

BIRDS, POLLINATION RELIABILITY, AND GREEN
FLOWERS IN AN ENDEMIC ISLAND SHRUB,
PAVONIA BAHAMENSIS (MALVACEAE)

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ABSTRACT. *Pavonia bahamensis* (Malvaceae) is a shrub that is endemic to the southeastern Bahama Islands. Here I present the first detailed description of its pollination biology. On San Salvador Island, *P. bahamensis* appears to be pollinated exclusively by two bird species, Bananaquits and Bahama Woodstars. This pollination dependence was dramatically demonstrated in one season when hurricanes decimated these bird populations, and pollen deposition and fruit set of *P. bahamensis* was significantly reduced. However, the lack of pollination limitation of fruit set during two other flowering seasons and the relatively low pollen/ovule ratio (607) suggests that pollination of *P. bahamensis* by these birds is generally reliable. Flowers show traits typical for a bird pollination syndrome, except that the corolla is green. Flowers are held horizontally on the shrub, rather than vertically, suggesting that passerine birds (Bananaquits) rather than hummingbirds have been the most effective pollinator and major selective agent for the floral traits in this species. Individual Bahama Woodstars are ineffective pollinators, depositing few or no pollen grains on stigmas per visit; however, they maintained pollination in one season when visits by Bananaquits were infrequent, and they contributed to the reliability of pollination for this endemic species.

Key Words: bird pollination, breeding system, endemic plant pollination, flowering phenology, fruit set, green flowers, hummingbird pollination, island pollination, nectar production, passerine pollination, pollen/ovule ratio, pollen deposition, pollination limitation, pollination syndrome

Islands typically have fewer pollinator species than mainlands (Barrett 1996; Carlquist 1974; Elmqvist et al. 1992; Feinsinger et al. 1982; Inoue 1993; Spears 1987; Woodell 1979). As a consequence, many island plant species are generalized for pollination and have inconspicuous flowers (Carlquist 1974). Plants that are specialized for a pollinator type, such as hummingbirds, can be especially vulnerable to pollination limitation if only one or a few pollinating species are present (Rathcke 1988a, 1988b, 1998; Rathcke and Jules 1993; Wolf and Stiles 1989), unless those pollinators are abundant and predictable. Visitation to flowers has

been demonstrated to be lower on islands for some species (Feinsinger et al. 1982; Spears 1987), but pollination limitation has not been measured. Many island plant species reduce or avoid pollination limitation by auto-pollination and selfing (Baker 1955; Barrett 1996; Carlquist 1974).

If plants have only a few, similar pollinating species, they could experience stronger, directional selection for a specific pollination syndrome (i.e., a suite of predictable floral traits adapted to the most effective pollinator type, such as butterflies or birds; Faegri and van der Pijl 1979; Stebbins 1970). For example, hummingbird-pollinated flowers in western North America are typically red and tubular with large amounts of nectar and no fragrance (Brown and Kodric-Brown 1979; Grant and Grant 1976). Recently, the concept of the pollination syndrome has been criticized for being limited and misleading because flowering species often have many different pollinators that vary over space and time (Herrera 1996; Ollerton 1996; Waser et al. 1996). Studies show that flowers categorized in one pollination syndrome may be pollinated effectively by other types of pollinators (Baker et al. 1971; Feinsinger 1987; Schemske 1983; Schemske and Horvitz 1984; Waser 1983). As a consequence, selection on floral traits may be weak or inconsistent (Ollerton 1996; Waser et al. 1996). In contrast, an island plant with few pollinator species may be more likely to exhibit a floral syndrome that accurately predicts its pollinator type. Species on islands have been found to evolve different pollination syndromes from their mainland ancestors (Carlquist 1974; Inoue 1993), but the reliability of pollination and pollination limitation has seldom been quantified for island species.

In this study I present the first detailed description of the pollination and reproductive biology of an endemic island shrub, *Pavonia bahamensis* Hitchc. (Malvaceae; Bahama swamp-bush), growing on San Salvador Island, Bahamas. The pollination of *P. bahamensis* has only recently been described in brief reports, and it appears to be pollinated exclusively by birds on San Salvador (Rathcke 1998, 2000; Rathcke et al. 1996). I describe the breeding system and the floral traits of *P. bahamensis*. I compare the pollen/ovule ratio of *P. bahamensis* to the ratios categorized by Cruden (1977) for plants with different breeding systems and different probabilities of pollination. I compare the floral traits with those predicted for a classic bird pollination syndrome, and I dis-

cuss the traits associated with passerine versus hummingbird pollination.

Reliability of pollination may be especially crucial for this endemic island species. *Pavonia bahamensis* grows only on the southeastern islands of the Bahamas in limited habitats near mangroves (Correll and Correll 1982). Populations tend to be relatively small and isolated, which may make this species especially sensitive to changes in pollinator species or behavior (Rathcke 1998, 2000; Rathcke and Jules 1993). In general, species on islands may be vulnerable to environmental changes such as global warming, habitat destruction, or introduced species (Loope and Mueller-Dombois 1989; but see Simberloff 1995). Species on small islands such as San Salvador, which is only 150 km², may be especially vulnerable to environmental changes (Eshbaugh and Wilson 1996). Therefore, documentation of the pollination biology and the reliability of pollination may be valuable in providing baseline data for future comparisons, as was found in Hawaii for lobeliad plant species after the extinction of the Hawaiian Honeycreeper (Smith et al. 1995).

STUDY SPECIES

Pavonia is in the family Malvaceae (the mallow family), which has about 1800 species throughout the world (Fryxell 1999). *Pavonia* is the largest genus in the tribe Malvaceae and has an estimated 100 to over 200 species that are mostly subtropical and tropical (Fryxell 1999). The species are most diverse in South America, but species are also found in Africa and other parts of the Old World and in the West Indies, Central America, and Mexico, reaching the southern United States (Fryxell 1999; Howard 1989).

Pavonia bahamensis is endemic to the Bahamas and is found only on the southeastern islands (i.e., San Salvador, Long Cay, Crooked Island, Acklins Islands, and the Turks and Caicos; Correll and Correll 1982). The northernmost limit is San Salvador Island. *Pavonia bahamensis* was first described by Hitchcock in 1893 from a specimen collected in 1890 on Fortune Island (now called Long Cay) in the Bahamas (Hitchcock 1893). It is a shrub or small tree that grows in rocky coastal thickets (Correll and Correll 1982) and inland adjacent to mangroves (Rathcke et al. 1996; Smith 1993). Its pollination and reproductive biology have

been only recently briefly described (Rathcke 1998; Rathcke et al. 1996). Little is known about the pollination biology of any *Pavonia* species (Fryxell 1999).

SAN SALVADOR ISLAND

San Salvador is one of the easternmost islands in the Bahama Archipelago (24°05'N, 74°30'W; Shaklee 1996), and it lies about 600 km east southeast of Miami, Florida and 340 km north of Cuba (Smith 1993). San Salvador is a low, carbonate island, about 19 km long and 10 km wide (Smith 1993). Although many of the Bahama islands have been isolated and reconnected with the fall and rise of the ocean during the glacials and interglacials of the Pleistocene (Sealey 1994), San Salvador has remained separated by a deep ocean trench (Carew and Mylroie 1997).

Total annual mean rainfall on San Salvador is 1007 mm (Shaklee 1996), with a rainy season from August to November (the hurricane season) and a lesser rainy season in May and June (Smith 1993). Annual temperature variation is 6°C (Shaklee 1996) with the coolest months averaging 22°C (January–February) and the warmest months averaging 28°C (July–August; Shaklee 1996). The major vegetation of San Salvador is a scrubland or coppice (Smith 1993). *Pavonia bahamensis* grows in a zone between the scrubland and the mangroves that line the inland hypersaline lakes and the tidal basin of Pigeon Creek (Smith 1993). San Salvador has about 440 species of vascular plants that are native or naturalized, and 6–8% of these species are endemic to the Bahamas (Smith 1993).

MATERIALS AND METHODS

I studied *Pavonia bahamensis* near the Bahamian Field Station at the northeastern end of San Salvador Island. Most data were collected on shrubs growing adjacent to mangroves on the southern edge of Reckley Hill Pond about 500 m southeast of the field station. Most of the flowering shrubs along the path are permanently tagged and studied. These shrubs included most of the local population in this area. Studies were done during three winter flowering seasons (December–January) 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.

This period encompasses the major flowering period on San Salvador.

All animals observed visiting flowers of *Pavonia bahamensis* were recorded throughout each study period over three winter flowering seasons. I typically spent 2–6 hours a day in the local site during most days for the entire research visit. Flower dimensions, such as corolla length and stigma–anther distances, were measured in the field using a metric ruler. Stigma–anther distances were measured from the bottom edge of the lowest lobe of a stigma to the upper surface of the nearest anther. The age or developmental stage of each flower was recorded to determine if measurements changed over time. Individual flower phenology was documented by marking and following flowers daily over their life span, and their developmental stages were categorized. Both unbagged, naturally-pollinated flowers and bagged, unpollinated flowers were observed to determine if pollination-induced floral senescence occurred.

The flowering phenology of shrubs was quantified by counting the numbers of open flowers per day per shrub. Total fruit set per shrub was censused in June 1995 by counting fruit or enlarged, dried peduncles remaining on each shrub. Seeds (mericarps) were counted in fruits that had not dehisced. Ovaries that were developing one week after pollination typically matured fruit. Therefore, fruit set data are based on ovary development after a minimum of one week. Ambiguous cases have been excluded, so estimates of fruit set are conservative. A flower can produce a maximum of five seeds, and most fruits sampled had five seeds ($\bar{x} = 4.6$, $SD = 0.62$, $n = 25$ fruits; 4 plants). Therefore, most of the variation in seed production was due to fruit set, and those values are reported here.

Nectar production reported here is based on the amount of nectar in open flowers (standing crop) in 1996/97, because pollinator visitation was so rare that nectar was seldom removed. These nectar volume values are similar or even higher than those recorded previously for bagged flowers (Rathcke 1998; Rathcke et al. 1996). Measurements were not included if nectar had overflowed the corolla. Nectar removals did not appear to stimulate nectar production. To determine if nectar could be resorbed, nectar was also measured in bagged flowers, which never had nectar removed until the end of their floral life (day 3 or 4). Sugar concentrations of nectar were measured using a Bellingham re-

fractometer. Sugar concentrations are estimated as sucrose equivalents and calculated from Brix values according to Bolten et al. (1979).

To determine the breeding system, large flower buds were tagged and given one of the following four pollination treatments: 1) bagged with no subsequent hand-pollination, 2) bagged with self-pollen added, 3) open and augmented with cross-pollen from at least two other individual shrubs, and 4) open and exposed for natural pollination. The pollen-ovule ratio was calculated based on the average number of anthers and the average number of pollen grains per anther. Pollen numbers in upper and lower anthers were measured but were not significantly different.

Pollination limitation of fruit set was tested by augmenting flowers with cross-pollen from at least two other shrubs and by comparing this subsequent fruit set with the fruit set of naturally pollinated flowers. Results of the pollination treatments are reported in detail in Rathcke (2000). Pollination limitation (PL) was estimated using a relative index based on fruit sets (FS—fruit per flower) of pollen-augmented flowers (P+) and naturally pollinated flowers (NP) using the following equation:

$$\%PL = 100 \frac{(\%FS \text{ of } P+) - (\%FS \text{ of } NP)}{(\%FS \text{ of } P+)}$$

If the percentages of fruit set of naturally pollinated flowers and augmented flowers were equal, then $PL = 0\%$. If fruit set was zero for naturally-pollinated flowers and 100% for pollen-augmented flowers, then % PL would equal 100% (Rathcke 2000).

The number of pollen grains necessary for maximum fruit set was determined by comparing fruit set in bagged flowers that had a known number of pollen grains deposited by hand on the stigmas. Cross-pollen from at least two other plants was used for each flower. Pollen grains deposited by pollinators on exposed stigmas by the end of floral life were counted in the field using a 10× hand lens.

The effectiveness per flower visit of Bahama Woodstars was measured by counting the number of pollen grains deposited per individual visit to virgin flowers in 1995. Because overall pollinator effectiveness is determined by the frequency of visits as well as by the amount of pollen transferred by a single visit, overall effectiveness of the two bird pollinators was also based

on average pollen loads on stigmas and pollination limitation of fruit set over the three years.

Statistical analyses were done using SYSTAT ver. 5.01. Non-parametric tests (Mann-Whitney U or Kruskal-Wallis tests) were used due to small sample sizes and because the data were non-normally distributed. These tests are conservative. Sample sizes were based on the averages per plant unless otherwise noted, but the total number of flowers is also shown for each sample. Most flowers in the population were tagged and studied, so the data nearly comprise the entire available flower population.

RESULTS

Pollinators. During three winter flowering periods, two bird species were the only major pollinators seen visiting *Pavonia bahamensis* flowers: Bananaquits (*Coereba flaveola*; Emberizidae, Coerebinae), also called the Bahama Honeycreeper, and Bahama Woodstars (*Calliphlox evelynae*; Trochilidae; Rathcke 1998). Bananaquits are resident birds and are common flower visitors to many plants (White 1991). The Bahama Woodstar is the only hummingbird on San Salvador, and it is also a resident (White 1991). I observed a single foraging bout by a Bahama Mockingbird (*Mimus gundlachii*; Mimidae) in January 1997. I saw a single visit by a wasp in 1996, but it visited between the petals to collect nectar and did not effect pollination.

Flower visitation. Flower visitation by bird pollinators decreased greatly between 1994/95 and 1996/97. In 1994/95, Bananaquits were the most common visitors to *Pavonia bahamensis* flowers. They were in small flocks of 5–7 birds and appeared to remain in the local area, visiting flowers continuously throughout every day during 10 research days in 1994/95. Bahama Woodstars were seen visiting flowers several times each day. In 1995/96, Bananaquits were infrequently seen or heard in the site, but Bahama Woodstars appeared to visit about as frequently as in 1994/95. In 1996/97 after the severe Hurricane Lili, I never observed either Bananaquits or Bahama Woodstars visiting flowers (see also Rathcke 1998, 2000).

Description of flowers and fruits. Because of the apparent specialization for bird pollination, I compared the observed floral

Table 1. Floral traits of *Pavonia bahamensis* on San Salvador Island, Bahamas, compared to those considered typical for a bird-pollination syndrome, including passerine vs. hummingbird pollinators (based on Howe and Westley 1988 and see discussion in text); * denotes non-matching traits. Table modified from Rathcke 2000.

	"Typical" Bird Flower	<i>P. bahamensis</i>
Corolla		
Color	*vivid; red	*green; yellow anthers
Odor	none	none
Shape	tubular corolla	tubelike corolla, 18.1 mm
Orientation	horizontal (passerine) *vertical (hummingbird)	horizontal
Anthesis	diurnal	diurnal
Phenology	steady-state	seasonal steady-state
Nectar	ample	ample (>100 µl/flower/day)
Concentration	20% sucrose	20% sucrose
Volume	>100 µl/flower/day	>100 µl/flower/day
Secretion	continuous	continuous

traits of *Pavonia bahamensis* with those predicted for a bird pollination syndrome (based on Howe and Westley 1988; Table 1; see Figure 1). In contrast to the classic bird pollination syndrome, the corolla and calyx of these flowers are green (see also Correll and Correll 1982) and blend into the leaves, but the exserted anthers with yellow pollen are highly visible (Figure 1). Other traits appear to fit a bird pollination syndrome. Flowers have no detectable odor. Flowers have five separate petals joined to the staminal column. The calyx and corolla form a cup that retains large amounts of nectar (Table 1). Although the petals are not fused, they remain somewhat closed and form a tubelike corolla that was 18.1 mm (SD = 1.74, n = 12 plants; 50 flowers) from the edge of the corolla to the base for flowers measured in this study. The average total length of the flower from the base to the upper surface of the exserted stigma at maximum exsertion was 31.1 mm (SD = 3.15, n = 11 plants; 42 flowers). Correll and Correll (1982) reported that petals were about 2 cm long and the stamen column was 3 cm or more.

Flowers are perfect. The style typically had 10 stigmas on short branches (n = 5 plants; 5 flowers). Anthers are located on the stamen column that surrounds the style, and flowers I observed had an average of 41 anthers (SD = 0.19, n = 14 plants; 26 flowers). On average, each anther contained 74 pollen grains (SD



Figure 1. Flower of *Pavonia bahamensis* on San Salvador Island, Bahamas.

= 17.5, $n = 7$ plants; 13 flowers, 24 anthers). The number of pollen grains per anther did not vary significantly with location on the stamen column (upper versus lower). Although the anthers encircle the stamen column, the filaments on the underside of the column curve upward causing the anthers to be arranged on the upper side of the stamen column (Figure 1). This arrangement of the anthers probably ensures more effective transfer of pollen to the body of a visiting bird (Figure 1).

Flowers exhibit herkogamy (spatial separation of male and female parts). On average, for the flowers I sampled, the uppermost anther was separated from the nearest stigma lobe by 4.6 mm (SD = 1.88, range = 1–10 mm, $n = 8$ plants; 85 flowers). However, occasionally flowers showed distances of 1 mm or less (2% of flowers, $n = 85$). Even in this case, however, the few pollen grains that could be transferred would not be sufficient alone to promote fruit set where usually around 20 grains are needed (see below). Pollen grains are large, spiny, and sticky and are not easily moved by wind or by other movements. Typically pollen must be transferred by a visitor.

Flowers are solitary and are displayed singly on branches (see also Correll and Correll 1982). The flowers are oriented horizontally or at a slight upward angle (Figure 1).

Fruits (schizocarps) are dry, and the mericarps (each with one seed) separate for dispersal. Each fruit has a maximum of five mericarps. Most intact mature fruits had 4 or 5 seeds ($\bar{x} = 4.6$, $SD = 0.62$, $n = 25$ fruits on 4 plants). No mature fruits had 1 or 2 seeds and only 6% had 3 seeds. Total fruit production censused in June 1995 ranged from 0–44 fruits per shrub ($\bar{x} = 16$, $SD = 16.8$, $n = 8$ plants; 130 fruits). Based on these averages, each shrub produced 74 seeds in June 1995. I never saw any evidence of pre-dispersal seed predation. Fruits have spongy tissue and can float for two weeks or more in the lab in fresh water.

Individual flower phenology. Flowers open throughout the day, and stigmas are receptive for 2–3 days. Flowers are partially protogynous (i.e., the stigma is receptive before the anthers dehisce and remains receptive until all the anthers have dehisced). Stages of flower development are described below (based on 15 flowers on 5 plants; see also Rathcke et al. 1996). Day 1 (Stage 1): The stigma emerges through the closed corolla and gradually the stigma lobes open and spread. Flowers are occasionally visited at this point and may have pollen deposited on the stigma. Next, the corolla begins to open, the stigmas become exerted beyond the corolla to their maximum length and the many anthers on the upper half of the style sheath begin to emerge beyond the corolla. Day 1–2 (Stage 2): The upper anthers begin to dehisce. Day 2–3 (Stage 3): The lower anthers begin to dehisce. Later, the stigma lobes begin to contract and move close together. Day 3–4 (Stage 4): All anthers are dehisced, the stigma lobes contract, the style starts to retract into the corolla, and the corolla begins to close. The stigma remains exerted beyond the corolla. Day 4–5: The corolla and the stamen column fall. The style becomes withered and brown. Subsequently the ovary either stays green and begins to enlarge in size, or the ovary, sepals, and calyx turn yellow and abscise, usually within about 10 days. Pollination does not induce floral senescence.

Flowering and fruiting phenologies. The major flowering of *Pavonia bahamensis* occurred in winter, November through January, on San Salvador. Other flowering during the year ap-

Table 2. Nectar production of different flower stages of *Pavonia bahamensis* in December 1996. Microliters of nectar per flower per day and mg sucrose-equivalents per ml are shown with means and standard deviations. n = number of flowers from 7 tagged plants.

Stage (days of age)	n	Secretion Rate $\mu\text{l/day}$	Sugar Concentration mg/ml sucrose
Stage 1 (day 1)	19	72 ± 90.9	1.30 ± 1.646
Stage 2 (day 1–2)	6	162 ± 129.9	3.00 ± 2.665
Stage 3 (day 2–3)	7	184 ± 82.5	3.35 ± 1.495
Stage 4 (day 3–4)	4	33 ± 35.7	0.66 ± 0.731

peared to be minor and I only saw a few flowers at other times. However, Correll and Correll (1982) have reported flowering throughout the year in the Bahamas.

Flowering showed a seasonal steady-state pattern (after Gentry 1974). Most individual shrubs had only 1–3 flowers open each day during the major flowering season ($\bar{x} = 2.3$, $SD = 2.42$, $n = 3$ years; 9 plants). Flowering of each shrub lasted for more than a month, and new buds were produced as flowering continued.

Fruits developed from flowers produced in November–February were dispersing mericarps 5–6 months later in June.

Nectar production. Nectar was relatively dilute, with average sucrose concentration equal to 19.5% or 0.195 mg/ml ($SD = 0.048$, $n = 7$ plants; 43 flowers; $Brix = 18.1 \pm 4.1$; measured in winter 1996/97). Nectar tasted sweet and had no other noticeable flavor.

Nectar production was highest for Stage 3 (day 2–3) flowers when it averaged 184 μl per flower (Table 2). Average lifetime nectar production per flower was 458 μl . Nectar production was continuous throughout the day and accumulated over the night to high levels in the morning. Nectar in old flowers could be re-sorbed. Bagged flowers in which nectar was never collected each had no nectar or less than one microliter of nectar each (6 plants; 11 flowers) at the end of floral life. There was no evidence that nectar removal stimulated nectar production.

Breeding system and pollen-ovule ratio. *Pavonia bahamensis* plants depended upon birds for fruit set. Plants did not autogaminate, and they were self-incompatible or weakly self-com-

Table 3. Breeding system of *Pavonia bahamensis* on San Salvador Island, Bahamas. Average fruit set is shown for bagged flowers with no hand-pollination, bagged flowers augmented with self-pollen, open flowers augmented with cross-pollen, and naturally pollinated flowers. % Fruit set equals 100 (fruits/flowers). ¹ Pollen was not augmented by hand but pollen grains were counted on naturally pollinated flowers. ² Two of five flowers on one plant produced fruit. Means within each season with different superscript letters are significantly different; Mann-Whitney U tests, * $P < 0.10$.

Treatment	Number		% Fruit Set
	Plants	Flowers	$\bar{x} \pm \text{SD}$
1994/95			
Bagged, no hand-pollination	5	7	0
Bagged, self-pollen	5	11	0
Abundant pollen, >50 grains ¹	5	18	93 \pm 13.4 ^a
Natural pollination	6	22	82 \pm 30.9 ^a
1995/96			
Bagged, self-pollen	4	6	0
Augmented cross-pollen	11	47	51 \pm 50.5 ^b
Natural pollination	11	67	40 \pm 49.4 ^b
1996/97			
Bagged, self-pollen	4	16	10 \pm 20.0 ^{c*}
Augmented cross-pollen	7	31	43 \pm 46.5 ^{d*}
Natural pollination	7	64	11 \pm 17.9 ^{c*}

patible (Table 3). Bagged flowers typically produced no fruit if pollen was not deposited on the stigmas by hand. Flowers hand-pollinated with self-pollen did not set fruit in 1994/95 or 1995/96 (and see Rathcke 1998; Rathcke et al. 1996). However, in 1996/97 two flowers on one shrub produced fruit in the treatment with added self-pollen (Table 3).

The pollen-ovule ratio for *Pavonia bahamensis* was estimated to be 607. This was based on the following measurements: Flowers had an average of 41 anthers (SD = 0.19, $n = 14$ plants; 26 flowers). Each anther contained an average of 74 pollen grains (SD = 17.5, $n = 7$ plants; 13 flowers, 24 anthers). Using these two averages, I estimated that flowers had an average of 3034 pollen grains. Flowers typically had five ovules.

Pollination limitation and pollen deposition. Fruit set was not significantly pollination limited in either 1994/95 or in 1995/96 (Table 3; Rathcke 2000). Fruit set of naturally pollinated flow-

ers and that of pollen-augmented flowers were not statistically different (Rathcke 2000). However, fruit set was strongly pollination limited in 1996/97 after Hurricane Lili when populations of the two bird pollinators were decimated (Murphy et al. 1998; Rathcke 1998, 2000). Using the equation given in the methods, percent pollination limitation = $(43\% - 11\%) / 43\% = 74\%$ (see also Rathcke 2000). Pollen deposition on stigmas was also much lower in 1996/97 than in the previous two years (Rathcke 2000).

Effectiveness of pollinators. Pollination effectiveness of a flower visitor reflects both pollen transfer by an individual pollinator per visit and the frequency of visits. Bahama Woodstars were not very effective as pollinators of *Pavonia bahamensis*, both because individuals transferred little or no pollen to stigmas and because they were relatively infrequent visitors. Because Bahama Woodstars have long bills, and because they could probe through the sides of the flowers between the petals, these birds could access nectar without touching either the stigma or the anthers. In 1995/96, no pollen was transferred by individuals in 27% of the visits to flowers ($n = 11$). For the visits that did transfer pollen, the majority of visits (73%) transferred < 20 pollen grains ($\bar{x} = 16$, $SD = 19.5$, $n = 11$). A minimum of ca. 20 pollen grains is needed for maximum high fruit set (Rathcke 2000). In 1995/96 when Bananaquits were rare and Bahama Woodstars were the most frequent flower visitors, both pollen deposition and fruit set were lower than in 1994/95, although flowers were not significantly pollination limited (Table 3; Rathcke 2000). Bahama Woodstars were relatively infrequent visitors to flowers. During a day, typically only one or two birds were observed visiting flowers in 1994/95 and 1995/96. In 1996/97, no birds were seen or heard in the site.

Bananaquits appeared to be effective pollinators, although the effectiveness of single visits was not quantified. Bananaquits probed flowers in two different ways; most often they probed with their heads up so that the anthers contacted their breasts but occasionally they probed with their heads upside down so the anthers contacted their foreheads. The bright yellow *Pavonia bahamensis* pollen was often evident on the foreheads of these birds but was less obvious on their yellow breasts. Very rarely, birds probed through the side of the flower between the petals and did not transfer or collect pollen. Bananaquits tended to remain in

small flocks and to visit flowers throughout the day. In 1994/95 when Bananaquits frequently visited flowers, pollen deposition on stigmas was high and fruit set was not pollination limited (Table 3).

Although I observed one Bahama Mockingbird visit flowers, this occurred in 1996/97 when nectar was overflowing and dripping from the flowers. It is unlikely these mockingbirds could reach the nectar when other birds were removing it to low levels in the flowers. The mockingbird had pollen covering its chest and it is possible that it could have transferred some pollen. However, pollen deposition in this winter period (1996/97) was low (51% of the flowers had no pollen deposition by the end of flower life) and fruit set was low and pollen-limited (Table 3; Rathcke 2000). Therefore, Bahama Mockingbirds were not considered effective pollinators, possibly because they rarely visited flowers and/or were poor at transferring pollen.

DISCUSSION

As is common for many island plants, *Pavonia bahamensis* has few pollinator species; its pollination appears to depend totally on two bird species, Bananaquits and Bahama Woodstars. Perhaps because it has only bird pollinators, the floral traits of *P. bahamensis* closely fit those predicted by the bird pollination syndrome, except for corolla color (Table 1). The corolla is green and is neither vivid nor red as is typical for hummingbird-pollinated flowers in western North America (Grant and Grant 1976; Howe and Westley 1988; Raven 1972; Stiles 1976).

The red color of flowers that is typical for hummingbirds in western North America is apparently not preferred by hummingbirds, but red is conspicuous to them and not to insect pollinators, which may explain its selective advantage (Melendez-Ackerman et al. 1997; Raven 1972). Because red is conspicuous, it has been hypothesized that there is an advantage for plants to converge on this single, distinctive flower color to attract migrating hummingbirds (Raven 1972). This color convergence would not be necessary for plants on San Salvador where nectarivorous birds are non-migratory. In fact, flowers visited by short-billed hummingbirds, like the Bahama Woodstar, in Central and South America and the West Indies often show a diversity of colors (Feinsinger 1987) although green is highly unusual. For *Pavonia bahamensis*,

the yellow pollen of the exerted anthers may provide the vivid visual cue rather than the corolla. It is also possible that the flowers exhibit an attractive color in the ultraviolet (Bleiweiss 1994; Goldsmith 1980), but this was not tested for this species. Green or greenish-yellow flowers are also found in three close relatives of *P. bahamensis* (*P. paludicola*, *P. troyana*, and *P. rhizophorae*) (Fryxell 1999), so green is not an unusual color in this lineage. However, the maintenance of the green color may also reflect a lack of selection for more vivid colors in areas where birds are not migratory. Green corollas may also have an adaptive advantage because they can contribute to photosynthesis and reduce resource limitation of fruit set (Bazzaz et al. 1979; Jurik 1983).

Other characteristics of *Pavonia bahamensis* flowers are typical of a bird pollination syndrome (Grant and Grant 1976; Howe and Westley 1988; Table 1). Flowers have no detectable odor. The calyx and corolla form a tube where nectar collects. Nectar per flower is ample (> 100 microliters per day) with a sugar concentration of 20%, which is typical of bird-pollinated species (Baker 1975; Bolten and Feinsinger 1978; Feinsinger 1983; Feinsinger et al. 1985; Hainsworth and Wolf 1976; Opler 1983). Insects can access nectar by forcing their way between the petals, as one wasp was observed to do. However, during three winter flowering periods, only this single wasp individual was ever observed to visit the flowers. This lack of visitation may support the hypothesis that the dilute nectar deters bees and wasps, which may need higher rewards (Bolten and Feinsinger 1978). Although ants fed on the nectar when flowers were placed on the ground, they were never seen in the flowers on the plant.

Pavonia bahamensis plants show a seasonal steady-state flowering pattern, which is a common flowering pattern for plants that support long-lived pollinators such as birds (Gentry 1974). Different flowers continued to open throughout the day, and nectar was secreted throughout the day as is characteristic of many bird-pollinated species (Howe and Westley 1988).

The pollinator specialization of *Pavonia bahamensis* is partly enforced by pollinator availability: Bananaquits and Bahama Woodstars are the only nectarivorous birds on San Salvador (Murphy et al. 1998; White 1991). However, other bird species, especially migratory warblers, occasionally visited the flowers of other nearby species (see also Murphy et al. 1998). Insects, especially wasps and butterflies, can be common flower visitors to

other plant species (Rathcke et al. 1996; pers. obs.). However, these species were never seen visiting the flowers of *P. bahamensis*, with two exceptions. I saw a single wasp visit one flower by pushing its way between the petals into the corolla tube; it appeared to access nectar as it stayed for some time. I observed one foraging bout by a Bahama Mockingbird feeding at flowers overflowing with nectar during winter 1996/97 when the main bird pollinators were scarce (Rathcke 1998, 2000). This bird had yellow pollen on its breast and head and may have transferred pollen. However, it is unlikely it could have reached the nectar if nectar removal was at the levels seen in the previous two winters (Rathcke 1998, 2000). Generalist pollinator species can provide compensatory pollination for plants, especially when nectar accumulates in flowers and becomes available to more species, and prevent or reduce pollination limitation (Wolf and Stiles 1989), but this was not the case for *P. bahamensis*. When populations of two bird pollinators, Bananaquits and Bahama Woodstars, were decimated by the severe Hurricane Lili in October 1994, the fruit set of *P. bahamensis* was strongly pollination limited the following December–January (Rathcke 1998, 2000). This species has no “fail-safe” mechanism (Wolf and Stiles 1989) to maintain pollination if these two bird species decline, and as such, it is highly vulnerable to changes in their behavior or population densities (Rathcke 1998, 2000).

Bird pollination is generally reliable for *Pavonia bahamensis* when either Bananaquits or Bahama Woodstars are present, as evidenced by the lack of pollination limitation in the two years before Hurricane Lili decimated their populations in 1996 (Murphy et al. 1998; Rathcke 1998; 2000). Hurricane Lili was a Category 2 storm with winds up to 105 miles per hour (Rathcke 2000). In September 1999 an even more intense, Category 4 hurricane, Hurricane Floyd, passed directly over San Salvador with winds up to 150 miles per hour (Bahamian Field Station records), but nectarivorous bird populations did not seem to be reduced; both Bananaquits and Bahama Woodstars appeared to be at typical population levels (M. Murphy, pers. comm.; pers. obs.). Although hurricanes affect San Salvador about every three years on average (Shaklee 1996), few hurricanes may be severe enough to reduce the nectarivorous bird populations. The strong pollination limitation seen in 1996/97 may seldom occur. However, pollination limitation could also occur if birds are unreliable pollinators

for other reasons. For example, in 1995/96 Bananaquits rarely visited although they were common on the island (Murphy et al. 1998; Rathcke 2000). In that year Bahama Woodstars appeared to be sufficiently effective to prevent pollination limitation although pollen deposition and fruit set were lower. It is possible that this island species usually has reliable pollination despite its specialization, in contrast to some other island plants where pollination is less certain with fewer pollinators (Feinsinger et al. 1982; Spears 1987).

The low pollen-ovule ratio (P/O) of 607 also suggests that pollination by these two bird species is generally reliable. The value of 607 is similar to the average ratio reported for plant species with facultative xenogamy (\bar{x} = 797) whereas the pollen-ovule ratio for plants with obligate xenogamy (i.e., obligate outcrossers) is much higher (P/O = 5860; Cruden 1977). Facultatively xenogamous species have more certainty of pollination than obligate xenogamous species because they typically can auto-pollinate and are self-compatible, although some species require pollinators (Cruden 1977). Given that *Pavonia bahamensis* could be classified as an obligate outcrosser, the low pollen-ovule ratio suggests that this species may have unusually reliable pollination. Flowers are unlikely to self-pollinate and outcrossing is usually required for fruit set. The production of fruit by two selfed flowers in 1996/97 may represent the breakdown of the compatibility system when cross-pollination is low, or it may reflect pollen contamination.

What is the evidence that either Bahama Woodstars or Bananaquits is the "most effective pollinator" and hence the stronger selective agent molding the pollination syndrome (Stebbins 1970)? The morphological match of bill and floral tube lengths suggests that the Bahama Woodstar was the more effective pollinator. The tube-like corolla was 18.1 mm and the bill length of the Bahama Woodstar is ca. 17 mm (based on one museum male specimen collected on New Providence in 1949 and deposited in the Museum of Zoology at the University of Michigan). In contrast, the average length of Bananaquit bills measured from nares to tip was 10.8 mm (SD = 0.902, min = 7.95, max = 13.47, n = 221; M. Murphy, unpub. data). Tongue lengths would also determine morphological matching, but data are unavailable. A visual estimation of tongue length in Bananaquits from a slide indicated that tongues could extend $1.2\text{--}1.4 \times$ beyond the bill length (ca. 13–15 mm long or a total of 24–26 mm; Bruce Hallett, pers. comm.).

Regardless of the morphological matching between bills and tongues and corolla lengths, Bahama Woodstars were not effective as individual pollinators because they typically visited the flowers through the side of the corolla and usually transferred little or no pollen per visit. They were also relatively infrequent visitors to flowers compared to Bananaquits, which foraged in small flocks. Other evidence suggests that Bananaquits are more effective pollinators than Bahama Woodstars. Bananaquits commonly had dense pollen loads on their foreheads and breasts and they usually contacted the stigma and anthers when visiting flowers. Pollen deposition was especially high when Bananaquits were the major flower visitors in 1994/95 (Rathcke 2000) although it is not known if this occurred because they transferred more pollen per visit or because they were very frequent visitors. Bananaquits usually visited the flowers so that pollen was deposited on their chests, but they occasionally visited flowers while hanging upside down so that pollen was deposited on their foreheads. In either case, pollen could be easily transferred to the extended stigma if the bird retained the same position during other floral visits. *Pavonia bahamensis* appears to be an important floral resource for Bananaquits on San Salvador (Murphy et al. 1998), and Bananaquits may be reliable pollinators over years. However, relatively few were seen in 1995/96 and the reason for this is not clear, suggesting that their foraging patterns may change and pollination reliability over years may vary.

A second line of evidence also suggests that Bananaquits are more effective pollinators than Bahama Woodstars. The horizontal flower orientation in *Pavonia bahamensis* supports the syndrome for passerine pollination, rather than hummingbird pollination. Flowers that are held horizontally, rather than vertically, allow passerine birds to perch on nearby branches while feeding (Bruneau 1997; Cruden and Toledo 1977). Another test for passerine versus hummingbird pollination would be to examine sugars in the nectar, but this remains to be done. Nectars of passerine-pollinated species tend to have low sucrose/hexose ratios (< 0.499) whereas hummingbird-pollinated species tend to have high sucrose/hexose ratios (Baker and Baker 1983; Bruneau 1997).

Bird pollination of *Pavonia bahamensis* may be relatively unusual for the genus *Pavonia*. Most species of *Pavonia* are thought to have relatively generalized pollination (Fryxell 1999). However, hummingbirds are reported to be pollinators for several spe-

cies that have tubular corollas and exerted stigma and anthers, including *P. schrankii* with a yellow corolla (Gottsberger 1972), *P. viscosa* (as *P. montana*) and *P. malvaviscoides* with red flowers (Sazima 1981), and *P. dasypetala* (McDade and Davidar 1984; Roubik 1982; see also Porsch 1929). The green flowers of *P. bahamensis* are unusual for a bird-pollinated flower. The three closely related species (*P. paludicola*, *P. troyana*, and *P. rhizophorae*) all have green or greenish-yellow flowers (Fryxell 1999). Whether these species will also prove to be pollinated by birds, or specifically by passerines or hummingbirds, remains to be determined. Among these four species, *P. bahamensis* is unique in having single flowers displayed among the leaves; the other three species have racemose inflorescences that rise above the leaves. If they are bird-pollinated, the more vertical, racemose inflorescence may reflect hummingbird pollination rather than passerine pollination (see Cruden and Toledo 1977).

For *Pavonia bahamensis*, a species of passerine bird (Bananaquits) may be a more effective pollinator than hummingbirds, but whether Bananaquits are more reliable over the long term remains to be determined. Although Bahama Woodstars are ineffective at transferring pollen, they maintained pollination one flowering season when Bananaquits were infrequent visitors. Having two pollinator species increased pollination reliability for *P. bahamensis*, although it still incurs a risk of pollination limitation if these two species decline or change their foraging patterns (Rathcke 1998, 2000).

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