CHAPTER 26

Effect of Capture on the Physiology of *Crocodylus porosus*

Roger S. Seymour[1], Grahame J. W. Webb[2], Albert F. Bennett[3] and David F. Bradford[1]

IN recent years, crocodile management programmes in northern Australia have more frequently required the capture of nuisance animals which are relocated into unpopulated areas or into crocodile farms. Since the saltwater crocodile *Crocodylus porosus*, was fully protected in the Northern Territory in 1971, the number of capture incidents involving large, mature animals has increased. However, attempts to capture crocodiles larger than about 4 m in total length (TL) with traps and harpoons have often resulted in the crocodile's death, although the causes were not immediately apparent. A common feature in the capture of large animals is a prolonged period of struggling to exhaustion, which has been necessary to subdue them to a point where it is possible to manoeuvre them onto a vehicle for transport. The crocodiles appear alive when subdued, but die shortly afterwards.

We felt that if the struggling during capture was intense and prolonged enough, it might produce death as a consequence of the severe lactic acid load and acid-base disturbance. Therefore we investigated anaerobic metabolism and acid-base balance in a series of different sized crocodiles exercised to exhaustion (Seymour *et al.* 1985; Bennett *et al.* 1985).

EFFECTS OF EXERCISE IN REPTILES

There are essentially two metabolic pathways available to all vertebrates: aerobic and anaerobic. When oxygen is present, energy from carbohydrates, fats and proteins is used via the tricarboxylic acid cycle and electron transport chain. Thus the foodstuffs are oxidised into carbon dioxide and water and oxygen is consumed. If oxygen is limited, on the other hand, most vertebrates can still gain energy by converting ketopyruvate to lactate. This pathway is known as the anaerobic pathway or anaerobic glycolysis. The aerobic pathway is used by practically every resting vertebrate known and there is a good reason for it. Aerobic metabolism produces about 18 times the energy as does anaerobic metabolism for the same input of carbohydrate. So aerobic metabolism is utilized by animals which have adequate supplies of oxygen to the cells. However, there are times when oxygen can become limited in the cells. This occurs when the cardiovascular and respiratory systems fail to deliver enough oxygen to the cells, either because the environment has become hypoxic, such as in diving animals, or because the rate of oxygen demand by the cells exceeds the supply capacity of the cardiovascular system.

Of all vertebrates, reptiles rely most heavily on anaerobic metabolism (Bennett 1982), and there are two reasons for them having this capacity. Firstly, many species use water for escape. When they dive into the water, they hold their breath and can become anoxic. Secondly, the energetic demands during exercise can greatly exceed the capacity of the cardiovascular system to supply oxygen. Thus, large amounts of lactic acid are produced in active reptiles, even though they continue to consume oxygen and pump blood (e.g., Gleeson *et al.* 1980). There appears to be a severe oxygen diffusion resistance at the tissue level in reptiles (Seymour 1982). Therefore during strenuous exercise, the muscles operate anaerobically, in virtual anoxia, and thereby produce large amounts of lactic acid. The lactic acid produced in the muscles dissociates into the lactate and hydrogen ions which diffuse out into the blood and cause a general acid-base disturbance known as lactacidosis or metabolic acidosis. The pH of the blood drops and this has detrimental effects on the metabolism of the whole body.

Therefore when a reptile becomes intensely active, it can quickly reach a state of exhaustion or fatigue, at which time it no longer responds to stimulation. Then it must rest and re-establish the normal acid-base balance. To appreciate the temporal pattern of anaerobic metabolism and recovery, it is necessary to measure blood gases, lactate and pH. Blood lactate values do not indicate the total amount

[1]Department of Zoology, University of Adelaide, Adelaide, South Australia 5001, Australia.
[2]Conservation Commission of the Northern Territory, P.O. Box 38496, Winnellie, Northern Territory 5789, Australia.
[3]School of Biological Sciences, University of California, Irvine, California 92717, USA.
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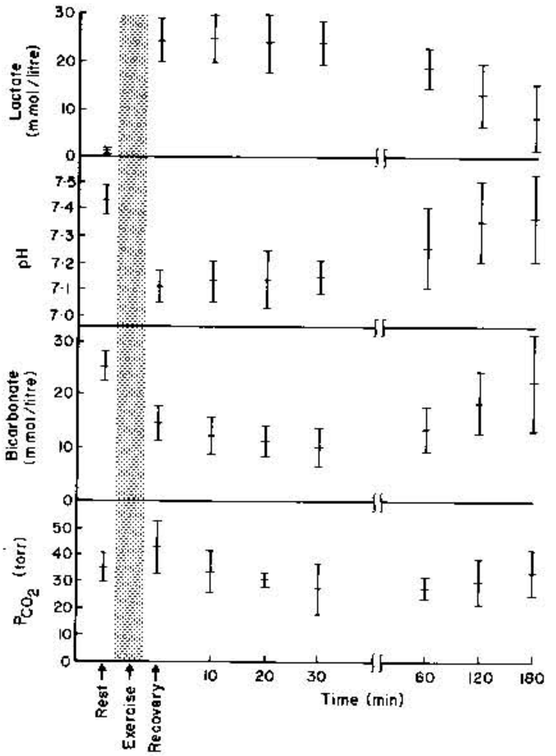

Fig. 1. Acid-base parameters of the blood of five laboratory *Crocodylus porosus* before and after 5 min of forced exercise. Data are means ± standard deviations and are derived from Seymour *et al.* (1985).

of anaerobic metabolism during activity, but they are a good index of it. Invariably, lactate is higher, and pH lower, in the muscles than in the blood.

ACID-BASE BALANCE IN LABORATORY CROCODILES

To obtain resting values, six small crocodiles were fitted with catheters and then exercised in laboratory conditions (Seymour *et al.* 1985). After 5 minutes of forced exercise in a bathtub, which was sufficient to exhaust the small animals, blood samples were taken during recovery. Within 10-20 min following exhaustion, blood lactate values peaked (Fig. 1). At the same time, pH decreased, the partial pressure of CO_2 (P_{CO_2}) increased and bicarbonate decreased. The latter changes occurred because the hydrogen ions produced by the lactic acid combined with bicarbonate to liberate CO_2.

ACID-BASE BALANCE IN FIELD CROCODILES

Because it was impractical to catheterize large crocodiles and exercise them in a bathtub, we decided to capture animals of selected sizes in the field. They were exercised to exhaustion during capture, and blood samples were taken during recovery to determine the extent of acid-base disturbance and the time course of its resolution (Bennett *et al.* 1985).

Small crocodiles were captured by hand and exercised to exhaustion by manipulation. The large animals were secured with a skin-penetrating harpoon and line (Webb and Messel 1977), which caused them to swim and thrash violently until they were exhausted and could be pulled in. They were turned over on their backs and a blood sample taken by heart puncture with a strong needle. The blood was analysed immediately in the field for pH and respiratory gases and another sample was preserved for subsequent determination of lactate concentration. The animals were then allowed to recover on shore for a few hours, during which time one or two more samples were obtained, before being carefully released.

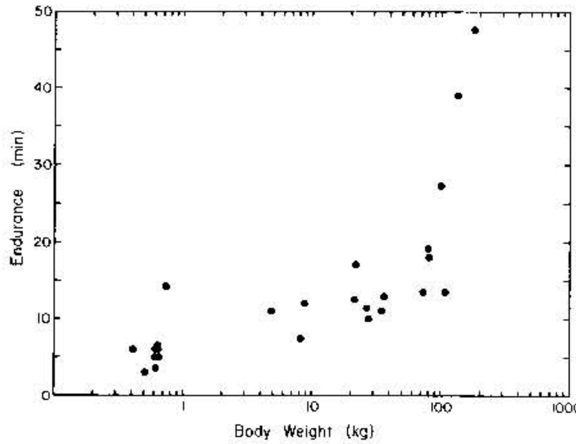

Fig. 2. Effect of body size on the length of time of exercise to exhaustion in *Crocodylus porosus* captured in the field. Data are from Bennett *et al.* (1985).

Large crocodiles had a greater capacity for exercise before they became exhausted (Fig. 2). Small animals became exhausted in about 5 minutes, but the largest ones required up to 40 to 50 minutes to subdue. In every case, the animals appeared completely exhausted when they stopped fighting. The pattern of activity was the same in both large and small ones; the large ones just lasted longer.

Increased endurance and stamina are probably of selective advantage in the larger mature animals. Adults engage in supremacy battles, mating, and defence of territories and nests. Female *C. porosus* reach maturity when they are about 2.25 m TL and males at about 3.3 m TL (Webb *et al.* 1978). These lengths correspond to body weights of about 36 kg and 128 kg respectively (Webb and Messel 1978), and are associated with the marked increase in endurance shown in Figure 2.

The greater endurance in the large animals was due to a greater capacity for anaerobic metabolism, as indicated by blood lactate levels (Fig. 3A). The largest animals had levels exceeding 50 mmol l^{-1}. These are the highest values recorded in any animal (not simply in reptiles) as a result of activity. Some

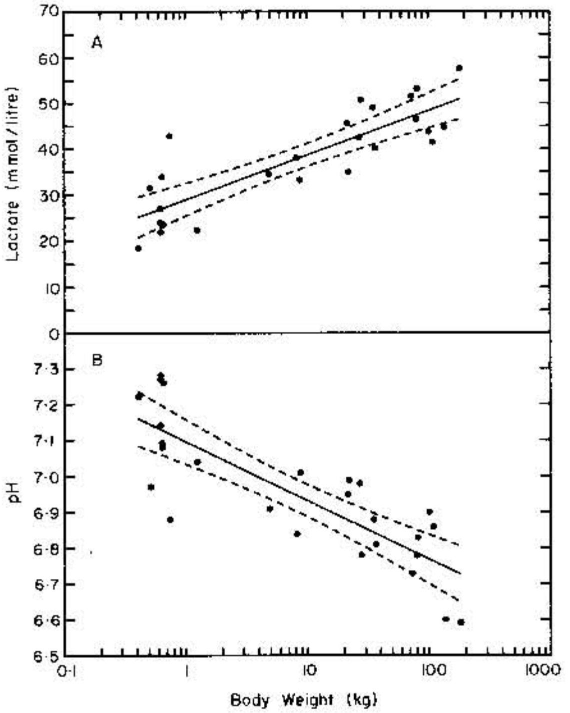

Fig. 3. Effect of body size on blood lactate (A) and pH (B) measured shortly after exhaustion in field captured *Crocodylus porosus*. The linear regressions are shown with their 95% confidence belts. Data are from Bennett *et al.* (1985).

species of turtle produce higher levels if held underwater for weeks or months (e.g., Ultsch and Jackson 1982), but no other animal is known to produce these levels by activity alone.

Accompanying the lactate buildup in crocodiles was a dramatic decrease in blood pH (Fig. 3B). Again we know of no other animal that can produce blood pH as low as 6.6 as a result of activity. Most reptiles become fatigued or are dead when blood pH drops much below 7.0 (Bennett 1973; Seymour and Webster 1975; Ruben 1979; Mitchell *et al.* 1981). In man, pH below 7.0 is accompanied by serious depression of central nervous system function (Guyton 1982). But 6.6 represents a hydrogen ion load 2.5 times larger than does 7.0. Large crocodiles are truly exceptional.

Recovery from exercise was slow. In general, the first compensatory response to the acidosis was hyperventilation to reduce the P_{CO2} and allow more bicarbonate to combine with excess hydrogen ions, thus raising the pH. This was accompanied by a longer term metabolic compensation as lactic acid was removed from the blood and either oxidised or reconverted into glycogen. Large field animals required more than 4 h to recover. In fact one large animal took about 30 h to recover from a profound acidosis. Two hours after exercise its blood pH decreased to about 6.4. At 4 and 14 h, it was still markedly acidotic despite deep breathing that reduced blood P_{CO2} to low levels.

This extremely acidotic crocodile was completely unresponsive during the first hours of recovery. We have seen other animals in a similar condition after capture. If they are left on the river bank, they will not voluntarily enter the water for sometimes over a day. In this condition, they are very weak but can swim slowly away if forced into the water. Perhaps these crocodiles are reluctant to enter the water because they are liable to drown if further harassed.

MANAGEMENT IMPLICATIONS

We suspect that the profound acidosis caused by capture of large crocodiles may be an important factor in their mortality. With blood pH's of 6.4 to 6.6, they must surely be close to death. It would take only a little added insult to push them over the brink. After capture, crocodiles too large to be lifted into the boat are usually moved from the site by being pulled through the water. Although care is usually taken to keep the head out of water, death of the fatigued animals may result from relatively brief submergences that would otherwise be easily tolerated by animals in good condition. It is significant that the first response to fatigue is hyperventilation. Low blood pH in man results in marked increases in depth and frequency of ventilation (Guyton 1982). Perhaps the drive to breathe in exhausted animals overpowers the response to submersion that normally prevents inhalation of water.

Other techniques of capture and relocation of large crocodiles sometimes involve injecting them with gallamine triethiodide (trade name: Flaxedil), which is a blocking agent at the nerve-muscle junction (Loveridge and Blake 1972). This drug therefore relaxes the muscles and the animals are easier to handle and are less likely to damage themselves in transit. However, respiration involves voluntary muscles in reptiles, and, although we have found that gallamine does not greatly affect breathing or recovery from acidosis in small crocodiles with low acid-base disturbances, the muscles that drive respiration or close the upper respiratory tract may be critically impaired in large animals when exposed simultaneously to extreme acidosis and a relaxant. Therefore, it may be unwise to use the drug in exhausted animals. However, if administered before the animal struggles excessively, the drug would prevent the extreme acidosis. It should be possible to inject it, with a dart gun or a syringe on a pole, soon after a harpoon is securely attached to the animal to prevent it from drowning when the drug takes effect.

What treatment should be given to acidotic crocodiles? Unfortunately, almost all of our work was directed at understanding the changes occurring without intervention, but a few pilot experiments were performed which suggest that intraperitoneal injections of sodium bicarbonate tend to restore normal blood pH more quickly. Eight small crocodiles, weighing less than 1 kg, were exercised to exhaustion. During 2 h of recovery, blood pH increased an average of 0.11 units in six animals. The two others were given an injection of sodium bicarbonate at a dosage of 6.4 mmol kg^{-1} immediately after exercise and the pH increased 0.29 units in 2 h, or almost three times faster. Whether this increase was actually good for the animals is not known. There was no obvious difference in the behaviour of the injected animals, and it may just be simpler to let the animals recover by themselves on land.

We made another observation during the experiments that may relate to survival of severely acidotic animals. When we were developing the technique of catheterizing crocodiles, we initially chilled the animals by submerging them in ice until the cloacal temperature dropped to 4-6°C. These cold animals did not breathe, but it was felt that the low temperature would produce such a low metabolic rate that this would not be a problem. However, after the catheter was in place and the animals rewarmed to 27°C, they still did not breathe. There was no response from touching the eye, the pupils were dilated, and the body was limp and without any reflexes. The animals were presumed dead so the catheters were cut. A blood sample taken from one was very dark and had a pH of 6.8 and a lactate level of 27.5 mmol l^{-1}, indicating severe anoxic acidosis. However, the heart was still beating in one animal so it was decided to try artificial resuscitation via a tube inserted into the glottis. About once every 15 seconds, air was forced into the animals from our lungs and allowed to escape passively. After 5-10 min in one, and 45 min in the other, spontaneous breathing was resumed. Vital signs returned to the animals and they were returned to their tank. Over the next 4 h, blood pH returned to 7.4 and we thought that they had recovered. Unfortunately, both animals were dead the next day. Apparently considerable neurological damage was done during the period of anoxia which we estimate had lasted over 1 h. After this experience we routinely artificially ventilated the crocodiles as they warmed after surgery and no subsequent deaths occurred.

These results point to the possibility of artificially resuscitating morbid crocodiles that are not breathing or are having difficulty breathing. Crocodiles that are presumed dead may in fact revive if artificial respiration is provided soon enough. Obviously, mouth-to-mouth resuscitation is not practical in large crocodiles, but standard resuscitation apparatus might be adapted for use on them by substituting the mouthpiece for a tapered fitting capable of being inserted tightly into the animal's glottis. Alternatively, compressed air from a tank might be used to periodically fill the animal's lungs.

A great deal of effort and expense is put into relocating large crocodiles. If they are successfully relocated at a crocodile farm, they are of considerable economic importance as an attraction for tourists and as valuable breeding stock. It would therefore be worthwhile to attempt to develop a successful method of capture and resuscitation that ensures these large, rare animals survive.

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