

Herpetologica, 51(2), 1995, 167-181
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RESOURCE PARTITIONING BY THE ESTUARINE TURTLE *MALACLEMYS TERRAPIN*: TROPHIC, SPATIAL, AND TEMPORAL FORAGING CONSTRAINTS

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ABSTRACT: We investigated the foraging ecology of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina by examining fecal samples for evidence of resource partitioning. From 76-79% of the dietary volume was the salt marsh periwinkle (*Littorina irrorata*); crabs (*Uca pugnax*, *Sesarma reticulatum*, and *Callinectes sapidus*), barnacles (*Balanus*), and clams (*Polymesoda caroliniana*) constituted the remainder. Dietary partitioning is related to the ontogenetic niche of terrapins. Sexual dimorphism occurs in terrapins with females having larger heads and bodies than males. Terrapins with large head widths ingest significantly larger periwinkles and a wider diversity of prey than terrapins with small head widths. Dietary overlap between males and females is greatest when females are small and decreases as females develop larger enlarged heads. Sexual dimorphism in terrapin trophic structures appears to be partially driven by ecological divergence through resource partitioning.

High tides permit terrapins to forage aquatically in upper reaches of the salt marsh. Prey size and distribution are variable and changing tidal heights affect the spatiotemporal availability of prey to foraging terrapins. Divergent foraging strategies for terrapins of different head widths may result in habitat partitioning. Food accessibility rather than food abundance may be a limiting factor for terrapins in areas of high tidal variability. Terrapins are clearly prominent but unrecognized macroconsumers in salt marsh ecosystems.

Key words: Resource partitioning; Turtle; *Malaclemys*; Dimorphism; Salt marsh; Foraging ecology; *Littorina*; Trophic structure

THE diamondback terrapin (*Malaclemys terrapin*) is a common reptile in salt marshes of the southeastern United States (Carr, 1952). Despite having a latitudinal distribution that extends from Massachusetts to Texas (Ernst and Barbour, 1989), their functional role as predators in salt marsh ecosystems is poorly known (Adam, 1990; Day et al., 1989; Pomeroy and Wiegert, 1981). In captivity, terrapins readily

consume snails, shellfish, fish, crustaceans, and beef (Allen and Littleford, 1955; Carr, 1952; Coker, 1906, 1920; Davenport et al., 1992; Hildebrand, 1929; Hildebrand and Hatzel, 1926), but dietary studies of wild terrapins are limited to descriptive or anecdotal accounts. Items recorded for the terrapin's diet include snails (*Littorina irrorata*, *Melampus lineatus*), small crabs (*Gelasimus*, *Uca*), marine annelids (*Nereis irritabilis*), mussels (*Mytilus edulis*), clams (*Anomalocardia cuneiformis*), captured or scavenged fish (*Menidia menidia*), and plant material (*Sargassum*, unidentified

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grass fragments) (Bishop, 1983; Ernst and Barbour, 1972; Hay, 1892; Hurd et al., 1979; Middaugh, 1981; Spagnoli and Marganoff, 1975). Davenport et al. (1992) studied feeding behavior of captive male terrapins, but no quantitative studies have examined dietary preferences of varied size classes or of both sexes of terrapin in the wild.

We chose to investigate dietary preferences among size classes of terrapins because of the extreme sexual size dimorphism shown by adults (female to male body size ratio of 1.45) (Gibbons and Lovich, 1990). The prevalence of size dimorphism among vertebrates (Camilleri and Shine, 1990; Shine, 1989) has provoked several hypotheses concerning food size selectivity relative to predator body size (Pianka, 1974; Slatkin, 1984; Wilson, 1975). Differences in body size can function to promote coexistence by allowing associated differences in food size selection (Brown and Lieberman, 1973; Wilson, 1975) and thereby reduce niche overlap and competition (Colwell and Futuyma, 1971; Schoener, 1967). Ontogenetic shifts in resource utilization are recorded in many reptilian groups, including the chelonians (Berry and Shine, 1980; Clark and Gibbons, 1969; Dalrymple, 1977; Hart, 1983; Mahmoud, 1968; Marchand, 1942; Moll, 1990; Parmenter and Avery, 1990; Plummer and Farrar, 1981; Pope, 1939; Tinkle, 1958; Vogt, 1981). Divergence in food resource utilization may occur through habitat selection, prey choice, or gape limitation (Schoener, 1974; Shine, 1991), particularly for species with pronounced dimorphism such as *Malaclemys*. Larger body size and enlarged head width in adult females may contribute significantly to ontogenetic or intersexual resource partitioning.

Dietary composition can reflect either resource availability or dietary selection, because many turtles are opportunistic feeders. As food resources are unlikely to be distributed uniformly in the salt marsh (Kneib, 1984), foraging involves searching for food patches as a function of the distribution, density, and relative energetic return of available prey items (Pyke, 1984).

Daily fluctuations in tidal amplitude may also affect resource availability; if so, then changes in prey quantity or composition would be predicted (Ross, 1986). Thus, if resource partitioning has occurred among terrapins, segregation along dietary, spatial, or temporal resource dimensions would be detectable by changes in intraspecific niche breadth or overlap.

We investigated the functional ecology of diamondback terrapins to test predictions of resource partitioning by (1) analyzing the diets of terrapins, (2) calculating coefficients of dietary overlap by gender and size class, (3) determining spatial patterns of prey distribution in the intertidal salt marsh, and (4) determining if prey availability and dietary intake were affected by tidal cycles. In addition, our findings quantify the predatory role of terrapins in salt marsh food webs.

MATERIALS AND METHODS

Study Site

Kiawah Island, South Carolina (80°08'W, 32°36'N) is an Atlantic barrier island bounded by extensive stands of *Spartina alterniflora* on the mainland side. The Kiawah River and its tributaries form a broad expanse of mesotidal euryhaline salt marsh bordering the west side of the island. We determined tide levels from published National Oceanic and Atmospheric Administration charts with the closest correction site (Kiawah River Bridge) to our study site. Maximum tidal height at Kiawah Island varies from 1.4–2.2 m during the year. During spring tides, great expanses of marsh are flooded while at neap tides, the *Spartina* remains largely unflooded. Salinity levels in the Kiawah River are the same (T. Zimmerman, unpublished data) as recorded for preferred salinity ranges (10–15 ppt) of terrapins in the Ashley and Wando River estuaries (Bishop 1983), some 25 km north. Further descriptions of the region are found in Gibbons and Harrison (1981).

General Methods

We conducted a mark-recapture study of terrapins from 1983–1993 to provide

information on demographics, feeding ecology, and movement patterns of diamondback terrapins (Gibbons and Harrison, 1981; Lovich and Gibbons, 1990; Lovich et al., 1991; Tucker and FitzSimmons, 1992). We collected terrapins ($n = 1102$ initial captures, 819 recaptures) using trammel nets and seines (Memphis Net and Twine, Inc.) during mid-ebb through mid-flood tides and transported them in pillow cases to a field laboratory for measurements of head width, carapace length, plastron length, and mass. We measured plastron length with a plastic ruler, carapace length with 50-cm forestry calipers, and head width with vernier calipers at the posterior edge of the upper tomium. All measurements were taken to the closest 1 mm. We aged terrapins by counting external annuli on the right humeral scute of the plastron (Dunham et al., 1988). Any turtles with smoothed or eroded annuli that could not be aged reliably upon first capture were excluded from age-related analyses. We marked all terrapins uniquely by notching marginal scutes (Cagle, 1939) and returned them to the same creeks from which they were collected.

Dietary Studies

During 22 June–27 July 1991, we collected 294 terrapins, separated them by sex, and grouped them into size categories based on mandible width measured across the posterior edges of the upper tomium (<20 mm = small, 20–30 mm = medium, and >30 mm = large). We kept terrapins of different head categories in separate fiberglass holding bins for 24–48 h to collect their feces. Terrapin feces that were excreted during transport were added from each pillow case to the appropriate bin and the pillow cases were cleaned before reuse. Fecal samples were washed into U.S. Standard Testing sieves (1 mm mesh), air dried, and winnowed (Tucker and FitzSimmons, 1992) to separate shell fragments. We identified fecal fragments by visual comparison to a locally gathered sample of marine invertebrates. We estimated gut passage times to be from 24–36 h based upon published values for emydids of similar size and under similar temperature (28–

32 C) regimes (Cagle, 1950; Kepenis and McManus, 1974; Parmenter, 1980, 1981; Parmenter and Avery, 1990). The estimates of digestive turnover rate linked each sample to food ingested on the previous day.

To determine the size of snails that terrapins ate, we collected 270 *Littorina irrorata* representing all size classes and measured them to the nearest 0.1 mm with vernier calipers to determine shell length (apex–spire) and operculum length. To minimize measurement errors from the flexible opercula on live snails, we microwaved snails to keep the operculum and shell together, then detached and measured the operculum. The relationship between operculum length and snail length was $y = 2.9x - 1.1$ ($r^2 = 0.90$, $P < 0.001$) where y is shell length and x the operculum length (Tucker and FitzSimmons, 1992). This relationship allowed sizes of ingested snails to be estimated from the opercula recovered in a fecal sample. Measurements of shell lengths are reported in this study, but to facilitate comparisons with studies using shell width, the formula width = length/1.3 provides a convenient transformation (calculated from Baxter, 1983).

In 1992, additional components of the diet were quantified. We separated fecal samples by prey species and quantified them by percent occurrence, percent mass, mass/turtle, and number of opercula/turtle. Percentages were arcsine transformed prior to statistical testing.

Niche breadth was quantified by Shannon indices for diversity (H') and evenness (J') (Magurran, 1988):

$$\text{diversity: } H' = - \sum_{i=1}^S P_i \log P_i;$$

$$\text{evenness: } J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log S},$$

where S is the number of prey species, P_i is the proportion of prey species i , and H'_{\max} is the log of S . Diversity (H') increases as the number of species (S) represented in the diet increases. Low H' values represent dietary specialists and high values represent generalists. The evenness index (J')

gives a measure of relative diversity in that the quantity $1 - J'$ is an expression of dominance on a 0-1 scale. Low values indicate low dominance and high values a high dominance in prey representation.

We measured dietary overlap (a similarity index) by the expression developed by Schoener (1968):

$$\theta = 1 - \frac{1}{2} \left(\sum_{i=1}^s |P_{ij} - P_{ik}| \right),$$

where P_{ij} and P_{ik} are the proportions of the food resource i used by category j and k , and s is the total number of different resources used by each category. The fewer the numbers of commonly used resources, the higher the divergence measure. Dietary overlap was considered minimal if values (scaled: 0 = no overlap to 1 = complete overlap) were <0.4 (Ross, 1986) and of biological significance in terms of resource partitioning if values exceeded 0.6 (Zaret and Rand, 1971).

Food Resource Distribution

In 1991, we measured prey density and distribution along 14 transects perpendicular to the channels of the main tidal creeks (Fiddler Creek, $n = 4$; Terrapin/Marsh Creek, $n = 3$; Oyster Creek, $n = 4$; and Stingray Slough, $n = 3$). Terrapins encounter prey in this manner as they travel outward from creek drainages, and our systematic sampling reflected a biologically meaningful continuum with respect to terrapin foraging patterns. Plots (1 m^2) were selected at 5-m intervals along the transect (mean length of transect = 66 m, $SD = 22.5$, range = 30-115 m) extending across the intertidal marsh from the creek bank to the edge of the high marsh (sensu Pomeroy and Wiegert, 1981) to quantify food resource availability. All plots ($n = 199$) were contained within an area of 4 km^2 .

Within each plot, we counted all crab burrows to estimate crab abundance (Warren, 1990), recorded the number and height of stems of *Spartina*, and collected all *Littorina* for enumeration and measurement. Prey and habitat associations were de-

scribed by regression analysis for each transect. Snail sizes were also categorized as $\leq 10 \text{ mm}$ or $> 10 \text{ mm}$ to trace patterns of distribution for juvenile and adult *Littorina* (Bingham, 1972). The dispersion of prey items across each transect was determined from Morisita's index of dispersion (Morisita, 1959):

$$I_d = n \frac{\sum X^2 - N}{N(N-1)}$$

where n is the number of plots, N is the total number of individuals counted on all n plots, and X is the number of individuals per plot. If dispersion is random, then $I_d = 1.0$; if perfectly uniform, $I_d = 0$; and if maximally aggregated, $I_d = n$.

Temporal Variation in Resource Availability

To investigate the role of tidal effects on prey availability, we collected 285 terrapins over 24 June-1 August 1992 to determine dietary intake relative to tidal height. Terrapins were classified by tomium width as before and included 176 small males, three small females, 73 medium females, and 33 large females. The three small females ranged from 19.4-19.9 mm tomium width and their samples were subsequently pooled with the males for a total of 179 small terrapins. We adjusted for dietary turn-over rates by linking each sample to the high tide of the previous day. The sample period included the variation between spring and neap high tides (1.55-2.05 m) and spanned a complete lunar cycle so that rising and falling phases were equally represented. To examine prey consumption relative to tidal amplitude, we used least squares linear regression to examine general trends and interpolation to search for switches in prey consumption that would otherwise be masked by linear regression.

Statistical Analysis

Statistical procedures (Chi-square, Pearson's correlation coefficient, t -tests, and regression analysis) were performed on data that met the assumptions of normality and equality of variance. Statistical signifi-

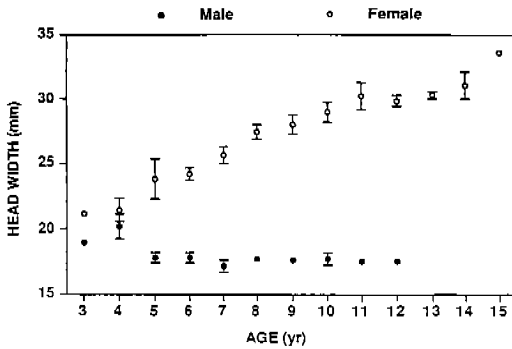


FIG. 1.—Size dimorphism in *Malaclemys terrapin* at Kiawah River, South Carolina. Growth in head size for a given age and sex are indicated. Means ± 1 SE are plotted.

cance was inferred for $\alpha = 0.05$. Groupings that were significantly different by ANOVA were followed by a multiple range test to determine which means differed. Means reported in this paper are followed by ± 1 SD. Statistical analyses were completed with Statview II and Superanova software.

RESULTS

Trophic Structure Dimorphism

Hatchlings and young terrapins were not seen or sampled adequately by our capture methods; only four 3-yr-olds were represented among 1102 individuals captured. All animals could be reliably aged between 4–7 yr, but as the epidermal scutes eroded over time, direct age determination became more difficult. Subsequent recaptures allowed us to age individuals up to 15 yr (age at first capture plus present duration of study) and generate growth curves (Dunham and Gibbons, 1990). Terrapins exhibited high site fidelity with 96% of recaptures occurring within the same creek drainage as recorded for the original capture.

Body size to age relationships (Gibbons, unpublished data) indicated that little growth in plastron length occurred in males after age 4–5 yr while females continued to grow in body size until about 10–11 yr. Relationships for head width to age exhibited a similar pattern between the sexes (Fig. 1). Head width remained small in males ($\bar{x} = 17.61$ mm, $SD = 1.047$, $n =$

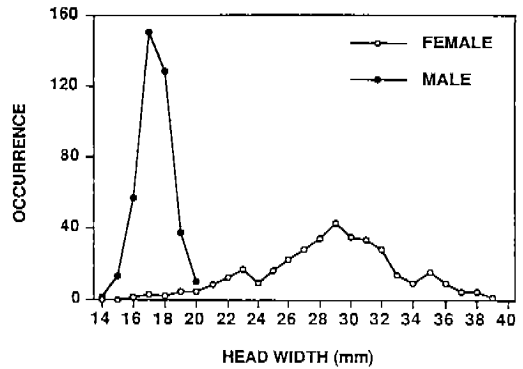


FIG. 2.—Frequency of occurrence for head width of male and female *Malaclemys terrapin* at Kiawah River, South Carolina. The x axis represents 1 mm size groupings.

396, range 14.6–20.5), and there was no correlation of head width to age. In contrast, there was a positive relationship between head width and age for females ($y = 11.09 + 2.75x - 0.09x^2$, $r^2 = 0.47$, $n = 163$, $P < 0.001$). Mean head width for all females was 28.88 mm ($SD = 4.29$, $n = 355$, range = 16.4–39.5). Only 3% of the females had head widths < 20 mm while 97.5% of the males were < 20 mm (Fig. 2).

Head width in medium and large females increased more than accounted for by an allometric increase in body size as projected from male growth relationships (Fig. 3). The relationship of head width (y) to plastron length (x) was different between males ($y = 0.12x + 5.30$, $r^2 = 0.35$, $n = 395$, $P < 0.0001$) and females ($y = 0.24x - 5.82$, $r^2 = 0.74$, $n = 346$, $P < 0.0001$) with the regression slope for females twice that of males. Mean head width for hatchlings was 7.2 mm ($SD = 0.4$, $n = 8$).

Dietary Divergence and Resource Overlap

Fecal samples were composed of the opercula of marsh snails (*Littorina irrorata*), the claws, legs, and carapace fragments of fiddler crabs (*Uca pugnax*) and marsh crabs (*Sesarma reticulatum*), legs of juvenile blue crabs (*Callinectes sapidus*), small marsh clams (*Polynesoda caroliniana*), and small barnacles (*Balanus*)

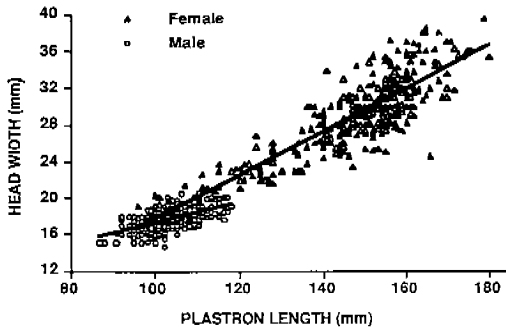


FIG. 3.—The relationship of head width to plastron length for *Malaclemys terrapin* at Kiawah River, South Carolina. Least squares regression lines are plotted for males ($r^2 = 0.35$, $P < 0.0001$) and females ($r^2 = 0.74$, $P < 0.0001$).

(Table 1). Sediment and fragments of *Spartina* comprised a negligible amount of the samples (<1–2%).

Littorina constituted 76–79% of the overall dietary mass for each size class of terrapin (Table 1), but both the mean size and range of snails consumed varied considerably between sexes and among size classes (Fig. 4, Table 2). Coefficients of skewness (S) for snail size distributions exhibited a shift from positive to moderately negative skewness (Table 2), indicating a shift from small to larger snails ingested as head width increased. Coefficients of kur-

tosis (K) changed from leptokurtic to a platykurtic frequency distribution (Table 2) indicating a broadened range of snail sizes ingested as head width increased. ANOVA tests for mean sizes of snail consumed by terrapins of different head width categories indicated significant differences among sexes and sizes. The mean sizes of snails consumed by small, medium, and large females were significantly different from one another (Fisher's protected LSD, $P < 0.001$ in each case) (Table 2). The mean snail size consumed by males differed significantly from small and large females (Fisher's protected LSD, $P < 0.001$ in each case) but not from medium females ($P = 0.48$) (Table 2). Males, small females, and medium females composed the majority of their diet with snails ≤ 10 mm while large females relied on snails > 10 mm.

Species of small crab (*U. pugnax*, *S. reticulatum*) were recorded in the diets of all turtles, but the large crab *C. sapidus* was strongly represented only in diets of medium and large terrapins (Table 1). Small clams (*P. caroliniana*) were ingested infrequently and comprised a small volumetric portion of the few samples in which they occurred (Table 1). Low numbers of barnacles were ingested by all size categories of turtles; it was unclear whether barnacles were ingested intentionally or

TABLE 1.—Prey items recovered from fecal samples of diamondback terrapins (*Malaclemys terrapin*) at Kiawah Island, South Carolina. Values are expressed as percent occurrence (% of samples containing a particular taxon), percent mass (% of total mass), and mass per terrapin (grams dry weight) of prey items for terrapins of three head width categories (S is < 20 mm, M is 20–30 mm, L is > 30 mm). Number of pooled samples = 33 (small $n = 12$; medium $n = 13$; large $n = 8$).

Prey	% occurrence			% mass			Mass		
	S	M	L	S	M	L	S	M	L
<i>Littorina irrorata</i> (Periwinkle)	100	100	100	79.1	76.2	78.3	0.50	2.72	3.80
a. (≤ 10 mm)	(100)	(100)	(100)	(64.9)	(59.1)	(25.0)	(0.41)	(2.11)	(1.21)
b. (> 10 mm)	(100)	(100)	(100)	(14.2)	(17.1)	(53.3)	(0.09)	(0.61)	(2.59)
c. <i>Uca pugnax</i> (Fiddler crab)	25.0	69.0	50.0	4.8	7.8	5.1	0.03	0.28	0.25
d. <i>Sesarma reticulatum</i> (Marsh crab)	25.0	31.0	63.0	3.2	1.4	6.2	0.02	0.05	0.30
e. <i>Callinectes sapidus</i> (Blue crab)	8.0	69.0	63.0	0.1	12.9	9.7	0.001	0.46	0.47
f. <i>Polynesoda caroliniana</i> (Marsh clam)	8.0	8.0	13.0	12.7	< 0.1	< 0.1	0.08	0.0015	0.0013
g. <i>Balanus</i> (Barnacle)	8.0	54.0	39.0	0.1	1.6	0.6	0.001	0.06	0.03

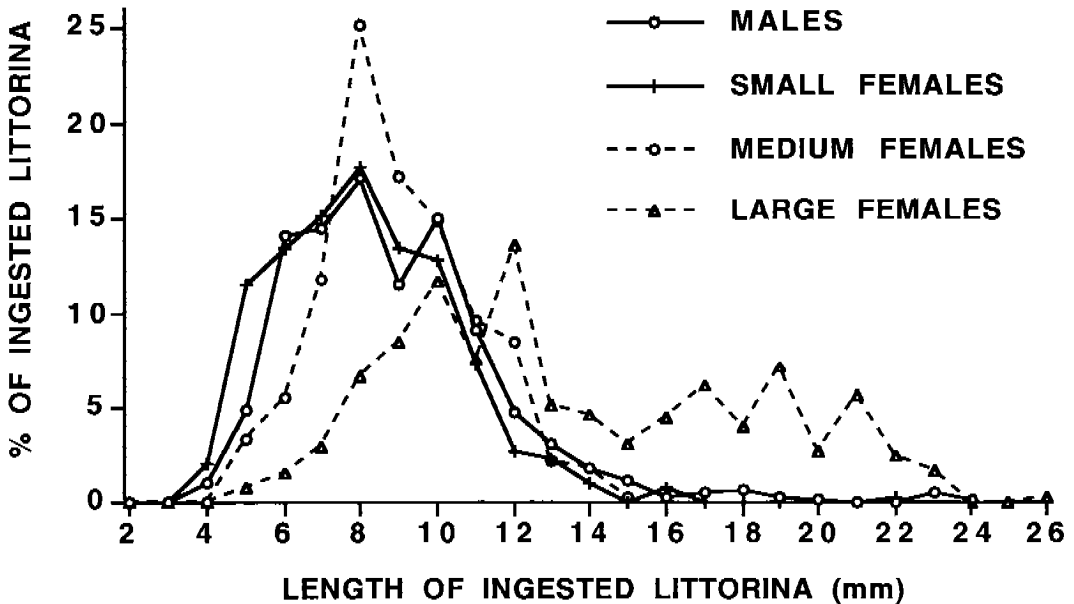


FIG. 4.—Size frequency distribution of periwinkles, *Littorina irrorata*, ingested by male and female diamondback terrapins, *Malaclemys terrapin*, in the Kiawah River, South Carolina. Terrapin head classifications are small if ≤ 20 mm, medium from 20–30 mm, and large if ≥ 30 mm head width.

incidentally as terrapins grazed snails from stems of *Spartina* (Table 1).

Because the size of snails consumed was related to the size class of terrapin (Tables 1, 2), snails < 10 mm and > 10 mm were considered as separate prey categories (Schoener, 1974) in calculations of dietary diversity and evenness. Dietary diversity (H') increased slightly with increasing head width but not significantly as all prey items were represented across the span of head widths (Table 3). Small headed turtles exhibited more dietary specialization than did turtles of larger head widths, although the overall difference was minor. Dietary evenness (J') rose slightly with increasing head width (Table 3) as a result of shifts in prey preference.

Terrapins consumed a similar range of prey species but in different proportions as indicated by the number of equally common prey (Table 3). Small terrapins specialized on small snails with large snails and marsh clams of lesser importance (Table 3). Medium terrapins still relied on small snails but apportioned more of the diet among large snails, blue crabs, and fiddler crabs (Table 3). Large terrapins

spread their dietary choices more evenly among large snails, small snails, blue crabs, mud crabs, and fiddler crabs (Table 3). Significant dietary overlap (θ) occurred between small and medium terrapins and between medium and large terrapins. Dietary overlap was least between small and large terrapins but not considered significantly different (Table 3).

TABLE 2.—Number and mean size of snails (*Littorina irrorata*) recovered from fecal samples of diamondback terrapins (*Malaclemys terrapin*) of different category head widths. Head width classifications for males (M) are 14.6–20.5 mm, small females (SF) are < 20 mm, medium females (MF) are 20–30 mm, and large females (LF) are > 30 mm. Mean snail sizes are followed by a letter (a–c) to indicate which values were significantly different by Fisher's protected LSD for a posteriori comparisons. K and S represent values for kurtosis and skewness.

Head width classification	Sample n	Mean snail size (± 1 SD)	% < 10 mm	% > 10 mm	K/S
M	878	8.4 (2.7) b	78.0	22.0	4.41/1.50
SF	305	7.7 (2.4) a	85.9	14.1	3.62/1.10
MF	331	8.5 (2.0) b	77.6	22.4	-0.13/0.42
LF	411	13.0 (4.6) c	31.9	68.1	-0.86/0.42

TABLE 3.—Indices of dietary diversity calculated for prey items consumed by diamondback terrapins (*Malaclemys terrapin*) categorized by head width. Head widths are S <20 mm, M from 20–30 mm, and L >30 mm. Shannon diversity index (H'), evenness index (J'), and Schoener's niche overlap (θ) or similarity index were calculated from % dietary mass. Number of equally common prey species (a–g) are listed in declining order of dietary importance.

Head width	Diversity (H')	Evenness (J')	Number equally common spp.	Overlap (θ)
S	1.572	0.560	2.97 (a, b, f)	(S–M) 0.958
M	1.740	0.620	3.34 (a, b, e, c)	(S–L) 0.593
L	1.825	0.650	3.55 (b, a, e, d)	(M–L) 0.671

a = *Littorina irrorata* ≤ 10 mm, b = *Littorina irrorata* ≥ 10 mm, c = *Uca pugnax*, d = *Sesarma reticulatum*, e = *Callinectes sapidus*, f = *Polymesoda caroliniana*, g = *Balanus*.

Food Resource Distribution

Subtle differences in elevation, vegetation height, and density provided microhabitats that were reflected by zonal distributions of marsh organisms. Mean height (\bar{x} = 57.6 cm, SD = 24.9, range = 15–145 cm) and density (\bar{x} = 70.5/m², SD = 32.6, range = 0–186/m²) of *Spartina* varied across transects and were inversely related ($y = -0.28x + 77.56$, $r^2 = 0.13$, $P < 0.0001$). *Spartina* was distinctly zoned with greater heights and lower densities occurring along creek banks or drainage meanders.

Localized patches of prey abundance were associated with variance in vegetation height. Mean snail density was 42.4 snails/m² (SD = 41.9, range 0–277) with considerable variation among plots. Snail density was negatively related to vegetation height ($y = -0.64x + 79.05$, $r^2 = 0.15$, $P < 0.001$) and weakly related to vegetation density ($y = 0.2x + 28.21$, $r^2 = 0.02$, $P < 0.001$). Mean fiddler crab density was 140.2/m² (SD = 107.2, range 3–457) and was positively correlated with increased vegetation height ($y = 1.45x + 58.18$, $r^2 = 0.11$, $P < 0.0001$) and negatively correlated to vegetation density ($y = -0.63x + 185.31$, $r^2 = 0.04$, $P = 0.007$). Although zones of overlap occurred between snails and crabs at lower densities, regions of high density for each group generally did not coincide.

Two major patterns of snail distribution were observed. In 43% of the transects, mean snail size <10 mm was found

throughout the transects (Fig. 5). In 50% of the transects, mean snail size increased to >10 mm with increased distance from the creek drainage (Fig. 5). The exception to these general patterns was noted for a meandering creek where mean snail sizes of >10 mm were nearer the drainage in a vicinity where the creek looped back on itself. However, all transects exhibited increased mean snail size at increased snail density ($y = 0.12x + 4.41$, $r^2 = 0.79$, $P < 0.0001$).

Morisita's indices for spatial dispersion of crab abundance, overall snail abundance, and snail abundance by size class ranged from near random ($I_d = 1.1$) to moderately aggregated ($I_d = 1.7$) for all transects. Mean snail size was <10 mm in 78% of the plots. Densities higher than the mean (42 snails/m²) occurred in 35% of the plots; densities of twice the mean occurred in 18% of the plots. High densities or snail sizes >10 mm were uncommon and generally occurred farther away from a creek drainage (Fig. 5).

Temporal Variability in Resource Utilization

Tests for correlations between snail consumption (g/turtle) and tidal heights indicated that small terrapins exhibit low levels of snail consumption regardless of tidal height ($y = 0.61x - 0.62$, $r^2 = 0.07$). Medium ($y = 2.17x - 1.19$, $r^2 = 0.04$) and large females ($y = 10.13x - 14.23$, $r^2 = 0.22$) increased their consumption of snails at higher tides although the correlations were not significant. Because linear relationships were insufficient to discern a complex relationship, data points were refitted by interpolation (Fig. 6a). Threshold patterns of snail consumption were related to tidal height with the most obvious pattern being an increase in snail consumption by large females at tidal heights that flood the marsh. Small terrapins exhibited no increase in snail consumption, and medium sized terrapins had levels of consumption intermediate between small and large terrapins (Fig. 6a).

Crab consumption by terrapins (g/turtle) also varied with tidal height. Small terrapins consumed virtually no crabs over

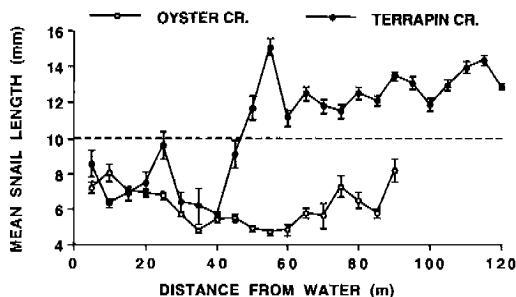


FIG. 5.—Two general patterns observed for spatial distribution of *Littorina irrorata*. Mean lengths (± 1 SE) are shown for snails collected in 1 m² plots at 5-m intervals along transects from creek channel to high ground. The Oyster Creek transect (17 July 1991) illustrates a pattern recorded for 43% of the transects. The Terrapin Creek transect (3 July 1991) illustrates a pattern recorded for 50% of the transects. The dashed horizontal line distinguishes juvenile (<10 mm) from adult (>10 mm) *Littorina*.

the range of tidal heights ($y = 0.17x - 0.25$, $r^2 = 0.13$) while medium and larger females increased levels of crab consumption with rising tidal height (medium females: $y = 1.33x - 1.53$, $r^2 = 0.20$; large females: $y = 0.99x - 0.70$, $r^2 = 0.03$). The linear relationships were not significant, and a more complex relationship was sought by refitting the data by interpolation (Fig. 6b). A fluctuating relationship was evident for large females that could not be simply explained as increased crab consumption with increased tidal height. Medium size females exhibited moderate and fluctuating crab consumption rates over a range of tidal heights but at levels intermediate to smaller or larger terrapins (Fig. 6b).

DISCUSSION

Ontogenetic Shifts in Diet

Substantial differences in the foraging ecology of immature and adult female terrapins were discovered. As divergence in body size and feeding structures occurred, dietary divergence resulted, as expected for an ontogenetic niche shift (Mittelbach et al., 1988). The most frequently consumed prey in this study, *Littorina irrorata*, was apparently size-selected as a functional constraint of terrapin head size.

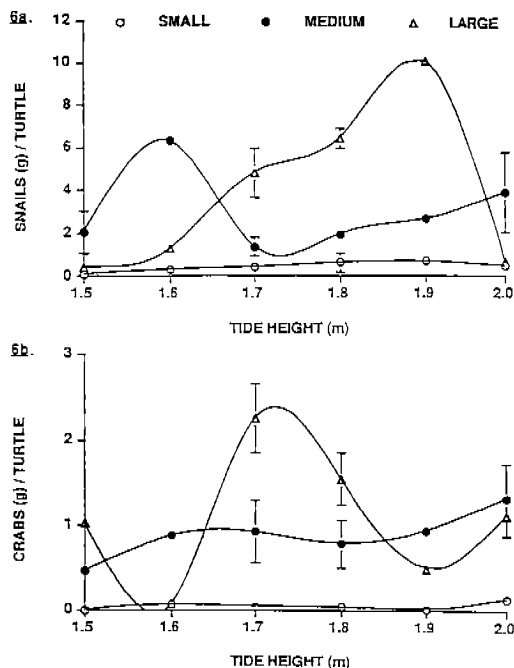


FIG. 6.—Quantities of (a) snails and (b) crabs consumed by different size classes of diamondback terrapins (*Malaclemys terrapin*) during different tidal conditions in the Kiawah River, South Carolina. Terrapins are categorized by mandible width as small if ≤ 20 mm, medium if 20–30 mm, and large if ≥ 30 mm head width.

Crabs of two small species were ingested (*U. pugnax* and *S. reticulatum*) by all terrapins whereas primarily the rear legs from the large blue crab, *C. sapidus*, were ingested by medium and large size terrapins. These size-related differences in feeding behavior likely result from variation in both terrapin head and body sizes, with larger jaws required to grasp the appendages of blue crabs and a larger body and stouter arms required to handle prey with minimal risk.

Gape limited feeding strategies were also reported by Davenport et al. (1992) when differently sized *Carcinus maenas*, the green crab, were offered to captive male terrapins. Their terrapins ate small crabs whole, while preferentially cropping the hind legs from medium crabs and avoiding large crabs altogether. Cropping limbs of the crab's hind legs was clearly a profitable

strategy when the size of the crab or its large chelipeds deterred consumption by a terrapin (Davenport et al., 1992).

Estimates of niche breadth (H' and J') were in concordance with results predicted by foraging theory, in that large predators should eat large prey as well as a greater range of prey sizes (Schoener, 1974), although the magnitude of the differences appears slight. Indices of niche overlap (Table 3) suggest that should intraspecific competition be occurring, it would be most likely between males and small females or between medium and large females which evidenced the greatest extent of resource overlap. However, it must be demonstrated that food resources are limiting to terrapins before concluding that competition is responsible for any observed shifts in niche overlap.

Studies of resource partitioning have noted increasing dietary overlap in some species of turtles and increasing specialization in others following changes in resource availability. For example, in the transition from wet to dry season, *Staurotyphlops triporcatus* became more generalized in its diet but *Kinosternon leucostomum* and *K. scorpiodes* increased in dietary specialization (Moll, 1990). Through the same period, *Trachemys scripta* retained a generalized diet despite male, female, and juvenile diets differing substantially from one another (Moll, 1990). Dietary shifts within a species (Clark and Gibbons, 1969; Hart, 1983; Moll and Moll, 1990) are likely to occur whenever environmental conditions modify prey availability.

Ontogenetic dimorphism lessens dietary overlap by the establishment of divergent feeding capabilities in *Malaclemys*. Resource acquisition is often related to body size (Werner and Gilliam, 1984), and the niche of female terrapins does grade from specialist to generalist in a size structured manner. It remains unknown whether males or small females compete indirectly with adult females by consuming small *Littorina* prior to the snails' growth into larger size classes of prey. In the present study, a high degree of dietary overlap may simply reflect superabundant food re-

sources (Pianka, 1974) rather than competition (Zaret and Rand, 1971).

Ecological divergence of terrapins or their ancestors is suggested by the exaggeration of female trophic structures, because it cannot be accounted for simply from body scaling (Berry and Shine, 1980; Selander, 1972). When dietary variation between the sexes has allowed for the operation of selection and resultant ecological divergence, trophic structures may develop independently of body size scaling (Selander, 1972). Terrapins are but one of the aquatic turtles (*Cuora*, *Graptemys*, *Emydura*, and *Phrynops*) that consume mollusks and are noted to have females with enlarged heads and intersexual dietary differences (Shine, 1989). Alternative mechanisms such as sexual selection or physiological and reproductive constraints might influence the allometric relationship of body size (Gibbons and Lovich, 1990) but do not explain enlarged head sizes when divergent head size confers no reproductive advantage to either sex (Shine, 1989). For terrapins, ecological causation via niche divergence provides a parsimonious mechanism for trophic differentiation despite the admitted difficulty in testing that hypothesis.

Resource Distribution

Sampling transects indicate that prey abundance and distribution are variable (Kneib, 1984; this study) and agree with descriptions of distinct zonation in salt marsh fauna and flora (Teal, 1958). Studies of the intertidal ecology of *Littorina* mention seasonal patterns of vertical movement; e.g., *Littorina* lives on the marsh mud in winter and early spring but moves onto the stems of *Spartina* in summer (Smalley, 1959). Changes in size distribution by snails in higher regions of the salt marsh were attributed by Chow (1975) to horizontal movement by adults. However, recorded distances moved by *Littorina* are but 1–3 m annually (Bingham, 1972; Hamilton, 1978; Vaughn and Fisher, 1992) and cannot account for the broad shifts of size and density noted across our transects (30–

120 m). Alternative possibilities that may define patterns of size and density for snails include larval settlement patterns, availability of suitable substrates, and predation (Gibson, 1969; Kneib, 1984; Stiven and Kuenzler, 1979), particularly by terrapins in regions where they are abundant.

Small marsh crabs were associated with tall, dense *Spartina* along creek banks or among swaths of *Spartina* associated with muddy depressions (Daiber, 1982), where the root matrix supports the burrow systems of the crabs during repeated tidal inundations. Dense expanses of stems of *Spartina* may provide structural shelter from predators such as terrapins. Even so, active foraging by small crabs keeps them at risk of incidental predation. *Uca pugnax* is active primarily at low tide but continues to feed underwater at high tide while *S. reticulatum* is active mainly at high tide or throughout cloudy days (Teal, 1958). Small crabs were recorded in the diet at less than their proportional occurrence in the marsh, perhaps due to their agility in evading predators and the availability of burrow refuges.

Large blue crabs, *Callinectes sapidus*, were not strongly represented in the diet even though they move from drainages into the *Spartina* during high tide. Smaller individuals of *C. sapidus* (<11 cm wide) were prevalent beneath mats (debris) of *Spartina* in the high marsh even at low tide (Baxter, 1983; Hamilton, 1976; Tucker, personal observation) and were the predominant size consumed by *Malaclemys* in this study. Interestingly, large individuals of *C. sapidus* also feed upon *Littorina* (Baxter, 1983; Hamilton, 1976) and exhibit the preference shown by large terrapins in consuming larger snails. It is noteworthy that *C. sapidus* has been the only predator considered in two field studies of *Littorina irrorata* (Baxter, 1983; Stanhope et al., 1982); although the study sites are clearly within the range of *Malaclemys*, it was not stated whether terrapins were present at their specific study sites.

Marsh clams, *P. caroliniana*, were recorded sporadically in fecal samples. Preferred habitats for this bivalve are current-scoured sandy bottoms at the mouths of

tidal creeks, and clams were noted only from terrapins captured near these bottom types. Benthic fauna from subtidal flats should be sampled in the future to characterize the importance of this prey species. Patchy dispersions of benthic bivalves are common because an appropriate substrate is required for settlement and establishment of larval stages (Daiber, 1982). If clam abundance is aggregated, then predation upon buried clams might involve subtidal searching behavior by terrapins. Unfortunately, water turbidity precluded any visual confirmation of underwater foraging at this study site.

We considered that other soft-bodied prey items might be poorly represented in fecal samples (i.e., intact annelids might be recovered before digestion via gastric lavage yet not found in sieved samples) and their dietary importance underestimated (Parmenter and Avery, 1990; Tucker and FitzSimmons, 1992). However, no remains of annelids were detected when sieving fecal samples (mesh size was adequate to retain the indigestible setae or mandibular cuticles), and we conclude that soft-bodied prey were not a major dietary component during the sample period.

Terrapins are obviously prominent but unrecognized macroconsumers in many salt marsh systems. Recent views of salt marsh food webs omit them entirely (Daiber, 1982; Day et al., 1989; Montague et al., 1981; Teal, 1962), perhaps because contemporary studies of salt marshes are conducted during a time of population depletion for terrapins in many regions (Ernst and Barbour, 1972). Terrapins are inconspicuous at low population levels, and a need for special capture techniques may tend to underestimate their predatory significance. Our study has indicated that where robust populations of terrapins remain, they are significant macroconsumers, particularly of *Littorina*. This finding revises the assumption that the only major predators of *Littorina* are large *C. sapidus* (Baxter, 1983; Hamilton, 1976) or marsh birds such as the clapper rail (*Rallus longirostris*) (Heard, 1952) or oystercatcher (*Haematopus ostralegus*) (Boates and Goss-Custard, 1992).

Tidal Constraints on Resource Acquisition

Both field and laboratory studies with terrapins have demonstrated strong tidal synchronization in activity patterns (Muehlbauer, 1987; this study). Activity periods in synchrony with local tidal regimes were exhibited by wild-caught terrapins although the circadian cycle could be constrained when water salinity and temperature were varied independently in the laboratory (Muehlbauer, 1987). Swimming activity was strongly associated with high tide while inactivity or basking activity was exhibited at lower tides (Muehlbauer, 1987). The range of prey taken by terrapins plainly indicates that they are not sit-and-wait predators. We surmise that feeding must coincide with swimming activity at high tides as more snails are available and marsh-dwelling crabs more active with the rising tide (Teal, 1958). A concurrent telemetry study of terrapins at our study site provides some support for this view. We tracked six large females independently as they used the creeks and tidal drainages as primary travel corridors both with and against the currents during all tidal levels. At high tide levels, these females left the channels and swam through flooded *Spartina* to areas where high densities of large snails were located. Here we observed the terrapins feeding on snails either by consuming snails within reach or by pushing over *Spartina* to feed on snails further up the stems. As tide levels ebbed, females either remained nearby and buried in the mud or followed tidal drainages back into the main channels. We hypothesize that habitat partitioning occurs between sexes and size classes of terrapins which additional telemetry studies may verify.

The fecal samples indicate that prey encounter rates change from neap to spring tide cycles. Because terrapins are inactive at night (Carr, 1952; J. Lovich and W. Gibbons, personal observations), access to prey is constrained to diurnal high tides and to occasional encounters of prey found along creek margins. Consequently, searching for patches of sufficient quality

may affect the energy budget of terrapins, particularly of large females. In contrast, foraging by small terrapins may be less affected by tidal height as snails <10 mm are widespread and common and small terrapins apparently take advantage of marsh clams found within the drainages.

Resource Partitioning by Terrapins

The findings of dietary specialization, of differently dispersed food resources, and constrained prey availability pose the question of whether resource partitioning by diamondback terrapins reflects intra-specific competition. Terrapins appear to be faced with several constraints on foraging behavior when functionally grouped by their trophic structures (head width). For small terrapins, prey choices are limited by feeding structure size and prey availability is less constrained by tidal cycles as small snails are available at nearly all levels of high tide. For large females, greater gape capacity permits greater prey choices, but the availability of preferred prey (only 22% of the plots had snails >10 mm) is strongly limited by tidal height. While foraging, large females may exhibit switching behavior between frequently encountered, but lower quality, food items and less available prey of higher energetic value (Gilliam and Fraser, 1988). Thus, whether to pursue an energetically valuable but scarce prey or the search for an area of high snail density depends at least upon terrapin size and tidal cycle. Food resource abundance may not be limiting for terrapins; rather, food availability may be the limitation. In salt marshes with less extreme tidal amplitudes, terrapins may not be as constrained in resource availability as those inhabiting the Kiawah River.

Prey vary not only in their availability and in handling time required by predators (J. Lovich, unpublished data), but also in energetic value. Energetic equivalents are listed as 2.0 kcal/g for gastropods, 3.2 kcal/g for bivalves, and 3.9 kcal/g for decapod crustaceans (Cummins and Wuycheck, 1971). Estimates of prey consumption (Table 1) when multiplied by the caloric equivalents affirm that larger terra-

pins consumed both greater quantities and higher proportions of energetically valuable prey. Yet, diet profitability is relatively similar despite the observed shifts in dietary composition (calculated energetic returns are 55.1 J for small terrapins, 57.8 J for medium terrapins, and 57.3 J for large terrapins).

Overlapping regions of prey distribution in the marsh are spatially limited for terrapins; food resources generally exist as clumped aggregations of high prey profitability (crabs or snails >10 mm) or as random distributions of low prey profitability (snails <10 mm). Such a prey distribution presents a coarser-grained resource environment to large female terrapins than that encountered by males. The occurrence of resource partitioning among terrapins provides an opportunity to test additional working hypotheses. At one extreme, we predict that foraging patterns of large females will alternate between searching for small snails (a time minimizing strategy) at modest tidal heights to seeking larger prey as they become accessible at higher tides (an energy maximizing strategy) in response to fluctuating prey availability. In contrast, males or small females might devote more of their time budget to locating and consuming small prey than large females do to offset their limited capacity for consuming larger prey. We expect that shifts in dietary overlap and diversity will reflect associated changes in tidal amplitude and prey species composition over the broad geographical scale inhabited by *Malaclemys*. Finally, we anticipate that additional studies that incorporate telemetry, cafeteria-style feeding trials, or experimental manipulations of prey distribution and density will provide a clearer understanding of terrapin foraging ecology and their role in salt marsh ecosystems.

Acknowledgments.—We thank the volunteers from Earthwatch, Inc. during 1990–1992 for the tedious job of separating and counting scat samples. B. Willis collected transect data in 1991 and was supported by the National Science Foundation Young Scholar Program. H. Solovei constructed a winnowing device to simplify sample processing. The herpetology group at the Savannah River Ecology Laboratory provided field assistance during all years of the study. We thank

S. Colley, M. Fulmer, J. Greene, D. Kling, and T. Zimmerman for assistance, and J. Lovich for thoughtful perspectives from his study of sexual size dimorphism in turtles. K. Buhlmann, V. Burke, N. Frazer, T. Jensen, and J. Lovich provided helpful comments on early drafts of the manuscript. T. McAdory and the Kiawah Island Community Association arranged use of the Inlet Cove dock. Terrapins were collected under a scientific permit issued by South Carolina Wildlife and Marine Resources. Manuscript preparation was supported by contract number DE-AC09-76SRO0819 between The University of Georgia and the U. S. Department of Energy.

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Accepted: 19 May 1994

Associate Editor: Daniel Formanowicz, Jr.

