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BIRD POLLINATION OF THE ENDEMIC BAHAMA SWAMP-BUSH, *PAVONIA BAHAMENSIS* HITCHC. (*MALVACEAE*): THE RISK OF SPECIALIZATION

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ABSTRACT

Bahama Swamp-bush (*Pavonia bahamensis* Hitchc.: Malvaceae), a shrub endemic to the Bahama Islands, appears to be exclusively pollinated by birds. On San Salvador, Bananaquits and Bahama Woodstars were the only major pollinators. Flowers cannot self-pollinate and plants are typically self-incompatible. Such specialization and dependence was predicted to be a risky strategy for pollination if environments change and affect pollinators. Here I report data that support this hypothesis.

Hurricane Lili, October 1996 appears to have caused nectarivorous bird populations to decline. During the winter flowering period in 1996-7, these birds were rarely seen in the area, whereas in winter 1994-5, both Bananaquits and Bahama Woodstars were frequent visitors to the flowers. In 1994-5, only 2% of the flowers had received no pollen whereas in winter 1996-7, 51% of the flowers received no pollen. Fruit set of Bahama Swamp-bush decreased dramatically from 82% in 1994-5 to 11% in 1996-7, and fruit set became strongly pollination-limited with the loss of bird visitation as predicted.

Declines in nectarivorous bird populations after hurricanes have been documented for a number of areas and have been attributed to the lack of flower resources. These results on Bahama Swamp-bush indicate that the decline in bird populations can subsequently cause pollination-limitation and lower fruit set in bird-pollinated plants. Any environmental change that affects the populations or behaviors of these birds could similarly cause pollination limitation of fruit set and possibly endanger the regeneration and long-term persistence of this endemic plant species.

INTRODUCTION

Specialization of a plant species for an effective pollinator type is usually assumed to be advantangeous for pollination (Stebbins 1970). However, specialization for one or a few pollinator species can also entail a risk of pollination limitation of fruit set if the essential pollinators visit flowers less often because of behaviorial changes or because their populations decline. For example, pollinator reduction due to habitat fragmentation causes pollination limitation of fruit set more frequently in pollinator-specialized plant species than in pollinator-generalized plant species (Rathcke and Jules 1993). Such pollination-limitation of fruit set could reduce subsequent recruitment of new plants and endanger the long-term persistence of populations.

The pollination biology of Bahama Swamp-bush (*Pavonia bahamensis* Hitchc.: Malvaceae), a shrub endemic to the Bahamas, has only recently been described in Rathcke et al. 1996 (Fryxell in press). Based on observations made in December-January 1994-5 on San Salvador, Bahama Swamp-bush appeared to be to be exclusively pollinated by two bird species, Bananaquits (*Coereba flaveola*: Coerebidae) and Bahama Woodstars (*Calliphlox evelynae*: Trochilidae) (Rathcke et al. 1996). Based on these initial observations, we predicted that this specialization for pollination could make the pollination of Bahama Swamp-bush especially vulnerable to any environmental changes that reduced the visitation of these essential bird pollinators (Rathcke et al. 1996).

Here I further document the specialization and dependence of Bahama Swamp-bush on bird pollination. I also present data that support our earlier prediction that pollinator specialization can increase the risk of pollination limitation of fruit set (Rathcke et al. 1996).

MATERIALS AND METHODS

Bahama Swamp-bush is a shrub (or small tree) that grows in rocky coastal thickets (Correll and Correll 1982; Smith 1993). On San Salvador, it also grows along the edges of inland saline ponds just inland and adjacent to mangroves and, therefore, grows in fairly restricted and limited areas. I studied shrubs growing near the trail along the southern edge of Reckley Hill Pond (Godfrey et al. 1994). Most shrubs grew along the path for about 300 m. Most of the individual shrubs are permanently tagged and followed. Flowering is seasonal and the major

flowering period occurs during winter (November-January) on San Salvador. A brief description of the floral biology was reported in Rathcke et al. (1996) and further details will be presented elsewhere (Rathcke mss. in prep.).

I studied the pollination biology of Bahama Swamp-bush for three winter flowering seasons during the following dates: December 23, 1994 to January 2, 1995, December 17, 1995 to January 4, 1996, and December 17, 1996 to January 5, 1997. I typically spent 2-6 hours a day during most days throughout these research periods in the Reckley Hill Pond site doing pollination measurements and noting visitors to flowers. I recorded all species visiting flowers throughout each research period. Other observations on fruit set were made in June 1995 and 1997 and by Dr. Lee Kass in mid-April 1996.

To determine the breeding system, large flower buds on 5-6 shrubs were tagged and were either bagged with no further pollination treatment, bagged with self-pollen added, or left exposed for natural pollination.

Pollen grains are large and can be counted on stigmas in the field with a hand lens. I counted pollen on tagged flowers every day. Here I present data on the percent of flowers that had received no pollen grains by the third day of floral life when the stigma was withering and was no longer receptive (Rathcke et al. 1996).

Fruits have five carpels, each with one seed (Correll and Correll 1982). Most fruit had five seeds with a few having four seeds. Therefore, most of the variation in seed production is in fruit set (fruit/flowers x 100), not seed number per fruit. Fruit set values were based on ovary development after 7-10 days because my previous studies indicated that this was highly indicative of whether a fruit would be matured or not. If a fruit is not going to develop, the ovary usually turns pale green and falls within 7 days (pers. obs.).

Daily nectar production by flowers was measured by bagging large flower buds with bridal veil netting and collecting nectar each day from marked flowers in the morning (usually c. 10:00 AM) from December 28, 1994 through January 1, 1995. These five days included the entire lifespan of the sampled flowers. Nectar was collected with either 2 or 5 microliter microcapillary tubes and volume was measured. In 1996-7, sugar concentrations (sucrose-equivalents) were measured in the field using a Bellingham refractometer and calculated according to Bolten et al. (1979).

RESULTS

Over the three winter research-periods from 1994-1997, birds were the only visitors observed at the flowers of Bahama Swamp-bush. The single exception was one wasp seen feeding on nectar between the petals so that it did not effect pollination. The major bird visitors were Bananaquits (*Coereba flaveola*: Coerebidae) with occasional visits by Bahama Woodstars (*Calliphlox evelynae*: Trochilidae). The only other bird species observed visiting flowers was a single Bahama Mockingbird (*Mimus gundlachii*: Mimidae). This individual visited two shrubs and four flowers during one foraging bout in January 1997. At this time, flowers were overflowing with nectar because other birds rarely visited (see below). These three bird species are common residents (White 1991, Sordahl 1996).

Bananaquits decreased significantly in the study site between winters 1994-5 and 1996-7. In winter 1994-5, they were the most common visitors to Bahama Swamp-bush. They were in small flocks of 5-7 birds and appeared to remain in the local area, visiting flowers continuously throughout the day. I observed birds visiting flowers every day during 10 research days in 1994-5. In 1996-97, I never saw or heard a Bananaquit in the research site during 13 research days.

Bahama Woodstars also declined in the research site between winter 1994-5 and 1996-7. In winter 1994-5, individuals (mostly males) were seen several times a day visiting 1-10 flowers before leaving the local site. However, in winter 1996-7, they were virtually absent from the site. I saw or heard individual Woodstars only three times during 13 research days and observed no visits to Bahama Swamp-bush flowers.

Plants depend upon visitors for fruit set. Bagged flowers, where pollinators were excluded, produced no fruit (Table 1). Plants are mostly self-incompatible; flowers that were augmented with self-pollen produced no fruit in 1994-5 (Table 1). However, in 1996-7, two flowers on one shrub with added self-pollen produced fruit. This could reflect pollen contamination, but it is possible that this plant was weakly self-incompatible. Flowers with natural pollination had high fruit set in 1994-5 (Table 1).

The percent of flowers that had received no pollen grains on their stigmas by the end of stigma receptivity (the end of the third day of floral life) increased greatly from 2% in 1994-5 to 51% in 1996-7 (Table 2). Flowers with no pollen deposition do not develop fruit.

Fruit set of naturally-pollinated flowers declined greatly from 82% in 1994 to 11% in 1997 (Table 2). This was related to both lower pollen deposition on stigmas and to the decline in flower

Table 1. Pollination and breeding system of Bahama Swamp-bush (*Pavonia bahamensis*) on San Salvador, Bahamas. Average percent fruit set is shown for bagged flowers with no hand-pollination, bagged flowers augmented with self-pollen, and open flowers that were naturally-pollinated. Data from 1994-5. Fruit set equals 100 (fruits/flowers). Means and standard deviations are shown.

TREATMENT	NUMBER OF PLANTS (FLOWERS)	% FRUIT SET x ± S.D.
Bagged, no hand-pollination	5 (7)	0
Bagged, self-pollen	5 (11)	0
Natural pollination	6 (22)	82±30.9

Table 2. Percent of flowers with no pollen deposition on stigmas by end of floral life, percent fruit set of naturally-pollinated flowers, and bird visitation to flowers of Bahama Swamp-bush (*Pavonia bahamensis*) over two winter periods (December-January) on San Salvador, Bahamas.

	1994-5	1996-7
% Flowers with no pollen deposition	2 %	51 %
Number of plants (flowers)	6 (110)	8 (41)
Fruit set	82 %	11 %
Number of plants (flowers)	6 (22)	8 (65)
Flower visitation	frequent	rare

Table 3. Nectar production of bagged flowers of Bahama Swamp-bush (*Pavonia bahamensis*) in relation to flower age in days during December 1994 on San Salvador, Bahamas. Microliters of nectar shown as means and standard deviations (N=number of flowers). Flower age is highly significant; Kruskal-Wallis statistic=13.5, df=3, P=0.004.

FLOWER AGE IN DAYS	NECTAR MICROLITERS
1 day	59 ± 42.5 (7)
2 day	140 ± 91.1 (5)
3 day	26 ± 46.2 (7)
4 day	0.2 ± 0.28 (4)

visitation by both Bananaquits and Bahama Woodstars (Table 2).

Daily nectar production of bagged flowers varied with flower age and was highest for two-day old flowers (140 microliters) (Table 3). Average percent sugar (sucrose equivalents) was 20% ± 4.8 (N = 7 plants, 42 flowers).

DISCUSSION

The flowers of Bahama Swamp-bush appear to be pollinated exclusively by two bird species, Bananaquits and Bahama Woodstars, as previously reported (Rathcke et al. 1996). Flowers cannot self-pollinate and typically require cross-pollination for fruit set. In winter 1994-5, when both species were frequent visitors to flowers, pollination was very successful (98% of the stigmas had received pollen) and fruit set was high (82%) and was not pollination-limited. The importance of these birds as pollinators was clearly demonstrated when both species became rare in winter 1996-7, and fruit set became strongly pollination-limited. At this time, pollination of flowers was very low (51% of the stigmas received no pollen), and fruit set was dramatically reduced to 11%. Such reduced fruit set could endanger the long-term persistence of such specialized plant species (Rathcke and Jules 1993; Smith et al. 1995; Buchmann and Nabhan 1996).

The conclusion that Bahama Swamp-bush is highly specialized for bird pollination is further supported by nectar characteristics. The high daily nectar production per flower (>100 microliters/day) and relatively dilute sugar concentration (20 % sucrose concentration) are fairly typical of bird-pollinated species (Bolten and Feinsinger 1978; Opler 1983).

Because Bahama Swamp-bush is so specialized for pollination by these two bird species, the flowers received no compensatory pollination by other flower visitors as is often seen for more generalized plant species (Rathcke 1988; Wolf and Stiles 1989). The only other possible bird pollinator seen visiting flowers was a single Bahama Mockingbird feeding on nectar that was overflowing from the floral tubes in January 1997 when Bananaquits and Woodstars were rare. The bird had pollen on its head and breast. However, even if Bahama Mockingbirds can act as pollinators, pollen deposition was low and fruit set was pollen limited. No other animals, such as insects, were ever seen pollinating the flowers. Ants were never seen on the flowers although they quickly collected nectar when flowers were placed on the ground.

The risk of specializing on a few pollinators is clearly shown by the dramatic reduction in fruit set that occurred when the two bird species became rare. In this case, the decline in Bananaquits appears to have been caused by Hurricane Lili that went directly over San Salvador on October 21, 1996 and stripped the leaves off plants (Murphy et al. 1998). Flower visitation by Bahama Woodstars also decreased from 1994-5 to 1996-7, but mist-net captures were too few to make any strong conclusions about population declines in the research site (Murphy et al. 1998).

Similar major declines in populations of nectarivorous bird species after hurricanes have been documented in several recent studies, and these declines have been attributed to a lack of floral food resources (Askins and Ewert 1991; Wunderle 1995; Murphy et al. 1998). The results from this study provide the first evidence that the population crash in nectarivorous birds after hurricanes can subsequently reduce pollination success and fruit set of bird-pollinated plants. Hurricanes can also cause resource-limitation of fruit set due to the destruction of plant tissue and other stresses, such as increased salinity (Rathcke unpub. data). However, the lack of pollen deposition on flowers demonstrates that pollination can be reduced enough to limit fruit set.

Other environmental changes may cause more severe, long-term effects on plant pollination and reproduction than hurricanes (Rathcke and Jules 1993; Smith et al. 1995; Buchmann and Nabhan 1996). Hurricanes occur frequently in the Bahamas and severe hurricanes, like Lili, occur on average about once every 10-15 years (from Shaklee 1996). Because severe hurricane effects are sporadic, populations have a chance to recover; bird populations can rebuild, plant reproduction can increase. Other environmental changes, such as habitat destruction and introduced species, may not allow this recovery. Islands, such as San Salvador, are experiencing many such environmental changes making conservation increasingly imperative (Eshbaugh and Wilson 1996).

These results indicate that conservation of the endemic Bahama Swamp-bush will depend not only upon the preservation of its limited habitat, rocky coastal thickets, but also upon the preservation of its essential bird pollinators and their pollination services. For any plant species that is highly specialized for a few pollinating species, pollination specialization can be a risky strategy that needs to be considered in conservation planning.

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