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Courtney M. Bass and David Bass

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Aquatic Invertebrate Community Structure in Water-filled Bracts of *Heliconia caribaea* (Heliconiaceae) on Saba, West Indies

Courtney M. Bass and **David Bass**
Department of Biology, University of Central Oklahoma, Edmond, Oklahoma, U.S.A. 73034.
dbass@uco.edu

ABSTRACT
The aquatic invertebrate community living in the liquid-filled bracts of *Heliconia caribaea* (Heliconiaceae) inflorescences was studied on Saba, a small island in the northeastern Caribbean Sea, during October 2006. Invertebrates were collected by inverting inflorescences (n=52) to drain all of the liquid and its contents from the bracts into zip-lock plastic bags. All 52 inflorescences had invertebrates present in their bracts. Totals of 15,282 individuals and 20 taxa were collected from the *H. caribaea* inflorescences, and all 20 taxa were found only in water-filled bracts of this plant on Saba. Immature dipterans and ascid mites comprised the most abundant groups found. An average of 6.2 species and a confidence interval of 294±101 individuals for each inflorescence were calculated. Spearman's rank order values indicated correlations between both the number of species and the population sizes and the volume of liquid in each inflorescence, findings that support the species-area aspect of island biogeography theory. The Mann-Whitney statistic indicated no significant differences in population sizes and species richness in collections made at different elevations. The Mann-Whitney statistic also indicated there were no significant differences in population sizes and species richness in collections made on the windward side of Saba compared with those from the leeward side of the island. Seventeen of the invertebrate taxa found living in the *H. caribaea* inflorescences are being reported from Saba for the first time.

Key words: Antilles, elevation, leeward, phytotelmata, Saba, species-area relationship, windward.

INTRODUCTION

Phytotelmata are structures formed by terrestrial plants that impound water. Such structures include modified leaves, leaf axils, flowers, stem holes or depressions, open fruits, and fallen leaves (Maguire 1971). The term "phytotelmata" is a Greek word meaning "plant pond" that was introduced by Varga who observed small bodies of water held in pitcher plants, bromeliads and teasel (Fish 1983). Lloyd (1942) cited observations by Rumphius in 1747 of surviving organisms among the dead remains of insects in the digestive fluid of Asian pitcher plants as the earliest record of the existence of an aquatic fauna inhabiting terrestrial plants. Scott (1914) noted the differences between fauna inhabiting terrestrial ponds and that of terrestrial plants, and referred to those plants containing aquatic fauna as "reservoir plants". Fish (1983) listed 29 families of plants forming phytotelmata from which aquatic insects have been reported.

Phytotelmata are formed by the highly modified bracts in the inflorescences of *Heliconia caribaea* L., commonly known as wild plantain or lobster claw (Fig. 1). This plant belongs to the family Heliconiaceae, which has a circumtropical distribution; however, *H. caribaea* is found primarily in the Caribbean region (Anonymous 2010). Water is pumped to the bracts through the roots of the plant (Bronstein 1986) with additional water accumulating through rainfall (Seifert and Seifert 1976; Seifert 1982). Often, aquatic invertebrate communities, dominated by dipteran larvae, develop in the fluid contained in the bracts (Richardson and Hull 2000). Although Skutch (1933) speculated that water-filled bracts may protect developing floral reproductive structures from herbivorous insects, Seifert and Seifert (1976) found that several species feed directly upon the submerged flowers. However, most of the invertebrates use nectar, bacteria, decaying floral structures and the bract lining as food resources (Seifert 1982; Naeem 1990). Very few quantitative investigations have examined these aquatic invertebrate communities in *Heliconia* inflorescences and none have been conducted with *H. caribaea* on Saba.

Objectives of this research were to: (1) determine how much water is present in the bracts of *H. caribaea* inflorescences; (2) determine the percent of *H. caribaea* inflorescences that contain invertebrates; (3) determine the invertebrate species present in *H. caribaea* bracts; (4) determine invertebrate population sizes for each inflorescence; (5) determine which invertebrates are most abundant in *H. caribaea* bracts; (6) compare *H. caribaea* inflorescence data from different sides of the island; (7) compare *H. caribaea* inflorescence data from different elevations; (8) compare the species occurring in *H. caribaea* bracts to the invertebrate species found in other aquatic habitats of Saba; and (9) compare the invertebrate fauna inhabiting water-filled bracts of *H. caribaea* in Saba to that found elsewhere in the Caribbean region.

MATERIALS AND METHODS

Study area

Saba is a small Caribbean island located in the northern end of the Lesser Antilles. The island is volcanic in

origin and is thought to have emerged from the ocean approximately 30,000 years ago, with its last major eruption about 5,000 years ago. Maximum elevation reaches 887 m and its surface area encompasses approximately 13 km^2 (McLean 2004). Samples from *H. caribaea* inflorescences were collected during October 2006 along the Mount Scenery Trail (17°37'44.0"-17°38'4.3"N, 63°14'6.1"-63°14'24.8"W) and the Sandy Cruz Trail (17°38'17.3"-17°38'24.6", 63°14.0'6.1"- 63°14.0'24.8"W) in Saba. The vegetation of these areas grows on steep slopes of a tropical seasonal forest with a closed canopy where *H. caribaea* occurs as an understory plant.

Fig. 1. *Heliconia caribaea* (L) inflorescence on Saba, West Indies.

Sampling and data analysis

Fifty-two plants bearing inflorescences were sampled and their locations, including elevations, were determined using a Garmin GPS. Each inflorescence was covered with a zip-lock plastic bag and inverted to drain all of the water and its contents into the bag. This non-destructive method of sampling may not have allowed for complete collection of some invertebrates that clung tightly to the floral structures. The volume of water from each inflorescence was measured using a graduated cylinder. Invertebrates were strained from the water through a 0.25 mm Nitex net, preserved in 70 percent ethanol, and transported to the laboratory. In the laboratory, the invertebrate samples were sorted, identified, and counted under a stereoscope. Identification of the invertebrates was determined primarily using keys by Merritt, Cummins and Berg (2008) and Thorp and Covich (2001), and the numbers were statistically analyzed following formulae provided by Brower *et al*. (1997) and using Sigma Plot 10.0 (Systat Software, Inc. 2006). All specimens were deposited in the Caribbean Invertebrate Section of the University of Central Oklahoma Natural History Museum. Several larval and pupal specimen of *Aedes* (*Howardina*) *busckii* (Coquillett) have been transferred to the Entomology Collection in the British Natural History Museum.

RESULTS

The number of bracts on the inflorescences in the samples ranged from 2-10, with an average of 7.0 bracts per inflorescence (Table 1). The volume of the water sampled ranged from 16-528 ml, with an average of 118.8 ml of fluid associated with each inflorescence. An average of 17.0 ml of fluid occurred in each bract (s^2=18.9).

All of the inflorescences sampled had aquatic invertebrates living in them, resulting in a total of 15,282 individuals and 20 taxa collected from the 52 inflorescences (Table 1-2). The ranges for the number of individuals and number of species per inflorescence were 7-1428 and 3-12 respectively. Ninety-five percent confidence intervals of 294±101 (193-395) individuals and 6.2±0.52 (5.65-6.69) species were calculated for each inflorescence (52). A Spearman's rank order correlation value of 0.585 (*P*=0.000001) was calculated when inflorescence volume and population size were compared, indicating a correlation existed between volume and the number of individuals. Furthermore, a Spearman's rank order correlation value of 0.335 (*P*=0.0155) indicated a correlation existed between inflorescence volume and species richness.

The most abundant taxa were *Aedes* (*Howardina*) *busckii* (Culicidae) and species belonging to the Ascidae (Gamasida), and the genera *Dasyhelia* (Ceratopogonidae), *Polypedilum* (Chironomidae) and *Alepia* (Psychodidae). Of these, *A. busckii* was the most frequently encountered comprising 71.1 percent of the individuals collected (Table 2). This culicid, known only from the Lesser Antilles, has been collected previously from Dominica, Martinique, Guadeloupe, Grenada and St. Eustatius (Stone 1969), and is likely the species reported as *Aedes* sp. from Saba by Bass (2008). The second most abundant taxon was an unidentified mite belonging to the

family Ascidae, making up 14.0 percent of the individuals. Single species each of *Polypedilum, Dasyhelia* and *Alepia* were the only other taxa collected that constituted over one percent of the individuals in the samples (Table 2).

Samples collected on the leeward side of Saba along the Sandy Cruz Trail were compared to samples taken on the windward side of the island along the Mount Scenery Trail (Table 1). Leeward side samples contained an average of 162.3 individuals per inflorescence, while those from the windward side had an average of 333.4 individuals per inflorescence. An average of 6.2 species was collected from each inflorescence on both sides of the island. Six species constituted over one percent of the in-

Table 1. Minimum, maximum, average per inflorescence, and total numerical for values number of individuals, number of species, volume of liquid, number of *H. caribaea* bracts, and elevation for all samples, leeward samples, windward samples, lower elevation samples, and higher elevation samples.

Sample Parameter	Minimum	Maximum	Average per Inflorescence	Total
All Samples (52)				
Number of Individuals	7	1,428	293.9	15,282
Number of Species	2	12	6.2	20
Volume of Liquid (ml)	16	528	118.8	6,179
Number of Bracts	2	10	7.0	363
Elevation (m)	489	820	696.0	
Leeward Samples (12)				
Number of Individuals	49	406	162.3	1,947
Number of Species	4	10	6.2	10
Volume of Liquid (ml)	52	154	96.7	1,160
Number of Bracts	5	9	6.9	83
Elevation (m)	536	665	579.2	
Windward Samples (40)				
Number of Individuals	7	1,428	333.4	13,335
Number of Species	2	12	6.2	20
Volume of Liquid (ml)	24	528	125.5	5,020
Number of Bracts	2	10	7.0	280
Elevation (m)	489	820	731.2	
Lower Elevation Samples (24)				
Number of Individuals	22	406	133.7	3,208
Number of Species	4	12	6.7	15
Volume of Liquid (ml)	16	209	108.1	2,594
Number of Bracts	2	9	6.8	163
Elevation (m)	489	713	565.4	
Higher Elevation Samples (28)				
Number of Individuals	7	1,428	431.2	12,074
Number of Species	2	10	5.8	20
Volume of Liquid (ml)	24	528	128.0	3,584
Number of Bracts	4	10	7.1	199
Elevation (m)	774	820	808.2	

dividuals collected on the leeward side, while only five species made up more than one percent of the individuals from the windward side. The most abundant species on both sides of the island was *A. busckii*. The average volume of liquid per inflorescence collected from the leeward side plants was 96.7 ml, whereas the average volume of liquid collected from inflorescences of the windward side plants was 125.5 ml. The average number of bracts per inflorescence, 6.9 and 7.0, differed very little between locations from plants on the leeward side and windward side respectively. The Mann-Whitney statistic (U=242.0, P=0.974) indicated there was no significant difference between invertebrate population sizes found in inflorescences existing on different sides of the island. In addition, the Mann-Whitney statistic (U=238.5, P=0.982) indicated there was no significant difference between invertebrate species richness found in inflorescences existing on different sides of the island.

The 52 collections were divided into two groups, based on elevations from where they were taken (Table 1). One set of samples was collected from an average elevation of 565.4 m asl (489-713 m asl), while the other set came from an average elevation of 808.2 m asl (774-820 m asl). Samples collected at the lower elevation had eight species that made up over one percent of the individuals, whereas those taken at higher elevations contained only four species that constituted over one percent of the individuals. The average number of individuals collected in the lower elevation samples was 133.7, while the average number of individuals in samples collected at higher elevations was 431.2. Samples collected from the lower elevations yielded a total of 15 species (average = 6.7 species/inflorescence) and samples taken from the upper elevations contained all 20 species (average = 5.8 species/inflorescence). At both elevations the dominate species was *A. busckii*. Samples taken from lower elevations contained an average volume of liquid per inflorescence of 108.1 ml, whereas samples taken from higher elevations had an average of 128.0 ml per inflorescence. The average number of bracts on inflorescences at lower elevations was 6.8, while inflorescences at higher elevations possessed an average 7.1 bracts. The Mann-Whitney statistic (U=435.0, P=0.071) indicated there was no significant difference between invertebrate population sizes found in inflorescences at different elevations. The Mann-Whitney statistic (U=250.5, P=0.111) also showed there was no significant difference between species richness found in inflorescences at different elevations.

Table 2. Taxa, average number of individuals per inflorescence, total number of individuals per inflorescence, and percent of total number of individuals for all samples.

Taxa	Average per Inflorescence	Total	Percent of Total
Tubificidae	2.69	140	<1
Cyclopoida	0.06	3	<1
Ascidae	41.17	2141	14.0
Isotomidae	0.21	11	<1
Aedes (*Howardina*) *busckii*	208.96	10,869	71.1
Alepia sp.	4.54	236	1.5
Ceratopogonidae sp. 1	0.02	1	<1
Dasyhelia sp.	12.21	635	4.2
Dolochopodidae	0.57	29	<1
Ephydridae sp. 1	0.23	12	<1
Ephydridae sp. 2	1.87	97	<1
Metriocnemus sp.	0.02	1	<1
Orthocladiinae	0.04	2	<1
Orthocladiinae Genus E Epler	0.02	1	<1
Polypedilum sp.	17.42	906	5.9
Syrphidae	1.23	64	<1
Stratiomyidae	1.04	54	<1
Diptera sp. 1	1.08	56	<1
Diptera sp. 2	0.42	22	<1
Diptera sp. 3	0.04	2	<1

DISCUSSION

Population sizes and species richness

Very little information regarding invertebrate population sizes and the number of taxa inhabiting water-filled bracts of *H. caribaea* exists in the literature. Richardson and Hull (2000) reported averages of 232 and 258 individuals per *H. caribaea* inflorescence from field studies in Puerto Rico during 1996 and 1998 respectively. Their studies also found seven taxa constituted 94 percent of the total number of individuals in 1996 and 93 percent of the total number of individuals in 1998. Twenty-one and 22 taxa were recorded from their samples in 1996 and 1998 respectively. Data recorded by Richardson and Hull (2000) in Puerto Rico are somewhat similar to data we collected in Saba: an average of 294 individuals per

inflorescence and a total of 20 taxa were obtained from *H. caribaea* inflorescences (Table 1). Five taxa comprised 97 percent of individuals present in inflorescences of *H. caribaea* from Saba. Both larval and pupal stages of *A. busckii*, *Polypedilum* and *Dasyhelia* were collected. Sixteen of the 20 taxa found in these collections were dipterans, a finding similar to that reported by others (Richardson and Hull 2000) who studied inhabitants of *Heliconia* inflorescences. As noted earlier, the Saban collections were made by simply pouring water from the inflorescences, a non-destructive method that may have resulted in an underestimate of invertebrate populations.

Much variation exists in both the number of individuals present and species richness in different inflorescences. This is likely a reflection of the differences in ages of the inflorescences from which each collection was taken. Some inflorescences were relatively old and the dipteran larvae which developed in them had probably matured and emerged, hence the lower numbers in the collection from those inflorescences. Other inflorescences were younger, so they had not been present as a microhabitat for aquatic larval development as long.

The inflorescences of *H. caribaea* are seasonal. Although they are present for five to six months, the bracts deteriorate and hold water for only about 60-70 days (Richardson and Hull 2000). Therefore, invertebrates living in the bracts are specialized and have evolved faster life cycles than many of their relatives living in more permanent environments. Fish (1983) suggested that species which live in phytotelmata with higher turnover rates, such as *Heliconia*, are more specialized and exhibit greater habitat specificity than do those that inhabit phytotelmata with lower turnover rates. Many species of mosquito exist in temporary aquatic habitats and *A. busckii* is no exception. In addition to flower bracts of *Heliconia*, immature *A. busckii* have been found in rock holes, tree holes, broken and cut bamboo, fallen leaves, fruits and pods, and in the leaf axils of bromeliads and aroids (R. Harbach, pers. comm.). Dobkin (1990) described how ascid mites exhibit a specialized behaviour allowing them to be dispersed among *Heliconia trinidatis* L. inflorescences by visiting hummingbirds; a similar situation probably exists in this *H. caribaea* invertebrate community, as they were frequently observed near the plants.

Bass (2008) reported 18 invertebrate species from aquatic habitats such as forest pools, open cisterns, and small artificial ponds on Saba. Only three of those 18 taxa collected previously by Bass were associated with *H. caribaea* on the island: *Aedes, Dasyhelia* and Stratiomyidae. Elsewhere on the island, Bass did not find any *Polypedilum* or Ascidae, two of the more abundant taxa in the 52 collections from *H. caribaea* inflorescences. Therefore, 17 of the 20 taxa collected from these *H. caribaea* inflorescences were previously not known to exist on Saba and all 20 taxa associated with *H. caribaea* inflorescences were limited to that habitat on the island.

Studies of the *H. caribaea* fauna by Machado-Allison *et al*. (1983) in Venezuela and by Richardson *et al.* (2000) in Puerto Rico reveal many taxa similar to those found in the Saban phytotelmata, although fewer species were reported in the Venezuelan study. Machado-Allison *et al*. (1983) stated there should be more species of insect living in *Heliconia* bracts of mainland plants than in those of island plants. Interestingly, Machado-Allison *et al*. (1983) reported only about half the amount of water present in bracts as compared with Saba. Because the volume of water represents the habitat size, this may explain the lower species richness of the Venezuelan phytotelmata.

Species-area relationship

An aspect of island biogeography theory (MacArthur and Wilson 1967) predicts a positive correlation would exist between the size of the habitat and species richness. A Spearman's rank order correlation value of 0.335 (P=0.0155) was calculated when the volume of water in bracts and the number of species in each inflorescence were compared, indicating a correlation did exist. It is likely only a few invertebrate species are capable of inhabiting temporary aquatic habitats and a small amount of water is sufficient to support these species associated with *H. caribaea* inflorescences. However, this increase in species richness as volume increases may be limited because populations of common insects may increase more rapidly than additional species invading the liquid in the bract (Seifert 1975). A correlation value of 0.585 (P=0.000001) existed when comparing the amount of liquid in the bracts with the number of individuals inhabiting each inflorescence. This correlation was expected because a larger habitat has the potential to support more individuals.

Community succession

Richardson and Hull (2000) followed succession of the *H. caribaea* fauna in a mountain forest of Puerto Rico. They reported larval Ceratopogonidae were most abundant in younger bracts and declined in older bracts as decaying materials accumulated. Larval Psychodidae followed a similar pattern, although they lagged behind slightly. Those same trends were observed in the *H. caribaea* phytotelmata faunal samples collected in this current study from Saba. Because all instars of *A. busckii* larvae were present in all samples, these mosquitoes ap-

peared to have no preference for bract age – they simply required the liquid to be present in sufficient quantities for a long enough period to allow development to be completed.

CONCLUSION

The nine objectives originally proposed were addressed. Results of this investigation in Saba generally agree with other studies of aquatic invertebrate populations inhabiting *Heliconia* inflorescences in different tropical locations, including the presence of similar taxonomic groups. All 20 taxa reported in this study were found only in water-filled bracts of *H. caribaea* on Saba, and 17 of the 20 taxa are being reported from this island for the first time, increasing the total number of aquatic invertebrates known from Saba to 35 taxa.

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