

**PROCEEDINGS
OF THE
SIXTH SYMPOSIUM
ON THE
NATURAL HISTORY OF THE BAHAMAS**

Edited by
Nancy B. Elliott
D. Craig Edwards
and
Paul J. Godfrey

with additional editorial assistance from
Linda A. Swift and Melinda M. Godfrey

Production Editors
Daniel R. Suchy
Nicole G. Suchy

**Bahamian Field Station, Ltd.
San Salvador, Bahamas
1996**

Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

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Printed in USA by Don Heuer

ISBN 0-935909-60-5

BIOGEOGRAPHY OF BAHAMIAN WASPS

Nancy B. Elliott
Department of Biology
Siena College
Loudonville, NY 12211

William M. Elliott*
Department of Biology
Hartwick College
Oneonta, NY 13820

* Died August 23, 1994

ABSTRACT

Geologically there are three distinct groups of Bahamian Islands. The northern and central Bahamas lie on one of two shallow banks, the Great and Little Bahama Banks, which were united into two larger land masses during the Pleistocene. Islands of the southeastern Bahamas are isolated from each other by several deep channels. San Salvador and Rum Cay lie between the banks and the southeastern islands. We compared wasp species composition for groups of islands to test the hypothesis that the islands' geologic history had affected their faunas.

The mean proportion of species shared by pairs of islands on the same bank (Mean + SE = 0.57 + 0.02) was greater than that for islands on different banks (0.43 + 0.04). The southeastern islands shared a mean of 0.21 + 0.03 species with each other and between 0.24 and 0.06 of their species with the banks. San Salvador shared 0.34 + 0.04 of its species with the Little Bahama Bank, 0.44 + 0.04 with the Great Bahama Bank, and 0.17 + 0.03 with the southern islands.

INTRODUCTION

Geologically and historically there are three groups of islands in the Bahamas Archipelago. The islands of the northern and central Bahamas lie on one of two shallow bank systems; the Little Bahama Bank unites the northernmost islands of Grand Bahama and the Abacos, and the Great Bahama Bank underlies the islands of the central Bahamas

including Andros, New Providence, the Biminis, Eleuthera, the Exumas, Long and Cat Islands. These banks are so shallow that during the Wisconsin Glaciation, they formed two large but distinct land masses (Correll, 1979; Pregill and Olsen, 1981). Another group of islands in the southeastern Bahamas lie on isolated banks and were not joined during the Pleistocene. They include Crooked Island, separated from the Great Bahama Bank by the Crooked Island Passage, Mayaguana, which is further separated by the deep water of the Mayaguana Passage, and Inagua, separated from the first two by the Caicos Passage (Buden, 1981; Correll, 1979; Miller et al., 1992). A pair of islands (San Salvador and Rum Cay) lie intermediate between the banks and the southern islands.

Since 1992 we have conducted studies to test the hypothesis that the geologic history of the Bahamas has affected the composition of its wasp faunas. Islands united on the same bank system should have more species in common with each other than with islands on the other bank. Each of the isolated islands of the southern Bahamas should have a distinctive fauna. Because of the intermediate position occupied by San Salvador, it should have faunal similarities with the islands of the banks as well as the southeastern islands.

MATERIALS AND METHODS

Between January and May 1992, we collected wasps on Grand Bahama and Great Abaco Islands on the Little Bahama Bank, and on Andros, Great Exuma, Long Island, Cat

Island, and Eleuthera on the Great Bahama Bank. Additional collecting on these banks was done as follows: June 1993: Grand Bahama and Great Abaco; June 1994: North Andros and Eleuthera. We had also collected specimens on Long Island in July 1990. We collected on the southeastern islands as follows: Great Inagua, December 1992 and early January 1993; Mayaguana, December 1992 and early January 1993; Crooked Island, June 1995. Wasps have been collected on San Salvador Island by the senior author and students from Hartwick and Siena Colleges since 1975. In all cases, collecting involved walking along roads and trails and netting the wasps seen.

We calculated an index of similarity for each pair of islands by dividing the number of shared species by the total number of species on both the islands. We then averaged the

values obtained for each island pair to determine the relative proportion of shared species for each group of islands we wished to compare. Values reported are means + standard error.

RESULTS

Family distributions and the total number of species collected on each island are listed in Table 1. So far a total of 69 species of aculeate wasps have been collected, including 29 species from the islands of the Little Bahama Bank, 44 from the islands of the Great Bahama Bank, 31 from San Salvador, and 25 from the southeastern islands. There were an average of $22 + 2.5$ species per island; the islands on the Little Bahama Bank averaged $23.5 + 1.5$; those on the Great Bahama Bank

TABLE 1

Number of Species of Aculeate Wasps by Family for 11 Bahamian Islands Families are SCOLiidae, TIPHiidae, MUTillidae, POMPilidae, VESPidae and SPHECidae

ISLAND	SCOL	TIPH	MUT	POMP	VESP	SPHEC	TOTAL
Grand Bahama	3	1	0	1	7	13	25
Gt. Abaco	3	0	0	1	7	11	22
N. Andros	3	1	0	3	7	11	25
Eleuthera	2	0	1	6	10	15	34
Gt. Exuma	2	1	1	2	7	12	25
Cat Isl.	3	0	1	2	8	12	26
Long Isl.	2	0	0	5	7	12	26
San Salvador	2	3	0	6	8	12	31
Gt. Inagua	1	0	0	4	1	8	16
Mayaguana	2	1	0	0	1	4	8
Crooked Is	1	0	0	1	1	5	8
Total Species	4	4	1	15	16	29	69

averaged 27.2 ± 1.7 and the three southern islands averaged 10.7 ± 2.7 . We collected the greatest number of species (34) from Eleuthera and only 8 from both Crooked Island and Mayaguana.

Comparisons of the mean proportion of wasp species shared by pairs of islands in various categories are shown in Figure 1. The proportion of shared species for islands on the same bank system was 0.57 ± 0.02 , and 0.42 ± 0.04 for islands on different banks. The average proportion of species shared among the three isolated southeastern islands was 0.21 ± 0.03 .

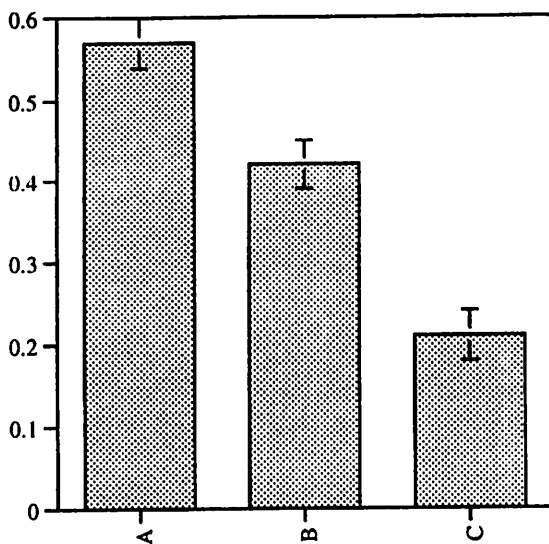


Figure 1. Comparison of mean proportion of wasp species shared by pairs of islands in the following categories: A. Islands on the same bank, B. Islands on different banks, C. The isolated southeastern islands: Crooked Island, Mayaguana and Great Inagua. (Error bars represent a mean standard error of 0.03).

The proportion of wasp species that the three southern islands had in common with the Little Bahama Bank was 0.10 ± 0.01 , and with the Great Bahama Bank 0.14 ± 0.01 ; they had a mean of 0.17 ± 0.03 of their species in common with San Salvador (Fig. 2a). Crooked Island shared between 16 and 24% of its species with the other islands groups (Fig. 2b). This was the highest percentage of species any of these islands shared with the others.

Mayaguana and Inagua each shared 11% or fewer of their species with the islands of the Bahama Banks (Fig. 2 c, d). Mayaguana had 11% of its species in common with San Salvador, and Great Inagua 20%.

The proportion of wasp species San Salvador shared with islands of the Little Bahama Bank was 0.34 ± 0.04 , and with the islands of the Great Bahama Bank, 0.44 ± 0.04 ; the proportion of wasp species it shared with the southern islands was 0.17 ± 0.03 (Fig. 3).

Table 2 reports island records for thirty-five of the common species collected during the study. Omitted are those species represented by a single specimen, and most for which specific names have not yet been obtained. Only two species, the scoliid, *Campsomeris trifasciata nassauensis* and the sphecid *Sphex jamaicensis*, occurred on every island. We collected nine species on at least some of the islands of both banks and on San Salvador. Five more occurred on some or all the islands of the Great Bahama Bank and on San Salvador. Four species were found on some or all the bank islands, on San Salvador and on Crooked Island.

A few species were restricted to islands on the eastern flank of the Great Bahama Bank; they included *Pepsis marginata*, an *Ammophila* species, and an as yet undetermined mutillid.

Some species had more restricted distributions. Eight of the fifteen pompilids so far determined were found on only a single island. A pompilid of the genus *Poecilopompilus* occurred on San Salvador and on Great Inagua; the sphecid, *Cerceris wallingensis* had a similar distribution. Mayaguana and Great Inagua each had an endemic species or subspecies of *Pachodynerus*: *Pachodynerus linda* on the former, and *Pachodynerus tibialis barbouri* on the latter. San Salvador was the only island on which *Tachytes tricinctus* was found, but there was another species in the genus on Great Inagua. Inagua had three additional species of pompilids, including one in the genus *Pepsis* that was collected nowhere else during the study.

DISCUSSION

Our findings that islands on the same

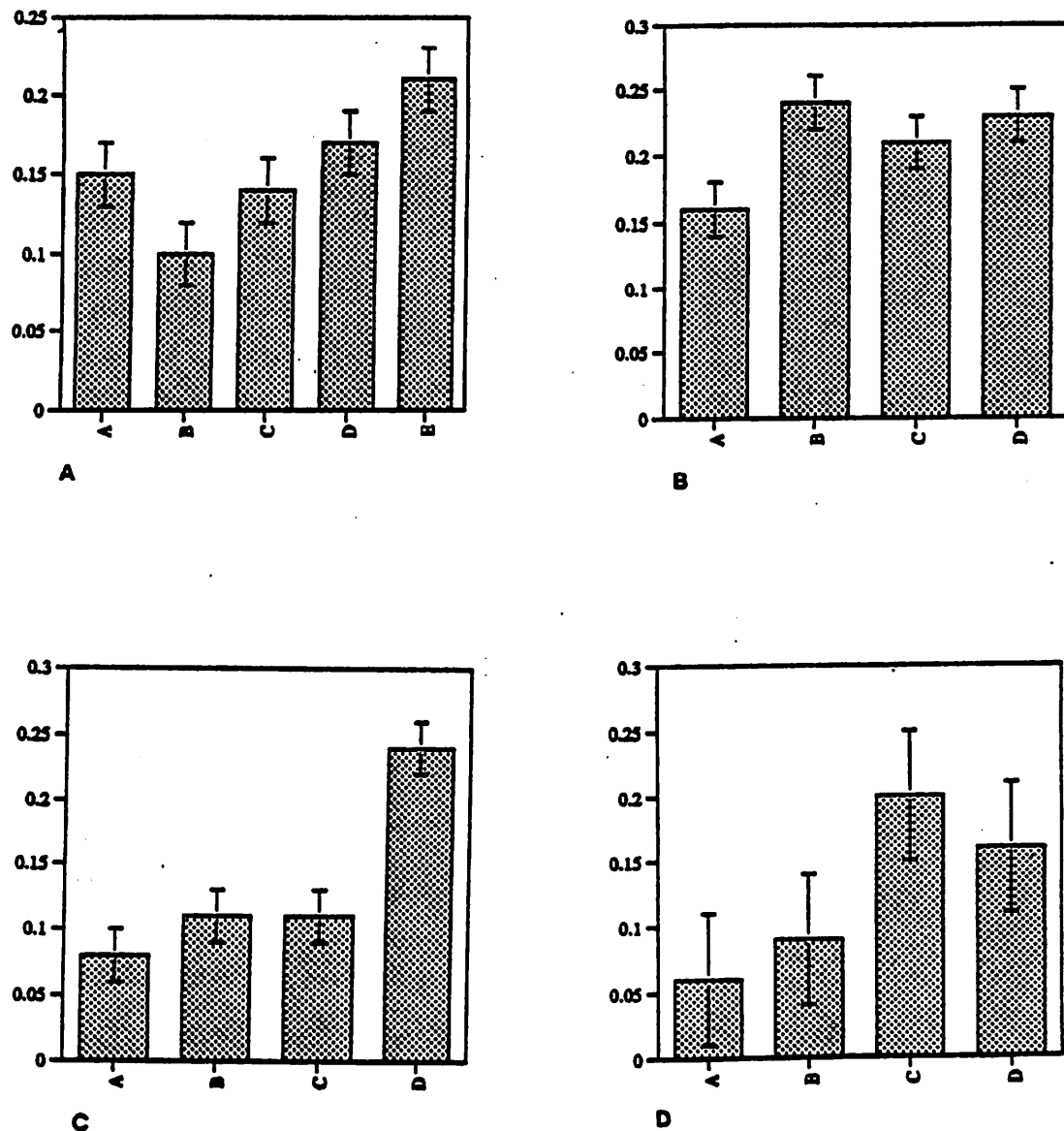


Figure 2. Faunal comparisons between the three southeastern islands (Crooked Island, Mayaguana, and Great Inagua) and other groups of islands.

- 2A. Mean proportion of species all three islands shared with other groups of islands as follows: A. All islands of the Bahamas, B. Islands of the Little Bahama Bank, C. Islands of the Great Bahama Bank, D. San Salvador, E. Other southeastern islands. (Error bars represent an average standard error of 0.02).
- 2B. Proportion of wasp species Crooked Island shared with other groups of islands as follows: A. Islands of the Little Bahama Bank, B. Islands of the Great Bahama Bank, C. San Salvador, D. Other southeastern islands. (Error bars represent an average standard error of 0.02).
- 2C. Proportion of wasp species Mayaguana shared with other groups of islands as follows: A. Islands of the Little Bahama Bank, B. Islands of the Great Bahama Bank, C. San Savador, D. Other southeastern islands. (Error bars represent an average standard error 0.02).
- 2D. Proportion of wasp species Great Inagua shared with other groups of islands as follows: A. Islands of the Little Bahama Bank, B. Islands of the Great Bahama Bank, C. San Salvador, D. Other Southeastern Islands. Error bars represent an average standard error of 0.05).

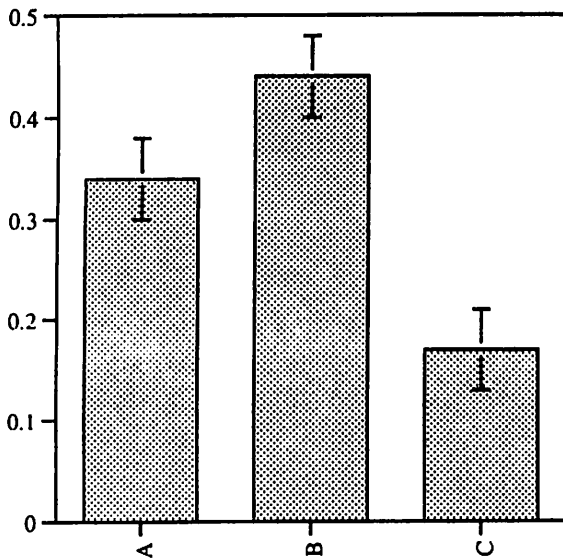


Figure 3. Proportion of wasp species San Salvador shared with other groups of islands as follows: A. Islands of the Little Bahama Bank, B. Islands of the Great Bahama Bank, C. Southeastern Islands. (Error bars represent an average standard error of 0.04).

bank shared a larger proportion of species with each other than with islands on the other bank support our general hypothesis. The values we report here differ slightly from those previously reported (0.56 ± 0.03 for islands on the same banks, and 0.44 ± 0.03 for islands on different banks; Elliott & Elliott, 1994) because of additional collecting on Grand Bahama and Abaco in 1993 and North Andros and Eleuthera in 1994. Also, as predicted, the faunas on islands of the southeastern Bahamas differed markedly from the islands of both banks and from each other.

Results for San Salvador are certainly affected by our many years of collecting there. In fact, the thirty-one species reported probably represent the complete wasp fauna of the island; I have collected no new species there since 1986. However, Buden (1981) reported that the intermediate position of San Salvador between the Great Bahama Bank and the southeastern islands of the Bahamas played a role in the diversity of its vertebrates, resulting in faunal affinities with both the Great Bahama Bank and the islands to the South. I have found the same to be true for

San Salvador's wasp community. Nine of the wasp species that are widely distributed on both the Great and Little Bahama Banks also occur on San Salvador but no further south. Five additional species occur only on the islands of the Great Bahama Bank and on San Salvador, and three more occur on one or both of the banks, on San Salvador and on Crooked Island. The latter three species include a widely distributed subspecies of *Polistes exclamans*, *P. e. picturatus*, a pompilid endemic to the Bahamas, *Anoplius insignis bahamas*, and a widely distributed North American sphecid, *Tachysphex similis*. There were also a few species that occurred on some or all the islands of the banks, San Salvador, and one or more of the southern islands in addition to or instead of Crooked Island. These distributions seem to indicate that San Salvador's geographic position affects the species composition of its insect community and also that it may serve as a steppingstone between the Bahama Banks and the southeastern Bahamas.

The widely distributed species *Polistes exclamans* has several subspecies occurring in the Bahamas (Bequaert and Salt, 1931). The most widely distributed of the subspecies, *P. e. picturatus*, occurs on the Little Bahama Bank, most of the islands of the Great Bahama Bank, and on San Salvador and Crooked Islands. A different subspecies, *P. e. bahamensis*, occurs on Andros and a third subspecies, *P. e. bilineolatus* occurs on Bimini (Kromein, 1953). Two other species of Polistinae, *Polistes major* and *Mischocyttarus cubensis* have similar Bahamian distributions, occurring on all islands of both banks and on San Salvador. We did not collect any social vespids from either Mayaguana or Great Inagua. However, Alan Bolten (personal communication) says that there are *Polistes* on the latter island, and Elliott et al. (1979) reported examining museum specimens of *P. e. picturatus* from Mayaguana. Social wasps are usually easily collected, and occur around human habitations, so at the very least, our failure to collect them on these islands must indicate that they are relatively rare there.

There are five species of *Pachodynerus* in the Bahamas (Menke, 1986). Both *P. scrupeus* and *P. cubensis* are Cuban species, although Bequaert and Salt (1931) described a

TABLE 2

Occurrences of 35 Species of Wasps on the Little Bahama Bank (LBB), Great Bahama Bank (GBB), San Salvador (SS), Crooked Island (CR), Mayaguana (MY) and Inagua (IN). For the banks, X = species occurred on all the islands surveyed; integer = number of islands where the species occurred.

SPECIES	LBB	GBB	SS	CR	MY	IN
SCOLIIDAE						
<i>Campsomeris trifasciata nassauensis</i> Bradley	X	X	X	X	X	X
<i>Campsomeris atratus</i> (F.)	X	X	X			
TIPHIIDAE						
<i>Myzinum ephippium bahamensis</i> Krombein	1		X		X	X
MUTILLIDAE						
undetermined species		3				
POMPILIDAE						
<i>Pepsis marginatus</i> Beauvois		2				
<i>Pepsis saphyrus</i> Beauvois	1	X				
<i>Pepsis</i> sp.						X
<i>Anoplius insignis bahamas</i> Krombein		X	X	X		
<i>Anoplius fulgidus</i> (Cresson)		2	X			
<i>Poecilopompilus</i> sp.			X			X
VESPIDAE						
<i>Polistes exclamans picturatus</i> Beq & Salt	X	4	X	X		
<i>Polistes exclamans bahamensis</i> Beq & Salt		1				
<i>Polistes major</i> Palisot de Beauvois	X	X	X			
<i>Mischocyttarus cubensis</i> Saussure	X	X	X			
<i>Pachodynerus scrupeus</i> Zavattari	X	X	X			
<i>Pachodynerus cubensis bahamensis</i> Beq&Salt	X	X	X			
<i>Pachodynerus nasidens</i> (Latreille)		2	X			
<i>Pachodynerus tibialis barbouri</i> Bequaert						X
<i>Pachodynerus linda</i> Menke					X	
<i>Zeta abdominale</i> (Drury)		X	X			
SPHECIDAE						
<i>Tachysphex alayoi</i> Pulawski	1	2	X			
<i>Tachysphex similis</i> Rohwer	X	X	X	X		
<i>Tachytes tricinctus</i> (F.)			X			
<i>Tachytes</i> sp.						X
<i>Trypoxylon</i> sp.		4	X			
<i>Sceliphron jamaicense</i> (F.)		4	X	X		X
<i>Sphex jamaicensis</i> (Drury)	X	X	X	X	X	X
<i>Prionyx thomae</i> (F.)		4	X	X	X	X
<i>Ammophila</i> sp.		4				
<i>Stictia signata</i> (L.)	X	X	X			
<i>Microbembix monodonta</i> (Say)	X	3	X			
<i>Cerceris wallingensis</i> Elliott & Salbert			X			X
<i>Cerceris cubensis</i> Cresson		2	X			
<i>Ectemnius auriceps</i> Cresson	X	1	X			X
<i>Oxybelus analis bimini</i> Krombein	X	X	X			

Bahamian subspecies of *P. scrupeus*, *P. s. bahamensis* which Menke (1986) has now assigned to *P. cubensis* instead. In the Bahamas, both species are restricted to the islands on both Bahama Banks and San Salvador. The distribution of these species suggests that the Pleistocene island of Paleoprovidence might have been the point from which these Cuban species spread throughout the Bahamas. A similar distribution occurs for another Cuban vespid, *Mischocyttarus cubensis*. *Pachodynerus nasidens* has a disjunct distribution in the Bahamas, but it has a similar kind of distribution on Pacific Islands (Menke, 1986), suggesting its ability to hitchhike on human transportation. *Pachodynerus linda* was described from Mayaguana (Menke, 1986) and as far as is known, is endemic to that island. *P. tibialis* is found on Hispaniola, and a subspecies, *P. t. barbouri* was described from a single specimen collected on Great Inagua (Bequaert, 1948). The specimens we collected there are identifiable as this form. Menke (1986) suggests that examination of a larger series of specimens might indicate that it is a separate species; it is at least an endemic subspecies. Thus among the *Pachodynerus*, there are two species found throughout the banks and on San Salvador, one opportunistic species, and two endemics from the southeastern islands.

Among Bahamian tarantula hawks in the genus *Pepsis* the most widely distributed species, *Pepsis saphyrus*, occurs on Grand Bahama and on all the islands of the Great Bahama Bank that we sampled; we did not collect it from any of the other islands. Perhaps the absence of the large ground spiders that are its prey precludes its occurrence on some of these islands. *Pepsis marginata* was collected on Eleuthera and Long Island during our study, but is also reported from Bimini (Krombein, 1953) and New Providence (Campbell, 1978). A third species of *Pepsis*, as yet unidentified was collected only from Inagua.

As is the case for *P. marginata*, several other species were confined in their distribution to the islands along the eastern margin of the Great Bahama Bank. These include an as yet undetermined species of mutillid, and an *Ammophila* species, probably

Ammophila apicalis Guerin-Meneville (Menke, 1970). As we reported previously (Elliott and Elliott, 1994), Andros shows a number of distinctive differences from the other islands of the Great Bahama Bank, including an endemic subspecies of *Polistes exclamans*, *P. e. bahamensis*.

The tiphiid, *Myzinum ephippium bahamense*, shows an unusual distribution among the islands. It was originally described from females (holotype and 1 paratype) collected from Mayaguana and from males (allotype and 1 paratype) collected from Grand Bahama (Krombein, 1942). It has now also been collected from San Salvador and Inagua, and presumably populations must occur on islands of the Great Bahama Bank as well.

It is not surprising that Great Inagua has a distinctive fauna. As other authors have noted (e.g. Clench and Bjorndal, 1980; Miller et al., 1992), it is very arid, even in comparison with the nearby islands. Besides three distinctive pompilids, including a *Pepsis* species, and the *Pachodynerus* already mentioned, it had a unique species of *Tachytes*, and a nyssonine unlike those seen on other islands. There are also a few species which occur only on Inagua and San Salvador; these include a pompilid in the genus *Poecilopompilus* and the sphecid *Cerceris wallingensis*, which was previously considered to be endemic to San Salvador (Elliott et al., 1979).

In conclusion, the results of our study have supported our overall hypothesis. The islands on the same bank showed greater faunal similarity with each other than with islands on the other bank; the southern islands differed from the other islands in their faunas and had a higher degree of endemism. Mayaguana has at least one endemic, Inagua may have several. The intermediate geographic position of San Salvador has been a factor in the characteristics of its wasp community.

ACKNOWLEDGEMENTS

We thank the staff of the Bahamian Field Station on San Salvador for decades of support for our work there and for assisting us in arranging travel to the other islands. We are particularly grateful to Dr. and Mrs. Donald

Gerace for many years of friendship and support and to Dr. and Mrs. Daniel Suchy for their assistance in recent years. The staff of the Forfar Field Station assisted us during our collecting trip to Andros in 1992. We thank Dr. Maurice Isaacs, Bahamian Ministry of Agriculture, for permission to collect wasps throughout the Bahamas. Beth Wren Elliott assisted with collecting on Crooked Island in 1995.

Dr. F. E. Kurczewski, SUNY College of Environmental Science and Forestry, Syracuse, NY, determined the pompilids we collected during the study; Dr. W. J. Pulawski, California Academy of Sciences, determined the *Tachysphex* species, and Dr. A. S. Menke, USDA ARS, determined *Campsomeris atratus* and *Zeta abdominale* from our 1986 collections on San Salvador.

This research was supported in part by a grant from the National Geographic Society as well as by faculty research grants from our home institutions.

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