FACULTATIVE AESTIVATION IN A TROPICAL FRESHWATER TURTLE *CHELODINA RUGOSA*

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Abstract-1. *Chelodina rugosa* dug from aestivation sites at the end of the dry season were immediately alert and well coordinated.

2. Compared with non-aestivating animals, aestivating turtles had 20% higher plasma osmotic pressure and 7% higher sodium. Coupled with a small, but significant weight gain upon return to the water, this suggested the occurrence of minor dehydration in aestivating animals.

3. Plasma lactate levels of aestivating animals were low, averaging 1.99 mmol/1, consistent with aerobic rather than anaerobic metabolism having sustained their long period under ground.

4. No evidence was seen of dramatic physiological specialization. Aestivation in this species is interpreted as a primarily behavioural adaptation, made possible by typically reptilian abilities to tolerate a wide range in plasma electrolytes and to survive long periods without feeding.

INTRODUCTION

The northern snake-necked tortoise, *Chelodina rugosa* (Chelidae), occurs in tropical Australia from Cape York to the Kimberley district of western Australia, where it is found in freshwater swamps, billabongs, waterholes and slow-flowing rivers (Cogger, 1975). The climate throughout its range is markedly seasonal, with the summer monsoon lasting from about November to March and little or no rain in the intervening dry season. The summers are hot and humid, winters warm and less humid. Many of the water bodies in which turtles are found are seasonal, being resplendent with emergent and floating vegetation and wildlife during the wet season, but drying out completely during the ensuing dry season. Turtles in these waterholes survive by aestivating buried in the soil. They are a significant traditional food item for aborigines who seek them with great skill, wading in shallow billabongs and capturing them by hand or digging them from their aestivation sites.

Little is known about aestivation in reptiles, although it is reported in lizards, snakes, chelonians and crocodilians (Gregory, 1982). Saint Girons (1953) identified aestivation as a period of inactivity during dry seasons at any time of the year in tropical habitats. Seidel (1978) considered aestivation (and hibernation) to be a "behavioural strategy accompanied by physiological adjustments". We were curious about what physiological adjustments *Chelodina rugosa* might make to enable it to survive buried in the earth for months awaiting the onset of the next wet season and the regeneration of its aquatic habitat, particularly whether blood lactate levels would indicate aerobic or anaerobic metabolism while underground.

MATERIALS AND METHODS

In October 1981, aboriginal women collected six aestivating turtles for us from a dry billabong at Bulgai on the floodplain of the Tomkinson R near Maningrida, northern Territory, Australia. The billabong is likely to have been dry for a minimum of five months. The method of collection is sufficiently interesting to record here. The collection site showed no sign to the untutored eye that it was a waterhole in the wet season, comprising an extensive grove of paperbark trees *(Melaleuca sp.)* which formed a canopy over hard-packed bare loamy soil from which all signs of vegetation had been burnt. The women fanned out, scanning the ground and prodding and tapping the earth with digging implements made by inserting a sharpened steel rod a metre in length into a short wooden handle. They detected the presence of a turtle either from surface signs or from the hollow sound of the struck earth. As they dug at a likely prospect they would examine the removed clods, looking (they told us) for the impressions of turtle carapace. Six turtles were found at 5-15 cm, at which depth there was no apparent moisture in the soil. There was no aestivation cavity, and mud/earth was caked so firmly onto many of the turtles that we could only scrape it away with difficulty. The animals were alert and well coordinated when lifted from the soil, showing no signs of being torpid. The shells of two turtles were pierced accidentally by the seeking probe tip.

All animals were weighed, including two collected previously by hand from a permanent waterhole at Gadji near the Cadell R. Enough blood was drawn from the jugular vein of each within a few hours of capture to allow determinations of plasma osmotic pressure, electrolytes and lactate. Lithium heparin was

used to prevent clotting. The animals were then put into water and weighed again after 3 hr to measure the extent of short-term water uptake. Two more turtles were caught subsequently from a different permanent billabong near Gadji and all samples and turtles were returned to the University of Sydney where the turtles were kept in water and adapted well to captivity. In January 1982, further sets of blood samples were taken for plasma electrolyte and osmotic pressure determinations. Osmotic pressures were measured with a Knauer Semi-Micro Osmometer, chloride was analysed by coulometric titration (Radiometer CMT 10) and potassium and sodium by flame photometry (Corning 435). Versatol was used as a standard for electrolyte analyses.

RESULTS

Aestivating turtles had on average a 20% higher plasma osmotic pressure than those measured in animals from the permanent waterhole, and also the January and December 1982 determinations on all turtles kept in water in the laboratory in Sydney (Table 1). There were no significant differences between wild-caught and captive turtles in fresh water. Aestivating turtles also showed about 7% higher plasma sodium than nonaestivating turtles. Chloride and potassium values were similar in all groups.

Turtles collected in aestivation showed small and variable, but significant, weight gains within 3 hr when returned to water (Table 2). Blood lactates were low, the only elevated values being from the two animals which had been injured at collection (Table 2).

Table 1. Comparison among blood plasma values of *Chelodina rugosa* taken from the wild in October 1981, some in aestivation and some aquatic, and the same animals kept in aquatic captivity for more than one year

	In the wild (October 1981)		In captivity	
	Aestivation (dry earth)	Aquatic (permanent billabong)	Aquatic (January 1982)	Aquatic (December 1982)
Osmotic pressure (mOsm/1)	307.3 ± 8.22 (6)* (281-334)	260.5 ± 5.5 (2) (255-266)	244.7 ± 6.07 (7) (230-277)	251.0 ± 2.93 (9) (232-265)
Sodium (mmol/1)	133.0 ± 1.59 (6)* (130-140)	125.0 ± 3.00 (2) (122-128)	123.3 ± 2.55 (6) (115-130)	123.4 ± 2.56 (9) (112-I34)
Potassium (mmol/1)	3.88 ± 0.221 (6) (3.3-4.8)	3.60 ± 0.100 (2) (3.5-3.7)	4.03 ± 0.139 (7) (3.4-4.6)	4.20 ± 0.159 (9) (3.3-4.7)
Chloride (mmol/1)	89.9 ± 1.64 (6) (84-94)	89.0 ± 2.00 (2) (87-91)	86.1 ± 1.47 (7) (82-93)	86.4 ± 1.07 (9) (81-92)

Data presented as X ± SE (N), range in brackets below. *Denotes significant difference, $P < 0.05$ (t -test).

Table 2. Weights and plasma lactate in aestivating and nonaestivating *Chelodina rugosa* and percentage weight gain by aestivating tortoises 3 hr after being placed in water

Animal No.	Captive wt (g)	Plasma lactate (mmol/1)	Weight gain (%)
Aestivating			
1	1471	1.317	1.9
2	1971	1.537	6.7
3	1472	1.255	4.7
4	565	7.023*	6.4
5	411	3.834	0.04
6	374	7.632*	4.4
Non-aestivating			
7	1905	1.794	
8	2854	3.737	

*Shells pierced at capture.

DISCUSSION

Blood lactate values suggest that aestivation in *Chelodina rugosa* is undertaken aerobically. The two animals which had been pierced at the time of collection had moderate values (≈ 7-8 mmol/1), which may have reflected their stress, while the mean of the other four animals was 1.99 (± 1.24 SD). Plasma lactate values are modified by handling and general disturbance, so comparison of these values with a series drawn from the literature will assist with interpretation. Grigg and Cairncross (1980) reported plasma lactates of 4.41 mmol/l in 42 field-caught *C. porosus* sampled within 12 hr of capture and 9.31 mmol/1 in five samples taken immediately after the moderate struggle associated with capture in a pen at Taronga Zoo. Coulson and Hernandez (1964) reported values of "trace" to 1.0 mmol/1 in alligators kept undisturbed in a sound-proofed box. Seymour (1979) interpreted values of 0.5-3.8 mmol/l in diving sea-snakes to indicate aerobic diving, and a value of 12.2 mmol/1 to indicate an anaerobic dive. Values of 6.5 mmol/l were measured in *Chelonia mydas* during nesting, thought to represent moderate exertion (Jackson and Prange, 1979). The most relevant data for comparison with lactate levels in the present study are, however, those reported from hibernating turtles *(Chrysemys picta)* by Ultsch and Jackson (1982). Among turtles kept at 3°C for 189 days, those with access to air had plasma lactates ranging to 14 mmol/1, compared with 39-64 mmol/l in a group denied access to air. In another group kept in N_2-equilibrated water, lactates rose to over 200 mmol/1. Applying these considerations to the present study it can be concluded that values of 1.99 and 7-8 mmol/1 indicate that the previous months underground had been supported by aerobic rather than anaerobic metabolism. This is hardly surprising for, unlike turtles which hibernate in winter at the bottom of ponds and which may not, therefore, have the option of remaining aerobic, *C. rugosa* burrows to only a shallow depth in the soil where gas exchange can, presumably, still occur. It can be expected that fat reserves would be adequate to sustain aerobic metabolism at resting rates for many months. Using data on oxygen consumption from Bennett and Dawson (1976), and fat metabolism equivalents from Schmidt-Nielsen (1975), aerobic metabolism at resting rates in a 1.5 kg turtle will result in a reduction of fat reserves of less than 1 % per month at 20°C and less than 2% per month at 30°C. However, in the North American mud turtle, *Kinosternon flavescens,* which seems to aestivate in similar circumstances, Chilian (1976) found mean plasma lactate values of (approx.) 3.7 mmol/l aquatically, compared with 6.3, 7.8 and 9.0 mmol/1 after 2, 4 and 6 months in aestivation. Chilian, therefore proposed a shift to anaerobic metabolism during dormancy, a view supported by Seidel (1978) who found that oxygen consumption increased at the end of dormancy in this species, suggesting the repayment of an oxygen debt. However, the lactate values are modest and are very unlikely to indicate major anaerobic metabolic support during the six months of experimental dormancy. Furthermore, Seidel measured reduced oxygen consumption during dormancy. Unfortunately the oxygen consumption data

were apparently drawn from a large size range (15-362 g) and insufficient information was given to allow a proper analysis of the information with the weight effect removed.

Higher plasma osmotic pressures and sodium values in aestivating turtles suggest that some dehydration had occurred, a conclusion reinforced by the weight grains that occurred when animals were placed in water. Seidel (1978) found that *Kinosternon flavescens* suffered a 27% weight loss in three months aestivation. Chilian (1976) found that this species sustained dramatic increases in plasma osmotic pressure, sodium, potassium and chloride, during aestivation. All of these variables more than doubled at the end of six months experimental dormancy. Being a smaller species than *C. rugosa, Kinosternon flavescens* is likely to lose water more rapidly under similar conditions and whether or not *C. rugosa* can tolerate similar departures from its normal plasma constituency and survive really extended periods of aestivation is unknown. The length of aestivation tolerated by this species must be variable, depending as it does on the time of drying of the waterhole, and it is not improbable that survival will, at times, depend upon an ability to survive two or more seasons without an aquatic phase. Consequently, maximum tolerances to dehydration are likely to be very much greater than those we saw in this study. Most reptiles can tolerate very wide variation in body ion concentration and total body water (Dessauer, 1970; Shoemaker and Nagy, 1977; Minnich, 1982), and the physiological specializations accompanying aestivation in *C. rugosa* appear to be minimal.

The stimulus for aestivation in *C. rugosa* is, presumably, the drying out of the waterhole. Anecdotal evidence from aborigines is that the turtles move to dry land and then burrow. This makes sense if they are to remain aerobic, for they could not if they burrowed into the mud before the water retreated. Once burrowed, water loss is retarded and thermal changes are damped by the surrounding earth which provides a secure retreat in which to await the return of water. On the other hand, turtles remain active if the water hole does not dry.

In summary, aestivation in *C. rugosa* occurs facultatively with the drying out of its habitat and is a primarily behavioural strategy, apparently without major physiological specialization, by which water and energy are conserved in a thermally benign environment while the animal is protected encased in earth until the rains come.

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