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Salad with Clams: Prey Choice of an Intentionally Carnivorous Turtle

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Abstract - Prey choice is the non-random foraging and consumption of prey species by their predators, and is therefore the basis for studies of topics as diverse as quantifying food webs, predator–prey relationships, and optimal-foraging models. *Malaclemys terrapin* (Diamond-back Terrapin) is a diet generalist with a large geographic distribution: the US Atlantic and Gulf coasts from Massachusetts to Texas. Individual terrapins have relatively small home ranges and feed primarily on local mollusc species. In feeding trials with 1 prey species and 2 prey species, wild-caught terrapins from New York readily consumed *Mya arenaria* (Soft-shelled Clam) and *Geukensia demissa* (Atlantic Ribbed Mussel), preferring them over a wide range of other prey species commonly eaten by terrapins at other sites. Our correlation test indicated that *Ulva latuca* (Sea Lettuce), common in the diets of this population, is ingested incidentally when terrapins forage for Soft-shelled Clams. The impact of consumption of algae by this primarily molluscivorous turtle is unexplored, but could have important impacts on their energy balance and contaminant intake.

Introduction

Diet studies are greatly enhanced by studies of prey choice, because the latter can indicate where predators are on the spectrum of the generalist-to-specialist continuum, enhance studies of predator–prey relationships, and form the basis for optimal-foraging models, including providing insights associated with nutrient-specific foraging (Kohl et al. 2015). However, prey-choice experiments can be difficult to conduct under natural conditions because they often require measurements of prey availability relevant to the predator's search capabilities (Suryawanshi et al. 2017). These types of studies can be more challenging when individual predators specialize, making prey choice a characteristic of individuals, as well as populations and species.

Prey choice can have ecosystem-level implications. For example, *Malaclemys terrapin* (Schoepf) (Diamond-back Terrapin) is an estuarine North American turtle that inhabits Western Atlantic salt marshes and mangrove swamps from Massachusetts to Texas. It is important to investigate Diamond-back Terrapin diets and prey choice because they may play a vital role in the top-down control of ecosystems, based on their selective predation on *Littoraria irrorata* Say (Marsh Periwinkle) in

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some parts of their range (Levesque 2000). Uncontrolled populations of March Periwinkles, in turn, consume large amounts of *Spartina alterniflora* Loisel. (Smooth Cordgrass), leading to widespread marsh die offs (Silliman and Bertness 2002). The broader implication of Diamond-back Terrapin prey choice and predation on invertebrates has not been explored but could have been ecologically important when Diamond-back Terrapins occurred in large numbers (Carr 1952, Kennedy 2018).

Diamond-back Terrapin diets have been studied in much of their range, resulting in numerous papers and 2 recent reviews (Erazmus et al. 2019, Tucker et al. 2018). These studies show that Diamond-back Terrapins exhibit high levels of molluscivory, feeding mostly on snails (Marsh Periwinkles and *Nassarius* (= *Ilyanassa*) *obsoleta* (Say) [Eastern Mudsnail]; Coker 1906, Petrochic 2009, Tucker et al. 1995) and clams (*Mulinia lateralis* (Say) [Dwarf Surf Clam] and *Mya arenaria* L. [Soft-shelled Clam]; Butler 2000, Roosenburg et al. 1999). Terrapins are also known to eat crabs, including *Callinectes sapidus* Rathbun (Atlantic Blue Crab) and introduced *Carcinus maenas* (L.) (European Green Crab) (King 2007, Petrochic 2009, Spivey 1998). Studies of captive terrapins found they readily ate Atlantic Blue Crabs, fish, *Crassostrea virginica* (Gmelin) (Atlantic Oyster), clams, *Uca pugilator* (Bosc) (Atlantic Sand Fiddler Crab), canned fish, liver, beef, and small molluscs (Allen and Littleford 1955, Hildebrand 1928).

Diamond-back Terrapin diets are similar throughout their large range, apparently behaviorally adapting to feed on mollusc and crustacean species that are locally available (Erazmus et al. 2019). The diets of the Diamond-back Terrapins of Jamaica Bay (JB), NY, are particularly well studied, including over 7 consecutive years (Erazmus et al. 2019), multiple sub-populations (Zostant 2018), and comparisons with other local populations (Kudman 2021). Jamaica Bay Diamond-back Terrapin diets have 2 unusual characteristics. First, they frequently consume *Ulva lactuca* L. (Sea Lettuce), sometimes occurring in as much as 54% of Diamond-back Terrapin fecal samples (Erazmus et al. 2019). This high level of Sea Lettuce consumption by JB Diamond-back Terrapins is not typical among Diamond-back Terrapin populations (Tucker et al. 2018). Second, JB Diamond-back Terrapins consume relatively few Eastern Mudsnails (average 2% of terrapin fecal samples; Erazmus et al. 2019), which are exceedingly common in JB (R.L. Burke, pers. observ.). Eastern Mudsnails are often eaten by Diamond-back Terrapins elsewhere (Tucker et al. 2018), and Eastern Mudsnails were found in 16% of fecal samples in another Diamond-back Terrapin population only 42 km away from JB (Oyster Bay, NY; Herrel et al. 2018).

While Diamond-back Terrapin consumption patterns are well studied, prey choice relative to prey availability is unexplored. We tested prey choice of Diamond-back Terrapins in JB using wild-captured individuals in short-term captive studies. We offered a variety of commonly consumed prey species in 1-species and 2-species trials to better understand Diamond-back Terrapin prey choice in a simplified environment.

Methods

Jamaica Bay is a polyhaline urban embayment at the extreme southwestern end of Long Island, NY, part of the boroughs of Brooklyn and Queens, NY, and connected to the Atlantic Ocean through Rockaway Inlet. *Mercenaria mercenaria* L. (Northern Quahog), Soft-shelled Clams, and *Mytilus edulis* L. (Blue Mussel) are abundant in JB mud flats and littoral waters (R.L. Burke, pers. observ.). *Geukensia demissa* (Dillwyn) (Atlantic Ribbed Mussel) and *Semibalanus balanoides* (L.) (Northern Rock Barnacle) are common in the upper half of the inter-tidal zone and both Eastern Mudsnails and *Crepidula fornicata* (L.) (Atlantic Slippersnail) are common in tidal creeks (R.L. Burke, pers. observ.). Additionally, Sea Lettuce and Smooth Cordgrass are abundant, especially in the summer (R.L. Burke, pers. observ.). Jamaica Bay history and ecology are well described elsewhere (Erazmus et al. 2019, Handel et al. 2016).

Feeding trials

During June, July, and August of 2009, we retained 56 recently collected wild female Diamond-back Terrapins that had just nested on the western half of Ruler's Bar, an island centrally located within JB. After capture, we initially soaked these Diamond-back Terrapins, without feeding them, for 5 days in individual containers with ~23 L of fresh water each, to facilitate collection of fecal samples for diet analysis (Erazmus et al. 2019). At the conclusion of fecal collection, we transferred the Diamond-back Terrapins to individual housing in 37.8-L tanks that each contained ~20 liters of freshwater that had been treated with Instant Ocean (Spectrum Brands, Inc., Miramar, FL) to raise the salinity to ~18 ppt. We kept these Diamond-back Terrapins and tanks outdoors under shading and randomly assigned them to experimental trials in which potential prey species in different combinations were offered. We placed only single Diamond-back Terrapins in a tank at a time and used each turtle for just 1 feeding trial.

We collected potential prey live from JB. In some treatments, a single prey species was offered; in other treatments, 2 prey species were offered (Table 1). Individual prey specimens were of similar sizes, and numbers of each prey type given were distributed equally based on weight. On the first day of each trial, we presented each Diamond-back Terrapin with potential prey and observed them briefly, then left them with prey items in the tanks for 2 additional days and recorded the number of prey individuals remaining in the tank daily.

Potential prey species in single species trials were *Littoraria* sp. (periwinkle) (each trial offering 1 periwinkle), *Glycera* sp. (bloodworm) (single bloodworm), Sea Lettuce (each trial offering four 5 cm x 5 cm squares), Eastern Mudsnails (each trial offering 5 mudsnails), Atlantic Ribbed Mussels (30 g [1–2 individual mussels] per trial), and Soft-shelled Clams (30 g [3–4 individual clams] per trial). We used Periwinkles and Eastern Mudsnails because they were consumed heavily in other terrapin populations (Herrel et al. 2018, Tucker et al. 1995). We chose bloodworms because they are soft-bodied and cannot be detected through fecal analysis, and we were concerned we might have failed to detect them in diet studies dependent on fecal analysis. We included Soft-shelled Clams, Sea Lettuce, and Atlantic Ribbed Mussels to further investigate findings from previous fecal analyses (Erazmus et al. 2019).

Combinations of prey items offered were the following pairs: Soft-shelled Clams and Ribbed Mussels (30 g each [3–4 individual clams and 1–2 individual mussels] per trial)*, Hemigrapsus sanguineus* (De Haan) (Asian Shore Crab) and Atlantic Ribbed Mussels (30 g each [2–3 crabs and 1–2 individual mussels] per trial), Asian Shore Crabs and Atlantic Sand Fiddler Crabs (20 g each [1–2 shore crabs and 1–2 fiddler crabs] per trial) and Soft-shelled Clams and Soft-shelled Clams wrapped in Sea Lettuce (20 g each [2–3 clams] per trial).

In addition to the feeding trials, we investigated Soft-shelled Clam and Sea Lettuce consumption patterns using the fecal samples of individual terrapins in the 2008–2010 data reported by Erazmus et al. (2019). We used a correlation test using the Soft-shelled Clam and Sea Lettuce occurrence data to test for non-random patterns in a presence–absence matrix (Gotelli and Graves 1996). Using the observed presence–absence data from the fecal samples, we created a presence–presence unit (the opposite of a checkerboard unit described by Stone and Roberts [1990]) for Soft-shelled Clams and Sea Lettuce. We calculated the equivalent to a C-score, defined as the mean number of checkerboard units per species pair (Stone and Roberts

Table 1. Diamondback Terrapin prey-choice experiments: prey offered, number of trials, and outcomes. Each terrapin was used in only a single trial.

Prey species	# of trials	Quantity eaten, comments
Littoraria sp. (periwinkle), 1/trial	2	0
Glycera sp. (bloodworm), 1/trial	1	1, within 2 minutes
Ulva latuca (Sea Lettuce), four 5 cm x 5 cm squares/trial	7	0
Tritia obsolete (Eastern Mudsnail), 5/trial	6	0
Geukensia demissa (Atlantic Ribbed Mussel), 1–2/trial	13	6 trials: ≥1 mussel in each trial, 7 trials: none eaten
Mya arenaria (Soft-shelled Clam), 3–4/trial	3	3
Soft-shelled Clams and Atlantic Ribbed Mussels, 3–4 clams and 1–2 mussels/trial	13	All Soft-shelled Clams in all trials, ≥1 mussel in each trial
Hemigrapsus sanguineus (Asian Shore Crab) and Atlantic Ribbed mussels, 2–3 crabs and 1–2 mussels/trial	5	≥1 mussel in all trial and ≥1 crab in 3 trials
Asian Shore Crabs and *Minuca pugnax* (Atlantic Sand Fiddler Crab), 1–2 shore crabs and 1–2 fiddler crabs/trial	2	≥1 crab of each species in both trials
Soft-shelled Clams without Sea Lettuce and Soft-shelled Clams wrapped in Sea Lettuce, 2–3 clams/trial	4	In all trials, terrapins ate all Soft-shelled Clams without Sea Lettuce first, then unwrapped the remaining Soft-shelled Clams from Sea Lettuce and ate them

1990) from the presence–presence unit. The C-score measures the average pairwise species segregation for the entire matrix (Gotelli 2000), and in our case, we measured the average pairwise presence–presence species aggregation for the entire matrix. Next, we generated 5000 pseudo matrices by shuffling the observed data matrix using a SYM4 randomization algorithm that provides fixed species totals but creates random proportional site totals (Luiselli et al. 2007). We then compared the observed presence–presence score to the distribution of simulated presence–presence scores. We considered (presence–presence) patterns statistically significant if the observed index was significantly larger than 95% of the simulated indices (Luiselli et al. 2007).

Results

Wild-caught JB Diamond-back Terrapins readily ate many but not all prey species in captivity (Table 1). Soft-shelled Clams and crabs were eaten consistently in every trial offered, whereas periwinkles, Sea Lettuce, and Eastern Mudsnails were routinely rejected. Analysis of fecal sample data from Erazmus et al. (2019) showed that Soft-shelled Clams were associated non-randomly and more frequently with Sea Lettuce than expected by chance (C-score = 123.33, $P < 0.0001$).

Discussion

Our feeding trials demonstrated that wild-caught JB Diamond-back Terrapins preferred molluscs, specifically Soft-shell Clams, over all other prey species. In feeding trials, JB Diamond-back Terrapins did not consume periwinkles or Eastern Mudsnails; Erazmus et al. (2019) also rarely found these prey species in Diamond-back Terrapin feces. These results are especially surprising because Periwinkles were heavily consumed in other Diamond-back Terrapin diet studies throughout their range (Tucker et al. 2018), and Eastern Mudsnails were consumed heavily by Diamond-back Terrapins in nearby Oyster Bay, NY (Herrel et al. 2018). Eastern Mudsnails are common in JB, but periwinkles are not (R.L. Burke, pers. observ.). Jamaica Bay Diamond-back Terrapins may avoid eating Eastern Mudsnails because their shells are relatively difficult to crush (Tucker et al. 1997), but if so, then why are they commonly eaten by Diamond-back Terrapins elsewhere? It is unlikely that JB Diamond-back Terrapins avoid eating Eastern Mudsnails because of the availability of another, easier-to-crush prey species (Erazmus et al. 2019).

Jamaica Bay Diamond-back Terrapins readily consumed non-native, invasive Asian Shore Crabs in our feeding trials. Asian Shore Crabs have been in JB since at least 1994 (G. Frame, National Park Service, Gateway National Recreation Area, Middletown, NJ, pers. comm.), and we commonly observed them in near-shore JB habitats that they share with non-native invasive European Green Crabs. Although Erazmus et al. (2019) found crab fragments in JB Diamond-back Terrapin fecal samples, they could not identify them to species. Lindeman (2006) similarly noted that *Graptemys geographica* (Lesueur) (Northern Map Turtle) had sufficient dietary flexibility to add 2 non-native clam species to their diets.

Our analyses indicate that Diamond-back Terrapin consumption of Soft-shelled Clams was non-random and was more frequently associated with Sea Lettuce than expected by chance. Erazmus et al. (2019) reported a high percentage frequency of occurrence of Sea Lettuce in JB terrapin feces. However, Diamond-back Terrapins preferred Soft-shelled Clams and avoided Sea Lettuce in our feeding trials. Together these results suggest that Diamond-back Terrapins consume Sea Lettuce incidentally while foraging for Soft-shelled Clams. While accidental plant consumption by Diamond-back Terrapins had been suggested previously (Coker 1906, Tucker et al. 1995), our study provides the first direct evidence that Diamond-back Terrapins ingest plant material incidentally. Soft-shelled Clams are normally found buried in sand and mud, up to 25 cm deep. but their burial depth decreases in the presence of macroalgal (such as Sea Lettuce) mats (Auffrey et al. 2004). In JB, Soft-shelled Clams often live directly below Sea Lettuce mats, on top of sand, at low tide (R.L. Burke, pers. observ.), so Diamond-back Terrapins attempting to capture clams might easily consume Sea Lettuce simultaneously. Butler (2000) mentioned a small amount of "unknown plant" found in Florida Diamond-back Terrapin diets, and Petrochic (2009) found over 70% frequency of occurence of plant material in Diamond-back Terrapin diets in nearby Oyster Bay, NY, but did not identify this material to species. We suspect that at least some of the unspecified plant material found in other diet studies was likely associated with the consumption of invertebrate prey.

Jamaica Bay Diamond-back Terrapins may have non-typical prey availability because of the unusual conditions of JB. Urban pollution, specifically nitrogen loading, is associated with Sea Lettuce blooms (Hanson and Lindh 1993, Mackenzie 2005, Odum et al. 1984). The expansion of Sea Lettuce also reduces the number of macroinvertebrates (copepods, polychaetes, *Gemma gemma* (Totten) [Amethyst Gem Clam], Eastern Mudsnails, and Soft-shelled Clams) on estuary sediment surfaces (Franz and Freidman 2002, MacKenzie 2000, MacKenzie and McLaughlin 2000). Therefore, nitrogen loading may indirectly reduce the abundance of many typical Diamond-back Terrapin prey species, causing changes in terrapin diets.

Relatively high consumption of Sea Lettuce has unknown consequences for Diamond-back Terrapins. Sea Lettuce can accumulate large amounts of polychlorinated biphenyl (PCB; Cheney et al. 2014) and heavy metals (Haritonidis and Malea 1999, Scoullos et al. 2004), and Holliday and Holliday (2012) found that PCBs decrease bone density in juvenile Diamond-back Terrapins, which may affect survivorship. Although some of their close relatives (*Graptemys* spp. [map turtles]) apparently feed largely on algae (Lindeman 2013), it is unclear whether Diamond-back Terrapins can digest algal tissue. Thus, JB Diamond-back Terrapins' foraging for Soft-shelled Clams appears to lead incidentally to their consumption of Sea Lettuce, which may increase their intake of contaminants without significant nutritional benefit.

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