REPTILES & AMPHIBIANS

The Diet of Florida Box Turtles (*Terrapene bauri*) in a Coastal Ecosystem in Southwestern Florida

Juliana Loredo, Cristal Navarrete, and Jordan Donini

Florida SouthWestern State College – Collier Campus, Naples, Florida 34113, USA (jtdonini@fsw.edu)

Abstract.—North American Box Turtles are opportunistic generalists with omnivorous tendencies, but diets of box turtles are known to vary by population, region, and season. Relatively few studies have examined the diet of Florida Box Turtles (*Terrapene bauri*). By analyzing fecal samples and direct observations of feeding, we describe the diet of Florida Box Turtles in a coastal area in southern Florida. Fecal samples of turtles in this population contained four functional groups of plants and algae, 11 categories of animals, plus miscellaneous unidentifiable and mineral matter. Frequencies of occurrence differed significantly between wet and dry seasons but not between sexes. Seeds of the invasive Beach Cabbage (*Scaevola taccada*) were among the most frequently detected plant items, whereas Coffee Bean Snails (*Melampus coffea*) and ocypodid crabs were the most frequently encountered animal items.

Box turtles of the genus *Terrapene* are dietary generalists known to consume a diverse array of foods including plant matter, fruits, fungi, insects, birds, bones, and even soil (Dodd 2002). Frequency and abundance of food types vary by season and location (Klimstra and Newsome 1960; Figueras et al. 2021), but the majority of dietary studies on box turtles have focused on inland regions in the northern extent of their range (Dodd 2002). Studies of Florida Box Turtles (*Terrapene bauri*) have examined populations on Egmont Key (Dodd 1997, 1998; Dodd et al. 2006), the Florida Keys (Verdon and Donnelly 2005; Platt et al. 2010), and the Ten Thousand Islands (Jones et al. 2016). However, to the best of our knowledge, only Dodd et al. (1994) and Platt et al. (2009) examined the diets of *T. bauri* in Florida. Like those of congeners, the diets of Florida Box Turtles almost certainly vary across their range depending on habitats and the abundance of resources. Herein we describe observations of direct consumption of food and the results of fecal sampling in Florida Box Turtles in a coastal habitat in southwestern Florida.

Methods

We conducted this study at an undisclosed coastal site in southwestern Florida that is accessible by boat (exact coordinates are not provided in order to prevent illegal collection of wildlife). The survey area of approximately 50 ha consists of mangrove estuary, coastal scrub, dune, and hardwood hammock habitats. Primary vegetation includes Buttonwood (*Conocarpus erectus*), Red Mangrove (*Rhizophora mangle*), Black Mangrove (*Avicennia germinans*), White Mangrove (*Laguncularia racemosa*), Sea Grape (*Coccoloba uvifera*), Cocoplum (*Chrysobalanus icaco*), Beach Cabbage (*Scaevola taccada*), Seaside Goldenrod (*Solidago sempervirens*), Coinvine (*Dalbergia ecastaphyllum),* Brazilian Pepper (*Schinus terebinthifolia*), Australian Pine *(Casuarina equisetifolia)*, Sea Oats (*Uniola paniculata*), and Muhly Grass (*Muhlenbergia capillaris*).

We collected box turtles during weekly surveys from July 2020 to June 2021, locating individual turtles opportunistically via meandering surveys (Currylow et al. 2011) and by using wooden rake handles to detect turtles at the bases of vegetation or covered by leaf litter. Once captured, turtles were marked (Cagle 1939) and tagged with passive integrated transponders (PIT tags) (Buhlman and Tuberville 1998). Adult turtles (carapace length >100 mm) were sexed before being placed into plastic 3-gallon buckets, filled to approximately 5 cm, and soaked in a shaded area for 1–4 hours until defecation occurred (Platt et al. 2009). Fecal samples were passed through a fine 3-mm mesh kitchen strainer and stored in plastic vials at -20 °C. We subsequently examined thawed samples using a cell-phone-linked wi-fi digital microscope (Heitwon©) at 50–100X magnification.

We identified dietary material to the lowest possible taxonomic level and grouped items into corresponding categories to assess the frequency of dietary components between seasons (dry vs. wet) and between sexes. We determined the frequency of occurrence of food items in the diet per season and

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Table 1. Frequency of occurrence (FO%) of food items in fecal samples from Florida Box Turtles (*Terrapene bauri*) by season. N = total number of turtles per season; n = number of turtles containing a particular category of food.

Food Item	Season			
	Dry (n = 32)		Wet (n = 21)	
	n	FO%	n	FO%
Plants and Algae				
Grasses (Poaceae)	16	50.0	7	33.3
Beach Cabbage (*Scaevola taccada*)	9	28.1	15	71.4
Inkberry (*Scaevola plumieri*)	2	6.3	4	19.0
Unknown leaf, seed, or algal matter	14	43.8	10	47.6
Animals				
Arthropoda: Insecta				
Dragonflies (Odonata)	0	0.0	4	19.0
Ants (Formicidae)	0	0.0	1	4.8
Beetles (Coleoptera)	2	6.3	1	4.8
Mollusca: Gastropoda				
Coffee Bean Snails (*Melampus coffea*)	11	34.4	9	42.9
Periwinkles (*Littorina* sp.)	0	0.0	4	19.0
Truncatellas (*Truncatella* sp.)	6	18.8	0	0.0
Unidentified gastropods	1	3.1	1	4.8
Arthropoda: Crustacea				
Mangrove Tree Crabs (*Aratus pisonnii*)	1	3.1	1	4.8
Fiddler and Ghost Crabs (Ocypodidae)	7	21.9	9	42.9
Unidentified brachyuran crabs	4	9.4	1	4.8
Vertebrata: Aves				
Perching birds (Passeriformes)	1	3.1	0	0.0
Other				
Unidentifiable and mineral matter	4	12.5	0	0.0

per sex using the equation: FO% = n/N x 100 (Paralikidis et al. 2010; Xiao et al. 2017), in which FO = frequency of occurrence, n = the number of turtles in a confirmed dietary category, and N = the total number of turtles per category (wet/dry season or male/female). We used chi-squared tests to evaluate differences in diets between seasons and between sexes.

We also documented direct observations of foraging with food items identified to the lowest taxonomic level or specific descriptor. These observations were not included in any frequency-of-occurrence calculations.

Results

Fecal Sample Analysis.—We collected a total of 53 fecal samples (26 from males and 27 from females), 21 during the wet season (16 May–15 October) and 32 during the dry season (16 October–15 May). Samples from three turtles (two females and one male) were collected in both seasons but were treated as unique individuals for the purpose of this study. We documented three distinct taxa of plants and 11 animal taxa. Several samples had unidentifiable components that were labeled and categorized as accurately as possible but grouped together as unidentified plant, animal, or mineral matter.

Table 2. Frequency of occurrence (FO%) of food items in fecal samples from Florida Box Turtles (*Terrapene bauri*) by sex. N = total number of turtles of each sex; n = number of turtles containing a particular category of food.

Food Item	Sex			
	Males (n = 26)		Females (n = 27)	
	n	FO%	n	FO%
Plants and Algae				
Grasses (Poaceae)	10	38.5	13	48.1
Beach Cabbage (*Scaevola taccada*)	9	34.6	15	55.6
Inkberry (*Scaevola plumieri*)	3	11.5	3	11.1
Unknown leaf, seed, or algal matter	5	19.2	10	37.0
Animals				
Arthropoda: Insecta				
Dragonflies (Odonata)	1	3.8	3	11.1
Ants (Formicidae)	1	3.8	0	0.0
Beetles (Coleoptera)	1	3.8	2	7.4
Mollusca: Gastropoda				
Coffee Bean Snails (*Melampus coffea*)	8	30.8	11	40.7
Periwinkles (*Littorina* sp.)	2	7.7	2	7.4
Truncatellas (*Truncatella* sp.)	3	11.5	3	11.1
Unidentified gastropods	1	3.8	1	3.7
Arthropoda: Crustacea				
Mangrove Tree Crabs (*Aratus pisonnii*)	1	3.8	1	3.7
Fiddler and Ghost Crabs (Ocypodidae)	4	15.4	12	44.4
Unidentified brachyuran crabs	2	7.7	1	3.7
Vertebrata: Aves				
Perching birds (Passeriformes)	0	0.0	1	3.7
Other				
Unidentifiable and mineral matter	3	11.5	1	3.7

Frequencies of occurrence differed significantly between seasons (x^2_{15} = 28.27, P = 0.02), whereas those between sexes did not differ significantly (x^2_{15} = 8.29, P = 0.91).

The most frequently observed plant matter in the dry season consisted of grasses in the family Poaceae, which occurred in half of the turtles sampled (Table 1). Most were not identifiable past the family level based on digestion and fragmentation. The most frequently observed plant matter in the wet season consisted of seeds and fruits of invasive Beach Cabbage (*Scaevola taccada*), which we found in 15 of 21 sampled turtles. The most frequently observed animal matter in the dry season was the Coffee Bean Snail (*Melampus coffea*), which occurred in 11 of 32 sampled individuals. Coffee Bean Snails were present at an even higher frequency in the wet season (9 of 21), a frequency equaled by crabs in the family Ocypodidae.

In males, grasses in the family Poaceae made up he most frequently encountered plant matter (10 of 26), whereas Beach Cabbage (*Scaevola taccada*) was most frequently observed in females (15 of 27) (Table 2). The most frequently observed animal matter in males was the Coffee Bean Snail (8 of 26), whereas additional crabs in the family Ocypodidae where the most frequently observed in females (12 of 27).

Table 3. Direct observations of food items consumed by Florida Box Turtles (*Terrapene bauri*) in a coastal southwestern Florida population.

Food Item	Notes
Plants and Algae	
Cocoplum (*Chrysobalanus icaco*)	Multiple individuals feeding on fallen fruit in the wet season
Beach Cabbage (*Scaevola taccada*)	Multiple individuals feeding on fallen fruit in both the wet and dry seasons
Unknown algae	Juvenile under Muhly Grass (*Muhlenbergia capillaris*) on a moist substrate feeding on unidentifiable algal clumps growing on the soil surface of soil
Animals	
Roof Rat (*Rattus rattus*)	A single male scavenging a dead rat in the wet season
Perching birds (Passeriformes)	A single male scavenging a dead songbird (likely a Northern Mockingbird, *Mimus polyglottos*)
Striped Mullet (*Mugil cephalus*)	A single female scavenging a dead mullet in the wet season (fish probably died of algal bloom toxicosis)
Mangrove Tree Crabs (*Aratus pisonnii*)	Multiple individuals hunting and consuming tree crabs in both wet and dry seasons
Fiddler and Ghost Crabs (Ocypodidae)	Multiple individuals consuming Fiddler Crabs in both wet and dry seasons
Miscellaneous	
Northern Racoon (*Procyon lotor*) scat	Single male consuming raccoon feces in the dry season

Foraging Observations.—We observed turtles consuming 10 distinct food items (Table 3), several of which were identified in fecal samples (Beach Cabbage, Mangrove Tree Crab, ocypodids, and passeriform bird feathers). Other items of interest were Cocoplum (*Chrysobalanus icaco*), Striped Mullet (*Mugil cephalus*), a Roof Rat (*Rattus rattus*), and Northern Raccoon (*Procyon lotor*) scat (Fig. 1).

Discussion

Fecal Sample Analysis.—Our dietary data, with an abundance of both plant and animal matter (Fig. 2), were very similar to those in the published literature (e.g., Dodd 2002). However, we found a noticeable lack of fungi in the diet of this population when compared to those of other box turtles (Surface 1908; Strang 1983). The lack of fungal matter may be due to an environment with several ephemerally inundated regions, high dry dunes, and salt or brackish flood plains and, in fact, we found no mushrooms during our surveys. This is similar to the situation at the National Key Deer Wildlife Refuge (NKDWR), where very little fungal matter was found in fecal samples and fungi were seemingly rare in the xeric pineland ecosystem where the study was conducted (Platt et al. 2009).

Dietary composition was similar between seasons, but frequencies of items consumed differed significantly. The high frequency of grasses (Poaceae) and other unidentifiable ligneous plant material in the dry season might be indicative of a declining availability of fruits; however, Beach Cabbage fruits remained relatively abundant compared to other fruits that were readily available in the area. The abundance of grasses consumed by turtles in the dry season matches descriptions of shoots and leaves as a large portion of box-turtle diets in other regions (Stuart and Miller 1987; Dodd 2002); yet some of that might have been adventitiously ingested as leaves and shoots provide less energy than fruits and seeds (Golley 1961).

One noteworthy observation is the frequency of Beach Cabbage seeds and fruit in diets of males and females during both the wet and dry seasons. *Scaevola taccada* is a Florida Invasive Species Council Category 1 invasive species from the Indo-Pacific region that occurs throughout coastal southern Florida (Lockhart 2019). This species is closely related to the native Inkberry (*Scaevola plumieri*) that has been documented in the diets of box turtles on Egmont Key (Dodd 2002) and which we also found, albeit at much lower frequency than *S. taccada* in this study population. One notable difference between these species is that *S. plumieri* typically fruits in the summer wet season, whereas *S. taccada* is known to fruit throughout the year in southern Florida (Gilman 2015; Lockhart 2019). Although prolonged fruiting could increase consumption opportunities for box turtles, we also found many seeds in some samples (>10 in some instances), suggesting that box turtles might prefer an introduced species over a similar indigenous species, which also has been noted for the Santa Cruz Giant Tortoise (*Chelonoidis porteri*) in the Galápagos Islands (Blake et al. 2015). Furthermore, because box turtles are known to disperse seeds (Braun and Brooks

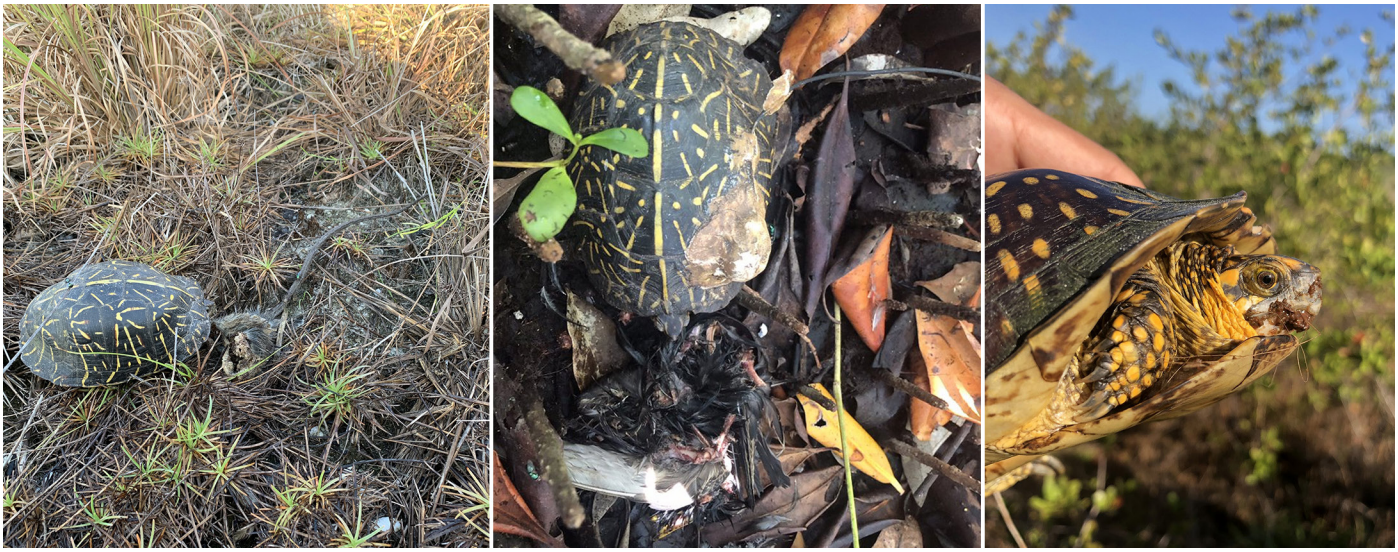

Fig. 1. A male Florida Box Turtle (*Terrapene bauri*) scavenging a dead Roof Rat (*Rattus rattus*) (left); a male scavenging on an unidentified passeriform bird (center); and a male captured while consuming Northern Raccoon (*Procyon lotor*) scat (right). Photographs by Jordan Donini and Adrian Rodriguez.

Fig. 2. Miscellaneous grasses (Poaceae) and unidentifiable plant matter (left); six Beach Cabbage (*Scaevola taccada*) seeds from a single fecal sample (center left); fragmented Coffee Bean Snail (*Melampus coffea*) shells (center right); and chelae from a fiddler crab in the family Ocypodidae (right). Photographs by Juliana Loredo and Cristal Navarrete.

1987; Liu et al. 2004), turtles in this population could be facilitating the dispersal of this invasive species.

We found evidence of turtles eating dragonflies (Odonata) and ants (Formicidae) only during the wet season. Although ants are not considered a primary prey item for box turtles, several studies (Klimstra and Newsome 1960; Worthington et al. 2017; Figueras et al. 2021) have indicated their presence in the box turtle diet. However, given that a single observation was the only evidence of predation on ants in the study, we cannot discount the possibility of incidental ingestion. The presence of Odonata in the diet only during the wet season coincides with migrations and life cycles of dragonfly species documented in the area (May 2013); this might explain the seasonal occurrence, suggesting that box turtles take advantage of seasonal congregations of dragonflies, perhaps scavenging adults as they reach the end of their life span.

That the diet of this box turtle population in both seasons included gastropods in three genera plus various other unidentifiable shell fragments is not unusual. Bush (1959) reported that over half of the dietary volume in Kentucky box turtles consisted of snails and slugs. Coffee Bean Snails (*Melampus coffea*) were the most frequently observed gastropods and were present at high frequencies in our samples

from both seasons. However, truncatellas (*Truncatella* sp.) were in 6 of 32 of dry-season samples but completely absent in the wet season, whereas periwinkles (*Littorina* sp.) were absent in the dry season but were observed in 4 of 21 of wet-season samples. Because all three gastropod taxa appear to co-occur in similar habitats, we are unable to explain the seasonal differences.

Crabs in the infraorder Brachyura are a rarely documented component of box turtle diets. Although the most likely explanation is that the large majority of dietary studies were conducted in areas far from coastlines (Dodd 2002), even in a study in similar habitat and a comparable latitude, Platt et al. (2009) provided only a single vague description of a crustacean in their data. To the best of our knowledge, the only other description of crab consumption by North American box turtles was in McCoy et al. (2016), who recorded crabs in two families (Ocypodidae and Grapsidae) consumed by Gulf Coast Box Turtles (*Terrapene carolina major*) in coastal Mississippi. We documented the presence of at least two families of crabs, the sesarmid Mangrove Tree Crab (*Aratus pisonnii*) and ocypodids (likely multiple species). The latter were most abundant in wet-season samples (9 of 21) but also present at lower frequencies (7 of 32) in the dry season.

Our data, like those in much of the primary literature, indicate that Florida Box Turtles in this population are dietary opportunistic generalists, consuming whatever food resources are most abundant, which was reinforced by the significant seasonal differences in dietary frequencies. Also, similar to our observations, Platt et al. (2009) stated that males and females do not appear to partition habitats and noted a lack of dietary divergence between the sexes.

Fecal dietary studies are largely limited to observations of hard-bodied or less digestible organisms or their parts, which limits the scope of such studies and the conclusions that can be made (Sung et al. 2016). This certainly contributed to missing some food items in the diet of this population, as indicated by observations of turtles consuming some items that were not detected in fecal samples. However, alternative techniques also have limits. For instance, DNA-barcoding of fecal samples might reveal the presence of additional dietary contents, but DNA sampling is expensive (US $2–8 per sample) (Valentini et al. 2009). Sacrifice-and-dissection and stomach-flushing techniques can provide more information (Fields et al. 2000) but, given the current risk of extinction that many chelonian species face (Stanford et al. 2020), we vehemently disagree with the unnecessary sacrifice of study animals, and stomach flushing can sometimes lead to injury or death (De Lima et al. 1997; Legler 1977). Thus, despite its drawbacks, we believe fecal collection and analysis is the most cost-effective and relatively noninvasive means of generating sufficient data to make basic assumptions about dietary frequencies and even preferences.

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