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THE BIOLOGY OF THE DIAMONDBACK TERRAPIN MALACLEMYS TERRAPIN (LATREILLE)

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INTRODUCTION

The diamondback terrapin Malaclemys terrapin (Latreille) is a medium-sized emydid turtle which inhabits saltmarshes and lagoons on the eastern coast of the United States, from New York State to Texas. This wide geographical distribution, perhaps coupled with limited gene flow between populations living in brackishwater habitats separated by open coast, has led to an unusual degree of recognized subspeciation. Pritchard (1979) describes the following subspecies (running from north to south in the species' distribution):- Malaclemys terrapin terrapin (northern race; found from Cape Cod to Cape Hatteras), Malaclemys terrapin centrata (a subspecies ovelapping with the northern race and stretching to Florida), Malaclemys terrapin tequesta ('Florida east coast terrapin'), Malaclemys terrapin rhizophora (a rather obscure subspecies found in Floridan mangroves), Malaclemys terrapin macrospilota (the omate diamondback of the southern part of the Gulf coast of Florida), Malaclemys terrapin pileata (the Mississippi diamondback, distributed to eastern Louisiana from the Florida Panhandle), and finally the Texas diamondback, Malaclemys terrapin littoralis, which is distributed from Louisiana to Corpus Christi in southern Texas.

Emydid turtles are normally characteristic of freshwater ecosystems in the Americas, Europe, North Africa and Asia. Although a handful of species have colonized productive estuarine areas, most cannot survive in full sea water for more than a few days because they become osmotically dehydrated and salt loaded. Such species can survive periodic exposure to high salinities by avoiding drinking or eating when salinities are high (e.g. Batagur baska; see Davenport & Wong, 1986; Davenport et at., 1992 [a]), but only Malaclemys is physiologically capable of spending several weeks in sea water without frequent access to fresh water. It has therefore attracted much physiological study. and, because it lives much of its life as a marine animal eating a marine diet, its feeding ecology is also being studied.

The diamondback terrapin is interesting historically too because it was, for a time, the object of a remarkable food fad. From the 1880's. through to the 1920's, there was increasing interest in diamondbacks as gourmet food items. Initially satisfied by capture of wild terrapins, by the turn of the century demand plus declining stocks had triggered the establishment of ranches and farms, particularly at Beaulieu, Georgia and Beaufort, North Carolina (see Gadow, 1901; Coker, 1906; Hatsel & Hildebrand, 1926; Hildebrand, 1932 for an account of terrapin culture). Diamondbacks were not only eaten in the U.S.A., but were exported to Paris, Berlin and even the Amazon city of Manaus, basking in the prosperity of a rubber boom before the Great War. The diamondback trade

collapsed with the American Recession, and populations have generally recovered, though there is some sign that the northern subspecies are again under hunting pressure, this time because of demand from Asiatic communities in the large cities of the eastern seaboard of the U.S.A.

PHYSICAL DESCRIPTION

A good description of Malaclemys terrapin is given by Pritchard (1979). Diamondbacks are relatively small emydids,but there is a strong sexual dimorphism in size; adult males being about 120mm carapace length, females about 160mm. Females are much more heavily built than males, and have proportionally larger heads. Diamondbacks take their name from strong concentric annuli on the carapace scutes. They also have generally spotted soft parts, particularly on the head and neck. The colour is extremely variable, ranging from dark and dull terrapins to yellow shelled animals with spotted cream heads. Seigel (1984) showed that Floridan diamondbacks grow to a significantly larger size than those from North Carolina, suggesting a latitudinal (and presumably thermal) effect on growth. This is consistent with the measurements collected by Pritchard (1979), who found that the largest female recorded (237 cm carapace length) was a member of the Mississippi subspecies.

PHYSIOLOGY AND RELATED BEHAVIOUR

Malaclemys terrapin is capable of surviving for long periods in full seawater (salinity ca. 34%) because it has an unusually low skin permeability to salts and water, plus a reasonably powerful lachrymal salt gland (Dunson 1970, 1976, 1985, Robinson & Dunson, 1975) that allows them to secrete sodium chloride or common salt in tears. However, diamondbacks cannot survive indef-initely in sea water; their blood gradually becomes more concentrated and loaded with urea (Gilles-Baillen, 1970). Davenport & Macedo (1990) recently demonstrated that diamondbacks have well-developed behavioural responses to rainfall which allow them to spend the summer months in fully-marine conditions. The turtles exploit the transient availability of freshwater during occasional rainstorms. They are able to detect the vibration of rainfall, even when submerged, and immediately swim to the edge of the water, climb out and drink rainwater from surface films on the muddy substratum using the drinking posture shown in Figure 1.

The posture, combined with the sloping jaws, permits drinking from films I- 2 mm thick (compared with a minimum depth of about 5 mm for box turtle (Terrapene carolina)). Diamondbacks will also seek out droplets of rainwater on plants and will even drink from the surface of each other's shells. When drinking from another diamondback's shell, the drinking terrapin either drinks from the curled posterior margin of the carapace, or drinks from a hindleg pocket. In either case the drinking turtle immobilizes the other by treading upon one or other of the latter's hindlimbs. Terrapins that have been in sea water for 2-3 weeks will drink as much as 15% of their body weight within 5-1 0 minutes. If they are interrupted or frightened when drinking, they have a vomiting reaction (Figure 2) which ejects all of the water taken, perhaps to make them lighter for escape.

LIFE HISTORY

Most data are available for the northern subspecies that encounters low enough temperatures for hibernation in winter. Usually hibernation takes place in submerged mud (Hay, 1904; Coker, 1906; Hay and Aller, 1913; Pope, 1939; Carr, 1952), though there has been an isolated report of hibernation in moist sand above high water (Lawler and Musick, 1972). The terrapins emerge from mud in the spring and mate immediately. Egg clutches (5-12 eggs) are laid in the early summer (May /June), usually in sand dunes. They hatch (August-September) at around 25 mm carapace length. It is not yet clear whether Malaclemys terrapin shows the temperature-dependent sex determination (TDSD) characteristic of many turtles (Bull and Vogt, 1979; Bull, 1980). Sachsse (1984) reported that a group of eggs incubated at 27+-20C resulted in 52 males and 2 females. This suggests that TDSD does operate, but unfortunately only 50% of Sachsse's eggs hatched and he did not sex the stillbirths, so it remains possible that temperature caused preferential mortality of female embryos (a different phenomenon from TDSD, and one known from some snakes). Mortality is very high during incubation; Burger (I 976) reported that 60% of nests in a New Jersey habitat were destroyed by foxes and raccoons; 4% failed to develop at all. Of the eggs in the remaining 36% of nests only 69% hatched, and of the hatchlings only 78% emerged successfully from the nest. This suggests that total mortality up to emergence is about 80%. Unlike sea turtles, almost all diamondback hatchlings emerge from the nest during daytime. However, they head for the nearest vegetation (irrespective of incline), rather than the sea, and this behaviour is probably effective against the main daytime predators (birds such as gull and herons). Until recently almost nothing was known about the habits of newly hatched or juvenile diamondbacks as they were hardly ever seen. However, in 1985 Pitler reported that northern diamondbacks in the 25-75 nun size range spent their time out of water living beneath surface debris and matted Spartina (cord grass; the major vegetation of salt marshes). Lovich et al. (1991) have confirmed this picture, reporting deliberate burrowing behavior into Spartina mats by hatchling terrapins. These workers also report that hatchlings released in water immediately swim ashore and bury themselves in the debris of saltmarsh vegetation. They also note that the Spartina mats provide a moist habitat which features high densities of winkles (Littorina irrorata) and young fiddler crabs (Uca sp.), both known to be important items of the diamondback diet (Coker, 1906). It seems probable that young diamondbacks avoid predation (by either fish or birds) by largely limiting themselves to a narrow zone of strandline debris at the high water mark, rarely straying either into open water, or onto exposed mud flats. A particular feature of the life history of diamondbacks that has attracted recent attention is the finding that populations of Malaclemys terrapin are heavily male dominated(1.78:1 in a South Carolinan population according to Lovich and Gibbons, 1990). The great statistician Fisher (I 930) showed that a 1: 1 sex ratio was generally a stable one in evolutionary terms. In a female-dominated population, a parent producing mostly males will, on average have more grandchildren than a parent that produces mostly females, thus (assuming an inherited tendency to the production of male offspring) correcting the population ratio towards 1:1 (the reverse situation will apply to a population dominated by males). Explanations for biased sex ratios are not easy, but in the case of Malaclemys terrapin the strong bias seems to stem from two things. Firstly, as stated above, there is a

strong sexual dimorphism in the species. Lovich and Gibbons (I 990) found that adult females in their study population had a mean shell length 45% greater than that of males, while the mean female body weight (705 g) was 2.91 times that of the average male (242 g). Secondly, early growth rate in the two sexes is similar in male and female terrapins (Seigel, 1984). To achieve sexual maturity therefore takes substantially longer in female diamondbacks (6 years) than in males (3 years). Assuming a 1: 1 sex ratio in hatchling Malaclemys terrapin, and assuming no differences in environmental effects on the two sexes, then it will be inevitable that the longer period before maturity in adult females will result in a higher total mortality experienced by sexually mature females (Lovich and Gibbons, 1990).

FEEDING /ECOLOGY

By exploiting estuarine and saltmarsh ecosystems, diamondbacks gain access to far richer food resources than are characteristic of freshwater ecosystems. Coker (1906) long ago showed that diamondbacks are predominantly carnivores which eat a range of saltmarsh invertebrates (crabs, littorinid snails, nereid worms). Captive animals at Millport readily take small intact mussels, crabs and even snails as small as Hydrobia ulvae (<4 mm shell height). Several studies have demonstrated that newly-caught wild diamondbacks defaecate fragments of mussel shells, while Pritchard (I 979) reported that diamondbacks ate a certain amount of vegetation too, so it would seem that Malaclemys terrapin exploits a large fraction of the available resources. Davenport and Ward (in press) have recently shown that diamondbacks have an unusually large appetite, eating satiation meals of 7.2% body weight (when fed on mussel flesh) at 25'C, and averaging 3.7% body wt d-1(since appetite returns fully in 48 h at this temperature). This compares with 0.5% body wt d-1 recorded for young painted turtles (Chrysemys picta Schneidei-) (Kepenis and McManus, 1974), and about 0.2% body wt d-1 found in adult male Mauremys caspica (Gmelin) of similar size (I 01 - 173 g) to the diamondbacks and at the same temperature (25'C) (Davenport and Kjorsvik, 1988).

All of these values have been corrected to the same basis (food as % wet wt of turtle), so it would seem that Malactemys terrapin eats more than ten times as much food as its freshwater relatives. To some extent this is a general characteristic of estuarine carnivores, which tend to eat large quantities of food, processed inefficiently, but another factor may be at work in diamondbacks. Although Malaclemys terrapin does eat while in full sea water, Davenport and Ward (in submission) found that diamondbacks progressively lose appetite under such conditions, to the extent that appetite after 18 days' exposure to sea water is only 22-54% of that shown when fresh water is readily available. Diamondbacks in their coastal habitats may well face periods of 2-4 weeks when no rain falls. All of their prey items are invertebrates that will be isosmotic with sea water, so will have body fluids more than twice as concentrated as terrapin blood. It is also probable that terrapins will take in some sea water with their food, though they avoid deliberate drinking of high salinity media (Davenport & Macedo, 1990). In consequence it is clear that diamondbacks have to restrict food intake when in sea water. Perhaps their great appetite when fresh water is available helps them to compensate.

Davenport et al. (1992 [b]) have recently investigated diamondback feeding behaviour on crabs. Saltmarshes on the east coast of the U.S.A. have a very diverse crab fauna, which includes several species of the genus of small fiddler crabs (Uca), the medium-sized

portunid crab Carcinus maenas (also found in Britain) and the large portunid Callinectes sapidus, the blue crab, which is a fierce predator up to 300 mm across, with chelipeds capable of tearing human flesh, let alone that of terrapins! Crabs are therefore a source of both food and danger as far as Malaclemys terrapin is concerned. Using the shore crab Carcinus maenas as a test prey species, it has been found that diamondbacks have a complex response to crabs. Firstly, like many animals they exhibit size selection of prey (see Figure 3), mainly eating whole crabs in the small size range, taking a few medium-sized crabs and no whole large crabs. However, further research showed that diamondbacks did exploit a wide size range of crabs, not by eating them whole, but by biting off legs, leaving the animal alive (see Figure 4). Small crabs were rarely 'cropped' in this fashion because they were eaten whole, but a few large (and dangerous) crabs were cropped too. Detailed investigation showed that diamondbacks make complex decisions when cropping medium-size and large crabs. Normally they attack from behind and bite off the rearmost walking limbs first, since these are the furthest from the dangerous claws (chelipeds). A significant number of crabs in the natural habitat are without one or both chelipeds (because of intraspecific aggression or because they have been preyed upon and escaped). Diamondbacks faced with a clawless crab are much more aggressive and attack from the front, even if the crab is large. If the crab has a single claw, they invariably attack from the less dangerous side.

DISCUSSION

Malaclemys terrapin is a relatively undistinguished chelonian as far as appearance is concerned, yet exhibits a remarkably complex suite of physiological and behavioural features that allow it to exploit one of the most productive of the world's ecosystems - the salt marsh. The species is a useful model for evolutionary biologists interested in how reptiles have repeatedly invaded the sea over geological time (e.g. sea turtles, sea snakes, ichthyosaurs, crocodiles), while its recently discovered subtlety of foraging on crabs suggests that diamondbacks may be useful in testing fundamental questions of feeding ecology.

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