A COMPARISON OF ISLAND AND MAINLAND
POLLINATION ECOLOGY

By

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In this study, I compared male and female reproductive success of island and mainland populations of two plant species, Opuntia stricta (Cactaceae) and Centrosema virginianum (Fabaceae) on the west coast of Florida. During the 1980, 1981, and 1982 breeding seasons, both male success, as measured by pollen dispersal, and female success, as measured by fruit or seedset, showed a significant reduction in island populations relative to mainland populations of these species despite the close geographic proximity of the study sites. The pollinator species that visited Opuntia stricta on the island site were a subset of the mainland pollinator assemblage. A complete shift in pollinating species of Centrosema virginianum occurred between the mainland and the island. On the island site, pollination was less effective for this species and less reliable for both species than on the mainland sites. Observational and experimental data suggested that pollinator scarcity was the cause of reduced reproductive success

on islands. On more distant, oceanic islands, these effects may be even more extreme and could either filter out inappropriate colonists or act as an agent of directional selection.

John C. Pimm
Chairman

INTRODUCTION

Floras of geographically isolated islands differ in many ways from the floras of mainlands with similar climates (Carlquist 1974, Rick 1966). The reproductive biology of island plants is often distinct from mainland plants when examined at the community level. A greater proportion of island plants is self-fertilizing than of mainland plants (Baker 1955, Baker and Hurd 1968, Linsley et al. 1966, Rick 1966). Differences also exist in the floral structure of island plants. The flowers of insect pollinated plants on islands tend to be unspecialized, open structures and are smaller and less showy than mainland flowers (Carlquist 1974). Finally, wind pollination is more common in island communities than in mainland communities (Whitehead 1969).

These differences in plant reproductive characteristics may have evolved in response to the depauperate pollinator communities usually found on islands (Baker 1955, Carlquist 1966, 1974). Island biogeographic theory predicts reduced diversity on islands for any guild or community of organisms, relative to mainland sites (MacArthur and Wilson 1967). Reduced diversity on islands has been found in insects (Simberloff and Wilson 1969) and birds (Diamond 1970), among many other taxa (see Carlquist 1974 and MacArthur and Wilson 1967 for reviews).

If pollinators follow the general trend of reduced diversity on islands, a flowering plant that has colonized an island may have a

lower chance of being visited than the same plant growing on the mainland. Island plants that require animal pollinators might suffer a decrease in reproductive output if visits are less common or certain. This would place such plants at a competitive disadvantage relative to other species or phenotypes that could self-fertilize, use a wide variety of pollinators, or use wind as a pollen dispersal agent.

Reduction in seed or fruit set, measures of female reproductive success, has been found in plant species growing in other conditions where pollinators are uncertain or rare. Examples include herbs flowering in early spring in temperate woodlands (Schemske et al. 1978) and insect-pollinated species in the Arctic (Kevan 1972). Pollen dispersal, a measure of male success, depends on pollinator visitation (Beattie and Culver 1979, Levin and Kerster 1974) and should be lower if pollinator visit rates are reduced. Linhart and Feinsinger (1980) demonstrated reduced pollen dispersal in Mandevilla hirsuta (Apocynaceae) on Tobago compared to a larger island, Trinidad, and attributed this to erratic bird visitation to Mandevilla flowers on the smaller island.

Pollinator scarcity could affect island plant communities by either 1) acting as a selective filter, inhibiting colonization of islands by plants with floral structures and breeding systems requiring pollinators, or 2) exerting directional selection pressure on plant populations established on an island, adapting the floral structures and breeding systems of these colonists to independence from pollinators.

Few studies have shown that pollinators are scarcer or less predictable on islands than on mainland sites. On the Galapagos

Islands, several orders of pollinating insects are represented by very few species, although the parts of the South American mainland with a similar climate have a diverse pollinator assemblage (Linsley 1966). Only a single species of flower-visiting bee is found on all the islands (Linsley et al. 1966). The diversity and density of nectarivorous birds are lower on a small, distant island (Tobago) than on a large, near island (Trinidad) (Feinsinger et al. 1979, 1982, Linhart and Feinsinger 1980). Even when pollinator scarcity has been demonstrated, the reproductive cost to the plant species on the island has almost never been estimated, except for one hummingbird-pollinated species on Trinidad and Tobago, where both pollen dispersal and seed set were reduced on the smaller island (Linhart and Feinsinger 1980).

Are the reproductive differences usually observed between island and mainland plant communities due to pollinator scarcity? To answer this question requires an examination of the reproductive success of a plant species with populations on an island and an adjacent mainland. In this study I examined two insect-pollinated plant species with populations growing on the mainland and on two off-shore islands, one smaller and more distant than the other. Three basic questions were addressed: 1) Are pollinators less abundant and less predictable on the island sites? 2) Is reproductive success, both male and female, reduced in island plant populations? 3) If reproductive success is reduced, can this be shown to result from pollinator limitation?

METHODS

Study Species

The two study species are Opuntia stricta (Cactaceae) and Centrosema virginianum (Fabaceae). These species were chosen because 1) they were the most abundant native species growing at the far island site, where the angiosperm community was least diverse, and 2) these species represent extremes in floral structural complexity.

Opuntia stricta, the prickly pear cactus, is a large, perennial, succulent plant. Often over a meter tall, plants can cover as much as three square meters at my study sites. Most species in the genus Opuntia undergo extensive vegetative growth. Sections of the stems, or "pads," are frequently lost from the parent plant (Rympe 1952). These pads can then grow into a full-sized plant. This form of vegetative propagation is common among Opuntia stricta growing at my sites.

The flower of Opuntia stricta has many petals and numerous stamens with a single pistil. The stigma is five-lobed. Each lobe is tightly appressed to the others when the flower first opens, but these separate and expose the receptive surfaces by the time the anthers dehisce. The flower is bright yellow and bowl-shaped, producing abundant pollen but little or no measurable nectar. At these sites, there is polymorphism in flower color and size within a study population. Some individuals had flowers with a noticeable orange tint and flowers that were usually larger than the bright yellow flowers of

other individuals. These individuals may contain characters transmitted from other species of Opuntia through hybridization, since the several Florida species apparently readily hybridize (Lyman Benson, personal communication). To reduce this potential source of variation, I chose only individuals with identical floral and pad morphology as study plants.

The open floral structure suggests that a wide array of flower-visiting insects could utilize Opuntia, but most of the pollinators that I observed visiting this species were pollen-foraging hymenoptera. In the field, most flowers last a single day, opening after sunrise and closing late in the afternoon. Timing of flower opening, stigma and anther dehiscence, and petal closing are largely temperature dependent. On cool, cloudy days flowers may open only partially and remain open for only a short time. Such flowers usually open again the next day. The inferior ovary of Opuntia stricta is large and fleshy by the time of flower opening. Mature fruits are approximately twice the size of the ovary of a newly-opened flower. At my study sites, Opuntia blooms from late April until early June, for approximately six weeks.

Centrosema virginianum, the butterfly pea, is a perennial, herbaceous vine. At my study sites, Centrosema plants grow in intertwined masses, which makes identification of individual vines impossible. Each vine is several meters in length and produces abundant flowers. The flower of Centrosema is highly specialized. Structurally it is an inverted flag flower adapted for pollination by large hymenopterans (Faegri and van der Pijl 1979). One petal is modified to act as a landing platform for the pollinator. The remaining petals form a structure surrounding the anthers and pistil,

which must be manipulated by a visitor to transfer pollen and expose the stigma. Flowers last a single day. After fertilization, the superior ovary must grow substantially to produce a mature fruit. In this area, Centrosema usually flowers from early August through September, for approximately nine weeks.

Study Sites

I chose study sites based on the presence of both plant species and on similarity of the habitat. The near island, Cedar Key, and the far island, Seahorse Key, had areas where both species were abundant. On the mainland, however, Opuntia stricta was found only as isolated individuals; I found no population large enough to include in this study. Comparisons among Opuntia populations were therefore limited to the larger, inshore island and the smaller, offshore island. Cedar Key, the larger, inshore island, is considered to be the mainland for the comparison of Opuntia stricta populations (similar comparisons using a large island as "mainland" were made by Diamond 1970, and Linhart and Feinsinger 1980). I found a suitable mainland site for Centrosema, so that three populations of this species were compared.

Seahorse Key, the smaller, offshore island, is located approximately eight kilometers off the west coast of Florida at 29° 07'30" (Figure 1). The island is 1.5 kilometers long and varies between 0.1 and 0.5 kilometers in width. My study transect extended 0.5 kilometers along the south beach, a sandy, low-energy beach dominated by sea-oats (Uniola paniculata) with live oak (Quercus virginianum) further inshore. Populations of both study species grow in the ecotone between the oak-dominated forest and the grassy shoreline.

Figure 1: Locations of Cedar and Seahorse Keys on the west coast of Florida. Study transects were on south-facing beaches of both islands.

Cedar Key is located midway between Seahorse Key and the mainland, connected to the latter by a man-made causeway. Cedar Key has approximately three times the surface area of Seahorse Key, approximately 3 kilometers long and between 0.2 and 1.0 kilometers wide. My Cedar Key transect was the same length as that on Seahorse Key, also along a south-facing, low-energy beach. Vegetation was similar to that on Seahorse Key, but appeared to be more strongly influenced by human habitation and richer in species.

I found a mainland site for Centrosema in 1981, a disturbed roadside area surrounded by a myrtle oak (Quercus myrtifolia) hammock. This Centrosema population is less extensive than the two island populations. As a consequence, my study transect was reduced to approximately 0.25 kilometers. I attempted to choose habitats as similar to each other as possible to use as study sites. This was done to reduce other potential sources of variation in these interpopulation comparisons so that any differences that I observed among the populations would be due to an "island effect" and not to habitat differences.

Breeding Systems

I determined the breeding system of Opuntia stricta by removing stem sections (pads) with well-developed flower buds and placing them in a greenhouse. Previous field observations had suggested that isolated pads of Opuntia would give rise to mature fruits provided that flower buds were already present. In 1982, approximately one week before the flowering season began, I removed a pad from each of twelve plants in each study population and potted the pads in a greenhouse. Each pad chosen had produced between six and seventeen flower buds. These pads were watered every other day for

approximately two months. When the flowers opened, I subjected them to one of three treatments: unmanipulated, self-pollinated, or cross-pollinated. Fruits were harvested after two months, before fruit maturation, but after sufficient time for fertilized seeds to develop fully. I counted all seeds in each experimental fruit and determined fruit abortion rates. Many seeds were much smaller than normal and were often discolored. I assumed such seeds were aborted and did not include them in further analyses.

To determine if the fruit abortion rates that I observed in the greenhouse were an artifact of growing conditions or the result of the experimental manipulations, I also bagged flowers in the field, using mosquito netting to prevent insect visitation. These flowers were either left unvisited or were cross-pollinated by hand. I compared abortion rates of these fruits to those of unmanipulated and hand-crossed flowers in the greenhouse.

Flowering Phenologies

A census of twelve plants of Opuntia stricta was made weekly at each study site in 1980, 1981, and 1982. Because it was difficult to distinguish individual plants of Centrosema virginianum, I chose three discrete patches at each site. If the flowers per patch exceeded 200, I estimated to the nearest twenty flowers. Centrosema was not chosen as a study species until the middle of its flowering season in 1980, and the Cedar Key study site was mowed in the middle of the 1982 Centrosema breeding season, so complete census data for this species are available only for the 1981 season.

Pollinators

In 1980, 1981, and 1982 I determined pollinator diversity and abundance by timed floral observations throughout the breeding seasons. Data for Opuntia stricta in 1980 consisted of hourly, three minute observations at each of the twelve study plants from the time of flower dehiscence in the morning until the flowers closed at approximately 16:00 EST, once a week at each site. A preliminary ANOVA of these 1980 data revealed no significant variation in visit frequencies or visitor diversity among the study plants at a given site. Therefore, I limited visitor censuses for the remaining seasons to observations of a single individual at each study site. The observation period was increased to fifteen minutes each hour. For each weekly visitor census, I chose the individual with the largest number of open flowers. I feel this technique is valid as a relative measure because this one plant would often contain from 25-50% of the total flowers in bloom on all the study individuals. This was a possible source of bias in determining visit rates; however, there was little difference among the study sites in the number of flowers that I observed for a given week during the breeding season. I determined visit rates and visitor diversity for Centrosema virginianum by observing the patch with the greatest number of flowers. As a relative measure of pollinator abundance, I estimated the number of insect visits / flower-hour based on a 15 minute observation period each hour the flowers were open. This was not an absolute measure of pollinator density because floral density strongly influenced the value. For example, if the number of pollinator visits that I measured on Seahorse and Cedar Keys were similar, but more flowers were under observation on Seahorse Key, visit rate would be

lower on Seahorse Key. Number of visits / flower*hour was, however, a valid relative measure of the visit frequency a given flower in a study population can expect.

Both study species received insect visits by numerous lepidopterans and small hymenopterans, which did not contact the female reproductive structures. I did not include these species in calculations of either diversity or abundance.

Reproductive Success

Both of these study species produce hermaphroditic flowers, flowers that produce both pollen and ovules. The male and female functions of these flowers can have different success under a variety of environmental conditions (Willson 1979) and both should be determined when comparing reproductive success. Female success of a plant can be measured as the number of fruits or seeds produced (Lloyd 1979). Seed set is probably a better measure, since each seed represents a potential individual in the next generation. To determine female reproductive success, I measured natural fruitset in both species and the seeds per fruit in Opuntia stricta. Each week of the 1981 and 1982 breeding seasons I tagged and left open to natural visitation 20 flowers of Opuntia stricta. For Centrosema virginianum the weekly sample size was 20 in 1981 and 30 in 1982. Centrosema fruits mature quickly; I harvested fruits of this species 1-2 weeks after tagging. Opuntia fruits required a longer development time and were harvested in September, by which time they had begun to ripen, as shown by the reddening of the "pear."

I conducted an additional experiment with Opuntia to determine the relationship between number of pollinator visits and resulting seedset. I bagged flowers of a randomly chosen plant before they

opened, removed the bags when the flowers opened, and rebagged each flower after a given number of visits.

Male reproductive success is the number of ovules fertilized by pollen from a given plant (Willson 1979). This is difficult to measure, however, so male reproductive success is often estimated by determining a plant's pollen dispersal pattern. I estimated pollen dispersal with fluorescent dyes, a standard technique (Stockhouse 1976) recently evaluated by Waser and Price (1982). Because floral density is known to affect pollen dispersal (Levin and Kerster 1974), I conducted these experiments only during times when flower densities were similar among the study sites during the 1981 and 1982 breeding seasons. The anthers of a marked flower were dusted with UV fluorescent dye early in the morning. At the end of the day, when the flowers began to wilt, I harvested flowers at 0.5, 1.0, 2.0, 4.0, and 6.0 meters from the dusted flower and examined them for the presence of dye with a hand lens under UV light. The data that I collected were percentages of flowers at each distance containing dye on their reproductive structures.

Pollinator Limitation

I conducted field experiments to determine whether pollination might be limiting female reproductive success in my study populations. Between 15 and 60 Centrosema flowers were hand-pollinated during the 1981 and 1982 flowering peaks (late September to early October), the only times when sufficient flowers were available at all sites for the experiment. I tagged but left unmanipulated an equal number of flowers to serve as controls. Whenever possible, the control flowers were the nearest neighbors of the experimental flowers. I carried out pollinator limitation experiments on Opuntia stricta only during the

1983 breeding season. Unfortunately, the results of this experiment cannot be easily compared to visit-rate or reproductive success data collected during earlier breeding seasons. Each week of the 1983 flowering season, I hand-crossed 13 to 20 Opuntia flowers at each study site. Again, an equal number of flowers was tagged and left untouched as controls. I determined fruitset for both species and seeds per fruit for Opuntia.

RESULTS

Breeding Systems

Table 1 compares fruitset among greenhouse plantings of Opuntia stricta from Seahorse and Cedar Keys for each of three treatments. Fruitset rates for unvisited and hand-crossed flowers in the field are also presented. These fruitset data were analyzed using a log-linear model (Sokal and Rohlf 1981) to determine which variables significantly influenced fruitset. Treatment was the only variable significantly affecting Opuntia fruitset ($X^2 = 23.98$, $p < 0.001$); neither locale nor growing condition (greenhouse or field) affected fruitset. There were no significant interactions among the main effects. A contingency X^2 showed no difference between the fruitset for greenhouse flowers that were selfed or crossed, but significant differences did exist among unvisited flowers and the other treatments (Unvisited vs. Selfed $X^2 = 5.20$, $p < 0.05$, Unvisited vs. Crossed $X^2 = 16.47$, $p < 0.01$). Also, hand-crossed flowers in the field were significantly more likely to set fruit than were unvisited flowers in the field.

Table 2 presents mean seedset for the Opuntia fruits from the greenhouse experiments. An ANOVA of mean seeds per fruit found no significant locale or among-plant variation. Mean seeds / fruit did differ significantly among treatments ($F = 148.6$, $p < 0.001$) and a Duncan's Multiple Range Test revealed that all treatment means in Table 2 are significantly different. To summarize the Opuntia stricta

Table 1: Fruitset in Opuntia stricta under three experimental treatments from pads growing in a greenhouse and plants in the field. No between-site differences in fruitset were significant, but unvisited flowers set significantly fewer fruits than did crossed or selfed flowers ($\alpha = 0.05$).

Greenhouse Data			
	Unvisited	Selfed	Crossed
Cedar Key	65.3%(N=52)	71.8%(N=39)	76.9%(N=39)
Seahorse Key	60.7%(N=61)	85.7%(N=35)	81.6%(N=38)
Field Data			
Cedar Key	81.0%(N=21)	---	90.1%(N=81)
Seahorse Key	54.5%(N=55)	---	88.8%(N=72)

Table 2: Mean number of seeds/fruit of *Opuntia stricta* from three experimental treatments ($\bar{X} + \text{S.E. (coefficient of variation)}$). No between site differences in seedset were significant, however, mean seedset for each of the three treatments were significantly different ($\alpha = 0.05$).

	Unvisited	Selfed	Crossed
Cedar Key	$5.8 \pm 1.8(189.2)$	$66.2 \pm 5.0(40.0)$	$73.6 \pm 3.4(41.4)$
Seahorse Key	$8.0 \pm 2.8(212.3)$	$61.3 \pm 5.6(40.8)$	$73.0 \pm 4.0(30.2)$

breeding system, no differences existed between Seahorse and Cedar Key populations in either fruit or seedset for my experimental treatments. Unvisited flowers set fewer fruits and had fewer seeds / fruit than did either selfed or crossed flowers. Selfed flowers had a similar fruitset rate to crossed flowers, but had fewer seeds / fruit on the average than did crossed flowers. Hand-crossed flowers had high rates of fruitset and the greatest mean number of seeds / fruit of the three treatments.

I analyzed only fruitset data for Centrosema virginianum (Table 3). Seeds / fruit ranged between 15 and 23 for all fruits that reached maturity, averaging approximately 18 seeds / fruit. Many of the experimental fruits, however, did not reach maturity due to heavy predation by unidentified herbivores, so I limited Centrosema reproductive data to fruitset. Pod predation could have been a possible source of bias in the fruitset data if fruits had been entirely consumed.. Only if the entire fruit and petiole were missing was the fruit considered to be aborted. Partially eaten pods were most abundant on the mainland, which suggested that predation may have been greater at that site. Because fruitset was predicted to be greater on the mainland, this bias would have been a conservative one.

I tested for locale and treatment effects on fruitset with a log-linear model and found treatment effect to be highly significant ($\chi^2=66.08$, $p<0.001$) but found no site effect or any higher order interactions between these two variables. Fruitset differed significantly among all three treatments (Unvisited vs. Selfed $\chi^2=19.52$, $p<0.001$, Unvisited vs. Crossed $\chi^2=63.98$, $p<0.001$, Selfed vs. Crossed $\chi^2=10.52$, $p<0.01$). The mainland and two island populations of Centrosema did not differ in their response to a given

Table 3: Fruitset in *Centrosema virginianum* under three experimental treatments from plants in the field. No among-site differences in fruitset were significant, however, each of the three treatments resulted in significantly different fruitset ($\alpha = 0.05$).

	Unvisited	Selfed	Crossed
Seahorse Key	0%(N=40)	23.3%(N=30)	30.0%(N=90)
Cedar Key	0%(N=7)	16.7%(N=18)	40.0%(N=50)
Mainland	0%(N=35)	6.7%(N=15)	48.4%(N=45)

experimental treatment. Unvisited flowers did not set fruits, and selfed flowers produced significantly fewer fruits than did crossed flowers.

Phenologies

Figures 2 and 3 represent the flowering phenologies of Opuntia stricta and Centrosema virginianum. I used a Kolmogorov-Smirnov 2-Sample Test (Siegel 1956) to compare the phenologies of Opuntia populations at the two locales for 1980 and 1981; the 1982 census was incomplete due to the destruction of several individuals at the Cedar Key study area. The flowering distributions of the two sites differed significantly for both years ($p < 0.01$). The Kolmogorov-Smirnov 2-Sample Test could not be used to compare three study populations; instead, I used the χ^2 test for k-independent samples (Siegel 1956), which tests for differences in frequency distributions, to compare Centrosema populations. The three sites differed significantly in flowering phenologies for the 1981 season. The 1980 and 1982 seasons appeared to have less among site variation, but the data were too limited for statistical analysis.

Different flowering phenologies between sites could be the result of individual plants flowering for a longer time at one locale, or the differences in phenology could be caused by a greater variance in blooming times among individual plants at a given site. To distinguish between these two possibilities, I calculated a "flowering diversity" value for each individual of Opuntia stricta. This was not possible for Centrosema. Simpson's C-inverse (Simpson 1949) was used,

Figure 2: Flowering phenologies of Opuntia stricta for the 1980 (A), 1981 (B), and 1982 (C) flowering seasons. Flowering season extended from late April until early June.

Figure 3: Flowering phenologies of Centrosema virginianum for the 1980 (A), 1981 (B), and 1982 (C) flowering seasons. Flowering season extended from early August through September.

$$C \text{ inv.} = \sum \frac{1}{P_i^2}$$

where P_i equals the number of open flowers observed during week i divided by the total number of open flowers observed for that individual. These values incorporate the number of weeks an individual was in bloom and the evenness of flowering over a season, i.e. how concentrated the flowering was within the breeding season. I log-transformed these individual "flower diversity" values and analyzed by ANOVA to determine which factors affected flowering diversity. Between year variation was highly significant ($F=24.91$, $p<0.001$). Between site variation was not significant. These data suggest that the observed differences in Opuntia phenology between the two study sites were due to greater among individual variance in blooming times on Seahorse Key, and not to a longer blooming time for each plant.

Pollinator Communities

Tables 4 and 5 present the pollinators of Opuntia stricta and Centrosema virginianum and the relative frequencies of their visits. I observed three species transferring pollen on Seahorse Key, although one species, Bombus pennsylvanicus, was found only one week in 1981. Cedar Key had a richer pollinator community than Seahorse Key for both species. The mainland population of Centrosema virginianum was visited almost exclusively by Bombus pennsylvanicus. Two of the pollinators that I observed visiting these two plant species are

Table 4: The relative abundance of pollinators of Opuntia stricta at both study sites. Relative abundance of a species was determined for each breeding season by dividing the number of flower visits observed for that species by the total number of observed visits. Number of observed visits to Opuntia stricta by each species is in parenthesis. Visitors that did not carry pollen were not included.

Seahorse Key	1980	1981	1982
<u>Agapostemon splendens</u>	56.5%(26)	46.4%(116)	95.0%(57)
<u>Megachile brevis</u>	43.5%(20)	47.6%(119)	5.0%(3)
<u>Bombus pennsylvanicus</u>	---	6.0%(15)	---
Cedar Key			
<u>Agapostemon splendens</u>	7.6%(20)	42.1%(128)	21.4%(36)
<u>Megachile brevis</u>	30.8%(79)	23.0%(70)	7.7%(13)
<u>Apis mellifera</u>	50.3%(130)	24.7%(75)	69.0%(116)
<u>Melissoides</u> sp.	10.2%(26)	6.6%(20)	1.8%(3)
<u>Campsomeris quadrimaculatus</u>	0.4%(1)	3.6%(11)	---

Table 5: The relative abundance of pollinators of Centrosema virginianum at all study sites. Relative abundance of a species was determined for each breeding season by dividing the number of flower visits observed for that species by the total number of observed visits. Number of observed visits to Centrosema virginianum by each species is in parenthesis. Visitors that did not carry pollen were not included.

Seahorse Key	1980	1981	1982
<u>Megachile brevis</u>	100%(210)	100%(20)	100%(68)
Cedar Key			
<u>Megachile brevis</u>	43.4%(29)	47.4%(36)	20.2%(50)
<u>Melissoides</u> sp.	56.7%(38)	51.3%(39)	52.0%(129)
<u>Bombus pennsylvanicus</u>	---	1.3%(1)	---
<u>Campsomeris quadrimaculatus</u>	---	---	27.3%(69)
Mainland			
<u>Bombus pennsylvanicus</u>	No Site	95.4%(902)	100%(296)
<u>Apis mellifera</u>		0.1%(1)	---
<u>Campsomeris quadrimaculatus</u>		4.4%(42)	---

colonial, Bombus pennsylvanicus and Apis mellifera. These forage for both nectar and pollen. All the remaining species are solitary; all but the scoliid wasp Campsomeris quadrimaculatus forage for pollen only. A relatively small subset of species was shared by the two plant species.

To quantify the apparent differences among the study sites, I calculated weekly Shannon-Weaver species diversity values ($H' = -\sum P_i \ln P_i$, where P_i = proportion of total individuals in species i), log-transformed these values to normalize them (Sokal and Rohlf 1981), and calculated an ANOVA. For Opuntia stricta, mean species diversity values were 1.49 for Seahorse Key and 2.49 for Cedar Key. This difference was highly significant ($F=10.45$, $p<0.005$). Opuntia pollinator species diversity values did not significantly vary from week-to-week within a breeding season or among breeding seasons. I found similar results with Centrosema; site significantly affected pollinator diversity ($F=8.54$, $p<0.01$) but among or within year variation was not significant. A Duncan's Multiple Range test indicated that Cedar Key had a significantly greater pollinator diversity ($SD = 1.56$) than did Seahorse Key ($SD=0.73$) or the mainland ($SD=1.07$); the latter two did not differ.

Tables 6 and 7 show mean weekly visit rates to flowers of Opuntia stricta and Centrosema virginianum. When analyzed for variance, among year variation ($F=8.74$, $p<0.01$) and between site variation ($F=39.25$, $p<0.001$) were significant for Opuntia; neither was significant for Centrosema. Although the ANOVA found no significant locale effect ($p=0.17$) a Duncan's Multiple Range test of mean visit rates of Centrosema indicated that Seahorse Key visit rates ($X=0.532$) differed significantly from mainland visit rates ($X=4.245$), though neither

Table 6: Mean pollinator visit rates to Opuntia stricta in number of visits/flower/hour ($\bar{X} \pm \text{S.E.}$ (coefficient of variation)). Among year and between site differences in visit rates are all significant ($p < 0.01$).

Year	Seahorse Key	Cedar Key
1980	0.17 ± 0.07 (97.2)	0.60 ± 0.20 (68.0)
1981	1.28 ± 0.61 (124.7)	4.22 ± 0.54 (25.5)
1982	1.40 ± 1.14 (140.6)	3.73 ± 0.54 (25.2)

Table 7: Mean pollinator visit rates to *Centrosema virginianum* in number of visits/flower/hour ($\bar{X} \pm$ S.E. (coefficient of variation)). Among-year differences were not significant, but a year-locale interaction was significant ($\alpha = 0.01$). When each year was analyzed separately, the only significant difference was between the mainland site and the two island sites in 1981 ($\alpha = 0.01$).

Year	Seahorse Key	Cedar Key	Mainland
1980	0.71 $\pm$ 0.19(54.9)	0.63 $\pm$ 0.22(49.4)	No Site
1981	0.19 $\pm$ 0.18(231.0)	0.61 $\pm$ 0.18(65.4)	5.27 $\pm$ 1.76(66.8)
1982	1.69 (N=1)	6.81 $\pm$ 1.48(30.8)	2.20 $\pm$ 0.89(57.2)

differed significantly from Cedar Key ($\bar{X}=1.996$).

Not only are visit rates lower for small island populations of both species, but Centrosema visit rates also show greater variation on the island sites than on the mainland (Tables 6 and 7). Dawkins and Dawkins (1973) describe a method to determine if significant differences exist in the variation around sample means that requires only the CV values and the numbers of observations. The resulting C-statistic is compared to a t-distribution to test for significance. By this measure, the CV for the visit rates of the Seahorse Key population of Centrosema virginianum is greater than the CV for the Cedar Key population ($C=2.37$, $p<0.05$) and the mainland ($C=2.32$, $p<0.05$). The differences in variation of visit rates between the Opuntia populations are not significant, probably due to the small sample size. In all years, however, the CV's for Opuntia visit rates are greater on the far island.

To analyze one source of variation in visit rates, I examined the relationship between weekly visit rates and flowering phenologies for the study species. Data for 1981 were more complete and are presented in Figures 4 and 5. The populations of both species on Seahorse Key have extremely low visit rates during the peak of flowering, and higher rates when flower densities are low. Neither Cedar Key nor mainland populations show a similar pattern.

Reproductive Success

Tables 8 and 9 show field fruitset data for the two study species. I analyzed these data with log-linear models. Neither locale nor year significantly affected Opuntia fruitset. Both year and locale had a significant effect on Centrosema fruitset (locale $\chi^2=12.38$, $p<0.01$, year $\chi^2=3.92$, $p<0.05$), and there was a significant

Figure 4: 1981 flowering phenologies and weekly pollinator visit rates of Opuntia stricta at (A) Seahorse Key and (B) Cedar Key. Note the different scales for visit rates for each site.

Figure 5: 1981 flowering phenologies and weekly pollinator visit rates of Centrosema virginianum at (A) Seahorse Key, (B) Cedar Key, and (C) the mainland. Note the different scales for visit rates for the three sites.

Table 8: Fruitset in Opuntia stricta from tagged, unmanipulated flowers in the field. Neither between year nor between site differences in fruitset were significant.

Year	Seahorse Key	Cedar Key
1981	59.2%(N=135)	58.8%(N=80)
1982	65.0%(N=60)	55.0%(N=60)

Table 9: Fruitset in Centrosema virginianum from tagged, unmanipulated flowers in the field. Both year and site significantly affected Centrosema fruitset.

Year	Seahorse Key	Cedar Key	Mainland
1981	4.0% (N=100)	18.8% (N=80)	30.0% (N=60)
1982	23.3% (N=60)	36.7% (N=60)	18.9% (N=90)

year-locale interaction ($\chi^2=19.45$, $p<0.01$) indicating that the fruitset pattern changed within the two year study period. In 1981 fruitset on Seahorse Key was significantly lower than on Cedar Key ($\chi^2=10.24$, $p<0.01$) and the mainland ($\chi^2=21.27$, $p<0.01$). In 1982, fruitset on the mainland was significantly lower than on Cedar Key ($\chi^2=5.70$, $p<0.05$) but no other sites showed significant differences.

Data from the breeding system experiments indicated that seeds / fruit was a more sensitive indicator of reproductive success than fruitset in Opuntia stricta. An ANOVA of Opuntia seeds / fruit determined that several factors had a highly significant effect on the number of seeds / fruit; locale ($F=17.57$, $p<0.001$), year ($F=20.44$, $p<0.001$), week of flowering within the breeding season ($F=21.44$, $p<0.001$), and individual plant at the site ($F=4.92$, $p<0.01$) all significantly affected the number of seeds / fruit. Table 10 summarizes these data. The coefficients of variation for seeds / fruit differ significantly between the two populations for each of the three breeding seasons during which I collected fruits (1980 C=4.64, 1981 C= 4.66, 1982 C=3.84, all $p<0.01$). The number of seeds / fruit varied more on Seahorse Key than on Cedar Key. Mean seeds / fruit for each study individual ranged from 27.3 ± 4.0 to 86.2 ± 6.9 on Seahorse Key, and from 58.2 ± 10.6 to 99.0 ± 8.0 on Cedar Key.

Figure 6 shows the relationship between number of pollinator visits and resulting seedset in Opuntia stricta. A single visit was enough to ensure a high level of seedset, much higher than was found in fruits of unvisited flowers. Mean seedset increased with increasing visitation, up to twelve visits, but the rate of increase was much lower after the first visit. This relationship between number of pollinator visits and the resulting number of seeds / fruit

Table 10: Mean number of seeds/fruit from tagged, unmanipulated Opuntia stricta flowers in the field ($\bar{X} \pm$ S.E. (coefficient of variation)). Both site and year significantly affected Opuntia seedset.

Year	Seahorse Key	Cedar Key
1980	60.6 $\pm$ 3.7 (44.8)	74.3 $\pm$ 2.2 (23.0)
1981	65.3 $\pm$ 4.8 (65.6)	86.5 $\pm$ 4.5 (35.7)
1982	67.5 $\pm$ 4.5 (41.7)	89.6 $\pm$ 3.1 (19.3)

Figure 6: The number of pollinator visits and the resulting seedset
in flowers of Opuntia stricta. Distance of bars indicates
standard error of the mean.

suggested that one source of the variation observed in mean seeds / fruit was the number of pollinator visits that a flower receives. The significantly higher variation in Opuntia seedset on Seahorse Key may have been a result of a greater variation in the number of pollinator visits that Seahorse Key Opuntia flowers received.

Figures 7 and 8 present the data for pollen dispersal of Opuntia stricta and Centrosema virginianum, i.e. the index to male reproductive success used in this study. A contingency χ^2 for each distance showed that the patterns of dispersal did not differ significantly between 1981 and 1982 at any of the study sites. Sample sizes for each distance were between 15 and 30 flowers for each season. These figures represent pooled samples for both years. I calculated contingency χ^2 's for the number of flowers receiving fluorescent dye at each site for each of the five distance categories. Pollen dispersal of Opuntia was significantly greater on Cedar Key than on Seahorse Key at every distance except the furthest distance, six meters. For Centrosema I found no difference in pollen dispersal between the two islands; however, the mainland had greater pollen dispersal at all distances except six meters when compared to the two islands.

Pollinator Limitation

Tables 11 and 12 present fruitset data from the pollinator limitation experiments on the two study species. Opuntia fruitset showed no difference between the hand-crossed and unmanipulated flowers at either site. Mean seeds / fruit of Opuntia appeared reduced in open flowers when compared to hand-crossed flowers on Seahorse Key (Table 13), but this difference is not significant ($F=2.51$, one-tailed $p=0.056$). A log-linear model indicated that both

Figure 7: Dye dispersal in Opuntia stricta, 1981 and 1982 data combined. Contingency χ^2 indicated significant differences in frequency of flowers receiving dye at all distances except 6 meters.

Figure 8: Dye dispersal in *Centrosema virginianum*, 1981 and 1982 data combined. Contingency χ^2 indicated no significant difference in frequency of flowers receiving dye between the two islands, but significant differences between both islands and the mainland at every distance except 6 meters.

Table 11: Fruitset in Opuntia stricta from the 1983 pollinator limitation experiment. Handcrossed and unmanipulated Opuntia flowers had similar fruitset rates.

Treatment	Seahorse Key	Cedar Key
Crossed	90% (N=81)	89% (N=72)
Open	89% (N=81)	85% (N=72)

Table 12: Fruitset in Centrosema virginianum from 1981 and 1982 pollinator limitation experiments. Only on Seahorse Key in 1981 did fruitset rates differ significantly between hand-crossed and open flowers ($\alpha = 0.05$)

Year	Treatment	Seahorse Key	Cedar Key	Mainland
1981	Crossed	30% (N=30)	45% (N=20)	67% (N=15)
	Open	0% (N=40)	40% (N=20)	55% (N=20)
1982	Crossed	32% (N=60)	37% (N=30)	40% (N=30)
	Open	23% (N=60)	43% (N=30)	23% (N=30)

Table 13: Mean number of seeds/fruit from the fruits of the 1983
Opuntia stricta pollinator limitation experiment ($\bar{X} \pm$ S.E.).
Differences between handcrossed and open flowers were not
significant at $p = 0.05$.

Treatment	Seahorse Key	Cedar Key
Crossed	84.2 $\pm$ 3.5 (N=75)	73.1 $\pm$ 2.4 (N=64)
Open	75.9 $\pm$ 3.9 (N=74)	71.5 $\pm$ 2.8 (N=61)

treatment ($X^2=6.31$, $p<0.02$) and locale ($X^2=15.94$, $p<0.01$) significantly affected fruitset in Centrosema. Contingency X^2 for each locale showed a significant difference in fruitset between open and crossed flowers only on Seahorse Key ($X^2=6.34$, $p<0.02$).

In addition to the experimental evidence for pollinator limitation of female reproductive success, correlative data also suggest pollinator limitation. I found a highly significant Spearman rank correlation coefficient ($r=0.898$, $p=0.015$) between weekly visit rates and the resulting fruitset from these flowers for the Seahorse Key population of Centrosema virginianum. This correlation was not significant at Cedar Key or the mainland. Neither weekly fruitset nor weekly mean seeds / fruit was correlated with pollinator visit rates for the Opuntia populations.

DISCUSSION

Breeding Systems

Island plant populations can be examined in the larger context of plant species expanding into new areas (Rick 1966). Island plant populations should, therefore, share characteristics with other plant populations at the limit of the species' range, or populations introduced into foreign soil. The breeding biologies of many such plant populations have been examined previously.

Baker (1955) noted that both animal and plant species capable of long-distance dispersal tend to be self-compatible or hermaphroditic. This restricts recombination in colonizing organisms, but new gene combinations will not be as important to individual fitness in new, unoccupied territory as they will in stable, established populations (Grant 1975). In a study of the breeding biology of exotic weeds in Canada, Mulligan (1972) found that most weed species were self-pollinating; the few species requiring cross-pollination were long-lived perennials. Rick (1966) examined the reproductive biology of 16 species of angiosperms on the Galapagos Islands and found that 13 of these species were automatically self-pollinating, requiring no external agent. Rick also noted that many plant families that were obligate outcrossers on the nearest mainland were missing from the island flora. Along a California transect, Moldenke (1975) found a decrease in the proportion of plants requiring insect visits as environmental severity increased. At the climatically least

predictable site, a coastal island, 70% of the flora habitually selfed. In a more detailed examination of the breeding biology of a single species (Gilia achilleifolia), Schoen (1982) found increased autogamy in the northernmost populations in this species' range where pollinators were rarer. Colonizing populations are, then, more likely to be autogamous than are established populations, or populations in equable habitats.

An obligately outcrossing angiosperm faces two obstacles as a potential colonist; 1) conspecifics must simultaneously be present and 2) some vector must be available for pollen transport. The autogamous colonist faces neither of these barriers. The most obvious advantage that autogamous plants have over obligate outbreeders is the ability to establish a new population without the presence of a conspecific (Baker 1955). An additional advantage exists: an individual can set seeds in the absence of specialized pollinating agents (Baker 1955, Baker and Hurd 1968, Carlquist 1974, Rick 1966, Schoen 1982, Solbrig and Rollins 1977). Those successful colonizing species that do out-cross tend to have open, generalized flowers, which can be visited by a wide variety of pollinators (Carlquist 1966, 1974, Mulligan 1972).

According to the above argument neither Opuntia stricta nor Centrosema virginianum is an ideal colonist. Both species have greatly reduced reproductive success when their flowers are not visited by pollinators. Unvisited Opuntia flowers produce some seeds and fruits, although the frequency of both is low relative to animal-visited flowers. This species appears to be largely self-compatible. Unvisited Centrosema flowers were never observed to set fruit. This species appears to be partially self-compatible; the

seeds / fruit from selfed flowers were lower than the number found in crossed flowers. The highly specialized flower of Centrosema is probably another handicap to colonization. Without a large hymenopteran species present, sexual reproduction in Centrosema should be severely limited. The persistence of these species on Seahorse Key is not surprising, however, considering the island's proximity to the mainland. Immigration rates of the plants and potential insect pollinators from the mainland are presumably high (MacArthur and Wilson 1967). Furthermore, once established, individuals of these perennial species are likely to persist and spread through vegetative propagation alone. In plant species that have the option of vegetative propagation, this type of asexual reproduction is often favored when the population density is low, as during early colonization of a newly invaded site (Abramson 1975). The success of these two species as colonists is probably due to this propagation. The Seahorse Key populations of both species achieve relatively high levels of sexual reproduction and, presumably, outcrossing, so effective pollination takes place even on the far island site.

Perhaps due to frequent gene flow from the nearby mainland, neither Seahorse Key population has differentiated in floral biology from Cedar Key or mainland populations. There has been no increase in the potential for autogamy of the island populations. Had evolved differences existed at the population level, objective comparisons of natural female reproductive success would have been difficult. As it is, however, any reproductive differences found among these populations can be attributed to ecological effects that vary among the populations, and not to evolved differences.

Phenologies

The flowering seasons of plants on oceanic islands are often longer than their mainland counterparts (Carlquist 1966, 1974). The explanation usually offered for this extended reproductive period is the milder maritime climate found on islands. Alternative explanations exist, however. The flowering phenologies of many mainland plant communities are thought to be highly structured by interspecific competition among plants for pollination (Heinrich 1975a, 1975b, 1976, Reader 1975, Thomson 1980). The more diverse a plant community is, the greater the probability of competition for pollination among the flowering plant species. Plants flowering before and after a particular species are competing with that species for pollination. Individuals that flower out of synchrony with the majority of conspecifics will be surrounded by flowers of other species and will receive few visits, or will be unlikely to receive conspecific pollen from and transmit pollen to a conspecific. This risk becomes greater as the number of species competing for pollination increases. Thus, a strong stabilizing selection on flowering time is expected in diverse plant communities (Thomson 1980). Phenological studies of alpine (Mosquin 1976, Pleasants 1980, Thomson 1980), northern temperate (Heinrich 1975b), and bog (Heinrich 1976, Reader 1975) plant communities have attributed the apparently non-random flowering patterns to displacement of flowering times through competition for pollination.

MacArthur and Wilson (1967) predicted and empirical studies have demonstrated (see Carlquist 1974 for references) reduced plant diversity on islands. Such a reduction in potential competitors should reduce the selective pressure on individuals for synchronous

flowering, which might lead to "ecological release" of flowering season length. In this study, I did not determine overall plant species richness for the study sites. I noted, however, that Centrosema and Opuntia appeared to be the most abundant insect-pollinated flowers at the far island site, Seahorse Key. The study species were members of a more diverse assemblage of flowering plants at the Cedar Key site, and the mainland site had many conspicuous, animal-pollinated species in flower in addition to Centrosema. Opuntia flowered longer on Seahorse Key than on Cedar Key. Individual plants from both sites had flowering times of the same duration, so the differences in phenological patterns that I observed were probably due to more among-plant variation at Seahorse Key. I doubt, however, that this difference can be ascribed to a reduced competitive pressure on Seahorse Key. Jackson (1966) has shown that small microclimatic changes can significantly affect flowering phenology. My study transect on Seahorse Key cut across a greater variety of microhabitats than did the Cedar Key transect. For example, some of the Seahorse Key Opuntia plants that I censused were exposed to full sunlight; others were almost completely shaded. The Cedar Key Opuntia were all at least partially shaded. The pattern for Centrosema suggests a similar length of breeding season for the three study populations, but the peak of flowering is slightly later on the two island sites. Without clearer evidence, including greenhouse experiments (Lack 1982), the phenological differences among the sites must be considered a reflection of differences in the habitats, and not a response to reduced pollinator competition on the island. Again, frequent gene flow from the nearby mainland may be responsible for the absence of conspicuous divergence.

Pollinator Communities

Plants colonizing a new habitat risk leaving their usual pollinators behind (Baker and Hurd 1968, Carlquist 1974). Often, the usual pollinators are replaced by new species of visitors. Exotic weeds that have invaded Canada did not bring their usual pollinators with them, rather, those that require animal visitors are pollinated by native, Canadian insects (Mulligan 1972). The introduced tomato has left its pollinators in the Andes, despite this species' extensive range in North America (Rick 1950). Self-sterile tomatoes planted in California had 1-2% fruitset, while a similar density of plants growing in Peru had 41-43% fruitset, a difference that Rick (1950) attributed to lowered pollinator efficiency. Tomatoes are "buzz" pollinated, which requires specialized behavior of visitors (Buchmann 1974, 1983, Thorpe and Estes 1975). Visitors unable to manipulate such flowers correctly are ineffective at pollen transfer.

Even colonization over short distances can result in a shift in pollinating species, as when a species colonizes a recently disturbed site. Beattie (1969) found an increased number of visitors to Viola at disturbed sites, but most were generalized foragers that deposited a great deal of foreign pollen on Viola stigmas. Even though the usual pollinators of a plant are often replaced by new species in a newly-invaded habitat, the colonizing plant may suffer from a reduction in pollination efficiency.

A plant colonizing a new habitat on the mainland may face a new, less well-adapted array of visiting species, but colonization of an island entails the additional problem of a depauperate fauna from which to recruit new pollinators. On the Galapagos Islands, the assemblage of pollinators includes only one bee species, seven

butterflies, twelve hawkmoths, and a few species of flies and beetles. In contrast, these taxa and other pollinator taxa are very diverse on nearby mainland areas of similar climate (Linsley 1966). Hummingbirds were an important component of the pollinating community on the large island, Trinidad, but diversity was much reduced on Tobago (Feinsinger et al. 1982). Tobago populations of Erythrina pallida, a plant species highly adapted to hummingbird visitation, had fewer species of visitors and a lower visit frequency than did Trinidad populations (Feinsinger et al. 1979).

Data presented here demonstrate both of the phenomena mentioned above: a shift in pollinating species, and a reduction in pollinator diversity and frequency on the distant island. Centrosema virginianum growing on the mainland was visited almost exclusively by Bombus pennsylvanicus, a pollinator to which the flower is well adapted. Every Bombus visit operates the floral mechanism, such that reproductive structures consistently contact the insect's back (for details of this type of pollination, see Macior 1967). On Cedar Key, Centrosema loses its Bombus pollinators and acquires a more diverse assemblage of visitors. Of the several visitor species, only one, the scoliid wasp Campsomeris quadrimaculatus, operates the floral mechanism. This species does not appear to be a reliable visitor to Centrosema; Campsomeris was observed visiting the Cedar Key population during only one of the three breeding seasons for which I made observations. During the 1980 and 1981 seasons, the only visits on Cedar Key came from two genera of solitary bees that rarely operated the flowers properly, although they did remove, and possibly did transfer pollen, which these genera are known to utilize as a larval food source (Linsley 1978, Mitchell 1962). Only one solitary

species, Megachile brevis, was observed to visit Centrosema on the far island, Seahorse Key. Opuntia stricta was visited by fewer species on Seahorse Key than on Cedar Key. The Seahorse Key pollinator assemblage was a subset of the Cedar Key pollinator community.

Eusocial species of pollinators were present on both the mainland (Bombus pennsylvanicus) and Cedar Key (Apis mellifera) but are absent on Seahorse Key. On Seahorse Key I saw a single Bombus foraging at Opuntia on one occasion during the 1981 flowering season. Why are colonial species missing from the Seahorse Key pollinator fauna?

I suggest that the energy required for colony maintenance renders island sites unattractive to eusocial apids. Colonial species require a rich and dependable food source. Observations on Agave (Schaffer et al. 1979), Cassia (Johnson and Hubbell 1975), and cultivated blackcurrant, raspberry, and strawberry (Free 1968) all indicate that eusocial species of pollinators concentrate their attention on rich floral resources and often ignore unprofitable, scattered, or unpredictable (Real 1981) resources. The more highly eusocial a species is, the more concentrated the food resources must be to attract foragers (Schaffer et al. 1979). The degree of coloniality exhibited by a species may affect that species' ability to exist in a resource-limited environment. One hypothesis explaining the rapid spread of the Africanized honeybee is the ability of this genotype to exploit a lower level of floral resources than can the European genotype (A.B. Bolten, personal communication). In European colonies, many Apis mellifera remain at the nest when resources are too low to warrant recruitment, unlike colonies of Africanized bees, that may switch to foraging individually at times of resource scarcity. Therefore, in marginal habitats with low or unpredictable

resource levels, European honeybees cannot maintain colonies, leaving these habitats open to colonization by the Africanized bees.

My only measure of floral resource availability is a subjective one. As I noted earlier, flower diversity appeared to be much lower on Seahorse Key than at either of the other sites. At many times of the year I noticed no animal-pollinated plants in bloom along my Seahorse Key study transects, unlike the Cedar Key and mainland transects. On Seahorse Key, resource shortages for flower visitors may occur sporadically throughout the year. These shortages would place severe stress on a colony of eusocial insects, which must feed and maintain large numbers of developing young. Highly eusocial species, such as Apis mellifera, are able to store resources to provision against periods of resource scarcity, but if these periods occur frequently such stored reserves may not be sufficient. A queen of a colonial species reaching a marginal site such as Seahorse Key would probably be unable to establish a successful colony.

The depauperate plant community on an island can affect the pollinator community of the island by filtering out those pollinators, such as most eusocial bees, that require a rich and consistent resource base. Solitary flower-visitors apparently can exist on Seahorse Key. Solitary bees can forage profitably at lower floral densities than can colonial species (Johnson and Hubbell 1975, Schaffer, et al. 1979). Males and females use flowers as nectar sources, flower species that may be different from their pollen sources (Linsley 1978). Females gather pollen to provision a larval cell and make as many cells as pollen and nest-site availability allow (Linsley 1978). Despite the abilities of some species to utilize a wide array of food sources, the life cycles, and especially emergence

times of solitary bees are often closely tied to their floral resources (Linsley 1978, Linsley and MacSwain 1958, Hurd et. al. 1971). A severe flower shortage may limit population sizes and adult life-spans of the solitary species but should not completely exclude these species from a resource-poor habitat, such as Seahorse Key.

These data suggest that population densities of solitary pollinators may be more limited at Seahorse Key than at the other sites. Visit frequency to flowers is greatest at the beginning and end of the flowering curves (Figures 4 and 5), and lowest when flowers are most abundant. This drop in visit frequency with increasing abundance is less pronounced or absent on Cedar Key and the mainland. The increased variation in visit frequency on Seahorse Key may be another indirect effect of the reduced plant diversity presumed to occur there. If pollinators can utilize several plants as floral resources, then the pollinator populations may be "buffered" from extreme fluctuations in size between seasons. If, however, only a few flowering species are available to a forager, then any changes in one species' abundance or time of flowering may seriously affect the population size of the pollinator for some time. A reduced pollinator population can, consequently, cause much between and within season variation in visit frequency to the plant, which may result in reduced pollinator service and lower reproductive success for plant species found on islands. In effect, a negative feedback cycle is generated; a depauperate plant community reduces pollinator diversity and numbers by excluding social species and limiting the population sizes of solitary species. This may, in turn, inhibit establishment of new plant species on an island since the appropriate visitors are less likely to be available to pollinate the plant.

Reproductive Success and Pollinator Limitation

The perfect plant colonist would be completely autogamous; reproductive success for an individual growing on an island would not differ from that for a mainland conspecific, provided the physical environment was equally suitable. Both species that I studied, however, have low seed and/or fruitset unless they are visited by an appropriate pollinator. Sexual reproduction in these species depends to a large extent on an external agent. Another source of potential variation in the sexual success of the different populations is the habitat. I have already suggested that some environmental differences occur among the sites (see Phenologies section). Are the significant among-site differences in sexual success of these populations due to variation in pollination service or environmental variation?

The flowers of Opuntia and Centrosema are hermaphroditic. Both male and female reproductive success must be considered, as the two functions may not always be correlated (Bertin 1982a, Charnov 1979, Janzen 1977, Lloyd 1979, Willson 1979). My measure of male success was the frequency of flowers receiving dye, and presumably pollen, at various distances from a donor marked flower. Pollen transfer in both species is insect-mediated. The differences in pollen-dispersal patterns for both species must be a direct result of reduced pollinator service to the island populations.

Female reproduction in plants, as in animals, is more energetically expensive than male reproduction (see Charnov 1979, Lloyd 1979, and Willson 1979 for references). It is, therefore, more subject to environmental influences than is male reproduction (Stephenson 1981). Resource availability is known to limit female reproductive success in a number of species (Lee and Bazzaz 1982a,

Sutherland unpublished m.s., Stephenson 1979, 1982, Udovic and Aker 1981, Wyatt 1976). Artificial reduction (Stephenson 1980) or enhancement (Lee and Bazzaz 1982a) of resources available to the maternal parent has been shown to influence fruitset. Other species appear to have abundant resources, though, and the number of fruits / plant appears to be pollinator limited (Bertin 1982a, Bierzychudek 1981, Dafni and Ivri 1979, Willson and Schemske 1980). It is probably incorrect to think of plants as being either pollinator or resource limited; the two factors may both play a role in limiting female reproductive success. Abortion of fruits or seeds is seldom random in plants that appear to be primarily resource-limited (however, see Casper and Wiens 1981), but may be selective (Janzen 1977). The number of fertilized ovules in a fruit (Lee and Bazzaz 1982b) or even the paternity of the developing fruit (Bookman 1983, Bertin 1982b, Wyatt 1976) influences its probability of abortion. Under most circumstances, pollination probably affects female reproductive success of a plant, although numbers of fruits and seeds produced may be too gross a measure to detect this effect.

Even using the unsubtle measures of fruit and seedset, female reproductive success was detectably lower at the far island site than elsewhere for both study species during at least one of the breeding seasons for which I made observations. My data suggest pollinator limitation was the cause of the lowered sexual success. Field hand-crossings resulted in similar fruit and seedset for both study populations of Opuntia stricta and resulted in similar fruitset among the three Centrosema virginianum populations although there was a trend in this latter species that suggested increasing resource limitation along the mainland-far-island gradient. When both species

were given identical pollination treatments (Unvisited, Selfed and Crossed), I found no significant variation among the study sites, yet natural Centrosema fruitset was significantly lower on Seahorse Key during the 1981 study season. Centrosema flowered earlier in 1982 and both pollinator visit rates and fruitset showed a different pattern in that season, with the mainland and far island both showing relatively low reproductive success compared to Cedar Key. Fruits of Opuntia growing on Seahorse Key contained a significantly lower and more variable number of seeds / fruit than did fruits from Cedar Key during the three breeding seasons. The pollinator limitation experiments, where hand-crossing was done with control populations of open flowers, demonstrated pollinator limitation for the Seahorse Key population of Centrosema in 1981 and suggested pollinator limitation for Opuntia growing on that island in 1983. Therefore, I conclude that Seahorse Key plant populations suffer reductions in both male and female reproductive functions, relative to Cedar Key or mainland populations, and that this is due to reduced pollinator service.

A cautionary note must be added to this conclusion. Time constraints and the relative scarcity of mainland populations of these species growing in a comparable habitat limited the number of populations that I was able to examine. The differences that I observed among these populations in visit rates and reproductive success are assumed to be due to an "island effect" and, indeed, the differences are all in the predicted directions. However, I was unable to determine the interpopulation variation among mainland plants of these study species. This weakness is mitigated to some extent by the duration of the study, but, just as temporal variation was often a significant factor, spatial variation within a study site

could affect these results.

Evolutionary Considerations

Seahorse Key populations of Centrosema virginianum and Opuntia stricta have not differentiated from the mainland populations in phenology or in breeding biology. Because these populations are separated by short distances, immigration rates to the island are probably high enough to prevent evolutionary divergence of these island populations. Nonetheless, even across such short distances, there is a difference in reproductive success. My data implicate the reduced abundance and reduced effectiveness of island pollinators as the cause of this difference. If such differences can be detected over distances as short as eight kilometers, the differences in pollinator effectiveness and reproductive success of entomophilous plant species may be much greater on distant, oceanic islands. This study suggests that pollinator limitation can exert a strong selective pressure on island plants, a pressure that eventually, through filtration of inappropriate colonists, or through directional selection operating on island plant populations, shapes the plant communities of islands.

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BIOGRAPHICAL SKETCH

Edwin Eugene Spears, Jr.

Edwin Eugene Spears, Jr. was born September 27, 1953, in Asheville, North Carolina, to Edwin E. and Sue R. Spears. He was followed at regular, non-random intervals by a brother, Jack R., and a sister, Susan A. Spears. He completed his undergraduate degree in biology at the University of North Carolina at Asheville in 1975, his Master of Science degree in zoology at the University of Florida in 1978 and his PhD in zoology at the University of Florida in 1983. His experiences in pollination biology began at an early age when he captured what he thought was a very small hummingbird with a glass jar as it was visiting a cultivated Malvaceae growing in his family's backyard. It was not a hummingbird, but a day-flying sphinx moth, that rapidly sufficated in the small jar because of its high metabolic rate. This early experience left Gene with two impressions that remain with him to this day: 1) the ephemeral, transitory nature of beauty, and 2) the pleasure of sneaking up on bugs and catching them in glass jars.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Peter Feinsinger, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School, and was accepted for partial fulfillment of the requirements of the degree of Doctor of Philosophy

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