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THE SUPRATIDAL FAUNA OF TWIN CAYS, BELIZE

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ABSTRACT

Previous supratidal surveys of Twin Cays have documented the role of insect diversity in forest structure and dynamics. Information on other supratidal groups is limited. During the winter and summer of 2004, decapods were surveyed using burrow counts, pitfall traps, time-constrained searches and arboreal counts. Lizard populations were measured in quadrat surveys, while snakes and crocodiles were subject to searches of specific habitat types. Crabs numerically dominated the non-insect fauna; the population of *Uca* spp. alone was estimated at over eight million individuals. Questions remain regarding the identification of bats seen at Twin Cays and the impact of a large feral dog population on the islands.

INTRODUCTION

The importance of subtidal mangrove fauna to marine biodiversity has been broadly established (Mumby et al., 2004). The role of the supratidal fauna is less well understood despite demonstrated critical importance to forest structure (Feller, 2002) and regeneration (McKee, 1995; Feller and McKee, 1999). The goals of this paper are: 1) to review literature relevant to our understanding of the supratidal fauna of Twin Cays, Belize; and 2) present new data on groups surveyed during the winter of 2003-2004 and summer of 2004.

The mangrove forest system of Twin Cays has been a study site for biologists since the creation of the Smithsonian Marine Field Station on nearby Carrie Bow Cay in the early 1970s (Rützler and Macintyre, 1982). Previous surveys of the supratidal community have focused primarily on the insect fauna. These studies indicated that insects are the most abundant and species-rich group of animals in the supratidal mangrove habitat (Rützler and Feller, 1988, 1996; Feller, 1995; Feller and Mathis, 1997). Nocturnal and endophytic feeding are common features among many of the mangrove-associated insect species. Because of these cryptic behaviors and the difficult environment for collecting, the complexity of the insect fauna associated with mangroves frequently has been underestimated. Huge arboreal nests (termitaria) and extensive carton-covered foraging trails of the termite *Nasutitermes* sp. are the most conspicuous signs of insect activity in the mangrove. However, ants (Formicidae) are ubiquitous and are clearly the most abundant terrestrial animals on these mangrove and coral cays. At

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least 20 of the 34 species known from the Belizean cays live in direct association with the mangroves, utilizing hollow twigs and branches as nest sites (Feller, 2002).

The saltwater surface and mudflats on mangrove islands provide habitats for aquatic and semiaquatic insects, including species representing several families of Diptera, Hemiptera, Odonata, and Coleoptera. Comparable habitats in the mainland mangrove support much greater diversity than the cays in this part of the insect fauna. The shore-fly family, Ephydridae, is particularly species-rich in mangrove habitats in Belize. So far, 55 species in this family have been collected along the margins of Twin Cays and other mangrove islands in the Stann Creek District and Turneffe Atoll (Mathis, 1989, 1990, 1991, 1992, 1993). Most species in this family are detritivores and feed on decaying vegetation along the shore. Like other taxa, shore-fly species occupying the cays are a subset of Belize's mainland fauna.

The mangrove canopy provides numerous supratidal habitats for insect herbivores. Each species of mangrove supports a distinctive suite of herbivores, but the damages are more apparent than the herbivores themselves (Feller, 1995). Some species are host specific. For example, *Ecdytophyla* sp., an apical bud moth, feeds exclusively inside the apical buds of *Rhizophora mangle*. The larvae of several moths, including *Megalopyge dyeri* (a puss moth) and *Oiketicus kirbii* (a bagworm), and crickets (Orthoptera) are generalists and feed on all species of mangrove at Twin Cays.

In addition to leaf-feeding herbivores, more than 35 species of wood-feeding insects have been collected from mangrove trees on the cays and mainland in Stann Creek District (Chemsak and Feller, 1988; Feller, 1995; Rützler and Feller, 1999). Although some of these woodborers feed on any available dead wood, several species specialize on living trees of a single species of mangrove. For example, live twigs on *R. mangle* host a feeding guild composed of at least seven species of specialized wood-boring beetles and moths (Feller and Mathis, 1997). Larval stages of these insects feed internally on these twigs, killing them in the process, and creating hollow cylinders of dead wood. Another group of woodborers feed opportunistically on these dead twigs, further modifying trees by constructing galleries and pupal chambers in living and dead woody tissue. These spaces provide critical habitats for ants and numerous other arthropods in the canopy that use them for food, nest sites, prey sites, and diurnal refuge. The animals that use these spaces include ants, spiders, isopods, myriapods, pseudoscorpions, scorpions, crickets, scales, psocopterans, mites, moths, roaches, thrips, buprestids, tenebrionids, anobiids, termites, and cerambycids. More than 70 species of arthropods are associated in some way with twigs in the *R. mangle* canopy (Plate 1).

On Twin Cays, some woodborers kill branches, which contributes more to the total leaf area lost from the canopy than do all of the leaf-feeding herbivores combined (Feller, 2002). For example, the larvae of the beetle *Elaphidion mimeticum* (Cerambycidae) feed on the wood of live trees and deeply girdle wood under the bark. This type of herbivory causes death of branches and boles distal to the girdled area. Frequent attacks by this beetle create numerous small gaps in the *R. mangle* canopy (Feller and McKee, 1999). Thus, insect population dynamics and herbivory have a direct impact on ecosystem-level processes such as forest regeneration, seedling dynamics, nutrient cycling, habitat diversity, and other factors related to light gaps.

Previous studies have suggested that mangroves do not host a characteristic or specialized fauna (Huffaker et al., 1984; Tomlinson, 1986). However, surveys of the insects at Twin Cays and other mangrove forests along the MesoAmerican Barrier Reef System provide evidence to the contrary. In these forests, *Marmara*, a genus of microlepidopteran tissue miners, is particularly diverse. *Rhizophora mangle* hosts at least four species of *Marmara,* each adapted and restricted to a single type of tissue in this host plant, including the leaf epidermis, propagule periderm, stem periderm, and aerial root periderm (Plate 1; Feller, 1995).

Other occupants of the mangrove supratidal at Twin Cays include two species of small snails: *Melampus coffeus* (the Coffee Bean Snail) and *Littoraria angulifera* (the Mangrove Periwinkle). *Melampus coffeus* is a detritivore, feeding on leaf litter at low tide (Proffitt et al., 1993), and may reach densities of 500 individuals/m^2 (Heard, 1982). Proffitt et al. (1993) found that the percentage of total mangrove leaf litter consumed by *M. coffeus* was unknown, but their data suggested that the snail's effects were considerable. *Littoraria angulifera* can occur in high densities near the mangrove shore, predominantly on *R. mangle* (Gutierrez, 1988). Juvenile snails, more prone to desiccation, are found closer to the waterline, but adults are found in all supratidal levels of the forest. This species is known to feed largely on fungi found just above the mean high water mark on mangrove prop roots and trunks (Kohlmeyer and Bebout, 1987).

Other than the fauna described above, little is known of other animal taxa that occupy the supratidal zone in Neotropical mangroves. To help fill this gap, the purpose of our study was to survey the decapod and reptile fauna of Twin Cays.

MATERIALS AND METHODS

Decapod Surveys

We conducted decapod surveys on Twin Cays during the winter of 2004 in the following habitat types described by Rodriguez and Feller (2004): Fringe, Mixed Woodland, Open Pond Dwarf, *Rhizophora* Dwarf, *Rhizophora/Avicennia* Dwarf, *Avicennia* Basin, Regenerated *Avicennia* Basin, *Avicennia* Orchard, *Avicennia* Scrub, Moribund, and Floc. We surveyed 30 1-m^2 quadrats with visual counts per habitat type, 10 Pitfall traps within a 25 m^2 area, and time-constrained searches of a 25 m^2 area.

Quadrats (1 m^2) were used to count *Uca* spp., *Goniopsis cruentata,* and *Ucides cordatus*, the three most common burrowing crabs on Twin Cays. After an initial study of burrow duration and occupancy, both crabs and crab holes were considered as part of these surveys. For *Uca* spp., burrows could not be distinguished conclusively among species and age classes and were consigned only to genus. Other burrows, most notably those of *G. cruentata* and *U. cordatus,* were distinctive.

Ten pitfall traps (Greenslade, 1964), consisting of 16 oz plastic keg cups, were randomly distributed in a 25 m^2 plot. The cups were sunk into the substrate level to the lip of the cup using a bulb planter. Using this size of pitfall limited the traps to smaller genera, but secured specimens not collected in any other manner. Traps were left in place overnight.

Time-constrained surveys used the same 25 m^2 plots as the pitfall traps. During a 1-hr time period, terrestrial debris was searched for decapods by overturning fallen branches, removing bark from stumps and snags, and sifting through coarse litter.

Aratus pisonii was targeted in species-specific searches of mangrove trees. To determine the density of this crab, a 1-m^2 quadrat was extended vertically from the ground through the top of canopy around the trunk. Two observers, one on either side of the tree, counted visible crabs. When only one observer was available, a plastic bag mounted on a pole was used to flush all crabs to one side of the tree where they were counted.

Reptile Surveys

Reptiles species were individually targeted in different survey types. Anoles and other diurnal lizards were counted within a 25 m^2 quadrat after a 15 min acclimatization period for the lizards to resume activity. Three surveys were conducted for lizards within each of eight dominant terrestrial habitat types. Boas were the focus of 1 hr time-constrained searches targeted on the limited raised sandy banks at the southern end of the East Island near Boa Flats. Crocodiles were surveyed at night along the interior of the Main Channel using a spotlight to reflect eyeshine.

RESULTS

Decapods

Uca spp. were relatively common in all habitat types with highest density in Mixed Woodland, *Avicennia* Orchard, and *Avicennia/Rhizophora* Dwarf stands (Table 1).

Table 1. Burrow surveys from 30 1-m^2 quadrats per habitat type at Twin Cays. Values are means ± 1 SD.

Habitat Type	*Uca* spp.	*Goniopsis cruentata*	*Ucides cordatus*
Mixed Woodland	42.9 ± 9.2	0.0 ± 0.0	0.1 ± 0.0
Fringe	15.8 ± 12.0	0.1 ± 0.0	0.0 ± 0.0
Avicennia Basin	18.3 ± 0.7	0.6 ± 0.0	0.6 ± 0.0
Avicennia Orchard	39.7 ± 10.8	0.0 ± 0.0	0.0 ± 0.0
Scrub	21.6 ± 7.8	0.1 ± 0.0	0.0 ± 0.0
Moribund	11.7 ± 7.1	0.0 ± 0.0	0.0 ± 0.0
Regenerated *Avicennia* Basin	10.8 ± 5.0	0.0 ± 0.0	0.0 ± 0.0
Avicennia/Rhizophora Dwarf	28.9 ± 2.8	0.0 ± 0.0	0.0 ± 0.0

Goniopsis cruentata and *U. cordatus* populations were patchy with highest densities, ~1 crab/m^2, in the *Avicennia* Basin stands (Plate 2). Using the area measurements of Rodriguez and Feller (2004), total crab numbers for habitat areas were extrapolated by multiplying the average density of crabs/m^2 by total area of habitat type. Based on this method, the total estimated *Uca* population of Twin Cays was ~ 8.3 million individuals (Table 2). *Goniopsis cruentata* and *U. cordatus* populations were approximately 23,000 and 20,000, respectively.

Table 2. Estimations of population sizes for *Uca* spp., *Goniopsis cruentata*, and *Ucides cordatus* at Twin Cays. Area for each habitat type is from Rodriguez and Feller (2004).

Habitat Type	Area (m^2)	*Uca* spp.	*Goniopsis cruentata*	*Ucides cordatus*
Mixed Woodland	115,102	4,941,725	3,837	15,347
Fringe	99,667	1,574,743	13,289	0
Avicennia Basin	5,842	106,909	3,310	3,505
Avicennia Orchard	12,033	477,309	0	0
Scrub	22,805	493,348	2,281	760
Moribund	3,124	36,645	0	0
Regenerated *Avicennia* Basin	8,174	88,279	0	0
Avicennia/Rhizophora Dwarf	19,166	553,259	0	0

Pitfall traps provided information regarding the distribution of several taxa not recorded in the burrow surveys (Table 3). *Eurytium limosum* occurred broadly within *Rhizophora* habitat types while *Panopeus herbstii* was restricted to the fringe. *Armases ricordi*, a crab common within coastal scrub and clearcut areas (see discussion below), was trapped twice in pitfalls away from these habitat types. *Aratus pisonii*, an arboreal species, was recorded from one pitfall in a Moribund stand where it was being consumed by *E. limosum* (Plate 2).

Table 3. Pitfall trap samples by habitat type. Values are number of animals in 10 pitfall traps per 25 m^2.

Habitat Type	*Uca rapax.*	*Eurytium limosum*	*Panopeus herbstii*	*Aratus pisonii*	*Armases ricordi*
Mixed Woodland	6	1	0	0	0
Fringe	0	1	4	0	0
Avicennia Basin	10	0	0	0	0
Avicennia Orchard	16	0	0	0	1
Scrub	3	0	0	0	0
Moribund	11	1	0	1	0
Regenerated *Avicennia* Basin	3	0	0	0	0
Avicennia/Rhizophora Dwarf	12	1	0	0	1
Floc Zone	2	0	0	0	0

Three species were added through time-constrained searches: *Coenobita clypeatus* in Regenerated *Avicennia* Basin, *Pachygrapsus transversus* in the Fringe and *Avicennia* Orchards, and *Sesarma curacaoense* in the Fringe.

Arboreal searches for *A. pisonii* revealed a patchy distribution favoring *Rhizophora* habitats, with a total population of approximately 68,000 individuals (Table 4). *Aratus pisonii* was found mainly in the Fringe, and was virtually absent in the Mixed Woodland, *Avicennia* Orchard, Scrub, Moribund, and Dwarf habitat types.

Table 4. *Aratus pisonii* by habitat type with estimates for population size at Twin Cays. Areal coverages of habitat types are given in Table 2. Values for *A. pisonii*/m^2 are means ± 1 SD.

Habitat Type	*Aratus pisonii*/m^2	*Aratus pisonii* per habitat type
Mixed Woodland	0 ± 0	0
Fringe	0.7 ± 1.7	66444
Avicennia Basin	0.1 ± .3	649
Avicennia Orchard	0 ± 0	0
Scrub	0 ± 0	0
Moribund	0 ± 0	0
Regenerated *Avicennia* Basin	0.1 ± 0.3	908
Avicennia/*Rhizophora* Dwarf	0 ± 0	0

Reptiles

Only *Anolis sagrei* were encountered during the daytime in the 25m^2 quadrat surveys (Table 5). The lizards were most common in the Mixed Woodland habitat type. As with the decapods above, the area measurements of Rodriguez and Feller (2004) were used to extrapolate *A. sagrei* numbers by multiplying the average density of lizards per 25 m^2 by area (m^2) of each habitat type. Approximately 18,600 *A. sagrei* are estimated to inhabit the surveyed habitat types of Twin Cays (Table 5).

Table 5. Number of *Anolis sagrei* per 25 m^2 with estimates for population size at Twin Cays. Areal coverages of habitat types are given in Table 2.

Habitat Type	*Anolis sagrei* /25 m^2	*Anolis sagrei* per habitat type
Mixed Woodland	2.3 ± 0.5	10743
Fringe	1.7 ± 0.5	6644
Avicennia Basin	1.0 ± 0.0	234
Avicennia Orchard	0.3 ± 0.5	160
Scrub	0.7 ± 0.5	608
Moribund	0.7± 0.9	83
Regenerated *Avicennia* Basin	0.3 ± 0.5	109
Avicennia/*Rhizophora* Dwarf	0 ± 0	0

An individual boa (*Boa constrictor*) was found in each of two 1-hr searches of the Boa Flats area of Twin Cays in January. In the July searches, we found no boas. A single, small adult (~2 m) American Crocodile, *Crocodylus acutus,* was observed in the Main Channel during the January survey. Upon our approach, it quickly fled into nearby Gator Creek. July surveys revealed no crocodiles in the main channel, but two individuals were spotted by another observer within Hidden Lake (Stephen Mitten, personal communication).

DISCUSSION

Decapods

Decapod crustaceans are the most visually conspicuous element of the supratidal fauna of Twin Cays (Plate 2). Associations of decapods with mangrove forests date from the Cretaceous Period and possibly earlier (Schweitzer et al., 2003). Often found in startling abundance, the group plays crucial roles as (1) consumers of mangrove leaf litter (Camilleri, 1992), (2) meiobenthic predators (Olafsson and Ndaro, 1997), (3) predators of mangrove propagules (McKee, 1995), and (4) aerators of mangrove sediments (Hines and Feller, unpublished data).

Fiddler crabs (*Uca* spp.) dominate the supratidal crustacean fauna of Twin Cays with several hundred individuals often occupying a single square meter of appropriate habitat. The most common species is *Uca rapax*, though a second species, *U. vocator*, is found in small numbers detected through the presence of burrows with chimneys. However, it was not collected in any of the sampling methods in this survey. As crabs of the genus *Uca* frequently have fine niche partitioning (Crane, 1975), it is likely that more species may be found on Twin Cays, particularly in minor habitat types that were not sampled in this study. Other members of the family Ocypodidae found on Twin Cays are the Hairy Land Crab, *Ucides cordatus,* and the Ghost Crab, *Ocypode quadrata*.

Ucides cordatus is a relatively large (≤89 mm carapace width, Warner, 1969) herbivorous/detritivorous crab. It maintains distinctive burrows, which are often found in "villages." These burrows provide haven to other species, including the Mangrove Rivulus, *Rivulus marmoratus*, a tiny hermaphroditic fish (Davis and Taylor, 1987). This crab is rarely seen during the daytime in Belize, coming out at night to feed on fallen leaves.

Ocypode quadrata, a Ghost Crab, is a fast, pallid, predator-scavenger of open beaches. It is uncommon on Twin Cays, being found primarily in areas that have been clearcut, burned, and filled with sandy dredge spoils. In other areas of its range, *O. quadrata* has been identified as a major predator on ground nesting birds and sea turtle hatchlings (Loegering et al., 1995).

The decapod family Grapsidae is also well represented on Twin Cays with five species ranging from arboreal to semifossorial lifestyles. *Aratus pisonii,* the Mangrove Tree Crab, is found throughout the study area though it appears to favor fringe stands dominated by *Rhizophora mangle*. It feeds on *R. mangle* leaves and propagules in the canopy, algae in the intertidal zone, and whatever animal material is available. We have observed *A. pisonii* preying on *Marmara* spp., other insects, and smaller conspecifics.

Goniopsis cruentata, a brightly colored crab with red legs and a midnight blue dorsum, is common in sheltered habitats, particularly among *R. mangle* prop roots and low branches. It occupies terrestrial burrows, which are normally found under debris. Frequently seen above ground, this crab moves very rapidly to shelter when disturbed. A predator of mangrove propagules (McKee, 1995), *G. cruentata* will also consume leaf litter and scavenge animal matter.

Armases ricordi occupies dry wrack lines and upland terraces. Infrequently encountered in the interior of the island, it is more typical of the leeward beaches and areas filled with dredge spoils. A closely related crab, *Sesarma curacaoense,* was found within coarse woody debris and the leaf litter of the *R. mangle* fringe.

The small grapsid crab *Pachygrapsus transversus* was uncommonly found in leaf litter in fringe zones and *A. germinans* orchards. Ovigerous females were found in the January samples, falling within the breeding period noted by Crane (1947) for Costa Rica. In their study of this species, Abele et al. (1986) noted that "individuals are active at all low tides as soon as their habitat is exposed." This observation also appears to be true for *P. transversus* on Twin Cays.

Mud crabs of the family Xanthidae were represented in the study by two species occupying similar habitats. A relatively large mud crab with white-tipped chelae, *Eurytium limosum*, is a predator-scavenger rarely encountered on the surface during the daytime. In the confines of pitfall traps, it quickly seized and consumed other crabs including conspecifics, *Uca* spp. and *A. pisonii.* When stranded in the pitfall traps, *E. limosum* were eaten by Rufous-Necked Woodrails, based on signs including rail tracks and crab remains. *Panopeus herbstii* is similar in form to *E. limosum*, though lacking the white-tipped chelae, and more restricted to the *R. mangle* fringe.

A common inhabitant of neighboring sandy islands, the terrestrial hermit crab *Coenobita clypeatus* is most frequently encountered in the limited coastal scrub zone of Twin Cays near Boa Flats. This species is a known egg-predator of ground-nesting birds (Meier et al., 1989) and scavenges the wrack line for animal and vegetable matter. Crabs of this genus are host to a commensal springtail of the monogeneric family Coenaletidae (Palacios-Vargas et al., 2000).

We also found the semiterrestrial shrimp *Merguia rhizophorae* in the coarse woody debris along the *R. mangle* fringe of Twin Cays. Largely nocturnal, the species is known from only a few locations throughout the Caribbean.

While more derived reproductive strategies have been observed in some Caribbean supratidal crab faunas (Diesel et al., 2000), all members of the Twin Cays assemblage have a standard life history consisting of a pelagic larval dispersal phase, followed by the adult reproductive form. The evolutionary importance of mangrove areas to the development of terrestriality was discussed by Diesel et al. (2000) who noted "one important key to the invasion of land by crabs is the evolution of reproductive and developmental traits that accompany independence from the marine plankton." It would be of great interest to learn more about the reproductive habits of the terrestrial crabs of Twin Cays, particularly if the assemblage uses the interior ponded areas for breeding.

One striking result of the decapod surveys was the absence of large burrowing crabs, *G. cruentata* and *U. cordatus*, from the Regenerated *Avicennia* Basin, despite relatively high densities of both species in mature stands. The importance of these species as seedling predators (McKee, 1995, Sousa and Mitchell, 1999) and detritivores (M^{c}Keon, personal observation) has previously been noted. With the additional commercial importance of *U. cordatus*, the loss of these species becomes an important factor in the discussion of land-use and clearing of mangroves in the Caribbean.

During the January study period, crabs were largely absent from the Floc zone with no burrows present and very limited captures from pitfall traps. Observations of hundreds of *Uca* spp. individuals in the same area in July suggest that during some times of the year these areas may be of greater importance to crabs, *Uca* spp., in particular. The seasonal or hydrological changes involved are unknown but may represent the influx of new floc material or fresh accumulation of senesced leaves. As this zone forms the leading edge of forest growth in the island interior (Feller, unpublished data), the point at which the floc stabilizes enough for crabs may be an important factor in understanding forest dynamics. The studies of Hines and Feller (unpublished data) demonstrate the importance of *Uca* spp. burrowing to the growth and survival of *Avicennia* in Florida, USA. While results of similar studies in Belize have been less clear, the role of crabs in these transitional zones is of interest for further study.

Sites at Twin Cays that had been altered from the original forest types (cut, burned, and filled), had a different decapod community. *Armases ricordi* was much more abundant in such areas, and the Ghost Crab *Ocypode quadrata*, otherwise absent from Twin Cays, was also common. The addition of these aggressive predator-scavengers to the Twin Cays community may have important ramifications to the island's food webs.

Reptiles

Unlike comparable forests in Southeast Asia and Africa, which are home to numerous aquatic reptile species (Karns et al., 2002; Luiselli and Akani, 2002), the reptile fauna of Belizean mangrove forests is "limited to a few ubiquitous, opportunistic species" (Stafford and Meyer, 2000). Their importance to the supratidal fauna cannot be overstated. With a few subtidal exceptions, reptiles are the dominant predators of the Twin Cays ecosystem, and the adult American Crocodiles and Boa Constrictors feed at high trophic levels. The reptile fauna of Twin Cays is limited to four species in four families: *Anolis sagrei* (Polycroatidae), *Phyllodactylus insularis* (Gekkonidae), *B. constrictor* (Boidae), and *C. acutus* (Crocodylidae).

Easily the most abundant and easily encountered reptile on the island is the Mayan Coastal Anole, *A. sagrei,* which is common throughout the Caribbean as a tramp species, often colonizing coastal areas and inland areas disturbed by humans. Adult males typically maintain a head-down position on vertical trunks for territorial displays of head-bobbing and dewlap extension. We have observed Anoles on Twin Cays eating insects, particularly ants, beetles, and termites. In other parts of their range, these lizards are known to consume many other types of insects, small crabs, and smaller members of the same species. The eggs of *A. sagrei* are deposited in tree holes and other arboreal refugia.

The abundance of *A. sagrei* on Twin Cays is likely to play a major role in the trophic dynamics of the island. Previous researchers have found that removal of lizards of the genus *Anolis* triggers dramatic increases in local arthropod abundance (Pacala and Roughgarden, 1984; Schoener and Toft, 1983). Within the mangrove ecosystem of the Bahamas, the effect of lizard predation on insect herbivores was tested by Schoener (1988). The study demonstrated that leaf damage to *Conocarpus erectus,* a common mangrove associate, was reduced on islands with lizards in comparison to those without.

A pale, large-headed lizard, *Phyllodactylus insularis*, is largely nocturnal at Twin Cays and elsewhere, emerging from under the bark and dead limbs at dusk to feed on insects and other small arthropods. Recorded only from Belizean cays, *P. insularis* is very similar to a closely related species *P. tuberculosus* and often confused with that taxon. Geckos from Twin Cays have keyed out as both species suggesting further study of the taxonomy is warranted. Like other geckos, *P. insularis* has adhesive friction pads on the toes of each foot enabling it to scamper about vertical surfaces with ease. This species is also quite vocal with individuals emitting a sound much like a high pitched squeak or click. Though counts of this species were not attempted in this study, casual observations by the authors suggest that *P. insularis* may approach the daytime densities of *Anolis sagrei* in some habitat types.

*Boa constrictor*s are large, heavy-bodied snakes found infrequently on Twin Cays with the exception of the appropriately named "Boa Flats" at the southern end of the East Island. In other parts of their range, boas are generalized predators on vertebrates, consuming lizards, mammals, and birds.

The threatened *C. acutus* is the only crocodilian to be found in the Twin Cays area. A smaller species, Morelet's crocodile *C. moreletii*, is found at mainland sites on the Yucatan peninsula but is not known from the Belizean cays (Campbell, 1998). American Crocodiles feed largely on fish supplemented with other reptiles, birds, and mammals as opportunity presents. Sexual maturity is reached at a total length of approximately 2.8 m in females-- a size not yet observed by the authors at Twin Cays.

Colonization of the islands by reptiles has been limited to ovoviviparous species (*B. constrictor*) and lizard species with arboreal egg deposition. Large lizards of the genera *Ctenosaura* and *Iguana* have been known to arrive at Twin Cays and neighboring Carrie Bow Cay but have not established populations. *Crocodylus acutus*, despite healthy breeding populations on other Belizean islands (Platt and Thorbjarnarson, 2000), have yet to be recorded breeding on Twin Cays. Due to a lack of high ground for nesting areas and the absence of fresh or brackish water sources needed by hatchlings (Mazzotti et al., 1986), the authors considered Twin Cays unlikely breeding habitat for the species until a juvenile crocodile, approximately 35 cm in total length, was observed during the July surveys. It is unlikely that a crocodile of such small size would attempt or survive the open water crossing from adjacent breeding populations.

Birds

As explored by Mitten et al. (2004), mangrove bird communities are poorly studied though authors have made significant recent additions (Sodhi et al., 1997), particularly with regard to Central America (Butler et al., 1997; Lefebvre and Pulin, 1997) and South America (Olmos and Silva-e-Silva, 2001). The role of nesting birds in the diversity of the supratidal fauna is largely unexplored and deserving of mention.

Rookeries in mangrove forests can affect both biotic and abiotic components of the ecosystem. At the Frigatebird and Brown Booby rookery on nearby Man-of-War Cay, increased availability of nutrients from the bird guano results in higher mangrove productivity and growth rates in comparison with nearby islands that are not rookeries. Unlike the tangled maze of stems and roots that typify the low-stature fringe forests of most of Twin Cays and most other nearby cays, the mangrove trees on Man-of-War Cay are tall (10-15 m) and straight-trunked with few buttressing prop roots. Under the canopy, this forest is relatively open. Although Man-of-War is a very small cay, the insect fauna associated with these tall trees is more species-rich than on much larger, nearby islands (Feller and Mathis, 1997). In addition, insect herbivory of mangrove leaves, stems, and roots on the tall trees at this rookery is greater than is suffered by mangroves on these other islands (Feller and Mathis, 1997). The input of nutrients from the guano also leads to increased decomposition rates in the substrate and affects nutrient-cycling processes.

Adjacent marine communities also respond to this naturally occurring nutrient enrichment. Some marine fungi and algae grow densely in the waters around Man-of-War Cay (Kohlmeyer and Kohlmeyer, 1987). Some of these species of algae, such as *Ulva* sp. and *Enteromorpha* sp., are typically associated with marine environments that are more eutrophic than the oligotrophic waters typical of Belize's coastal zone.

Mammals

Native terrestrial mammals are unknown from Twin Cays. At the time of writing, feral dogs are the only known mammals (other than humans) present on the island. As highly adaptable, social carnivores, they are likely to be second only to crocodiles in an island food chain. Five to 15 dogs are reported from the islands, often near the active dump site at the southern tip of the West Island. The impact of these animals is unknown but is likely to be significant. In the Galapagos, feral dogs have significantly impacted native populations of tortoises, iguanas, and birds (Green and Gipson, 1994). Similar situations have been found in the Hawaiian Islands (van Ripper et al., 2001). Ground nesting birds (including both rail species recorded from Twin Cays) are particularly vulnerable (Fuller, 2001).

An unknown number of bat species hunt above Twin Cays and neighboring islands in the dusk and dawn hours. It is highly likely that these animals reside in the forest during the day. Limited research has been conducted on mangrove bat communities with most research conducted on Australian species (McKenzie and Start, 1989; McKenzie and Rolfe, 1986). Several species known from studies on mainland Belize have strong associations with waterways and coastal habitats *(Noctilio leporinus, Rhynchonycteris naso)* and are likely in the area based on distribution (Reid, 1998).

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Plate 1

Plate 1. A. *Littoraria angulifera*; B. *Marmara* sp.; C. *Elaphidion mimeticum*; D. *Anolis sagrei*; E. *Phyllodactylus insularis*; F. *Boa constrictor*

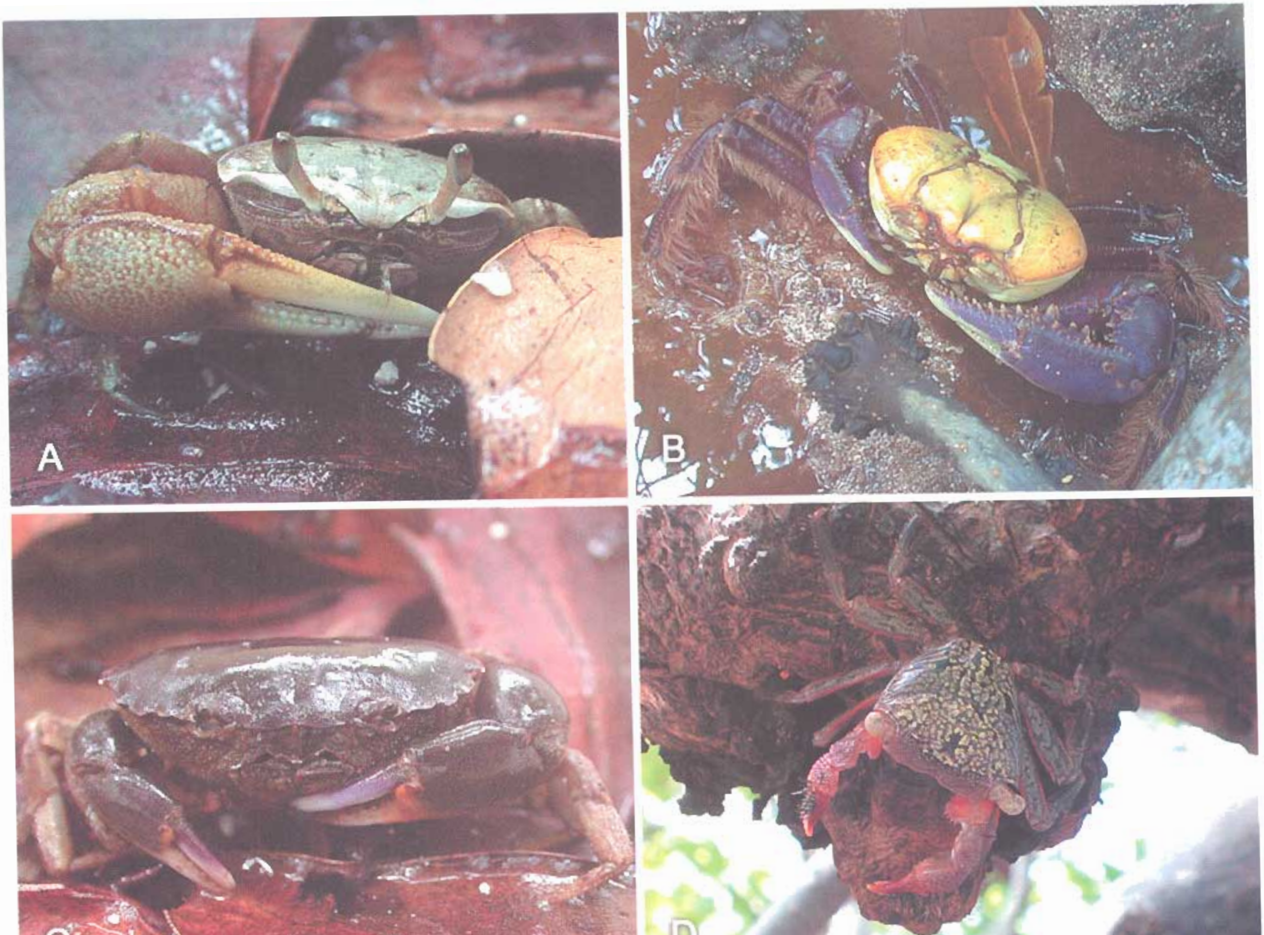

Plate 2

Plate 2. A. *Uca rapax*; B. *Ucides cordatus*; C. *Eurytium limosum*; D. *Aratus pisonii*; E. *Armases ricordi*; F. *Goniopsis cruentata*