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MASS-DEPENDENCE OF ANAEROBIC METABOLISM AND ACID-BASE DISTURBANCE DURING ACTIVITY IN THE SALT-WATER CROCODILE, *CROCODYLUS POROSUS*

BY A. F. BENNETT

School of Biological Sciences, University of California, Irvine, California 92717 U.S.A.

R. S. SEYMOUR, D. F. BRADFORD

Department of Zoology, University of Adelaide, Adelaide, S.A. 5001

AND G. J. W. WEBB

Conservation Commission of the Northern Territory, P.O. Box 38496, Winnellie, N.T. 5789, Australia

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SUMMARY

1. Lactate concentration ([lactate$^-$]), pH, P_{CO_2}, P_{O_2} and bicarbonate concentration ([HCO_3^-]) were measured in the blood of salt-water crocodiles (*Crocodylus porosus* Schneider) exhausted during field capture.

2. Body temperature after capture averaged 31·1 °C.

3. All animals underwent high levels of anaerobic metabolism and metabolic acidosis. The largest animals attained the highest blood [lactate$^-$] and lowest pH ever observed in any animal as a result of activity.

4. Peak levels of [lactate$^-$] increased with increasing body mass (slope = 9·72 mmol l^{-1} log M^{-1}; mass M in kg), indicating a greater anaerobic capacity in larger animals. Several large crocodiles had [lactate$^-$] in excess of 50 mmol l^{-1}.

5. Blood pH decreased with mass (slope = 0·163 pH units log M^{-1}) and reached 6·6 in the largest animals. One animal remained acidotic for several hours and had a minimal pH of 6·42.

6. Blood P_{CO_2} increased significantly and [HCO_3^-] decreased significantly with increasing body mass.

7. Struggling time before exhaustion was greater in larger animals, ranging from about 5 min in small (<1 kg) crocodiles to over 30 min in animals over 100 kg.

8. During recovery, mean blood [lactate$^-$] decrement after 2 h was 6·0 mmol l^{-1} and was not significantly related to mass. Proton elimination from the blood, however, was more rapid in larger animals (slope = 0·0443 μmol l^{-1} log M^{-1}).

9. The positive mass-dependence of acid-base disturbance could be related to the greater susceptibility of large crocodiles (>700 kg) to post-capture mortality.

Key words: Anaerobic capacity, pH, mass-dependence, reptile.

INTRODUCTION

Body size is related to numerous biological rate processes. Particular attention has been devoted to the scaling of different physiological factors associated with oxygen transport and consumption (see Kleiber, 1947; Heusner, 1982; Calder, 1984; Schmidt-Nielsen, 1984). In contrast, very little is known about the size-dependence of anaerobic metabolism. It has been tacitly assumed that mass-specific anaerobic capacity, the amount of energy formed anaerobically during activity to exhaustion (Bennett & Licht, 1972), is independent of body mass (Coulson, 1979; Coulson & Herbert, 1981; Coulson & Hernandez, 1983). Interspecific comparisons among reptiles support this view (Bennett, 1982); however, differences in behaviour among species create so much variability in these data that allometric trends may be obscured. The only intraspecific examination of anaerobic capacity is a study on the water snake *Nerodia sipedon* (Pough, 1978), which showed a significantly greater anaerobic capacity in larger snakes. As anaerobic metabolism is a major component of energy supply during intense activity in reptiles (Bennett, 1978, 1982), such a positive allometry of lactate formation should result in the capacity for longer or more intense periods of activity in larger animals. In fact, larger *Nerodia* were active for considerably longer periods before exhaustion than were smaller ones.

In view of the obvious behavioural consequences of differential activity capacity in differently sized animals, we undertook observations on the influence of body size on anaerobic metabolism during field capture in salt-water crocodiles (*Crocodylus porosus*). This species is ideal for an examination of size effects, as individuals range from post-hatching animals of approximately 0·1 kg to very large adults in excess of 900 kg (Greer, 1974; Webb & Messel, 1978; Montague, 1983). These crocodiles are very powerful animals, capable of violent bursts of activity, which are used in prey capture, escape or territorial disputes. Even the smallest animals are very difficult to subdue and handle. We measured blood pH and lactate concentration shortly after the struggling and violent activity associated with field capture. These crocodiles fight intensely to escape and can be secured and safely handled only after having fought to exhaustion. Before this time, these crocodiles are simply not manageable. We consider that they attained the limits of their activity capacity during capture and that our measurements accordingly represent the highest levels of activity-induced anaerobic metabolism of which they are capable.

The results of the present study may have management application. Within the Northern Territory of Australia, *Crocodylus porosus* in populated areas are frequently caught and relocated in the interest of public safety. In four instances, very large crocodiles (700–800 kg) have died during or immediately after capture, yet no obvious cause of death was detected. Smaller animals (<200 kg) are regularly caught using the same techniques with virtually no mortality. Fish often die after being caught (von Buddenbrock, 1938; Black, 1958; Jonas, Sehdev & Tomlinson, 1962; Beamish, 1966; Wood, Turner & Graham, 1983) and this is

associated with anaerobic metabolism and acid-base disturbance during and after activity. If these factors are involved in mortality and are positively allometric in crocodiles, they may be involved in the size-differential mortality observed for this species.

MATERIAL AND METHODS

Twenty-six salt-water crocodiles (*Crocodylus porosus*), ranging in body mass from 0·4 to 180 kg, were captured in the Adelaide River, approximately 60 km east of Darwin, in the Northern Territory of Australia during November, 1983. They were collected under Permit No. SL 41/83 issued by the Conservation Commission of the Northern Territory. All animals were subsequently released at their site of capture, and were active, alert and in apparent good health when released.

Crocodiles were captured from a boat by an experienced team of the Conservation Commission staff. A skin-penetrating harpoon connected to a rope (Webb & Messel, 1977) was used to capture animals larger than 1 kg. This method rarely results in tissue damage beyond a small skin puncture. Escape attempts after harpooning consisted of bouts of violent thrashing, rolling and swimming, mostly while submerged. Eventually the animals stopped struggling and were pulled to the surface with little resistance. They were then secured by tying their jaws together with cord. The time between harpooning and securing the animals was measured, and notes taken on the intensity and duration of the struggle. Secured animals were returned to a field camp on the river bank. A blood sample (approximately 2 ml) was taken by cardiac puncture with a heparinized syringe (McDonald, 1976). Cloacal temperature, measured with a quick-registering thermometer, averaged 31·1 °C($\pm$0·23 S.E., N=18, range=28·8–32·2 °C). Head and snout-vent lengths were measured subsequently. Crocodiles were then tethered by a snout-rope and their eyes were covered with a cloth bag. To monitor recovery, additional blood samples were taken 2 h after the first sample.

Eight smaller (0·4–0·7 kg) animals were captured by hand or noose and exercised separately so that we could be assured that they were totally exhausted prior to blood sampling. They were kept in wet cloth bags for approximately 8 h after capture. Cords were tied about the mouth and the pelvic regions, and each animal was exercised in a pond. These crocodiles were permitted to attempt to escape, swim and dive until they became exhausted (i.e. lost the righting response). Blood samples were taken by cardiac puncture 10 min after cessation of activity and again after 2 h of recovery as above. Mean body temperature was not significantly different from that of the former group ($\bar{x}$=30·9 °C$\pm$0·17 S.E., N=8, range=30·2–31·6 °C).

Blood samples were analysed in duplicate for pH, P_{CO_2} and P_{O_2} immediately after collection. A portion of each sample was deproteinized in 0·6 mol l^{-1} perchloric acid (0·100 ml of blood in 0·200 ml of acid) and stored directly for about 2 weeks before analysis of lactate content. Blood gases and pH were measured on a Radiometer model BMS Mk 2 blood microsystem connected to a model PHM 72

acid-base analyser. In the field, electricity was obtained from a gasoline-powered generator. The temperature of the electrodes was maintained at 31·1 °C (±0·30 S.E., range = 29·4–32·0 °C). Electrodes were calibrated before and after each sample reading with a Radiometer model GMA 2 gas mixing apparatus and Radiometer precision buffers. Bicarbonate concentration in true plasma was calculated from pH and P_{CO_2} according to the Henderson-Hasselbalch equation and constants derived from Severinghaus (see Seymour, Bennett & Bradford, 1985).

Lactate concentrations were measured on deproteinized blood samples with Boehringer-Mannheim enzymatic test kits (No. 149993) and a Varian model SuperScan 3 spectrophotometer. The samples were diluted with additional perchloric acid so that their concentrations were encompassed within the range of simultaneously-measured lactate standards (Boehringer-Mannheim No. 125440).

The body mass of each animal was estimated from its snout-vent length according to equations 122 and 123 of Webb & Messel (1978), which were derived for this species on specimens from northern Australia.

Either pH or $[H^+]$ may equally well be used in statistical analysis of acid-base data (Boutilier & Shelton, 1980). Linear, logarithmic and power (log-log) models were fitted to each data set relating concentrations of lactate $[lactate^-]$, protons ($[H^+]$) and plasma bicarbonate ($[HCO_3^-]$). Logarithmic and power models invariably had higher correlation coefficients than did linear models. Consequently logarithmic models ($y = a + b \log x$) are used to report these data as functions of $\log_{10}$ body mass (kg), and statistics are calculated on these transformed data. The coefficients and exponents of the power regression ($y = ax^b$) are also reported to facilitate allometric comparisons.

RESULTS

Crocodiles were judged exhausted when they ceased struggling and could be brought into the boat and secured without further efforts to escape; such animals made only feeble attempts to right themselves when placed on their backs. Smaller crocodiles became exhausted more rapidly than did larger ones (Fig. 1). Animals less than 1·0 kg struggled for only about 5 min, with the most violent escape attempts occurring during the first 1·5 min. After this activity, they lost most of their muscle tonus and were limp. Intermediate-sized animals (10–100 kg) usually fought for 10–20 min, and the largest animals (over 100 kg) sometimes required more than 30 min to subdue.

Blood samples were taken an average of 11·5 min after crocodiles were subdued and loaded into the boat (range: 4–20 min). Maximum changes in $[lactate^-]$, pH, P_{CO_2} and $[HCO_3^-]$ are reasonably constant in this species during a period of 5–30 min following bouts of exhaustive activity (Seymour *et al.* 1985). Therefore we are confident that the initial blood samples were not greatly influenced by recovery.

Analyses for mass-dependence of $[lactate^-]$, $[H^+]$, P_{CO_2} and $[HCO_3^-]$ were

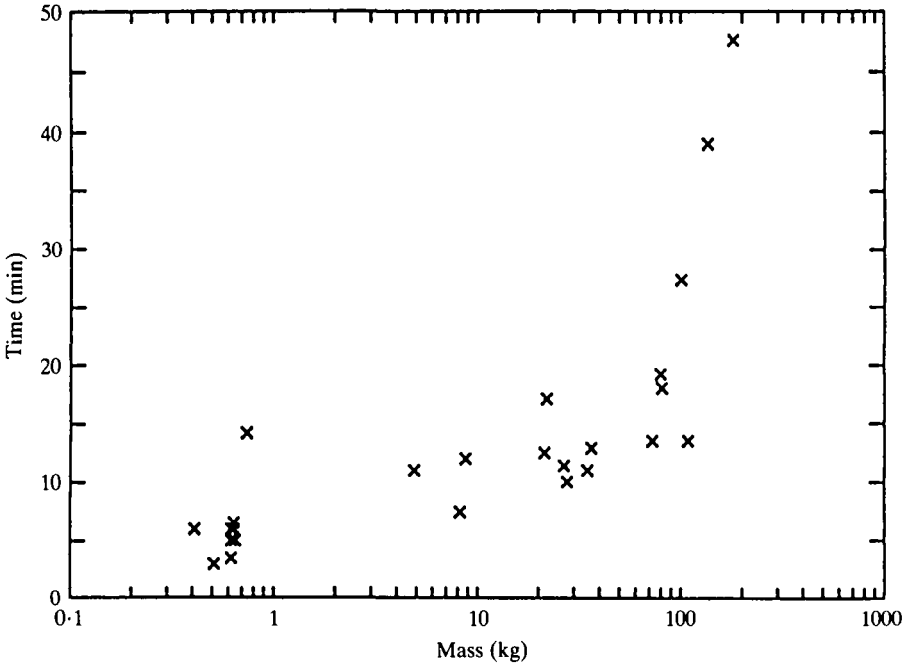

Fig. 1. Time to exhaustion in struggling *Crocodylus porosus*.

carried out separately for presumed arterial and venous bloods. P_{O_2} was used to determine which type of blood was obtained. The distribution of P_{O_2} values was unrelated to mass and was clearly bimodal: one group averaged 99 Torr (range: 79–122 Torr) and the other, 42 Torr (range: 22–60 Torr). Differences between arterial and venous blood samples were tested by multiple regression analysis with dummy variables (Kleinbaum & Kupper, 1978), which tests for differences in both slopes and elevations of the two data sets. There were no significant differences in arterial and venous samples in either [lactate$^-$] (slope, $P=0{\cdot}54$; elevation, $P=0{\cdot}61$) or [H^+] (slope, $P=0{\cdot}62$; elevation, $P=0{\cdot}20$). Therefore mass-dependent regressions were calculated for combined arterial and venous samples (Fig. 2A, Table 1). Blood lactate increased and pH decreased significantly with increasing body mass (Table 1, Fig. 2A,B). The largest animal (180 kg) had the highest [lactate$^-$] (57·5 mmol l^{-1}) and the lowest pH (6·59). Capture time (to exhaustion) was significantly related to lactate concentration according to the relationship: time $=0{\cdot}639$[lactate$^-$] $-10{\cdot}92$ ($N=24$, $r^2=0{\cdot}40$, $P<0{\cdot}01$, $s^2_{y.x}=72{\cdot}35$). The analysis confirmed that the P_{CO_2} was significantly higher in the venous samples, but there was no difference in slope of arterial or venous P_{CO_2} on log mass (slope, $P=0{\cdot}61$; elevation, $P=0{\cdot}004$). P_{CO_2} in both arterial and venous blood samples increased significantly with body mass (Fig. 2C, Table 1).

Mass-dependence of plasma [HCO_3^-] was analysed on values adjusted to a common P_{CO_2} value to eliminate variability resulting from different P_{CO_2} levels in the samples. The data were corrected to the standard P_{CO_2} of resting crocodiles

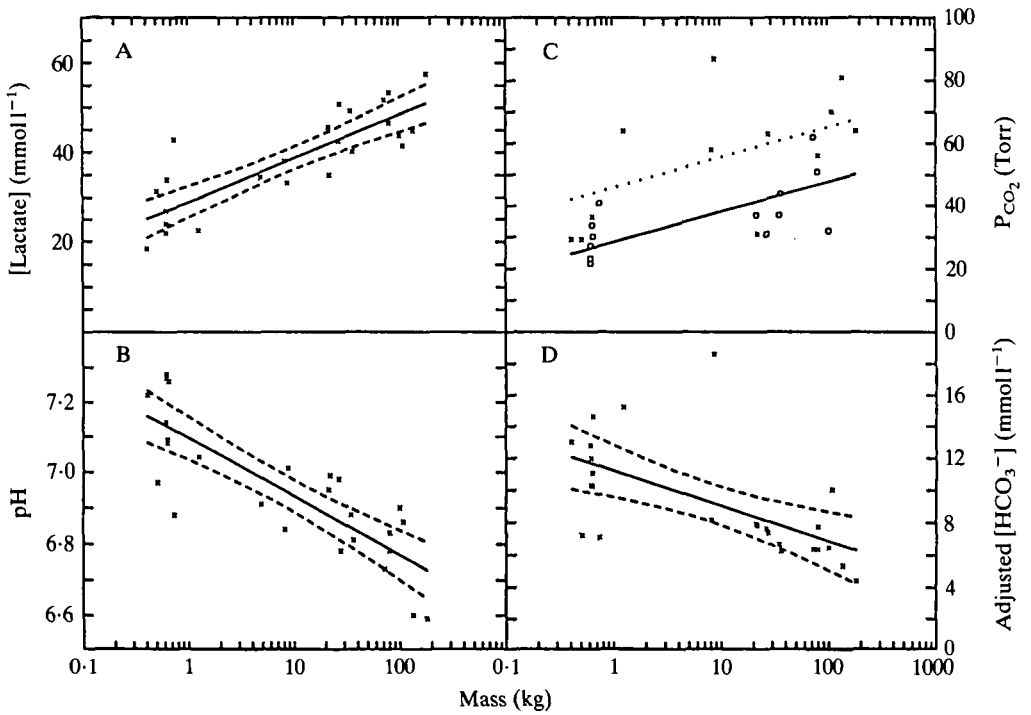

Fig. 2. Lactate concentration (A), pH (B), P_{CO_2} (C) and adjusted bicarbonate concentration (D) in the blood of exhausted *Crocodylus porosus*, captured in the field. P_{CO_2} values are shown for arterial (x) and venous (□) blood. Semilogarithmic regression lines and the 95 % confidence limits of the regressions in A, B and D. In C, regression lines are shown for arterial (dotted line) and venous (solid line) blood, and assume a common slope (ANCOVA, Table 1). Regression equations and statistics are given in Table 1.

(32·8 Torr; Seymour *et al.* 1985). This adjustment was done on a $[HCO_3^-]$-pH diagram by finding, with an iterative programme, the intersection of the P_{CO_2}= 32·8 Torr isopleth and the line which includes the uncorrected data pair. This line has a slope of $-12{\cdot}16\,\text{mmol}\,HCO_3^-\,l^{-1}\,pH^{-1}$, which is the mean *in vivo* buffer value of *C. porosus* (Seymour *et al.* 1985). Adjusted $[HCO_3^-]$ significantly decreased with increasing body mass (Fig. 2D, Table 1).

During the 2-h recovery period, blood [lactate$^-$] decreased and pH increased. The [lactate$^-$] decrement was independent of body mass ($r^2=0{\cdot}05$, $P=0{\cdot}59$); the mean decrement was small ($6{\cdot}0\,\text{mmol}\,l^{-1}$) but significant (S.E.$=2{\cdot}0$, $N=15$, $P<0{\cdot}01$). However, the decrease in $[H^+]$ was mass-dependent according to the relationship: $\Delta[H^+]=0{\cdot}0832+0{\cdot}0443\log M$ ($N=26$, $r^2=0{\cdot}62$, $P<0{\cdot}001$, $s^2_{y.x}=0{\cdot}00125$). Large animals eliminated protons more rapidly than did small animals.

Most animals had partially recovered from acid-base disturbance after 2 h. However, one animal (no. 4, 32 kg) initially developed greater acidosis and its recovery was followed for a longer period. Data on recovery for this animal were excluded from the previous analysis of recovery. Immediately after capture, its blood pH was 6·87 and blood [lactate$^-$] was $49{\cdot}1\,\text{mmol}\,l^{-1}$. Two hours later, the

Table 1. *Mass-dependence of blood properties in exhausted* Crocodylus porosus

		Semilogarithmic regression					Power regression	
Equation	Units	N	r^2	P	$s^2_{y.x}$	S.E.$_b$	Equation	S.E.$_b$
$[lactate^-] = 28{\cdot}91 + 9{\cdot}72 \log M$	mmol l^{-1}	25	0·71	<0·001	36·755	1·309	$[lactate^-] = 28{\cdot}0M^{0{\cdot}121}$	0·0167
$pH = 7{\cdot}095 - 0{\cdot}163 \log M$	pH units	26	0·68	<0·001	0·0121	0·0231	$pH = 7{\cdot}094M^{-0{\cdot}0101}$	0·0014
$[H^+] = 0{\cdot}0832 + 0{\cdot}0443 \log M$	μmol l^{-1}	26	0·62	<0·001	0·00125	0·0071	$[H^+] = 0{\cdot}0802M^{0{\cdot}163}$	0·0231
$P_{CO_2} = 28{\cdot}51 + 9{\cdot}63 \log M$ (arterial)	Torr	25	0·54	<0·005	173·94	2·788	$P_{CO_2} = 29{\cdot}04M^{0{\cdot}0976}$ (arterial)	
$P_{CO_2} = 45{\cdot}96 + 9{\cdot}63 \log M$ (venous)							$P_{CO_2} = 41{\cdot}49M^{0{\cdot}0976}$ (venous)	0·02522
$[HCO_3^-]_{adj} = 11{\cdot}20 - 2{\cdot}175 \log M$	mmol l^{-1}	25	0·36	<0·01	8·109	0·5983	$[HCO_3^-]_{adj} = 10{\cdot}87M^{-0{\cdot}063}$	0·0268

Statistics quoted are: N = number of animals; r^2 = square of correlation coefficient; P = probability level; $s^2_{y.x}$ = residual mean square; S.E.$_b$ = standard error of slope (semilogarithmic regression) or exponent (power regression). Analysis of convariance showed that regressions for arterial and venous P_{CO_2} did not differ in slope ($P = 0{\cdot}61$), but differed in elevation ($P < 0{\cdot}005$). Therefore P_{CO_2} equations assume the common slope.

pH dropped to 6·42 and [lactate$^-$] to 47·7 mmol l^{-1}. At 4 h, the pH was still below 6·5 and [lactate$^-$] was 69·1 mmol l^{-1}. During this period, the crocodile was completely unresponsive and maintained a regular pattern of deep ventilation, which was uncharacteristic of other animals. In spite of this prolonged and profound acid-base disturbance, the animal slowly recovered and was very active and aggressive upon its release about 29 h after capture. A more complete picture of this animal's recovery is presented elsewhere (Seymour *et al.* 1985).

DISCUSSION

Anaerobic capacity, the total amount of lactate produced during activity to exhaustion (Bennett & Licht, 1972), is properly measured by whole-body lactate analysis, which was impractical here. However, peak values of blood lactate after activity are a reasonable substitute to indicate general levels of anaerobic metabolism (Bennett, 1982). These crocodiles clearly undergo very high levels of anaerobiosis during struggling to exhaustion. Several of the larger animals had blood [lactate$^-$] exceeding 50 mmol l^{-1}, which are the highest values ever reported for activity-induced anaerobiosis for any animal. Blood [lactate$^-$] values of 22 and 47 mmol l^{-1} were reported for two *Crocodylus acutus* (Dill & Edwards, 1931), but these were moribund animals upon dissection. Average [lactate$^-$] values of approximately 20 mmol l^{-1} were measured after activity in *Alligator mississippiensis* (Coulson & Hernandez, 1979). Levels of [lactate$^-$] in *C. porosus* exceed those reported for *A. mississippiensis* (45 mmol l^{-1}, Andersen, 1961) or iguanas (*Iguana*, 36 mmol l^{-1}, Moberly, 1968; *Amblyrhynchus*, 33 mmol l^{-1}, Bartholomew, Bennett & Dawson, 1976) during struggling dives lasting 1 h or more. They even approach maximum levels reported for turtles subjected to diving or nitrogen-breathing for 1 day (109 mmol l^{-1}, Johlin & Moreland, 1933; 65 mmol l^{-1}, Robin, Vester, Murdaugh & Millen, 1964; 41 mmol l^{-1}, Altman & Robin, 1969; 37 mmol l^{-1}, Penny, 1974) or longer (62 mmol l^{-1} after 67 days, Gatten, 1981; 200 mmol l^{-1} after 180 days, Ultsch & Jackson, 1982). The values for *C. porosus* are all the more remarkable as they are attained during comparatively short periods of activity.

Anaerobic capacity (*sensu* Bennett & Licht, 1972) is mass-dependent in these crocodiles. The larger animals have substantially greater levels of lactate formation than do smaller ones, and these are accompanied by greater levels of acid-base disturbance. This greater anaerobic capacity indicates a larger anaerobic contribution in support of struggling to exhaustion in larger crocodiles. Anaerobic capacity is also positively mass-dependent in the water snake *Nerodia sipedon* (Pough, 1978), the only other reptilian species in which the size-dependence of anaerobiosis has been examined. With data on only blood lactate concentration and pH, it is not possible to determine rates of lactate formation (maximal rate = anaerobic scope, Bennett & Licht, 1972). Consequently, we do not know whether anaerobic scope is allometrically size-dependent in these crocodiles. It is also impossible on the basis of the present observations to know the causal factors

responsible for limiting lactate production. The basis of its differential size dependence is consequently undetermined. Such factors as size differential functional capacities of glycolytic enzymes, differential sensitivity of enzymatic function to intracellular pH, or differential product flux out of the skeletal muscle cells might be responsible. It is known, for instance, that the activities of skeletal muscle enzymes involved in lactate formation are positively and allometrically scaled with body mass among different species of fish (Somero & Childress, 1980). However, this relationship would suggest a greater rate of lactate synthesis in larger fish but not necessarily a greater anaerobic capacity. Another factor leading to higher anaerobic capacity in larger animals might be a greater proportional distribution of skeletal muscle in larger animals. Mass increases as the 3·24 power of snout-vent length in *C. porosus* (s.v. $>0{\cdot}4$ m, equation 122, Webb & Messel, 1978), a value greater than a geometric proportionality of 3·00, possibly indicating greater muscularity in larger animals. Interpretation of the present data is further complicated by the size-dependence of time to exhaustion (Fig. 1). What is clear, however, is that anaerobic capacity is far greater in larger crocodiles than in smaller ones.

Theoretical discussions of reptilian anaerobiosis (Coulson, 1979; Coulson & Herbert, 1981; Coulson & Hernandez, 1983) have a central assumption that total anaerobic capacity scales directly with body mass, that is, the mass-specific capacity to form lactate is independent of mass. It has been stated that this is the 'great equalizer' in activity capacity (Coulson, 1979), although no empirical data have been presented. Our results and those of Pough (1978) cast doubts on the validity of this assumption and consequently on arguments in which it plays an important role. It has also been assumed that recovery from exhaustion is slower in larger reptiles (Coulson, 1979). Our data demonstrate that the rate of lactate elimination, measured as mmol lactate $l^{-1}\,h^{-1}$, is independent of body size and that the rate of proton elimination is, in fact, faster in larger animals.

Lactate production is accompanied by severe acidosis, which is positively mass-dependent (Fig. 2B). Our largest crocodile had the lowest pH (6·59) ever reported for any animal as a result of activity. Comparable levels have been obtained in *A. mississippiensis* following epinephrine injections (6·54, Hernandez & Coulson, 1958; Coulson & Hernandez, 1983) and in turtles during forced dives of 1 day or longer (6·53, Robin *et al.* 1964). The level of acidosis reported for crocodile no. 4 ($pH = 6{\cdot}42$), accompanied by subsequent recovery, is to our knowledge unprecedented for any animal. This severe acidosis forces the carbonic acid reaction towards the production of more dissolved CO_2, thereby increasing P_{CO_2} and decreasing $[HCO_3^-]$ (Fig. 2C,D). Apparently in the early stages of recovery, ventilation is insufficient to reduce P_{CO_2} to normal levels, even in the arterial blood. As recovery progresses, however, respiratory compensation reduces P_{CO_2} to normal or below normal levels as normal pH is restored (Seymour *et al.* 1985).

The allometric size-dependence of anaerobic metabolism and acidosis in *C. porosus* could provide an explanation for differential mortality of large animals observed during field capture, although additional studies on very large crocodiles

are needed. The greatest anaerobic capacity and resulting acid-base disturbance may put the largest animals perilously close to their physiological limits. It has been reported that 1 in 10 alligators died after epinephrine injections that resulted in blood pH levels below 6·8 or blood lactate levels above 20 mmol l^{-1} (Hernandez & Coulson, 1958). Although none of our crocodiles died, the most acidotic animal (no. 4) was immobile and unresponsive and could have been expected to drown if it had been in the water. Large *C. porosus* may weigh over 1000 kg (Webb & Messel, 1978; Montague, 1983) and these specimens may be at even greater risk if size-dependent trends for anaerobic metabolism extend over this mass range. It would seem prudent that considerable care be taken after large crocodilians have been caught using a method inducing exhaustion, and that animals be given many hours to recover.

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