Diet of the Carolina Diamondback Terrapin
(*Malaclemys terrapin centrata*) in
Northeastern Florida

**Joseph A. Butler**¹, **George L. Heinrich**², and **Melinda L. Mitchell**¹

¹Department of Biology, University of North Florida, Jacksonville, Florida 32224 USA [jbutler@unf.edu];
²Heinrich Ecological Services, 1213 Alhambra Way South, St. Petersburg, Florida 33705-4620 USA
[george@heinrichecologialservices.com]
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JOSEPH A. BUTLER¹, GEORGE L. HEINRICHS², AND  
MELINDA L. MITCHELL¹  

¹Department of Biology, University of North Florida, Jacksonville,  
Florida 32224 USA [jbutler@unf.edu];  
²Heinrich Ecological Services, 1213 Alhambra Way South, St.  
Petersburg, Florida 33705-4620 USA  
[george@heinrichecologicalservices.com]  

ABSTRACT. – We evaluated the diets of 81 Carolina  
diamondback terrapins (*Malaclemys terrapin centrata*)  
from northeastern Florida by analyzing fecal samples.  
Female diets were significantly different from male  
diets (*p* < 0.01); fecal samples from females contained  
crabs, marsh periwinkles (*Littorina irrorata*), and  
dwarf surf clams (*Mulinia lateralis*) in that order of  
ocurrence, whereas fecal samples from males had  
dwarf surf clams and crabs in that order. We suggest  
that head-size dimorphism is advantageous to females  
during nesting forays when they experience a shift in  
prey availability.  

Diamondback terrapins (*Malaclemys terrapin*) inhabit  
brackish coastal ecosystems from Massachusetts to  
southern Texas (Ernst and Lovich 2009). This species  
exhibits sexual dimorphism with adult females being  
significantly larger than males and having wider heads  
(Tucker et al. 1995). Several food items have been  
anecdotally recorded in their natural diet, including  
snails, clams, mussels, small crabs, fish, and annelid worms  
(Coker 1906; Cagle 1952; Hurd et al. 1979; Middaugh  
1981). More detailed terrapin dietary studies demonstrat-  
ed resource partitioning between sexes in South Carolina  
(Tucker et al. 1995), and Petrochic (2009) studied bite  
force and jaw gape size between sexes in relation to prey  
selection in New York. Knowledge of terrapin dietary  
needs and preferences throughout their range can be  
valuable to the management of this species and its habitat.  
We studied the diet of Carolina diamondback terrapins  
(*Malaclemys terrapin centrata*) in northeastern Florida to  
ascertain which foods they use and determine whether
resources are partitioned between males and females in this region.

Methods. — The study area consists of tidal creeks, salt marshes, and coastal islands adjoining approximately 12 km of the Intracoastal Waterway between the Nassau and St. Johns rivers (Duval County, Florida). The environment is typical salt marsh dominated by smooth cordgrass (*Spartina alterniflora*) with intermittent stands of black needle rush (*Juncus roemerianus*), and is characterized by the most extreme tidal fluctuations in the state (Montague and Wiegert 1990). A more thorough assessment of the flora and fauna of the area is provided by Butler (2000).

We captured diamondback terrapins from 11 May through 28 June 1995 and from 6 May through 25 June 1996 as part of a larger project. We employed several capture methods, including gill netting, otter trawling, crab pots modified to prevent terrapin drowning, and hand capture. We collected terrapins from Deep Creek and Cedar Point Creek in the southern sector of the area and others from a nesting beach where the Nassau River meets Nassau Sound in the northern sector. We determined terrapin sex by evaluating carapace length, head width, tail length, and cloacal position (Ernst and Lovich 2009). We marked terrapins by drilling marginal scutes with a unique number system (Cagle 1939) and measured plastron length (PL) with tree calipers to the nearest 1.0 mm.

We maintained diamondback terrapins individually in clean, 19-liter plastic buckets with 2–3 cm of fresh water at air temperatures varying from 28–32°C for up to 48 hrs, a period which should be sufficient for defecation to occur (Tucker et al. 1995). Following this period, terrapins were released at their capture sites whether or not they had defecated. We recovered individual fecal samples from the buckets by carefully pouring off the water and scraping the remaining product into small plastic vials. Fecal samples dried by natural evaporation for 10–14 d, after which we capped and stored the vials until processing.

Throughout the field study we opportunistically collected samples of potential prey items as voucher specimens from the study area. We collected crabs from shorelines, marshes, and crab pots; we gathered snails from marsh vegetation, shorelines at low tide, and from the mud in creek bottoms; and we found clams on muddy creek bottoms and in intertidal areas. When fecal collection ended, we took the fecal vials and voucher specimens to the Florida Museum of Natural History (FLMNH, Gainesville) for identification with the assistance of museum staff. We separated components of each sample, identified them under a dissecting microscope, and compared fecal constituents to both voucher and FLMNH specimens. We passed samples containing large amounts of sand through a 0.25 mm sieve and discarded the sand. Because of the similarity of opercula between marsh periwinkles (*Littorina irrorata*) and eastern mud snails (*Nassarius obsoletus* [= *Ilyanassa obsoleta*]), we broke voucher specimens into small pieces and examined them along with their respective opercula for comparative purposes. We calculated the frequency of occurrence of prey species as the percent of fecal samples containing that species.

To determine whether there were differences among fecal contents, we did five comparisons: we compared fecal samples collected in 1995 with those from 1996, those from males with those from females, samples from females captured at the nesting beach site with those from females collected from tidal creeks, those from mature versus immature females, and samples from males versus immature females. In each comparison, we employed a G-exact test of population differentiation in Genepop using the default parameters (Raymond and Rousset 1995). This program compares genotype frequency data for multiple independent loci across populations. In our case, we treated each food item as an independent locus with two possible genotypes for each, “present” or “absent.” The exact test was then performed to test population differentiation across all loci (i.e., food items). We used a significance level of $p < 0.05$ in all comparisons. When means are presented, they are followed by standard errors.

Results. — In 1995, we collected fecal samples from 34 female and 12 male diamondback terrapins, and in 1996, we collected specimens from 26 females and 9 males. In both years, most females were collected by hand at the nesting beach as they came up to nest (total = 43). Fifteen females came from Deep Creek and 2 from Cedar Point Creek. We encountered no males at the nesting beach but collected 18 from Deep Creek and 3 from Cedar Point Creek.

Butler (2002) suggested that the smallest gravid female from this northeastern Florida population had a PL of 143 mm. Therefore, 9 females from the current study (all collected from creek habitats) were immature, ranging from 84–142 mm PL (mean $= 120.4 \pm 7.03$), and 51 (43 collected from the nesting beach and 8 from creek habitats) were mature, ranging from 143–180 mm PL (mean $= 161.9 \pm 1.16$). Male terrapins mature between 90 and 100 mm PL throughout their range (Cagle 1952; Seigel 1984; Lovich and Gibbons 1990; Roosenburg 1991); therefore two males in the current study with PLs of 86 and 87 mm were considered immature. The 19 mature males had PLs ranging from 93–114 mm (mean $= 102.2 \pm 1.39$).

We identified 9 categories of food items in fecal samples (Table 1). Most crab remains were so fragmented that species identification was not possible, but in several samples, we recognized wharf crabs (*Armases* [= *Sesarma* *cinereum*]). Samples also contained broken pieces of dwarf surf clams (*Mulinia lateralis*), opercula and shell fragments of the gastropods *L. irrorata* and *N. obsoletus*, and broken remains of small barnacles (*Balanus* sp.). Two samples contained fragments of other bivalves (*Lucina pensylvanica* and *Anadara* sp.), and two others contained fish bones from the family Cyprinodontidae, probably *Fundulus* sp. Gastropod opercula from two samples could not be identified to species and five samples contained unidentifiable animal matter (Table 1). Sand and plant material were found infrequently, and we
Table 1. Frequency of occurrence of food items identified from 81 fecal samples (21 males, 9 immature females, and 51 mature females) of Carolina diamondback terrapins (Malaclemys terrapin centrata) from northeastern Florida. Also shown are p-values for comparisons of fecal samples of male vs. female terrapins, females caught at a nesting beach vs. those caught in tidal creeks, mature females vs. immature females, and males vs. immature females. Bold values are statistically significant. Fecal samples of neither males nor immature females had Balanus sp., and this is indicated as No data.

<table>
<thead>
<tr>
<th>Food item</th>
<th>Males</th>
<th>Immature females</th>
<th>Mature females</th>
<th>Males vs. females</th>
<th>Nesting beach females vs. creek females</th>
<th>Mature females vs. immature females</th>
<th>Males vs. immature females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dwarf surf clam (Mulina lateralis)</td>
<td>95</td>
<td>100</td>
<td>27.5</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.31</td>
</tr>
<tr>
<td>Crabs</td>
<td>42.9</td>
<td>44.4</td>
<td>66.6</td>
<td>0.03</td>
<td>&lt;0.01</td>
<td>0.12</td>
<td>1.00</td>
</tr>
<tr>
<td>Marsh periwinkle (Littorina irrorata)</td>
<td>9.5</td>
<td>33.3</td>
<td>51.0</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.21</td>
<td>0.051</td>
</tr>
<tr>
<td>Eastern mudsnail (Nassarius obsoletus)</td>
<td>14.3</td>
<td>11.1</td>
<td>0.08</td>
<td>0.36</td>
<td>0.72</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Barnacle (Balanus sp.)</td>
<td>0</td>
<td>0</td>
<td>0.06</td>
<td>0.19</td>
<td>1.00</td>
<td>0.41</td>
<td>No data</td>
</tr>
<tr>
<td>Unidentified gastropods</td>
<td>4.8</td>
<td>0</td>
<td>0.02</td>
<td>1.00</td>
<td>0.33</td>
<td>0.62</td>
<td>0.57</td>
</tr>
<tr>
<td>Other bivalves</td>
<td>4.8</td>
<td>0</td>
<td>0.02</td>
<td>0.57</td>
<td>0.59</td>
<td>1.00</td>
<td>0.57</td>
</tr>
<tr>
<td>Fish</td>
<td>4.8</td>
<td>0</td>
<td>0.02</td>
<td>0.57</td>
<td>0.59</td>
<td>1.00</td>
<td>0.57</td>
</tr>
<tr>
<td>Unknown</td>
<td>4.8</td>
<td>0</td>
<td>0.08</td>
<td>0.73</td>
<td>0.70</td>
<td>0.28</td>
<td>0.57</td>
</tr>
</tbody>
</table>

Assumed they were ingested inadvertently and excluded them from our list of food items.

In our statistical comparisons, the only prey items determined to have significant differences were M. lateralis, crabs, and L. irrorata (Table 1). There were no significant differences between the two study years in proportions of fecal contents of either male (p = 0.66) or female (p = 0.10) diamondback terrapins; therefore we pooled results of both years. Prey proportions from males were significantly different from those of females (p < 0.01); males had higher proportions of M. lateralis (p < 0.01), whereas females had more crabs (p = 0.03) and L. irrorata (p < 0.01). Females collected at the nesting beach had fecal contents that were significantly different in proportions from those of females collected from tidal creeks (p < 0.01); those from the nesting beach again had more crabs (p < 0.01) and L. irrorata (p < 0.01), whereas females from the creeks had more M. lateralis (p < 0.01). Mature and immature female terrapins had significantly different fecal proportions (p < 0.01); the only difference was that immature females had more M. lateralis (p < 0.01). Males and immature females did not differ in the proportions of their fecal contents.

Discussion. — Tucker et al. (1995) reported 6 prey items (including 3 crab species and Balanus sp.) from diamondback terrapin fecal samples in South Carolina, whereas Petrochic (2009) listed 12 prey items (she included plants and excluded Balanus sp.) from New York. Our list of 9 prey items combines all crab species into one category, excludes plants, and includes Balanus sp. (Table 1). Petrochic (2009) found N. obsoletus to be the most frequently occurring prey item in the diet of New York terrapins. Mudsnails were an infrequent dietary component of both sexes in Florida (Table 1), and Tucker et al. (1995) did not find them from South Carolina terrapins. The barnacle Balanus sp. was identified in South Carolina and New York terrapin diets but in such low frequencies that researchers suggested that barnacles were taken inadvertently while terrapins were foraging on other items (Tucker et al. 1995; Petrochic 2009). In our study, only 3 fecal samples from females contained barnacle shards, indicating a low frequency of ingestion. We found fish bones in two fecal samples; however terrapins are not likely to attempt to capture fish for their diet (Petrochic 2009). Ehret and Werner (2004) suggested that terrapins may occasionally eat carrion, and it may be that the bones are the result of terrapins scavenging on fish. Tucker et al. (1995) found L. irrorata to be most heavily consumed by both terrapin sexes. Further, they found that males ate smaller periwinkles than did females and suggested this resource partitioning to be a driver in the evolution of larger female head size. Petrochic (2009) reported that larger N. obsoletus were eaten more often by mature female terrapins than by males or smaller females and attributed this to the mature females’ larger jaw gape size and stronger bite force. In the present study, mature female terrapins ate mostly L. irrorata and crabs, whereas males and immature females consumed mostly M. lateralis (Table 1). At first glance, the Florida data may appear to support the case for resource partitioning proposed by Tucker et al. (1995); however, we believe our findings suggest this to be a case of variation in prey availability.

Clams such as M. lateralis are relatively static, living in the mud and offering no resistance to predators other than their hard shells. Therefore, if small clams are abundant, it should be easier for terrapins of all sizes to use this source than to chase and struggle with crabs or search for periwinkles. Roosenburg et al. (1999) suggested that various smaller clam species dominate terrapin diets in Maryland. Although M. lateralis ranges from Maine to Texas (Kaplan 1988), overlapping and exceeding terrapin range, it has not been reported previously in their diet...
throughout their range (Tucker et al. 1995; Petrochic 2009; Cagle 1952) noted the presence of small clams and snails in the guts of terrapins from Louisiana. It may be that *M. lateralis* was not available to terrapins in the previous studies. Mannino and Montagna (1997) reported that in Texas *M. lateralis* were not collected at salinities below 20 ppt. Tucker et al. (1995) noted that salinities at their study site varied from 10 ppt and 15 ppt, which likely precluded the presence of dwarf surf clams. In a three-and-a-half–year study in Tampa Bay, Florida, Santos and Simon (1980) reported that *M. lateralis* exhibited several population rises and crashes, such that they varied from the most abundant taxon collected to not found at all. They attributed these fluctuations to variations in dissolved oxygen levels. These or other factors may have affected dwarf surf clam populations in previous terrapin dietary studies, and at the nesting beach in the current study. If *M. lateralis* was not present at the nesting beach, these terrapins would be forced to feed on other available prey.

The diets of female terrapins collected at the nesting beach differed significantly from those of females from the tidal creeks (Table 1). We identified *M. lateralis* in 100% of fecal samples collected from both mature (*n* = 8) and immature (*n* = 9) females from the tidal creeks, compared to only 14% of samples from the nesting beach. Conversely, 74.4% of fecal samples from nesting beach females had crabs, and 60.5% had *L. irrorata*, whereas fewer of those items were found in creek females (35.3% and 17.6%, respectively). Further, *M. lateralis* was identified in 95% of male fecal samples, all of which were from tidal creeks (Table 1). Prey items found in male fecal samples did not differ significantly from those of immature females that were also all collected from tidal creeks (Table 1). Therefore, both sexes and all age classes selected *M. lateralis* where it was available in the tidal creeks.

Terrapins nest above the high tide line in sandy soils that allow oxygen exchange between the developing embryo and the environment (Roosenburg 1994). Nesting sites may not be adjacent to resident creek habitats, and radiotelemetry studies have demonstrated that terrapins can travel several kilometers between resident creeks and nesting areas (Butler 2002). When they travel to nest, females may encounter differences in prey availability that affect their diet. Mortimer (1995) reported that Nicaraguan green sea turtles (*Chelonia mydas*) nest in areas where preferred foods are not available and shift to a diet of less preferred foods. Female terrapins collected at the nesting beach had higher proportions of crab and periwinkles in their fecal samples than did all terrapins from tidal creeks. Consequently, we suggest that another explanation for head size differences in terrapins beyond dietary resource partitioning (Tucker et al. 1995) could be that larger head size allows nesting females to use alternative food sources when forced to leave areas where smaller, more exploitable prey are abundant. Petrochic (2009) labeled diamondback terrapins dietary generalists, and it is clear they use a variety of prey throughout their range (Tucker et al. 1995; Petrochic 2009; this study). Our study suggests that variation in prey selection by nesting females also occurs on a local scale.

Our study was conducted during May and June for two consecutive years and, as such, revealed information concerning terrapin diet during the nesting season. Longer-term studies including active nonnesting months could support our prey availability explanation. Nonnesting adult females in northeastern Florida spend most of their time in the tidal creeks (Butler 2002). If dwarf surf clams, *M. lateralis*, remained abundant in the creeks during nonnesting months, we would expect them to be the most frequent prey item in all terrapin fecal samples. Future studies of terrapin diet should consider the importance of prey availability related to seasonal terrapin movements.

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