

THE EFFECTS OF SALINITY AND TEMPERATURE ON APPETITE IN THE DIAMONDBACK TERRAPIN *MALACLEMYS TERRAPIN* (LATREILLE)

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ABSTRACT

The appetite of saltmarsh diamondback terrapins (*Malaclemys terrapin*) is extremely large (mean satiation ration on a diet of mussel flesh at 25°C = 7.2% body weight), some 8-10 times that of closely related freshwater emydid turtles. When held in sea water without access to fresh water the appetite of diamondbacks is gradually depressed, reaching (after 18 days in sea water) 22-54% of the average satiation ration recorded when fresh water is available. Between 20 and 35°C appetite in *Malaclemys* is stable ($Q_{10} = 1.1$). Between 15 and 20°C $Q_{10} = 20.7$, indicating a shift to a hypometabolic state below 20°C.

INTRODUCTION

The diamondback terrapin *Malaclemys terrapin* (Latreille) is a small emydid turtle which inhabits saltmarshes and lagoons on the eastern coast of the United States, from New York State to 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 (e.g. Dunson & Seidel, 1986), 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 al.*, 1992), but only *Malaclemys* is physiologically capable of spending several weeks in sea water without periodic access to fresh water. The species has attracted a great deal of study by W. B. Dunson and co-workers who have demonstrated that the species can choose to drink only low salinities, has a low integumentary permeability to salts and water, plus a reasonably powerful lachrymal salt gland, and has the remarkable ability to increase extracellular fluid volume dramatically when fresh water is available (Dunson 1970, 1976, 1985; Robinson & Dunson, 1975). However, diamondbacks cannot survive indefinitely 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 direct behavioural responses to the vibration of rainfall which allow them to spend the summer months in fully-marine conditions. The turtles exploit the transient availability of freshwater during occasional rainstorms. However, in their coastal habitats they may well face periods of 2-4 weeks when no rain falls, yet they continue to feed. Coker (1906) long ago showed that diamondbacks are carnivores which eat a range of saltmarsh invertebrates (crabs, littorinid snails, nereid worms). All of these prey items will be isosmotic with sea water, so will have body fluids more than twice as concentrated as terrapin blood. Terrapins will take in some sea water with their food (Dunson, 1985; Dunson & Mazzotti, 1989), though they avoid deliberate drinking of high salinity media.

It therefore seemed likely that terrapins ought to respond to lack of availability of fresh water by reducing food intake; this hypothesis is tested in the present study. Experience of keeping *Malaclemys* and a variety of freshwater emydids in captivity also suggested that diamondback terrapins had an unusually large appetite; accordingly the study was broadened to investigate appetite, appetite return and the influence of temperature on food intake.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Six terrapins, all mature males, were used in these experiments. Initially purchased from a dealer, they had been held in captivity for several years, were extremely tame and fed readily in the presence of observers. They were held under constant illumination in large tanks of circulating sea water (34‰; 25±1°C) which had floating rafts on which vessels full of fresh water for drinking could be mounted. The terrapins were fed routinely upon flesh of mussels (*Mytilus edulis* L.) collected from the shore of the Menai Strait (North Wales).

FEEDING AND MEAL SIZE ASSESSMENT

During feeding experiments terrapins were each fed individually in a separate feeding tank. Each terrapin was weighed to the nearest 0.1 g on a Mettler P1200 toploading balance before a meal, so that the meal size could subsequently be expressed in terms of % body weight. To determine the size of a meal, a quantity of mussel meat was weighed out, and that amount offered piecemeal to the terrapin under investigation. When the animal had refused more food for a period of 10 min it was assumed to be satiated. Uneaten food in the feeding tank was retrieved, water drained from it, and added to the unoffered food. All of this food was weighed and the meal size obtained by deducting this weight of mussel flesh from the original weighed amount. In the light of pilot experiments it was found that maximal appetite occurred after a 48 hr food-deprivation period, and throughout this paper, a meal taken after such a deprivation period will be referred to as a 'standard satiation meal'.

RETURN OF APPETITE

To find out when food was first taken after a standard satiation meal, the terrapins were offered food at one hour intervals following a standard satiation meal. Food acceptance was first observed after 6 hr. This allowed the following experiment to be designed. Three of the terrapins were each given a standard satiation meal (i.e. after 48 hr of food deprivation). Each was then deprived of food for an experimental period before being fed to satiation. The sequence of 48 hr food deprivation, standard satiation meal, deprivation period and experimental satiation meal was repeated until all three animals had yielded data for the following deprivation times: 6, 12, 18, 21, 48, 60 and 72 hr.

APPETITE UNDER FULLY-MARINE CONDITIONS

Three terrapins were maintained under the standard feeding regime for four feeds (days 0-6) from which a mean standard meal size was calculated for each terrapin. Immediately after the fourth standard meal, the terrapins were deprived of fresh water. They continued to be fed to satiation at 48 hr intervals, the meal size being recorded in each instance. Fresh water was restored to the diamondbacks after 18 days of deprivation (i.e. after the feed on day 24 of the experiment); food consumption continued to be monitored at 48 hr intervals up to day 32.

EFFECT OF TEMPERATURE ON APPETITE

Three terrapins were maintained under the standard feeding regime for four feeds at a temperature of 25°C to allow a mean standard meal size to be calculated for each terrapin. After this the water temperature was changed to, and maintained at, an experimental temperature for 96 hr. Two satiation meal assessments were carried out, at 48 hr ('first feed') and at 96 hr ('second feed'). These two assessments were performed to test for adjustment of physiology to a new temperature. After the second feed the animal was transferred to the next experimental temperature and the whole process repeated. The terrapins were exposed to the following temperatures in an order designed to avoid either a systematic rise or fall in temperature throughout the period of study- 15°C, 25°C, 35°C, 30°C, 20°C.

RESULTS

In considering the results it has to be accepted that the sample size is rather small. Although the animals have been long-captive (carrying the risk of development of unusual behaviour patterns), this has the advantage that the turtles were not shy and would readily feed in the presence of observers.

RETURN OF APPETITE

The mean satiation ration recorded for the three turtles at 25°C was equivalent to 7.2% body weight. The results of the return of appetite study are shown in Fig. 1. Although no return of appetite occurs until six hours after a standard satiation meal, the diamondback is then capable of consuming 33-41% of a standard satiation meal. Appetite returns completely within 48 hr. Food intake probably reflects the amount of 'space' available in the stomach, but attempts to construct a 'square-root' gastric emptying model of the type described for lower vertebrates by Jobling (1981) failed be-

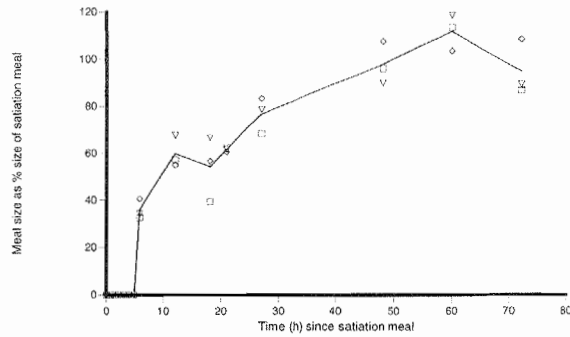


Fig. 1. Return of appetite in *Malaclemys terrapin* at 25°C. Solid line represents mean; symbols represent individual turtles.

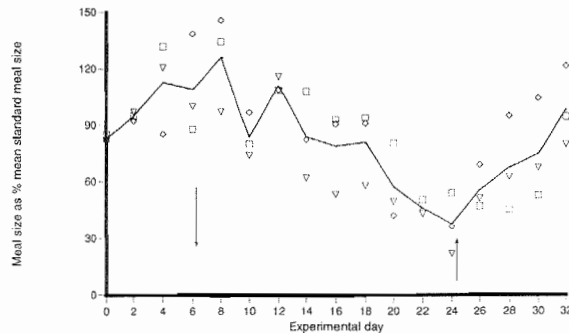


Fig. 2. Effect of lack of access to fresh water on appetite in *Malaclemys terrapin* at 25°C. Downwardly directed arrow indicates onset of water deprivation. Upwardly directed arrow indicates renewed access to fresh water. Solid line represents mean; symbols represent individual turtles.

cause of the steep rise in appetite between 5 and 6 hr after a standard satiation meal. After 60 hours of food deprivation there are signs of an overshoot to higher levels of appetite, but not to a statistically significant extent.

APPETITE UNDER FULLY-MARINE CONDITIONS

The data displayed in Fig. 2 demonstrate that exposure to full sea water without access to fresh water gradually depresses appetite so that, after 18 days of water deprivation, the diamondbacks' appetite has fallen to 22-54% of the average satiation ration recorded when fresh water was available. During this period there was a steady fall in body weight of the diamondbacks (Fig. 3), most of which is due to osmotic water loss as described by Robinson & Dunson (1976), since it may be seen that body weight rapidly climbs to its initial value as soon as fresh water is made available again, whereas appetite takes 6-8 days to recover completely (Fig. 2).

EFFECT OF TEMPERATURE ON APPETITE

The effects of temperature on appetite in *Malaclemys* are shown in Fig. 4. As would be expected, lowering the temperature depresses appetite, whereas a rise in temperature stimulates it. However, the temperature effects are far from linear (Fig. 4). At 15°C appetite is considerably depressed at the first feed (to around 16% of the average standard meal size at 25°C) and does not show significant signs of recovery by the time of a second feed. At 20°C the picture is different. Initially appetite is depressed, but there is a highly significant ($P < 0.001$) recovery of appetite by the time of the second feed. At 25°C there was no significant difference in appetite re-

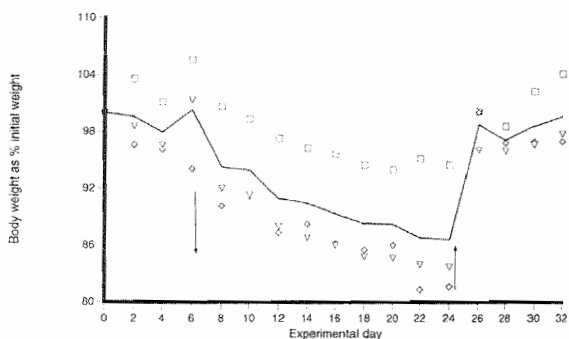


Fig. 3. Effect of lack of access to fresh water on body weight in *Malaclemys terrapin* at 25°C. Downwardly directed arrow indicates onset of water deprivation, Upwardly directed arrow indicates renewed access to fresh water. Solid line represents mean; symbols represent individual turtles.

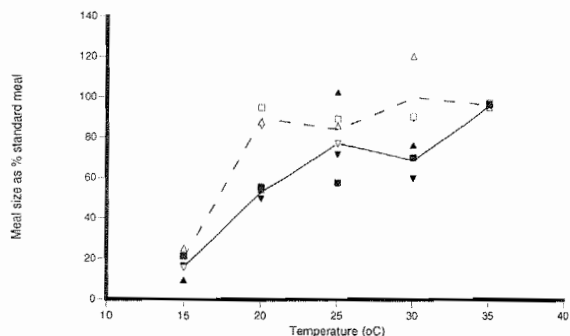


Fig. 4. Effect of temperature on appetite in *Malaclemys terrapin*. Data represent three individuals. Closed and open downward triangles represent one individual at first and second feeds after transfer to new temperature respectively (see text for details). Corresponding symbols for individuals 2 and 3 were closed and open boxes, and closed and open upward triangles respectively. Solid line represents mean appetite at first feed; dashed line represents mean appetite at second feed.

Temperature range (°C)	Q_{10} for appetite			
	Turtle 1	Turtle 2	Turtle 3	Mean
15-20	30.2	19.8	12.2	20.7
20-25	0.8	0.9	1.0	0.9
25-30	1.4	1.0	2.0	1.5
30-35	1.2	1.1	0.6	1.0
20-35*	1.1	1.0	1.1	1.1

TABLE 1. Effect of temperature on appetite in *Malaclemys terrapin*; Q_{10} values for second feed data. * Q_{10} is presented for this range to show contrast with that for 15-20°C range.

recorded between the two feeds, while at 30°C there was a significant difference ($P < 0.05$), with the appetite at second feed being higher. At 35°C there was no significant difference between appetite levels recorded.

Table 1 shows Q_{10} values for appetite calculated from the second feed data. Clearly appetite in *Malaclemys* is remarkably stable between 20 and 35°C, but is severely depressed below 20°C. The high Q_{10} value for the 15-20°C interval indicates a fundamental change in metabolism below 20°C, rather than a simple thermal response.

DISCUSSION

Diamondback terrapins with access to fresh water for drinking proved to have unusually large appetites (mean satiation ration 7.2% body weight at 25°C, corresponds to 3.6% body weight d^{-1} assuming complete return of appetite in 48 hr), particularly for carnivorous adult turtles past the phase of rapid growth. For comparison, Birse & Davenport (1987) recorded satiation rations of 3.7% body weight for juvenile (fast-growing) loggerhead sea turtles (*Caretta caretta* L.) at the same temperature, but values for freshwater emydid relatives of *Malaclemys* are much lower; Kepenis & McManus (1974) recorded $<0.5\%$ body weight d^{-1} for young painted turtles (*Chrysemys picta* (Schneider)), while Davenport & Kjørsvik (1988) recorded an intake rate of 0.045% body weight d^{-1} for adult *Mauremys caspica* (Gmelin) males (101-173 g body weight; also at 25°C) feeding on a dry pelleted diet, which corresponds to about 0.2% body weight d^{-1} on a wet weight basis. If mussel flesh is assumed to have a water content of 75-80%, then adult male diamondbacks consume about 7.9 g dry matter (kg body wt) $^{-1} d^{-1}$. This is 2-3 times the dry matter intake reported for a range of herbivorous turtles (Bjorndal, 1985) eating much poorer quality diets, so the available evidence indicates that *Malaclemys* has a relatively enormous appetite. Davenport *et al.* (1992) recently described a similarly large appetite in another estuarine emydid, the river terrapin *Batagur baska* (Gray) (a largely herbivorous species).

Davenport *et al.* (1992) suggested that river terrapins were responding to a food-rich estuarine ecosystem by maximizing food intake and processing food quickly and relatively inefficiently (a strategy compatible with the resource-utilization hypothesis of Sibly, 1981). This may also be true of *Malaclemys*, since their salt marsh habitats contain an abundance of littorinid snails and crabs (the main items of their diet), so they may be able to afford to waste energy in a manner not tolerable in food-poor freshwater systems. However, an additional factor needs to be considered. Diamondback terrapins spend much of the productive summer period in fully marine conditions, only able to fully-hydrate themselves when fresh water becomes available due to rainfall (there is strong element of water storage involved, since diamondbacks exhibit swollen subcutaneous tissues after a drinking bout; Robinson & Dunson, 1976). The results of the study reported here demonstrate that prolonged exposure to full sea water substantially depresses appetite, presumably because the animals have to strike a physiological balance between the intake of salts and energy. It therefore seems possible that diamondbacks are adapted to respond to the availability of fresh water by enhanced appetite (hyperphagia) and energy storage, so that average intake of energy is maximized.

Three features of the response of appetite of diamondbacks to temperature are interesting. First, the ability of the terrapins to adjust to temperatures between 20 and 35°C, but not to be able to acclimate (at least in the relatively short-term experiments reported here) to 15°C appears to be a novel observation in turtles. Second, the relative independence of appetite shown by acclimated terrapins between 20 and 35°C perhaps reflects the wide geographical range of the species (roughly from 26-41°N on the eastern coast of the United States), encompassing warm and cool temperate regions. It

contrasts with the limited data available for other chelonians, which tend to show temperature dependence (e.g. *Caretta caretta*; Birse & Davenport, 1987). Finally, a sharp decline in appetite below 20°C indicates that the species enters a depressed metabolic state at such temperatures.

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