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FLOWER VISITORS TO WHITE MANGROVE: A COMPARISON BETWEEN THREE BAHAMIAN ISLANDS AND FLORIDA

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ABSTRACT

White Mangrove (Laguncularia racemosa (L.) Gaertn. f.: Combretaceae) is a major species in the important mangrove zone in the Bahama Islands and Florida. Theory predicts that plants on islands should have fewer visitor species than plants on mainlands. Little information exists on the flower visitors (potential pollinators) of White Mangrove for any of these areas. Here we present and compare our species lists of flower visitors to White Mangrove for three Bahamian islands (San Salvador, Exuma, and Eleuthera) and mainland Florida. These data demonstrate that flowers of White Mangrove are visited by a diverse group of insects, including Coleoptera, Lepidoptera, Diptera, and Hymenoptera, and are occasionally visited by birds (Bananaquits). Hymenoptera (wasps and bees) comprised the majority of visitor species in Florida, Exuma, and Eleuthera whereas Lepidoptera (butterflies and moths) comprised the majority of visitor species on San Salvador. Fewer species were recorded on Bahamian islands than in Florida, but this could

partly reflect the smaller sample sizes we have from these islands. We are collecting more data to rigorously test whether plants on islands have fewer species of flower visitors.

Honeybees visited White Mangrove flowers in Florida and Eleuthera, where they have been introduced; they do not occur on San Salvador or Exuma. Introduced honeybees could exert a significant effect on the androdioecious sexual system of White Mangrove. They tend to forage more within than between plants, thereby transferring more self-pollen and reducing the mating opportunities for male plants. It is possible that honeybees could lead to the local extinction of male plants, leaving only hermaphroditic plants in those populations.

INTRODUCTION

Islands typically have fewer species of plants and animals than mainlands (MacArthur and Wilson 1967, Simberloff and Wilson 1969, Lack 1976). This also appears to be true for the pollinator communities that have been studied (Woodell 1979, Garcia 2000, Bernadello *et al.*

2001). Also, the types of pollinators on islands typically differ from those on the mainlands, and pollinators tend to be more generalized and small-sized islands on (Carlquist 1974, Feinsinger and Swarm 1982, McMullen 1993, Barrett 1996). Pollinator populations have also been assumed to be less abundant on islands (Feinsinger et al. 1982, Spears 1987, Anderson et al. 2001, Bernadello et al. 2001), although theory suggests that species populations may increase because there are fewer competitors or predators (MacArthur and Wilson 1967, MacArthur 1972, George 1987). Consequently, a plant species on an island may have a less diverse assemblage of pollinators than the same species on the mainland. Additionally, plant species may have different types of pollinators on islands and mainlands; some pollinator groups may be absent or pollinator species may be more generalized. Differences in the constituency of the pollinator community or in pollinator behavior may have consequences for the evolution of floral traits and breeding systems (Barrett 1996, Temeles and Kress 2003).

White Mangrove (Laguncularia racemosa (L.) Gaertn. f.: Combretaceae) is a major component of the important mangrove zone in the Bahamas and Florida; it is found throughout the Bahamas, Florida, and Mexico, through Central America and the West Indies to South America, and along the coast of northwest Africa (Correll and Correll 1982, Tomlinson 1994). In the Bahamas, plants often grow along the edges of inland saline lakes (Kass and Stephens 1990, Smith 1993). In Florida, plants grow along estuaries, canals, lagoons, and protected bays (Landry, personal observations). Despite its prevalence, few studies exist on the flower visitors or pollinators of White Mangrove (Rathcke et al. 1996), or on how they vary in different geographic areas. In this study we present a preliminary report on the flower visitors of White Mangrove in the Bahamas and on mainland Florida. We report the species and number of individuals observed visiting flowers and compare these between mainland Florida and four islands in the Bahamas (San Salvador, Great and Little Exuma (grouped together throughout this paper as "Exuma"}, and Eleuthera).

White Mangrove

White Mangrove is a tree or woody shrub usually found on the landward side of the intertidal region that defines the mangrove zone. It flowers primarily during June and July but may flower as early as April and extend into August (Tomlinson 1994). Flowering occasionally occurs in December and January (Tomlinson 1994, Rathcke *et al* 1996, Rathcke and Landry personal observations).

Flowers of White Mangrove are 3-5 mm in diameter with five rounded, white petals (Correll and Correll 1982) and are displayed on racemes. The calyx forms a tube that holds nectar. On San Salvador, nectar production was 0.43 microliters per flower per day (N= 6 plants, S.D. = 0.178) (Rathcke *et al.* 2001A). In Florida, nectar production was 0.51 microliters per flower per day (N= 20 plants, S.D. = 0.230) (Landry, unpublished data).

Some populations are androdioecious (sensu Darwin 1877), i.e. plants are male (with only male flowers) or hermaphroditic (with perfect flowers having male and female function) (Rathcke et al. 2001B). However, other populations have no males and all plants are strictly hermaphroditic. In the Bahamas, populations on Exuma and Eleuthera appear to be hermaphroditic (Rathcke and Kass, unpublished data) whereas many populations on San Salvador have males, ranging in frequency from 2-25% at different sites (Rathcke et al. 2001B). Both hermaphroditic and androdioecious populations occur in Florida, with males ranging in frequency from 2-67% in androdioecious populations (Landry, unpublished data).

Hermaphrodite flowers can self-pollinate and self-fertilize on San Salvador (Rathcke et al. 2001B) and in Florida (Landry, unpublished data); pollination studies have not been conducted elsewhere. Hermaphroditic flowers are open for two days (anthers dehiscent on Day 1, stigma receptive on Day 2) whereas male flowers are open for only one day (Rathcke et al. 1996, Landry, personal observations).

METHODS

Species Lists

Lists of species and number of individuals that were observed and/or collected on White Mangrove flowers at each site were compiled from all available data. Ants were excluded because they are probably not acting as pollinators but are stealing nectar (Rico Gray 1989), although some ants may occasionally act as pollen vectors between flowers and could increase transfer of pollen within flowers. The amount of time spent observing flower visitors differed for the sites; the species lists may reflect these differences. The details of sampling are described below for each site.

San Salvador. On San Salvador Island, collections and observations of flower visitors were made by Beverly Rathcke, Lee Kass, Carol Landry, Nancy Elliott, Wanza Munroe, and Susan Danforth. Most of the observations of flower visitors were made on plants growing along the shores of the inland hypersaline Osprey and Oyster Ponds, located south of the Gerace Research Center. We recorded pollinators during the following periods: May 7-18, 1995 (L. Kass); June 9-18, 1995 (B. Rathcke, L. Kass); May 22 and 26-28, 1996 (L. Kass, N. Elliott); June 9-21, 1997 (B. Rathcke, L. Kass); June 15-23, 1999 (B. Rathcke, L. Kass, W. Munroe, C. Landry); and June 15-17, 2001 (B. Rathcke, L. Kass, S. Danforth, C. Landry). Some earlier results were published by Rathcke and colleagues (2001A). Identifications were made by Nancy Elliott. Specimens held by the National Entomological Collection in Nassau and by the Gerace Research Center were used as references for identification purposes.

Exuma. On Great and Little Exuma Islands, collections and observations of flower visitors were made by Beverly Rathcke and Nancy Elliott. The following three localities were visited: Mosstown, Great Exuma on June 22, 2001 (B. Rathcke, N. Elliott); William's Town, Little Exuma on June 23, 2001 (B. Rathcke, N. Elliott); and Georgetown, Great Exuma along the shore of Victoria Lake, June 24, 2001 (N. Elliott). Identifications were made by

Nancy Elliott. Specimens held by the National Entomological Collection in Nassau were used as references for identification purposes.

Eleuthera. On Eleuthera Island, collections and observations of flower visitors were made by Rena Booth on July 1, 2002 for two populations (Deep Creek by the Methodist Church Causeway and near the Green Castle Cemetery). Identifications were made by Rena Booth and Nancy Elliott. Specimens held by the National Entomological Collection in Nassau were used as references for identification purposes.

Florida. In Florida, collections and observations of flower visitors were made by Carol Landry, Beverly Rathcke, Lee Kass, Mark Kaufmann, Paula Russo, and Susan Danforth in seven populations along the southeastern coast and in the Keys. Pollinators were observed during the following periods: June 5-18 and July 6-11, 2000 (C. Landry, M. Kaufmann); June 19-30 and July 2-16, 2001 (C. Landry, B. Rathcke, M. Kaufmann, Paula Russo); and June 25-29 and July 2-12, 2002 (C. Landry, B. Rathcke, L. Kass, S. Danforth, M. Kaufmann). In 2002, many insects were identified in the field using photographs of previously collected insects. Identifications were made by Mark O'Brien, Museum of Zoology- Insect Division, University of Michigan, Ann Arbor.

Composition of Visitor Assemblages at Different Sites

Because absolute numbers of species and individuals reflect different amounts of collection times, the percentage of species and individuals are calculated for comparisons. This method allows a direct comparison of the proportional importance of flower visitors among sites.

Voucher Specimens

For insect collections made in the Bahamas, vouchers were deposited in the National Entomological Collection held at Botanical Gardens in Nassau. For collections made on San Salvador, duplicate specimens, if any, were

also deposited in the insect collection at the Gerace Research Center. Nomenclature for flower visitors in the Bahamas was 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; M. Deyrup, personal communication; R. Dirig, personal communication).

For insect collections made in Florida, vouchers were deposited in the University of Michigan Museum of Zoology- Insect Division in Ann Arbor. Nomenclature for flower visitors in Florida was based on Brothers and Carpenter (1993), museum collections, and Internet resources.

RESULTS

Species Lists

San Salvador Island. We recorded and tentatively identified 16 species (45 individuals) of flower visitors to White Mangrove (Table 1). Lepidopterans and Dipterans were the most frequent visitors (22 and 15 individuals, respectively), while Hymenopterans and Bananaquits visited infrequently (5 and 3 individuals, respectively).

Exuma. We recorded and tentatively identified 18 species (25 individuals) of flower visitors to White Mangrove (Table 1). Hymenopterans were the most frequent visitors (19 individuals, 11 wasps and 8 bees), while Dipterans and Lepidopterans visited infrequently (4 and 2 individuals, respectively).

Eleuthera. We recorded and tentatively identified 12 species (17 individuals) of flower visitors to White Mangrove (Table 1). Hymenopterans were the most frequent visitors (9 individuals, 3 wasps and 6 bees), while Dipterans visited less frequently (5 individuals). Lepidopterans and Coleopterans visited infrequently (2 and 1 individuals, respectively).

Florida. In Florida, many more species and individuals were seen visiting White Mangrove flowers. We recorded and tentatively identified 41 species (999 individuals) of flower visitors to White Mangrove (Table 1). Hymenopterans were the most frequent visitors (763)

individuals, 202 wasps and 561 bees). Dipterans visited less frequently (178 individuals), while Lepidopterans and Coleopterans were infrequent visitors (40 and 18 individuals, respectively).

Composition of Visitor Assemblages at Different Sites

The relative composition of visitors observed at each site is shown as percentages of species and individuals (Table 2). Wasps and bees were the most common species and most frequent visitors on Exuma (67% of species, 76% of visitors), Eleuthera (50% of species, 53% of visitors), and the Florida mainland (54% of species, 76% of visitors), while butterflies and moths were the most common species (50%) and most frequent visitors (54%) on San Salvador. Wasp species were more common on Exuma, while bee species were more common on Eleuthera. Equal numbers of wasp and bee species were observed in Florida; however, honeybees (Apis mellifera) visited more than twice as frequently as all other bees combined (38% versus 18%), and accounted for half of all Hymenopteran visitors.

DISCUSSION

White Mangrove is generalized for flower visitors, but attracted Hymenopterans on mainland Florida and two of the three islands more frequently than other visitors; on San Salvador, Lepidopterans were the most frequent visitors (Table 2). Generalization for pollination is 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).

Among these four sites, overlap in species is rare (Table 1). Only three visitor species were found on both the Florida mainland and an island: Sphex jamaicensis (Sphecidae) on Exuma; Apis mellifera (Apidae) on Eleuthera; and Ascia monuste (Pieridae) on San Salvador (but possibly different subspecies). Species found visiting White Mangrove flowers on both San Salvador and Exuma are: Kricogonia lyside

(Pieridae), Centris versicolor (Anthophoridae), Megachile poeyi alleni (Megachilidae), and Campsomeris trifasciata (Scoliidae) (but different subspecies). Only one species was found visiting White Mangrove flowers on both San Salvador and Eleuthera- Palpada albifrons (Syrphidae). Exuma and Eleuthera did not have any visitor species in common. The lack of species overlap is not unexpected; many plant species that are distributed over broad geographic areas are known to have different pollinators in different regions, particularly if the plants' distributions are not continuous. While insect pollinators in the tropics and subtropics may have limited distributions, pollinator communities in different geographic areas include different species performing the same functional role (ie. pollinating White Mangrove flowers). However, our insect vouchers have only been identified to the generic level in many cases; further work on identification of the voucher specimens is needed to determine if a greater proportion of pollinator species overlap is present than indicated by these data.

Overlap in genera is also rare (Table 1). Genera represented at more than one site include: Palpada (Syrphidae) on San Salvador and Eleuthera; Megachile (Megachilidae) on San Salvador and Exuma; Pachodynerus (Vespidae) and Polistes (Vespidae) on Exuma and the Florida mainland; Campsomeris (Scoliidae) on San Salvador, Exuma, and the Florida mainland; and Agapostemon (Halictidae) on Exuma, Eleuthera, and the Florida mainland. Of these genera, only Palpada, Polistes and Campsomeris voucher specimens have been identified to the species level; it is possible that other genera listed here are represented by only one species. Again, additional work on voucher specimen identification is necessary for clarification.

Overlap in families is common (Table 1). Twenty-seven families are represented in four insect orders and one bird order. Fifteen of the insect families were represented at two or more sites (56% of all families); 14 of those families were represented on mainland Florida. Members of eight of the families were found at three sites, and no family was represented at all four sites.

Although a previous study described wasps and bees as the most frequent visitors on San Salvador (Rathcke et al. 2001A), when combined with data collected since that study. butterflies and moths are the most common visitors. We observed six butterfly species and two moth species (diurnal wasp mimics) visiting White Mangrove on San Salvador, fully 50% of the species recorded. The high frequency of butterfly visitors on San Salvador was surprising, as White Mangrove flowers do not produce much nectar and their small size and urn- or cup-like shape are not indicative of "butterfly flowers". The frequent visits by butterflies may reflect the proximity of Black Mangrove (Avicennia germinans), which is often visited by butterflies (Rathcke et al. 2001A). Miller and colleagues (1992) recorded eight butterfly species visiting Black Mangrove flowers on other islands, but did not report observations on White Mangrove. However, Black Mangrove is also found in close proximity to White Mangrove in Florida and the flowering phenology overlaps there as it does on San Salvador, yet butterfly visitors are proportionally uncommon in Florida. We documented 22 butterflies and moths visiting flowers on San Salvador and only 40 butterflies in Florida, despite considerably more time spent observing floral visitors in Florida.

Equal numbers of bee and wasp visitor species were observed on White Mangrove flowers in Florida, while twice as many wasp species visited White Mangrove as bee species on Exuma, and twice as many bee species visited as wasp species on Eleuthera. Whether the proportional differences of wasp and bee species on Eleuthera and Exuma is due to real differences in the distribution or foraging behaviors of insects on the two islands, or if it is an artifact of insufficient observation time, remains unknown. In Florida, bees have been reported as common visitors to flowers of White Mangrove (Tomlinson 1980, 1994). However, many of these bees were probably honeybees (Apis mellifera) or bumblebees (Bombus species). Bumblebees do not occur anywhere in the Bahamas. while honeybees have been introduced to a number of Bahamian Islands, Eleuthera, Grand Bahama, Long Island, North

Andros, and New Providence. Honeybees are a major component of the pollinator community in Florida and may have a large impact on the mating system of White Mangrove populations: they represent only 2.5% of the species recorded but account for 38% of all visitors to White Mangrove, and half of all Hymenopteran visitors. Honeybees are very aggressive pollinators. often excluding other pollinator species from flowers, and have been observed chasing other species away from White Mangrove (Landry and Kass, personal observations). Additionally, honeybees appear to increase the selfing rates of White Mangrove because individuals tend to stay and forage within plants, transferring selfpollen between flowers; most of the other visitor species tend to move between plants and transfer cross-pollen. Therefore, honeybees may also indirectly decrease cross-pollination and change the breeding system of White Mangrove. Additional research on pollinator behavior and male frequencies in different White Mangrove populations in Florida also supports this possibility (Landry, unpublished data). Large numbers of honeybees could lead to the reduction or elimination of male plants within populations of White Mangrove. Indeed, strictly hermaphroditic populations of White Mangrove in Florida have a higher proportion of honeybee visitors than androdioecious populations (Landry, unpublished data).

In general, many more visitors were recorded in Florida relative to the Bahama Islands and considerably more time was spent conducting observations in Florida. Therefore, differences in observation time may account for some portion of the difference in visitor numbers and in the number of species observed. Our data does not refute any of the predictions of island-mainland biogeography; fewer visitor species and fewer individuals were recorded on the Bahamian Islands than in Florida. However, more observation time is needed on the Bahamian Islands for a rigorous test of these predictions.

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Table 1: Species list of floral visitors to White Mangrove on three Bahamian Islands and mainland Florida.

Order Coleoptera	Family	Genus/Species	Florida	San Sal	Exuma	Eleuthera
	Buprestridae:	Acmaeodera confusa unidentified species	FL			EL
	Oedemeridae:	Oxacis sp. #1	FL			LL
	Occombination.	Oxacis sp. #2	FL			
	Scarabaeidae:	Euphoria sepulchralis	FL			
Lepidoptera	Sommer and the second s	zupnertu sepunem um				
Lopidopioia	Pyralidae:	unidentified species	FL			
	Ctenuchidae:	Empyreuma sp.		SS		
		Eunomia sp.		SS		
	Hesperiidae:	Copaeodes minima	FL			
		Phocides pigmalion	FL			
		Ephyriades brunnea		SS		
		unidentified species				EL
	Lycaenidae:	Brephidium exilis isophthalma		SS		
	Pieridae:	Ascia monuste	FL			
		Ascia monuste eubotea		SS		
		Kricogonia lyside		SS	EX	
		Phoebus sp.		SS	~	
	Nymphalidae:	Junonia evarete	FL			
	- · yL	Memphis echemus				EL
	Heliconidae:	Agraulis vanillae insularis		SS		22
Diptera						
_ 	Syrphidae:	Eristalis albifrons	FL			
	J 1	Eristalis sp.	FL			
		?Baccha sp.	FL			
		?Neascia sp.	FL			
		?Toxomerus sp. #1	FL			
		?Toxomerus sp. #2	FL			
		Volucella sp.	FL			
		Palpada albifrons		SS		EL
		Palpada hortorum		SS		
	Bombyliidae:	Villa sp. #1	FL			
		Villa sp. #2	FL			
		Anthrax insulanus			EX	
		Chrysanthrax sp.			EX	
	Calliphoridae:	Callitrega macellaria		SS		
		0.1				

		unidentified species	FL			
	Muscidae:	unidentified species			EX	EL
	Tachinidae:	unidentified species				EL
Hymenoptera	1					
	Braconidae:	Iphiaulax sp.			EX	
	Tiphiidae:	Myzinum sp. #1	FL			
		Myzinum sp. #2	FL			
		Myzinum sp. #3	FL			
	Scoliidae:	Scolia nobilitata	FL			
		Campsomeris trifasciata trifasciata		SS		
		Campsomeris trifasciata nassauensi	S		EX	
		Campsomeris sp.	FL			
	Vespidae:	Pachodynerus cubensis bahamensis			EX	
		Pachodynerus sp.	FL			
		?Parancistrocerus				EL
		Euodynerus sp.	FL			
		Polistes annularis	FL			
		Polistes exclamans	FL			
		Polistes metricus	FL			
		Polistes bahamensis picturatus			EX	
		Mischocyttarus cubensis			EX	
	Pompilidae:	Pepsis ruficornis			EX	
	Sphecidae:	Sphex jamaicensis	FL		EX	
		Stictia signata			EX	
	Chalcididae:	unidentified species				EL
	Megachilidae:	Megachile poeyi alleni		SS	EX	
		Megachile sp.		SS		
		Coelioxys sp.	FL			
	Halictidae:	Agapostemon sp.	FL		EX	EL
		Augochlora sp.	FL			
		Nomia sp.	FL			
		unidentified species				EL
	Anthophoridae:	Melissodes sp.	FL			
		Centris versicolor		SS	EX	
		Xylocopa virginica	FL			

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	Xylocopa sp.	FL	
Apidae:	Apis mellifera	FL	EL
	Bombus sp. #1	FL	
	Bombus sp. #2	FL	
	Bombus sp. #3	FL	
Unidentified	l bee		EX

Birds

Emberizidae: Coereba flaeveola SS

Table 2. Relative composition of flower visitors of White Mangrove on the Bahama Islands and Florida Mainland. Percentages of total number of species and total number of individual visitors observed at each site. Note that the Hymenoptera are subdivided into wasps and bees and the introduced honeybee, Apis mellifera.

	Florida	San Sal	Exuma	Eleuthera
COLEOPTERA				
% of Species	10 %	0	0	8 %
% of Visitors	2 %	0	0	7 %
LEPIDOPTERA				
% of Species	12 %	50 %	11 %	17 %
% of Visitors	4 %	54 %	8 %	13 %
DIPTERA				
% of Species	24 %	19 %	22 %	25 %
% of Visitors	18 %	29 %	16 %	27 %
HYMENOPTERA (no ants)				
% of Species	54 %	25 %	67 %	50 %
% of Visitors	76 %	10 %	76 %	53 %
Wasps				
% of Species	27 %	6 %	44 %	17 %
% of Visitors	20 %	2 %	44 %	27 %
Bees				
% of Species	27 %	19 %	22 %	33 %
% of Visitors	56 %	7 %	32 %	27 %
% Apis mellifera	38 %	0	0	7 %
BIRDS				
% of Species	0	6 %	0	0
% of Visitors	0	7 %	0	0