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Meat on the Move: Diet of a Predatory Turtle, *Deirochelys reticularia* (Testudines: Emydidae)

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The chicken turtle, *Deirochelys reticularia*, is a characteristic but rarely abundant inhabitant of shallow, lentic waters in coastal lowlands of southeastern United States. Inadequate knowledge of its diet has led to widespread speculation that the species is broadly omnivorous (Carr, 1952; Campbell, 1969; Ernst et al., 1994), although a few authors (Jackson, 1978, 1988; Pritchard, 1979) have suggested a more strictly carnivorous diet. Very limited evidence supporting the latter position is provided by Marchand (1942), Carr (1952), and Mitchell (1994), who reported glass shrimp, crayfish, tadpoles, a snail, a beetle, and only a trace of aquatic plants in chicken turtle natural diets.

Methods. - In conjunction with a study of the reproductive biology of the species (Jackson, 1988), I examined the gut contents of 24 chicken turtles; feces were collected from another that was retained alive for behavioral study. The sample included five adult males (103-137 mm plastron length [PL], 192-448 g), 19 adult females (147-190 mm PL, 645-1410 g), and one subadult female (137 mm PL, 410 g) collected from 1974 to 1977; shells of 12 were deposited in the Florida Museum of Natural History herpetology collection (UF 37555, 44210-44216, 44218-44220, 44231). All but one of the turtles were collected on land, either in association with nesting activity or with terrestrial wandering that presumably represented migration between bodies of water; several specimens were road-kills. Most of the turtles were from Alachua County (12) or nearby counties (Baker, Dixie, Levy, Putnam, and Marion) in northern peninsular Florida, where the subspecies D. r. chrysea and D. r. reticularia intergrade. The sample also included one specimen from the Florida panhandle (Wakulla County), two from the Florida east coast (Brevard County), and two from southern Georgia (Ware and Charlton counties). The entire alimentary tract of each animal was examined fresh within 24 hours of collection or refrigerated or frozen for analysis within a few days or weeks. Most food items were first identified to family, then preserved in 40% isopropyl alcohol for subsequent study.

Lengths of the three major segments of the digestive tract (stomach, small intestine, and colon) were measured for eight adult *Deirochelys* (seven females, PL 147–190 mm; one male, PL 110 mm) that had been dissected for reproductive information. For comparison, similar data were recorded from small series of adult emydid turtles of three primarily herbivorous, potentially microsympatric freshwater species: *Pseudemys floridana peninsularis* (three females, PL 269–332 mm; one male, PL 150 mm), *P. nelsoni* (two females, PL 283–303 mm; one male, PL 224 mm), and *Trachemys s. scripta* (one female, PL 183 mm; one male, PL 154 mm). For analysis, I compared the relative length of the digestive tract of each of the four species as a percentage of plastron length.

To observe *Deirochelys* feeding behavior, I maintained one large adult female with as many as four adult males in a 165 liter aquarium. Turtles were offered small amounts of a variety of potential foods (only one kind at a time) including crayfish, insects, earthworms, raw fish, and aquatic vegetation.

Results. — Nearly half of the digestive tracts were relatively empty, which may relate to the biased collection of reproductively active females during the cooler months of the year (see Jackson, 1988). The guts from 8 of 12 gravid females as well as all 3 pre-gravid females (i.e., bearing enlarged preovulatory follicles) were essentially devoid of food; the remaining 4 gravid females each contained only a small number of prey items. In contrast, the guts of all 4 post-reproductive females (March–June) were moderately full. All 5 of the males and the subadult female (collected late May – early October) contained several items each.

Table 1 summarizes the identifiable food items found in the sample; the diet consists principally of aquatic insects and crustaceans (Malacostraca), with some representation of terrestrial arthropods. Prey generally were chopped into fragments, which partially prevented quantitative analysis by species. Most specimens appeared to represent prey in the range of 8 to 20 mm in length, although a few were as small as 4 mm (Naucoridae and Hydrophilidae) and others as large as 55 mm (odonates and crayfishes [Cambaridae]). No substantive dietary differences were detected between the small sample of males and the larger female sample.

Plant matter was limited to < 3 cc of green algae in the colons of each of 5 individuals, a 1 cm woody twig fragment, and parts of the roots and leaves of a water hyacinth (*Eichhornia crassipes*) in an individual that contained numerous insect, spider, and decapod prey that typically dwell in the water hyacinth microhabitat. The guts of at least three individuals contained small semi-flattened stones that may have represented gastroliths from crayfish prey. Four turtles also contained small, yellowish, gelatinous spheres (one as many as 20) that may have been amphibian eggs.

Mean digestive tract length (stomach plus intestine and colon) as a percentage of plastron length for each of the four

Table 1. Gut contents of 25 *Deirochelys reticularia* mostly from northern peninsular Florida (see text for details). Frequency refers to number of turtles containing the item. Table does not include many insects too finely chopped to permit ready identification. Taxa followed by an asterisk (*) are generally terrestrial though they include species found in close association with water.

Taxon	No. Individuals	Frequency
Arthropoda	94+	14
Malacostraca: Decapoda	7	4
Palaemonidae: Palaemonetes	3	1
Cambaridae: Procambarus sp.	5	4
Insecta	53+	11+
Odonata	14	5
Aeschnidae: Anaxa	5	3
Libellulidae: Libellulab	1	1
Hemiptera	12	3
Belostomatidae: Lethocerus	3	2
Corixidae: cf. Hesperocorix	a 2	1
Naucoridae: Pelocoris	12 3 3 3 5 5	5 3 1 2 1 2 2 1
Nepidae: Ranatra	5	2
Orthoptera *	5	2
Gryllidae *	1	1
Tettigoniidae *	4	1
Coleoptera	14+	6+
Curculionidae *	3	1
Dytiscidae	3 4 2 5	2
Elateridae *	2	1
Hydrophilidae	5	2
Lepidoptera: cf. Noctuidaec*	7	2
Diptera: Stratiomyiidae ^a	1	1
Arachnida *	34±	2 1 2 1 2 1 2 6
Plant matter unquantified		6

a larvae or nymphs

^b adult

c all adults but one

species was as follows: *Deirochelys*, 390% (range 320–430, SD 38); *Pseudemys floridana*, 850% (range 630–1030; SD 180); *P. nelsoni*, 920% (range 740–1120, SD 191); and *Trachemys scripta*, 720% (range 580–860, SD 198). Only the differences between *Deirochelys* and the other species were significant (t-tests, P < 0.05).

In laboratory observations of feeding behavior, chicken turtles typically searched with extended necks until they detected prey movement. Slow stalking or swimming then brought them within striking range (ca. 10-12 cm), at which point the head remained stationary while the neck recoiled into the still-approaching body. The ensuing rapid strike usually occurred when the prey was stationary and followed the pattern of "pharyngeal feeding" described in detail by Bramble (1973) for Chelydra. Small prey were captured from all angles, but large and potentially dangerous prey such as crayfish generally were circled until a lateral strike could be attained; adult turtles of both sexes fed readily on crayfish in this manner. Dangerous prey such as large (> 35 mm) adult and larval dytiscid beetles and belostomatid bugs were avoided, sometimes after a single painful encounter, though some smaller individuals of those taxa were consumed in the wild (Table 1). Turtles watched but spent little to no effort in pursuing highly mobile prey such as sunfish (Lepomis), nor did they attempt to consume aquatic vegetation. However, most individuals readily accepted pieces of raw fish and even scavenged dead crayfish after a period of acclimation to captivity.

Discussion. — Despite statements by some authors that Deirochelys at least occasionally ingests plant matter (Carr, 1952; Campbell, 1969; Ernst et al., 1994), my data and observations indicate that this turtle is a carnivore that specializes on live, slow-moving prey. The diet consists almost entirely of arthropods, principally aquatic insects and crustaceans. The occasional consumption of terrestrial arthropods that presumably have fallen into the water underscores the importance of allochthonous input into aquatic food webs, as was noted by Georges (1982) for other freshwater vertebrates. The relatively anterodorsal position of the eyes of Deirochelys probably allows it to scan the water surface more effectively for such prey (Pritchard, 1984), as well as for those that normally live at the air-water interface (e.g., some spiders, water striders, and gyrinid beetles).

The degree to which individual turtles "specialized" on certain prey types, at least temporarily, was conspicuous. Thus, different individual turtles were responsible for nearly the entire consumption of glass shrimp (Palaemonidae), grasshoppers, moths, and spiders, respectively. Either individual turtles formed search images for certain prey types, or otherwise they foraged in localized microhabitats where those prey types were especially abundant. Dietary diversity might result from turtles moving among such microhabitats.

The small amounts of plant matter found in a few guts in this study, as well as the ingestion of plant parts reported elsewhere, presumably represent cases of incidental ingestion and mistaken identity. The acclimation of some captives to raw fish or commercial fish chow (Ernst et al., 1994; *pers. obs.*) does suggest the potential for scavenging in nature. The fact that chicken turtles rarely enter aquatic traps baited with sardines (*pers. obs.*) suggests, however, that the latter activity is infrequent. Nonetheless, Cagle (1950) believed that chicken turtles respond best to bait in advanced stages of decay; geographic differences in dietary preferences might account for this.

These conclusions are consistent with this turtle's specialized head and neck morphology, which represents a highly evolved suite of adaptations for pharyngeal feeding, a mode specifically adapted to the capture of mobile, aquatic prey (Bramble, 1973, 1974; Jackson, 1978; Pritchard, 1984). Narrow jaws, a greatly hypertrophied hyoid apparatus and cervical extensor musculature, elongated cervical vertebrae and skull, and relatively anterodorsal eyes combine to facilitate rapid strikes at living prey. My observations of captive animals revealed the technique to be equally effective at all adult body sizes, which might explain the lack of pronounced sex-related dietary differences despite the two- to three-fold disparity in body mass between typical males and females. Nevertheless, the wider gape of large females allows them to take somewhat more robust prey than can be effectively handled by males (pers. obs.).

Additional evidence of the carnivorous diet of *Deirochelys* is provided by the relatively short and simple gut when compared with that of sympatric herbivores (*Pseudemys*) and omnivores (*Trachemys*). The diet of *Deirochelys* shows no overlap with those of two large herbivorous emydids, *Pseudemys floridana* and *P. nelsoni*, which occupy some of the same bodies of water as chicken turtles. A higher level of overlap exists, however, with the sympatric *Trachemys s. scripta*, an omnivore that feeds upon many of the same prey (unpublished data). Dietary overlap may also occur with members of other freshwater turtle families (Chelydridae, Kinosternidae, and Trionychidae), juvenile alligators, and some fishes (e.g., *Micropterus*).

Among North American turtles, the feeding habits of *Deirochelys* are most similar to those of *Emydoidea blandingii* (Bleakney, 1963), an allopatric and distantly related but highly convergent emydine that appears to be the "northern equivalent" of the chicken turtle. Elsewhere, remarkably parallel diets and associated morphological adaptations occur in even more distantly related turtles, such as the South American chelid *Hydromedusa maximiliani* (Souza and Abe, 1995).

Interestingly, no fish were confirmed as prey of *Deirochelys*, even though several species of small body size were abundant in many of the waters from which the sampled turtles emerged. However, their lack of relatively large, indigestible parts comparable to the chitinous exoskeleton of arthropods facilitates rapid digestion and hence may conceal the presence of small fish in the diet. Still, fish are probably difficult prey for chicken turtles to capture and can be expected to be a minor dietary component, if eaten at all. In fact, in the southeastern US, *Deirochelys* is one of the few turtles (with *Kinosternon* spp.) that routinely inhabit fishfree temporary ponds. Perhaps not coincidentally, fish also seem to be absent from the diets of other turtles that specialize on aquatic arthropods (e.g., *Hydromedusa maximiliani* [Souza and Abe, 1995]).

The relatively small amount of food in most of the digestive tracts is probably attributable to collection bias. My sample over-represents turtles that had emerged to nest or to emigrate from ponds. Emigrating chicken turtles not only are unable to feed on land but also may be moving because of low prey densities. Many of the adult females in my sample were deliberately taken during the species' winter reproductive season (October-March) (Jackson, 1988), a time when arthropod prey may be relatively sparse. Furthermore, gravid female reptiles in general often reduce their food intake (Shine, 1980), with one explanation for this - a lack of physical space in the body cavity to accommodate prey items (Gregory and Stewart, 1975) - being particularly applicable to turtles. Additional sampling of non-reproductive turtles (males, subadults, and juveniles) during the winter reproductive season is necessary to determine whether the reduced feeding by reproductively active females observed in this study is a direct response to reproductive state or a more generalized seasonal response.

The carnivorous food habits of *Deirochelys* may have several ecological consequences. Relative to other sympatric freshwater emydids (*Pseudemys*, *Trachemys*), chicken turtles are relatively small; the largest species (*Pseudemys*) are all herbivorous, while the intermediate-sized *T. s. scripta* is omnivorous. Though perhaps more germane to mammalian than reptilian communities, population densities of predators are often substantially smaller than those of herbivores, and this also seems to hold within this turtle community. Even in fossil sites where *Deirochelys* is well represented (e.g., Miocene Love Bone Bed, Alachua County, Florida [Jackson, 1978; Webb et al., 1981]), it is still outnumbered roughly 4:1 by *Pseudemys*. And finally, though a confirmed basker, *Deirochelys* seems to spend less time engaged in this activity than herbivorous species, perhaps reflective of a difference in the relative digestibility of plant and animal matter.

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Kemp's Ridley Sea Turtle (Lepidochelys kempii) Tracked by Satellite Telemetry from Louisiana to Nesting Beach at Rancho Nuevo, Tamaulipas, Mexico

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The Kemp's ridley (*Lepidochelys kempii*) is considered the most endangered sea turtle in the world (Groombridge, 1982; Shaver, 1991; U.S. Fish and Wildlife Service, 1992). It is distributed throughout the Gulf of Mexico (Liner, 1954; Carr, 1957; Carr, 1980; Hildebrand, 1982; Manzella and Williams, 1992), but is most abundant in coastal waters from Texas to Florida (Ogren, 1989). It also occurs along the eastern shore of North America to Newfoundland and has been reported in the European Atlantic near the British Isles, Netherlands, and France (Pritchard, 1989). Despite this widespread distribution, almost all nesting occurs on about a 60 km stretch of beach near Rancho Nuevo, Tamaulipas, Mexico.

An adult female Kemp's ridley was tracked from Cameron, Louisiana to Rancho Nuevo, Tamaulipas, Mexico by satellite telemetry for 287 days from 13 August 1994 through 16 May 1995. The turtle measured 65.8 cm straight carapace length, 64.9 cm straight carapace width, and weighed 42.6 kg. The turtle was captured at Cameron, Louisiana in a 91.5 m turtle entanglement net (7.3 m deep, 12.7 cm bar mesh) by Texas A&M University biologists. It was fitted with a Telonics ST-10 satellite transmitter on 13 August 1994 and tracked by National Oceanographic and Atmospheric Administration's National Marine Fisheries Service Galveston Laboratory. It moved offshore of the upper Texas coast in late November 1994 and travelled south along the Texas coast into Mexican waters through early January 1995 (Fig. 1). It was offshore of the Rancho Nuevo nesting beach by 10 March 1995. It moved an additional 100 km to the south before returning to nest on 23 April 1995 and again on 19 May 1995, both nestings being recorded by Rancho