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FLOWER VISITORS TO BLACK MANGROVE AND WHITE MANGROVE ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Black Mangrove (*Avicennia germinans* (L.) L.: Avicenniaceae) and White Mangrove (*Laguncularia racemosa* (L.) Gaertn. f.: Combretaceae) grow together in the mangrove zone and overlap in their flowering during June on San Salvador Island, Bahamas. Both have small, white flowers with similar nectar production. To determine if these species are specialized for different pollinators or if they are generalized and share the same pollinators, we observed, counted and identified flower visitors to both species during studies over four years. Further pollination studies are needed to determine how many of these flower visitors act as effective pollinators.

Black Mangrove flowers were visited by many more species (32 total) and more individuals than White Mangrove flowers, although these differences partly reflect longer observation times and better species identifications for Black Mangrove. Black Mangrove was very generalized and was visited by many different types of species, including butterflies, moths, flies, wasps, bees, ants, and one bird species (Bahama Woodstar). Butterflies were the most frequent visitors to Black Mangrove flowers and ten species of butterflies were recorded on Black Mangrove. Butterflies seldom visited White Mangrove flowers and were not shared by these two mangroves. In contrast, White Mangrove appears to be more specialized for pollination by wasps and bees, but wasps and bees also visited Black Mangrove, and many of these species may be shared. These results are preliminary, and further studies are needed to confirm these differences in pollinator specialization and to determine the degree of pollinator sharing of these two mangrove species.

INTRODUCTION

Black Mangrove (*Avicennia germinans* (L.) L.: Avicenniaceae) and White Mangrove (*Laguncularia racemosa* (L.) Gaertn. f.: Combretaceae) grow together in the mangrove zone in intertidal areas throughout the Bahamas, Florida, and Mexico and extend through Central America and the West Indies to South America (Correll and Correll, 1982). On San Salvador Island they often grow intermingled in a narrow zone along the edges of inland saline lakes (Kass and Stephens, 1990; Smith, 1993). Black Mangrove typically flowers from April through June and White Mangrove flowers in June and July, so they can overlap in their flowering times during June (pers. obs.). Both species have

small, white flowers. However, few studies exist on the pollinators or the pollination biology of these species (Rathcke *et al.*, 1996), and no studies have determined whether these species are specialized for different pollinator species or if they share pollinator species. If pollinators are shared, these mangrove species could compete for pollinators (Rathcke, 1988), or they could show sequential mutualism where an earlier-flowering species attracts and supports pollinators for a later-flowering species (Waser and Real, 1979; Rathcke, 1988).

In this study we present a preliminary report on the pollinators of Black Mangrove and White Mangrove on San Salvador Island, Bahamas. We report on the total number of species observed visiting flowers of each species, visitation rates to flowers of each mangrove species during flowering overlap, and nectar production of flowers.

Floral Biology

Flowers of Black Mangrove are 11-13 mm in diameter with spreading rounded, creamy white petals. The calyx and corolla form a tube that holds nectar. Flowers are hermaphroditic (perfect) but self-incompatible so pollinators and outcross pollen are required for fruit set (Rico-Gray, 1989; pers. obs.). Flowers are displayed on spikes with only two flowers open at the same time (pers. obs.). Flowers are protandrous (Tomlinson 1994, Rathcke, *et al.*, 1996) and last three days, with flowers releasing pollen for the first two days and the stigma becoming sticky and receptive on the third day (Rathcke, *et al.*, 1996).

Flowers of White Mangrove are 4-5 mm in diameter with five rounded, white petals. The calyx forms a tube that holds nectar. White Mangrove is androdioecious, i.e. plants have either hermaphroditic flowers or male flowers, and the hermaphrodites can self-pollinate and self-fertilize (Rathcke, *et al.*, this volume). Flowers are displayed on spikes. Hermaphroditic flowers are open for two days whereas male flowers are open for one day (Rathcke, *et al.*, 1996).

METHODS

Most of the observations of flower visitors were made on plants growing along the shores of the inland hypersaline lake, Osprey Pond, south of the Bahamian Field Station on the northeastern coast of San Salvador Island. In June 1999, observations were also made at plants near Oyster Pond about 350 m southeast of the Osprey Pond site. We recorded pollinators on these two mangrove species during the following periods: May 7-18, 1995 (L. Kass only); June 9-18, 1995 (L. Kass, B. Rathcke); May 22 and 26-28, 1996 (L. Kass, N. Elliott), June 9-21, 1997 (L. Kass, B. Rathcke); June 15-23, 1999 (L. Kass, C. Landry, W. Munroe, B. Rathcke).

Flower visitors to both mangrove species were noted and recorded throughout the study. Spot surveys of all the trees were made periodically. Timed ten-minute watches of a known number of flowers (usually 20-100 flowers) were made throughout each day over several days. Data are reported as number of individuals seen visiting flowers during observation periods. The number of days each species was seen in surveys is noted to indicate the consistency of their visitation over time. Insect specimens are deposited in the insect collection at the Bahamian Field Station. Nomenclature for flower visitors is based on the following sources: Riley, 1975; White, 1991; Miller, *et al.*, 1992; Elliott, 1993; Smith, *et al.*, 1994; Carpenter, 1996; Raffaele, *et al.*, 1998; Deyrup, pers. comm.

Nectar production was measured during June 1995 in first-day flowers that had been bagged as buds by bridal veil netting. Nectar was collected with 1 or 2 microliter capillary tubes.

RESULTS

We recorded a total of 32 species visiting the flowers of Black Mangrove during our observations (Table 1). Butterfly species (N = 10) were the most common group of visitors to Black Mangrove flowers (Table 1), and

Table 1. Species seen visiting the flowers of Black Mangrove (BW), *Avicennia germinans* or White Mangrove (WM), *Laguncularia racemosa*, on San Salvador Island, Bahamas during May-June 1995 and May 1996. A "?" in the BM or WM columns indicates a tentative identification. This is not a complete list; other species observed were not identified.

	Scientific Name	Common Name	BM	WM
LEPIDOPTERA				
BUTTERFLIES				
Hesperiidae	*Epargyreus zestos zestos* Geyer	Zestos Skipper	X	
Lycaenidae	*Brephidium isophthalma pseudofea* Morrison	Eastern Pygmy BlueBM		
	Leptotes cassius theonus Lucas	Cassius Blue	X	
	Strymon sp.	hairstreak	X	
Pieridae	*Ascia monuste eubotea* Latreille	Great Southern White	X	
	Kricogonia lyside (Godart)	Guayacan Sulphur	X	
	Eurema chamberlaini Butler	Chamberlain's Sulfur	X	
Papilionidae	*Battus polydamas lucayus* Rothschild & Jordan	Polydamas Swallowtail	X	
Nymphalidae	*Junonia genoveva* Cramer	Caribbean Buckeye	X	
Heliconiidae	*Dryas iulia* (Fabricus)	Flambeau	X	
MOTHS				
Ctenuchidae	*Empyreuma heros* Bates	(wasp mimic)	X	X
	Eunomia sp.	(wasp mimic)		X
DIPTERA				
FLIES				
Syrphidae	*Palpada albifrons* Wied.	syrphid fly	X	
	Copestylum eugenia (Will.)	flowerfly	X	
Calliphoridae	*Callitrega macellaria*	blowfly	X	
HYMENOPTERA				
WASPS				
Tiphiidae	*Myzinum* sp.		X	
Scoliidae	*Campsomeris trifasciata nassauensis* Bradley		X	?
Eumeniidae	*Pachodynerus cubensis bahamensis* Bequaert & Salt		X	
Vespidae	*Polistes bahamensis* Bequaert & Salt (=*exclamans picturatus*)	social paper wasp	X	
Pompilidae	*Anoplius fulgidus* (Cresson)	spider wasp	X	
Sphecidae	*Ectemnius auriceps* (Cresson)	digger wasp	X	
	Stictia signata (Linn.)	digger wasp	X	
	Cerceris watlingensis Elliott & Salbert	digger wasp	X	
	Cerceris cubensis Cresson	digger wasp	X	
BEES				
Megachilidae	*Megachile* sp	leafcutter bee	X	?
	Coelioxys sp.	leafcutter bee	X	
Halictidae	*Agapostemon columbi* Roberts	sweat bee	X	
	unidentified species	sweat bee	X	
Anthophoridae	unidentified spp.		X	
UNKNOWN	Unidentified small bee		X	
ANTS				
Formicidae	*Monomorium ebeninum*		X	
	Pseudomyrmex sp.		X	
BIRDS				
Emberizidae	*Coereba flaveola*	Bananaquit		X
Trochilidae	*Calliphlox evelynae*	Bahama Woodstar	X	

Table 2. Visitors to flowers of Black Mangrove (*Avicennia germinans*) on San Salvador Island, Bahamas during May 7-18 and June 13-15, 1995. Data are summarized from 11 hours of observations over seven days. Total individual and species for major groups are shown in bold. N = number of. N dates = number of days visitor was seen. + means that more individuals or species were seen but were not counted or identified. See Table 1 for complete scientific names and common names. *species also visited White Mangrove flowers.

Visitor	N indivs.	N dates	N species
LEPIDOPTERA	57+		6+
BUTTERFLIES		54	
Brephidium isophthalma pseudofea	4+	3	
Kricogonia lyside	38	4	
Ascia monuste eubotea	1	1	
Junonia genoveva	7	3	
unidentified spp.	4+	4	?
MOTHS	3		
Empyreuma heros *	3	1	
DIPTERA (flies)	4+		2+
Copestylum eugenia	3	2	
unidentified spp.	3+		3?
HYMENOPTERA (ants excluded)	15+		6+
WASPS	5		
Campsomeris trifasciata nassauensis (Bradley) *	1	1	
Stictia signata	2	2	
other unidentified species	10+	3	?
BEES	2+		
Megachile sp.	1	1	
unidentified species	1	1	1
ANTS[a] (Formicidae)			
Monomorium ebeninum	10[b]	1	
Pseudomyrmex sp.	2	2	

[a]probably are not pollinators so are excluded in summary counts.

[b] all ants were in one flower

butterflies were the most frequent visitors (N = 54) to Black Mangrove flowers in June 1995 (Table 2). In June 1995, many visitors were not identified (Table 2), so in May 1996, we made a concerted effort to collect and identify species (Table 3). As a result, many more species of wasps and bees were identified on Black Mangrove (Table 3), although butterflies were still the most frequent visitors. Black Mangrove shrubs were often covered with butterflies, especially *Kricogonia lyside* (Pieridae), the Guayacan Sulphur. This abundant butterfly was never seen visiting White Mangrove flowers for nectar. At Pigeon Creek in June 1999, many (N = 7) Pygmy Blue Butterflies (*Brephidium isophthalma pseudofea* (Morrison): Lycaenidae) and one *Kricogonia lyside* were seen visiting Black Mangrove flowers during a ten-minute watch. A single visit by a Bahama Woodstar was observed.

Many wasp species (N = 9) visited Black Mangrove flowers (Tables 1, 2 and 3), but visits were less frequent than those by butterflies (Table 2). Bee species (N = 6) also visited

Table 3. Visitors to flowers of Black Mangrove (*Avicennia germinans*) on San Salvador Island, Bahamas during May 22 and 26-28, 1996. N = total number of species.

	Scientific Name	Common Name
LEPIDOPTERA butterflies and moths		
N = 6		
BUTTERFLIES		
Hesperiidae	*Epargyreus zestos zestos* Geyer	Zestos Skipper
Lycaenidae	*Leptotes cassius theonus* Lucas	Cassius Blue
	Strymon sp.	hairstreak
Pieridae	*Kricogonia lyside* (Godart)	Guayacan Sulphur
Papilionidae	*Battus polydamas lucayus* Rothschild & Jordan	Polydamas Swallowtail
Heliconiidae	*Dryas iulia* (Fabricus)	Flambeau, Orange Julia
DIPTERA		
Flies N = 2		
Syrphidae	*Palpada albifrons* Wied.	syrphid fly
Calliphoridae	*Callitrega macellaria*	blowfly
HYMENOPTERA		
Wasps, Bees and Ants N = 12		
WASPS N = 8		
Tiphiidae	*Myzinum* sp.	wasp
Scoliidae	*Campsomeris trifasciata nassauensis* Bradley	wasp
Eumeniidae	*Pachodynerus cubensis bahamensis* Bequaert & Salt	wasp
Vespidae	*Polistes bahamensis* Bequaert & Salt	social paper wasp
Sphecidae	*Ectemnius auriceps* (Cresson)	digger wasp
	Stictia signata (Linn.)	digger wasp
	Cerceris watlingensis Elliott & Salbert	digger wasp
	Cerceris cubensis Cresson	digger wasp
BEES N = 6		
Megachilidae	*Megachile* sp	leafcutter bee
	Coelioxys sp.	leafcutter bee
Halictidae	*Agapostemon columbi* Roberts	sweat bee
	unidentified species	sweat bee
Anthophoridae	unidentified spp.	
Unidentified small bee		
BIRDS N = 1		
Trochilidae	*Calliphlox evelynae*	Bahama Woodstar

Black Mangrove flowers (Tables 1, 2 and 3), but were very infrequent visitors in June 1999 (Table 2). Few fly species visited flowers (Tables 1, 2 and 3), and they were infrequent visitors (Table 2).

White Mangrove had many fewer species of flower visitors than Black Mangrove; we tentatively identified and recorded only five species (Table 1). Although many butterflies were seen visiting nearby Black Mangrove, White Mangrove flowers were visited by only one butterfly individual in 1995 (Table 4) and one in 1999. Two species of day-flying moths, which are wasp mimics, were seen visiting White Mangrove flowers (Table 4). Wasps, bees and flies were infrequent visitors (Table 4). At Pigeon Creek in June 1999, one megachilid bee was seen visiting White Mangrove flowers during a ten-minute watch. Bananaquits visited White Mangrove flowers on several occasions (Tables 1 and 4).

Only one species was determined with certainty to visit both Black and White Mangroves, and this was a distinctive moth (*Empyreuma heros*: Arctiidae/Ctenuchidae) with a black body and red wings that is a wasp mimic (Tables 1 and 4). One individual visited two flowers of White Mangrove and then flew directly to flowers of Black Mangrove. One wasp species (*Campsomerus trifasciata nassauensis*) is very common on San Salvador (Elliott, pers. obs.) and probably visited both mangroves, but the identification is not certain on White Mangrove. Other wasps may visit both mangrove species but were not identified so this cannot be confirmed. The Lycaenidae butterfly seen on White Mangrove (Table 4) may also visit Black Mangrove, but a positive identification was not made to confirm this.

During flowering overlap, no visitors were observed on flowers of White Mangrove during simultaneous ten-minute watches in both June 1995 and June 1999 whereas many visitors were seen on Black Mangrove flowers (Table 5).

The difference in visitation to White Mangrove and Black Mangrove cannot be explained by differences in nectar production. Nectar production (microliters/flower/day) in bagged flowers is not statistically different for White Mangrove and Black Mangrove (Table 6).

DISCUSSION

Black Mangrove attracted a diverse group of flower visitors and appears to have a very generalized pollination system. We recorded 32 species visiting Black Mangrove flowers, and they included butterflies, moths, flies, wasps, bees, ants and the Bahama Woodstar. In Mexico, butterflies, bees, wasps and ants were reported to be common flower visitors to Black Mangrove (Rico-Gray, 1989), which supports the pollinator generalization found here. Such generalization for pollination is proving to be common among plant species (Waser, *et al.*, 1996), although pollination studies are needed to determine how many of these visitors actually act as effective pollinators (Ollerton, 1996).

Black Mangrove appears to be more generalized for pollinators than White Mangrove because we tentatively identified only five species visiting White Mangrove flowers. However, our preliminary observations have three major limitations for comparing species of flower visitors to Black Mangrove and White Mangrove. 1) We spent longer times recording and collecting flower visitors on Black Mangrove. 2) We observed flower visitors to Black Mangrove during mid- and late-flowering whereas we observed flowers visitors to White Mangrove only during early flowering. The number of species and individuals visiting White Mangrove flowers may increase as flowering continues through June and July. 3) We determined species identifications for fewer of the visitors to White Mangrove than Black Mangrove. Therefore, further observations are likely to expand the list of flower visitors for White Mangrove.

Although Black Mangrove attracts many different types of pollinators, our preliminary data indicate that Black Mangrove is more specialized for butterfly-pollination than White Mangrove. We recorded ten species of butterflies visiting Black Mangrove whereas we observed only two butterfly individuals visiting

White Mangrove during our study. Miller, *et al.* (1992) recorded eight butterfly species visiting Black Mangrove flowers and have no records of butterflies visiting White Mangrove flowers. In Florida, Landry (pers. comm.) seldom saw butterflies visiting White Mangrove flowers. Although further observations may expand the list of visitors to White Mangrove, it seems unlikely that butterflies will prove to be frequent visitors to White Mangrove although this needs to be tested. During flowering overlap, butterflies almost never visited White Mangrove flowers, although they were the most frequent visitors to nearby Black Mangrove flowers. This difference in visitation cannot be explained by nectar production because nectar volume/flower/day was not significantly different for Black Mangrove and White Mangrove. Butterflies may be more attracted to Black Mangrove because the flowers have a corolla tube and a wide corolla that provides a landing platform. For whatever reason, butterflies appear to be a major group of potential pollinators of Black Mangrove that are not shared with White Mangrove.

In contrast, White Mangrove appears to be more specialized for pollination by wasps and bees than Black Mangrove. However, wasps and bees visited flowers of Black Mangrove as well, so this specialization would not necessarily reduce pollinator sharing or competition. In fact, we recorded more species and more individuals of wasps and bees on Black Mangrove than White Mangrove, but this could reflect differential sampling as noted above. In Florida, Landry (pers. comm.) observed that wasps and bees were the most frequent visitors to White Mangrove flowers. In Florida, bees have been reported to be common visitors to flowers of both Black Mangrove (Craighead, 1971) and White Mangrove (Tomlinson, 1980 and 1994). However, many of these bees were probably honeybees (*Apis mellifera*) or bumblebees (*Bombus* species), neither of which occur on San Salvador (Elliott, 1993). Landry (pers. comm.) saw bumblebees visiting both mangrove species in Florida. In general, bees are relatively rare on San Salvador, and both bees and wasps were infrequent visitors to these mangroves. Our lack of species identifications for visitors on White Mangrove prevents us from determining how many species of wasps or bees are shared. The one shared visitor that was positively identified was a ctenuchid moth (*Empyreuma heros*: Arctiidae), which is a wasp mimic. If species are shared, these two mangrove species may compete for these relatively rare pollinators during flowering overlap. However, the earlier-flowering Black Mangrove may also benefit White Mangrove by attracting and supporting pollinators that subsequently switch onto White Mangrove as has been reported for other sequentially flowering species (Waser and Real, 1979, Rathcke, 1988).

Another major difference between the pollination biology of Black Mangrove and White Mangrove was that Black Mangrove attracted many more flower visitors per flower per hour than White Mangrove during the period of flowering overlap. This greater attractiveness of Black Mangrove mostly reflected the high abundance of butterflies, which were major visitors to Black Mangrove and which rarely visited White Mangrove. Flowering phenology may also be important in explaining this differential visitation. Black Mangrove may have been maintaining visitors from earlier flowering whereas White Mangrove was just starting to attract new visitors when we ended our study. More data are needed to confirm whether White Mangrove is infrequently visited throughout its flowering period. Low flower visitation may be typical for White Mangrove; this species does not require pollinators for fruit set because it is self-compatible and hermaphrodites can self-pollinate and self-fertilize (Rathcke, *et al.*, 1996, Rathcke, *et al.*, this volume). In contrast, the more attractive Black Mangrove is self-incompatible and requires pollinators for fruit set (Rathcke, *et al.*, 1996, unpub. data). More observations on flower visitors and visitation rates to these mangroves are needed to confirm the differences reported here. Comparable quantitative data will also be necessary to test whether these island populations have fewer pollinator species

Table 4. Visitors to flowers of White Mangrove (*Laguncularia racemosa*) on San Salvador Island, Bahamas from June 13-15, 1995 when Black Mangrove (*Avicennia germinans*) was also flowering. Data are based on spot observations made throughout the day over 3 days because no visitors were observed during fourteen 10-minute watches. Total individuals and species for major groups are shown in bold. ? means a tentative identification. See Table 1 for complete scientific names and common names and Table 2 for a comparison with Black Mangrove flowering at the same time. N = number of. * indicates the species also visited Black Mangrove flowers.

Visitor	N indiv.	N dates	N spp.
LEPIDOPTERA	**5**		**3**
Butterflies: unidentified Lycaenidae	1	1	
Moths: *Empyreuma heros**	3	1	
Eunomia sp.	1	1	
DIPTERA (flies)	**1**		**1**
unidentified spp.	1	1	
HYMENOPTERA	**1**		**1**
Wasps: *Campsomeris trifasciata nassauensis*? *	1	1	
BIRDS	**3**		**1**
Bananaquit	3	2	

Table 5. Comparison of visitation rates to flowers of Black Mangrove (*Avicennia germinans*) and White Mangrove (*Laguncularia racemosa*) during June 13-15, 1995 and June 1999 on San Salvador Island, Bahamas. Plants were growing adjacent and 10-minute watches were made over the same periods of time. N flowers = range of the number of flowers per plant watched each 10-minute interval. N = number of. + means that more individuals were seen but were not counted.

	Year	Observation Time (min)	N flowers	N spp.	N indiv.	N/hr
Black Mangrove	1995	250	50-100	13	58+	13+
	1999	60	30-50	2	8	8
White Mangrove	1995	140	20-50	0	0	0
	1999	130	20-50	0	0	0

Table 6. Nectar production (microliters/flower/day) for Black Mangrove (*Avicennia germinans*) and for White Mangrove (*Laguncularia racemosa*) on June 14, 1995 at Osprey Pond, San Salvador, Bahamas. Means and Standard Deviations are shown. Nectar production is not significantly different for the two species (significance test by ANOVA: $P = 0.92$).

	Number of Plants	Nectar Production µl/flower/day
Black Mangrove	7	0.45 ± 0.462
White Mangrove	6	0.43 ± 0.178

and lower flower visitation than mainland populations as has been hypothesized (Carlquist, 1974; Barrett, 1996).

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