

SHORT NOTES

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THERMOREGULATION OR OSMOTIC CONTROL? SOME PRELIMINARY OBSERVATIONS ON THE FUNCTION OF EMERSION IN THE DIAMONDBACK TERRAPIN *MALACLEMYS TERRAPIN* (LATREILLE)

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The diamondback terrapin *Malaclemys terrapin* Latreille is a medium-sized emydid turtle that inhabits salt marshes and other brackish-water habitats on the east coast of the USA. (Pritchard, 1979). The osmotic physiology of the species has attracted much study, especially by Dunson and his co-workers (Dunson, 1970, 1976, 1985, 1986; Dunson & Dunson, 1975; Dunson & Mazzotti, 1989; Robinson & Dunson, 1976). *Malaclemys* spends much of the summer in an essentially marine environment, yet does not have such powerful salt glands as the marine turtles (Robinson & Dunson, 1976). When exposed to high salinity the turtles survive by virtue of an extremely low integumentary permeability to salts, a low permeability to water, a large interstitial fluid volume, (Robinson & Dunson, 1976) an ability to secrete salts from the lachrymal glands (Cowan, 1971), plus behavioural responses that allow them to select low salinity drinking water and to detect and exploit rainwater (Dunson, *op.cit.*; Davenport & Macedo, 1990; Bels *et al.*, 1995). They also exhibit a reduced appetite in sea water (Davenport & Ward, 1993) thereby minimizing uptake of salt in their invertebrate diet and by incidental swallowing of sea water whilst feeding (Dunson & Mazzotti, 1989).

The present study arose from three observations. Pritchard (1979) and Seigel (1984) both noted that diamondback terrapins are often to be seen in large basking aggregations on mudbanks. Davenport & Ward (unpublished data) found that terrapins used in feeding experiments spent increasing amounts of time out of sea water when deprived of access to fresh water; this observation was made under conditions of constant light and temperature.

Basking for thermoregulatory purposes is an extremely common phenomenon in reptiles, particularly in lizards (e.g. Cowles & Bogert, 1947; Bartholomew, 1966; Pearson & Bradford, 1976), but also in aquatic turtles (e.g. Spotila *et al.*, 1990). It has ecological costs (in terms of time unavailable for other activities, enhanced risk of predation etc), but the benefits in terms of maintenance of heightened body temperature

and possibly the inhibition of epiphytic growths on the shell, outweigh these disadvantages. For lizards and snakes a heightened body temperature will facilitate food capture and processing, but in aquatic turtles, basking can also be associated with quicker digestion of meals acquired in water at lower temperature (Hutchison, 1979).

Because Davenport & Ward had observed that animals deprived of fresh water spent increasing periods out of water, even though held at constant temperature, it seemed possible that 'basking' in *Malaclemys* might be in part a behavioural response to dehydration, rather than being solely a thermoregulatory response. This preliminary study tests this hypothesis.

Ten male diamondbacks (211 - 300 g) were used in these experiments. They were fed twice weekly, *ad lib.*, on flesh of scallops (*Chlamys opercularis*). They were held in a tank of circulating sea water (34‰) held at 25°C. The tank had a wooden platform onto which the animals could readily climb; it was fitted with a fixed drinking vessel that normally contained fresh water, but was filled with sea water during periods of experimental water deprivation. The tank was sited in a dimly-lit room where the air temperature ranged from 14 - 19°C; that is always at least 6°C cooler than the tank sea water.

To assess 'basking' (= emersion) frequency during experiments the terrapins were observed at 09.00 hr., 12.00 hr and 17.00 hr each day. The number out of water on the platform was counted and summed for the day (maximum possible frequency 30).

During 1992 and 1993, four experiments were performed. The first was a pilot experiment. The turtles had access to fresh water for several weeks. They were observed for basking frequency for five days, then deprived of fresh drinking water for ten days. In the light of this first trial, three further long experiments were performed, each lasting 36-40 days and separated from each other by 1-2 months of standard maintenance. In each case, turtles were observed for 9-10 days when fresh water was available, then for 13-16 days when it was not, followed by a further period of 10-14 days after fresh water access was restored.

To allow an assessment of the relative importance of respiratory and cutaneous water exchange, the following experiments were carried out in 1993-94. First, three groups, each of three well-fed terrapins, were fasted for 12 days. One group was held in fresh water, one in sea water and one in air (at 25°C). Their holding vessels were mounted next to one another to ensure a similar atmospheric humidity, but daily readings of relative humidity (RH) were taken by hygrometer (5 mm above the water surface in the case of the fresh water and seawater vessels). Animals were weighed each day, those held in water being thoroughly dried with paper towels before weighing (accuracy ± 0.05 g). Second, after several weeks during which the terrapins were again well fed and had access to fresh water, three ani-

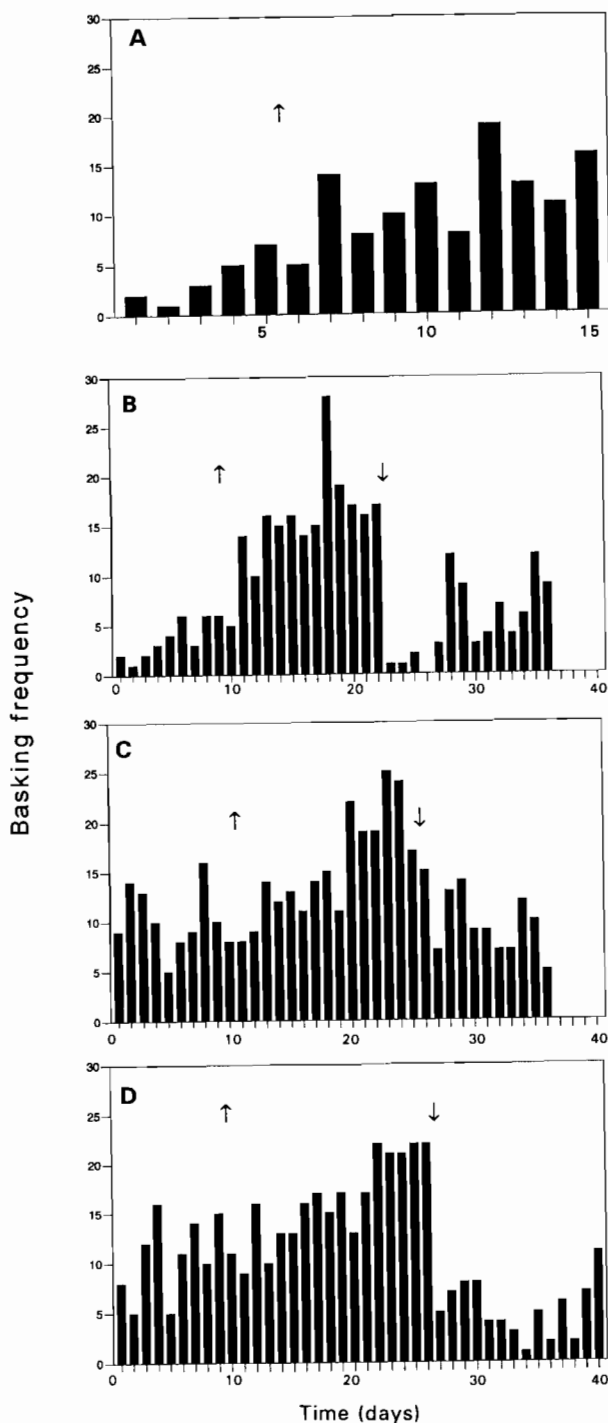


FIG. 1. A, basking frequency during preliminary trial. Fresh water was available on days 1-5 and absent on days 6-15. B, basking frequencies during experiment 1. Fresh water was available on days 1-9 and 23-36. It was absent on days 10-22. C, basking frequencies during experiment 3. Fresh water was available on days 1-10 and 26-36. It was absent on days 11-25. D, basking frequencies during experiment 3. Fresh water was available on days 1-9 and 27-40. It was absent on days 10-26. Up arrows indicate onset of fresh water deprivation; down arrows indicate restoration of fresh water availability.

mals, selected randomly from those available, were placed in an air-filled vessel in which a water tank and water-soaked absorbent paper (both inaccessible to the turtles) ensured a water-saturated atmosphere. They

were fasted for 12 days and weighed daily as described above.

Fig. 1A shows the results of the preliminary basking frequency trial. Terrapins deprived of fresh water spent more time out of water than they had previously in fresh water (on average 3.25 times the basking frequency), despite the lower temperature they encountered by doing so.

This is confirmed by the data shown in Figs 1B-1D. In each case a similar pattern of behaviour was seen. When fresh water deprivation started there was initially little change in basking frequency, but thereafter there was a progressive increase. When fresh water availability was restored there was an abrupt drop in basking frequency. Regression analysis confirmed that each period of water deprivation was associated with a rise in basking frequency (Table 1). Maximum basking frequency scores (22-28 out of a possible 30) indicated that terrapins deprived of fresh water were spending 73-93% of their time out of water.

During the period of the first mass change experiment, with terrapins held in fresh water, sea water and air, recorded relative humidities (RH) ranged from 61% to 85%. However, although there were differences in RH amongst the experiment vessels on each day, there was no significant pattern of difference, and no statistically significant difference between mean RH ($P > 0.05$). During the second experiment, with terrapins held in water-saturated air, RH values were always in the region of 98-100%.

All animals showed a similar pattern of rapid mass loss during the first four days of the experiments when they were defaecating. Thereafter, mass changes were much slower and very steady. Accordingly, regression analysis of mass changes was conducted from day 4 to day 12 of the experiment (Table 1). It is evident that rate of mass loss in air could be less or greater than the rate of loss in sea water, depending upon the RH.

Diamondback terrapins are vulnerable to avian and mammalian predation when on land (Seigel, 1984; Lovich & Gibbons, 1990). However, from the data collected it is evident that diamondbacks progressively spend more time on land when they lose access to fresh water. Under the experimental conditions employed in this study they consequently encountered reduced, not elevated temperature, so gained no thermal benefit. From the results of the mass change experiments it may be seen that they also experienced a heightened rate of water loss, when RH levels were in the range 61-85%, but a reduced rate of water loss at high RH (98-100%). Enhanced water loss in air of RH 61-85% presumably occurred across the skin and shell since respiratory water loss should have been similar for turtles held in fresh water, sea water or air. Dunson (1976, 1986) showed that diamondbacks lost mass in sea water at a rather lower rate ($0.32\% \text{ d}^{-1}$) than that recorded in this study ($0.56\% \text{ d}^{-1}$). This difference probably stemmed from the much smaller size (ca. 230 g) of our terrapins (and consequent higher surface area-to-volume ratio)

TABLE 1. (a) Rate of change of basking frequency during periods of water deprivation, where y = frequency of basking; x = length of period of water deprivation (days). (b) Rates of mass change in fasting diamondback turtles, where y = mean mass (g) and x = days of fasting. Regression equations are for the period between 4 and 12 days after initiation of fasting. From equations in Table 1 (b) it can be seen that the fasting diamondbacks lose little mass (0.15% d^{-1}) in fresh water, compared with 0.36% d^{-1} in water saturated air, 0.56% d^{-1} in sea water and 0.90% d^{-1} in air of 61-85% RH.

	Equation	r^2	P
(a)			
Experiment 1	$\log y = 0.028x + 0.29$	0.413	0.018
Experiment 2	$\log y = 0.023x + 0.73$	0.589	0.001
Experiment 3	$\log y = 0.021x + 1.02$	0.711	0.000
(b)			
In fresh water	$y = 232.5 - 0.36x$	0.66	0.007
In sea water	$y = 231.6 - 1.29x$	0.95	0.000
In air (61-85% RH)	$y = 224.6 - 2.02x$	0.97	0.000
In air (98-100% RH)	$y = 230.3 - 0.83x$	0.98	0.000

by comparison with those studied by Dunson (ca. 1000 g).

Cowan (1974) showed that blood concentration of terrapins rose from about 290 to 400 mOsmoles kg^{-1} during a four month exposure to full sea water. Taken with the flux studies of Robinson & Dunson (1976), it seems that all of the mass loss and rise in blood concentration that occurs in terrapins exposed to sea water may be accounted for by osmotic dehydration; salt influx and efflux are in balance. On the face of it therefore, terrapins would tend to suffer more osmoconcentration by leaving sea water and basking in air of 61-80% RH than they would if they remained immersed in sea water. However, when they do leave seawater salt influx will cease, but there would appear to be no reason for all salt efflux to cease during emersion. Minimal sodium efflux by the cloacal and lachrymal gland routes (65% of total efflux) should continue at around 4 - 7 μ moles Na $100 g^{-1} h^{-1}$ (calculated from Robinson & Dunson, 1976). Given a total body Na content of 108.6 μ moles g^{-1} (Robinson & Dunson, 1976) this corresponds to a loss of 0.9-1.55% of body sodium per day. So, by moving from sea water into air of 61-85% RH a terrapin will incur an extra water loss cost of 0.34% body mass d^{-1} (i.e. 0.9% minus 0.56% d^{-1}), but lose sodium at 0.9-1.55% d^{-1} . This suggests that basking animals will lose more body water by basking, but suffer significantly less overall osmoconcentration of the body fluids. Obviously the balance between these two influences will depend upon RH. At high RH levels (98-100%), which are perhaps more likely close to the muddy substrata of salt marshes, emersed terrapins will lose less water than they would in sea water, as well as avoiding salt influx and continuing to excrete salt in tears and urine.

Diamondbacks can withstand considerable loss of body water, first because they have large extracellular subdermal spaces that act as water stores, and second

because they partition water loss so that the intracellular compartment is maintained (Robinson & Dunson, 1976). Avoiding osmoconcentration of the body fluids is probably a higher physiological priority than preventing water loss; 'basking' (i.e. emersion) in response to lack of fresh water would appear to accomplish this aim, even when RH levels are below saturation. Obviously diamondbacks will bask for thermoregulatory purposes, just as do other emydids (the best studied being *Trachemys scripta*; Spotila *et al.*, 1990). However, the evidence presented in this paper demonstrates that basking might have an osmotic control function too.

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