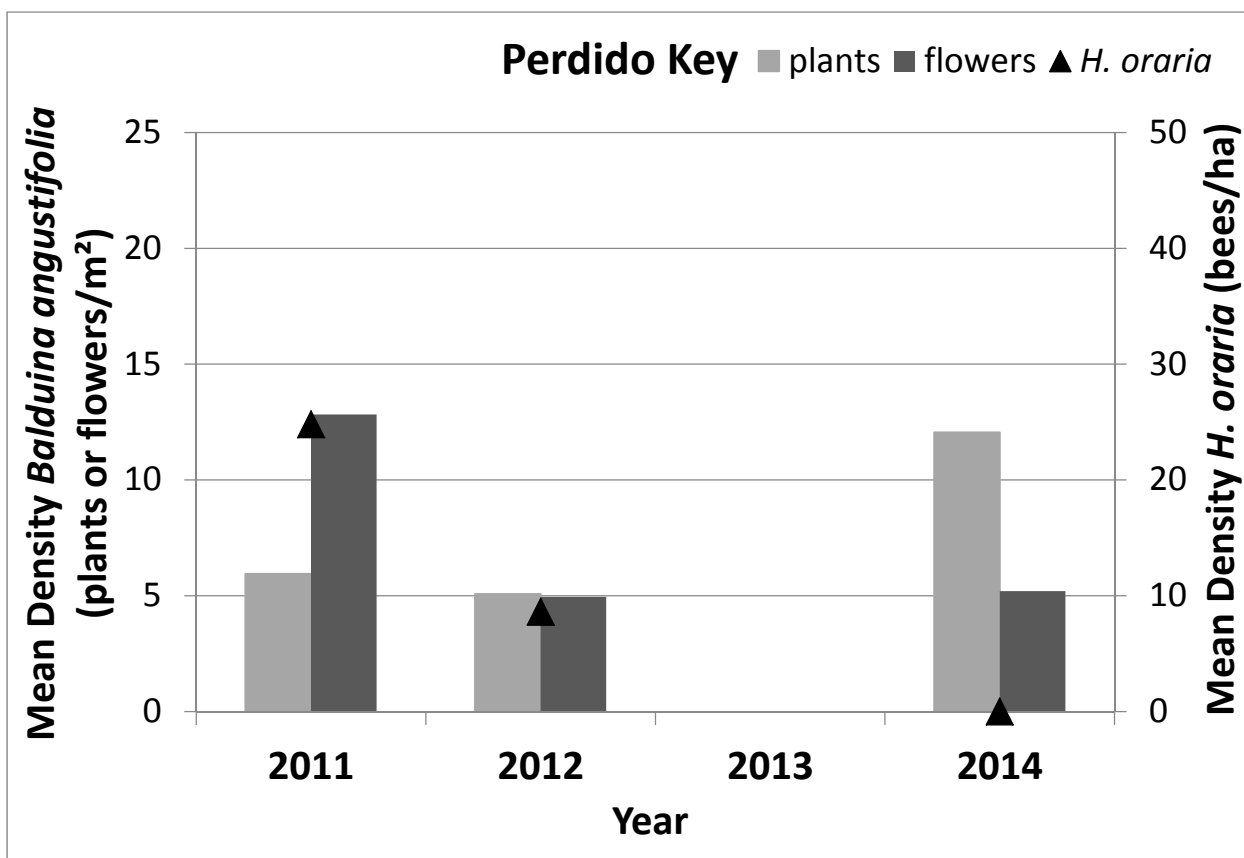
BIOGRAPHICAL SKETCH

Hannah was born in Butler, Pennsylvania but grew up in Fuquay-Varina, North Carolina. She earned a B.S. in environmental science from The University of North Carolina at Chapel Hill in August 2008. For over a year, she worked for the Student Conservation Association gaining a broad set of experiences in the natural resource management field. After a season working for the National Park Service in Texas, she was then hired by The Joseph W. Jones Ecological Research Center to collect data for a long-term study of longleaf pine ecosystem restoration and management at Eglin Air Force Base in Florida. She started her graduate studies in August 2011 majoring in interdisciplinary ecology. She concentrated on wildlife ecology and conservation and received her master's degree in the fall of 2013.

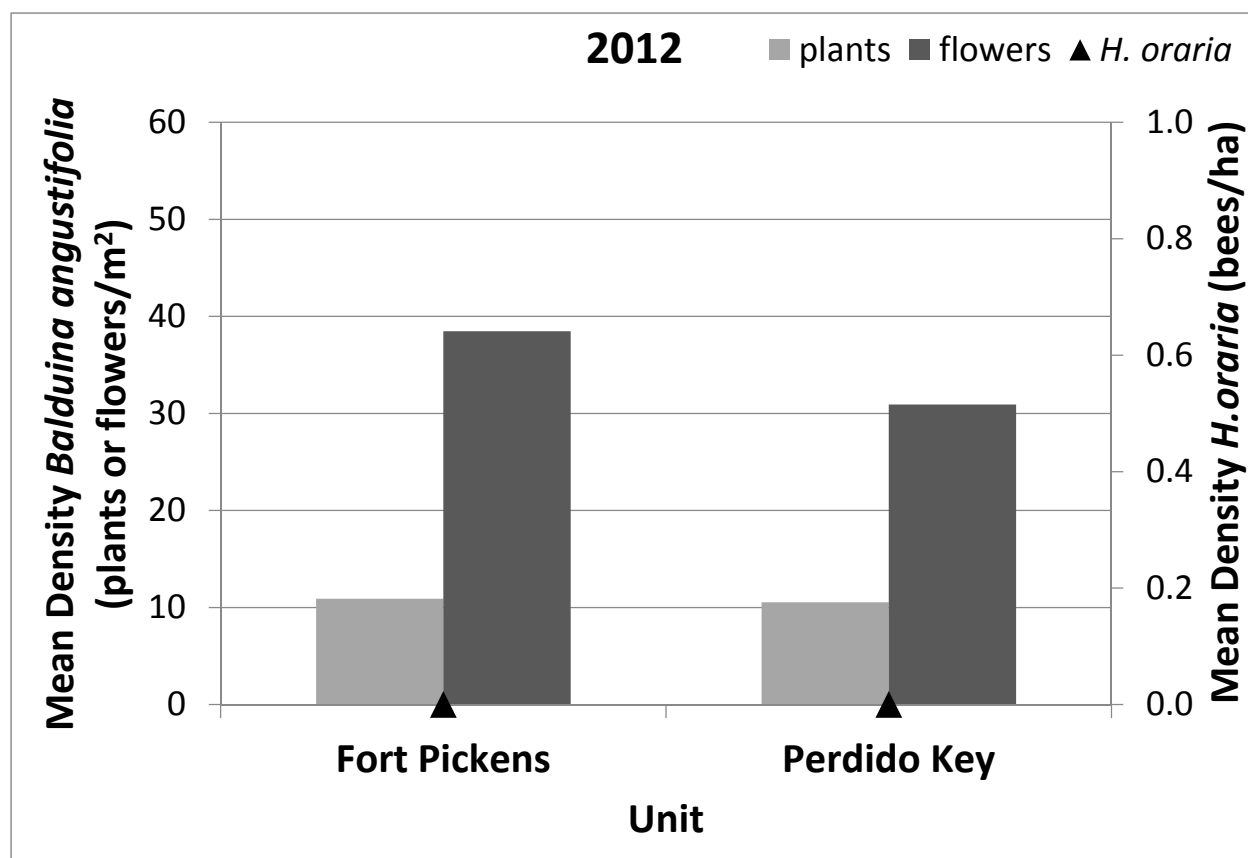
Chapter 5 final report bee-balduina graphs.docx follows:



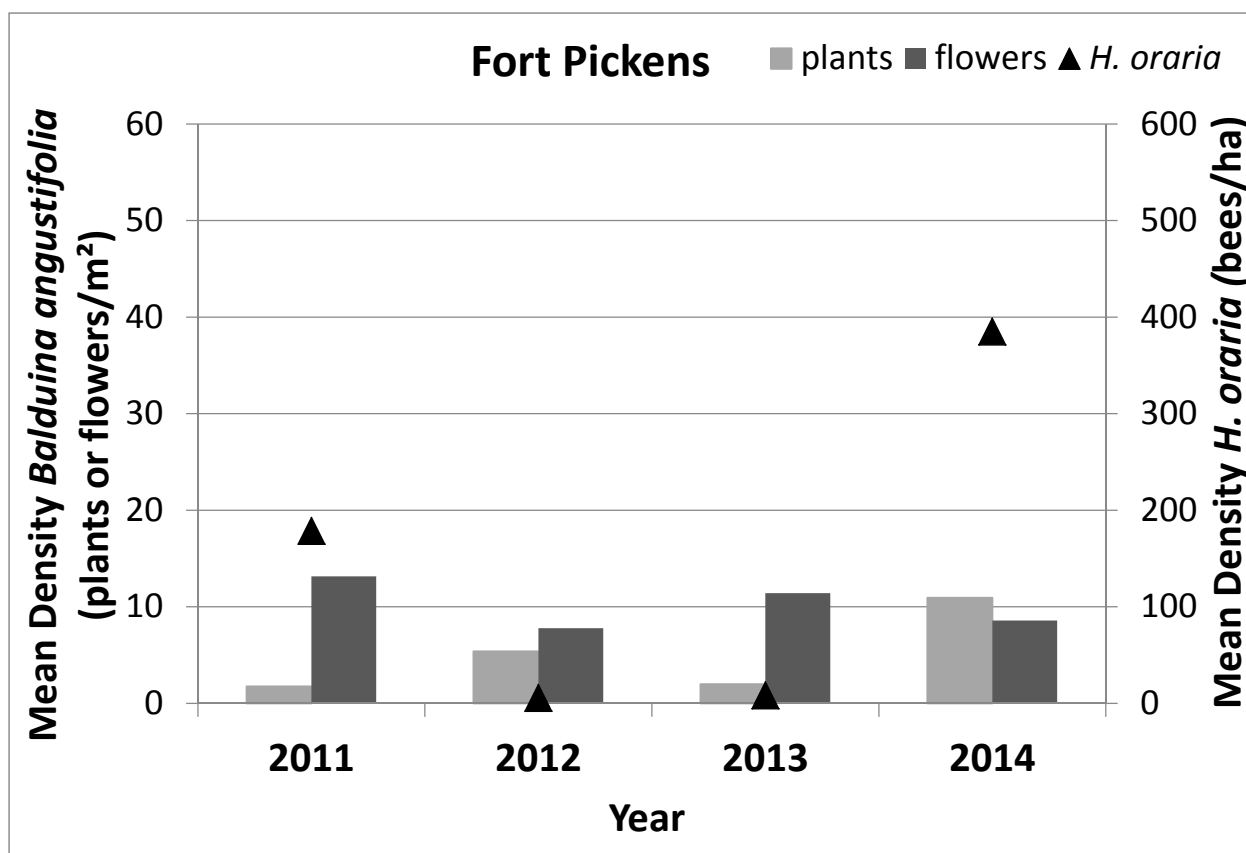
Fort Pickens	2011	2012	2013	2014
n	12	12	12	12
mean transect length (m)	15	13	12	10
plants/m ²	2	5	2	11
flowers/m ²	13	8	11	9
<i>H. oraria</i> /ha	179	6	8	385



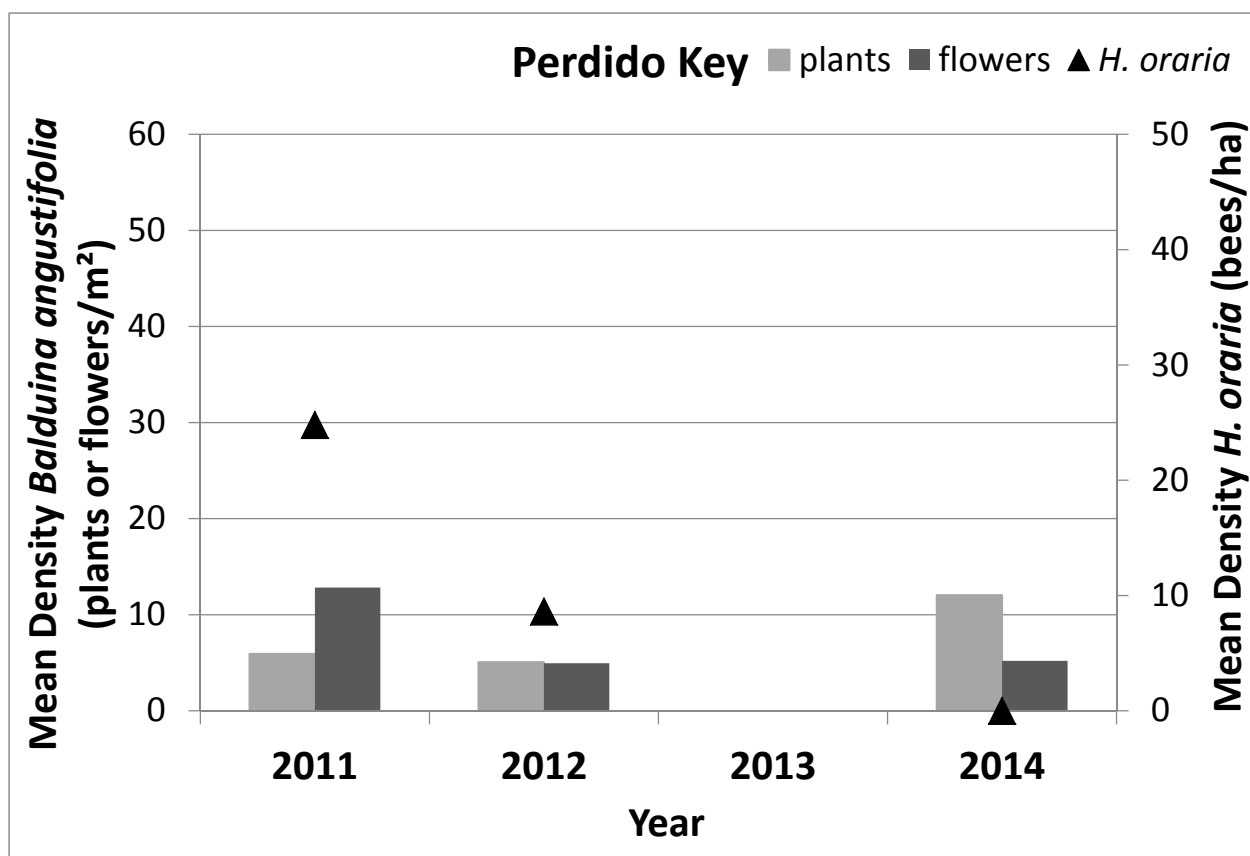
Perdido Key	2011	2012	2013	2014
n	15	15	n/a	15
mean transect length (m)	16	8	n/a	3
plants/m ²	6	5	n/a	12
flowers/m ²	13	5	n/a	5
<i>H. oraria</i> /ha	25	9	n/a	0



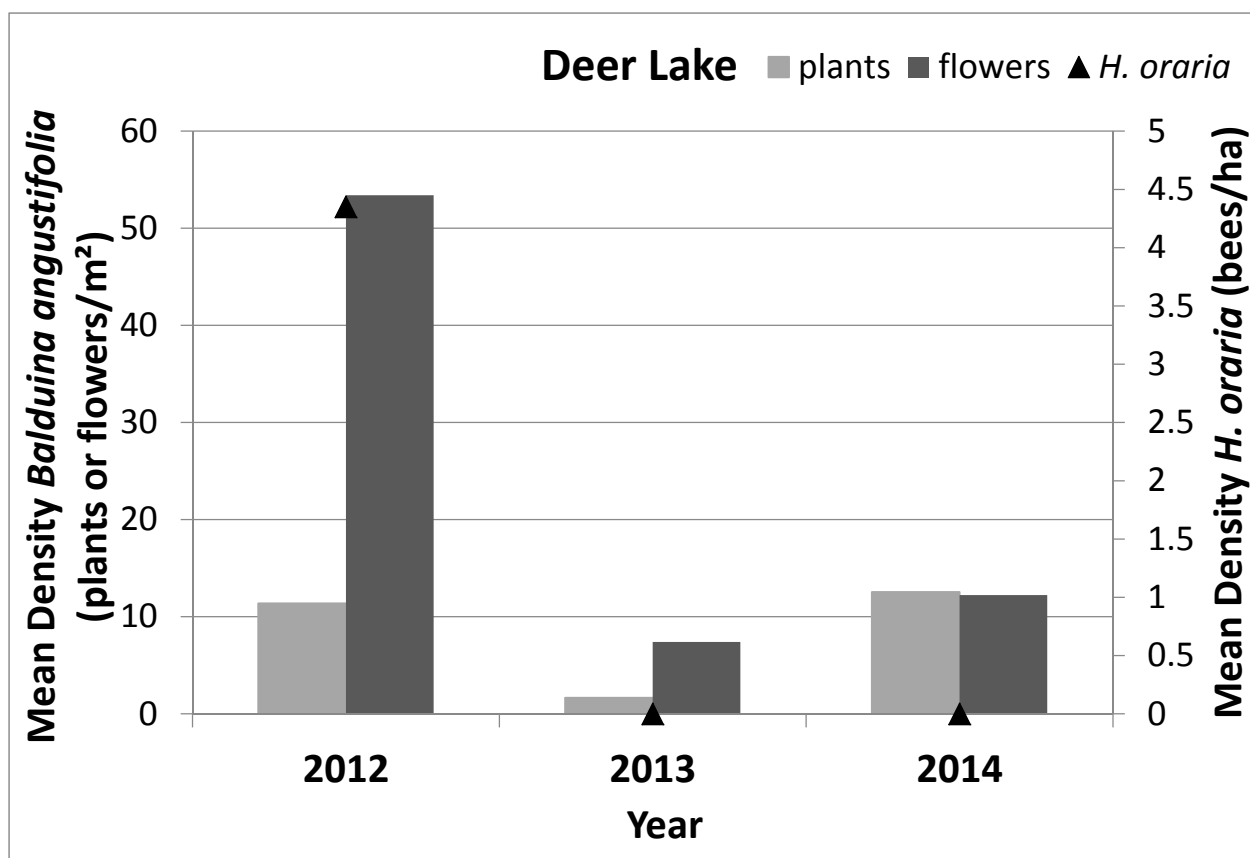
	Fort Pickens	Perdido Key
n	25	24
mean patch area (m ²)	156	158
plants/m ²	11	11
flowers/m ²	38	31
<i>H. oraria</i> /ha	0	0



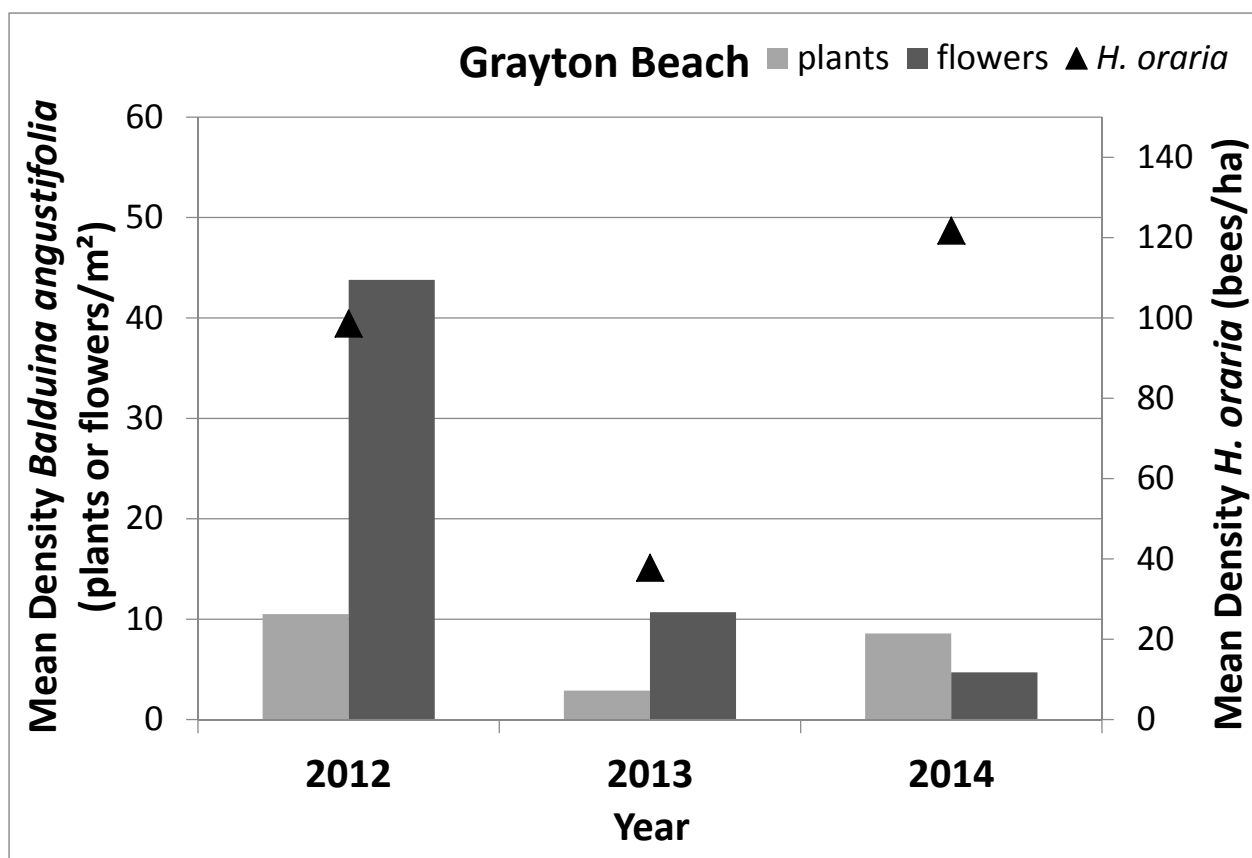
Fort Pickens	2011	2012	2013	2014
n	12	12	12	12
mean transect length (m)	15	13	12	10
plants/m ²	2	5	2	11
flowers/m ²	13	8	11	9
<i>H. oraria</i> /ha	179	6	8	385



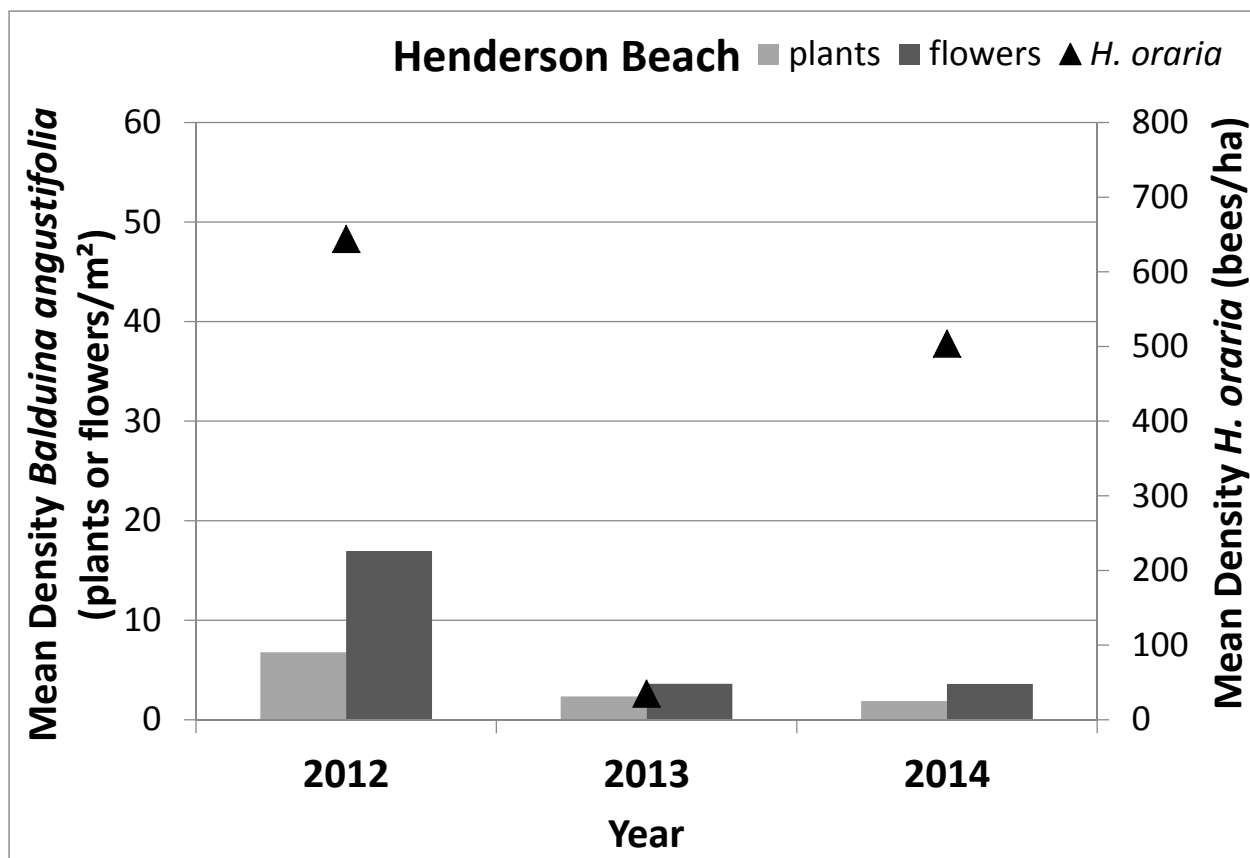
Perdido Key	2011	2012	2013	2014
n	15	15	n/a	15
mean transect length (m)	16	8	n/a	3
plants/m ²	6	5	n/a	12
flowers/m ²	13	5	n/a	5
<i>H. oraria</i> /ha	25	9	n/a	0



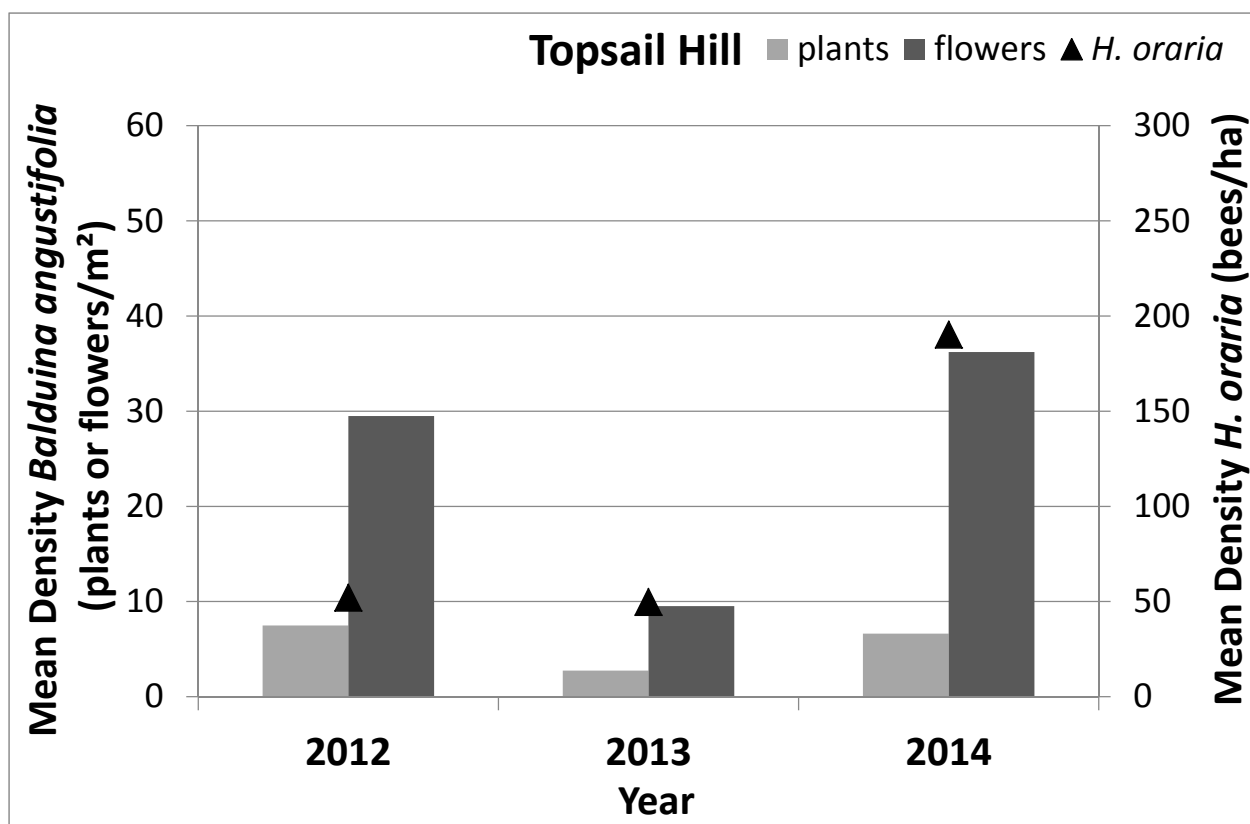
Deer Lake	2012	2013	2014
n	25	20	18
mean patch area (m ²)	897	131	189
plants/m ²	11	2	13
flowers/m ²	53	7	12
<i>H. oraria</i> /ha	4	0	0



Grayton Beach	2012	2013	2014
n	15	15	14
mean patch area (m ²)	923	1219	432
plants/m ²	11	3	9
flowers/m ²	44	11	5
<i>H. oraria</i> /ha	99	38	122



Henderson Beach	2012	2013	2014
n	13	12	10
mean patch area (m ²)	2275	835	52
plants/m ²	7	2	2
flowers/m ²	17	4	4
<i>H. oraria</i> /ha	644	35	504



Topsail Hill	2012	2013	2014
n	36	26	27
mean patch area (m ²)	147	126	90
plants/m ²	7	3	7
flowers/m ²	29	10	36
<i>H. oraria</i> /ha	52	50	190