

SHORT COMMUNICATION

ALLOMETRY OF LUNG VOLUME DURING VOLUNTARY
SUBMERGENCE IN THE SALTWATER CROCODILE
CROCODYLUS POROSUS

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During submergence, the volume of gas stored in the lungs of a reptilian diver functions not only as an O₂ store and CO₂ sink (Lenfant, Johansen, Petersen & Schmidt-Nielsen, 1970; Burggren & Shelton, 1979; Seymour, 1982) but can also be adjusted to achieve the desired buoyant state. Lung volume during voluntary submergence will often be a compromise between these two basic functions and should also increase with body mass. The relationship between submergence lung volume and body mass will depend on how tissue density and specific gravity selected by a submerged animal vary with body mass. Previous studies have determined the relationship between lung volume and body mass in reptiles from maximally inflated lungs of dead specimens and have calculated an interspecific scaling factor of 0.75 (Tenney & Tenney, 1970; Wood & Lenfant, 1976). This suggested that the lung volume of a reptile may scale in accordance with mass-specific aerobic metabolism which also has a scaling factor close to 0.75 (Tenney & Tenney, 1970). Although equations generated from interspecific data from maximally inflated lungs are useful for describing certain morphological characteristics of reptilian lungs (Perry, 1983), they are probably inappropriate for determining the lung volume selected by a conscious, undisturbed reptile while voluntarily submerged.

With the possible exception of studies of the ontogeny of buoyancy control in *Caretta caretta* (Milsom, 1974, 1975), the relationship between submerged lung volume and voluntary body mass has not been reported previously in the literature. As pulmonary oxygen often comprises a large proportion of the oxygen store of submerged reptiles (Seymour, 1982), the constraints placed on lung volume by buoyancy requirements and body mass will probably have a major influence on aerobic endurance and diving behaviour. The purpose of this study is to determine the relationship between lung volume and body mass in the saltwater crocodile, *Crocodylus porosus* during voluntary undisturbed submergence.

Lung volume at submergence was measured by whole body plethysmography for 24 juvenile *C. porosus* (mean body mass = 1301 g ± 211 g S.E.M.; range 271–3762 g). Water temperatures throughout experiments were maintained between

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23 and 25°C. The plethysmograph consisted of Perspex tubing (14.5 cm internal diameter; 80 cm in length and 0.4 cm thick) with a tight-fitting Perspex lid (1 cm) that could be clipped into place underwater following insertion of a crocodile. Two rigid tubes were inserted into one end of the plethysmograph to monitor pressure and to inject water. A Statham pressure transducer (model P23BC) was connected to a water-filled inlet tube to monitor water pressures inside the plethysmograph. The pressure transducer was connected to a low-level preamplifier (Grass instrument model 7P1E) and the output recorded on chart paper. Pressure transducers were calibrated against water columns of known height. A plethysmograph calibration curve was prepared by introducing known volumes of air into the chamber and recording the rise in pressure induced by injecting 2 ml of water into the plethysmograph.

Crocodiles were placed in a tank (120 cm × 60 cm × 80 cm) filled to a depth of 35 cm with fresh water, and were allowed to dive freely and undisturbed. Immediately following voluntary submergence, a crocodile was placed inside the plethysmograph and the lid secured without the loss of pulmonary gas. The whole apparatus was then removed from the tank. A previously calibrated Statham pressure transducer (model P23BC) was connected to one inlet and 2 ml of water was injected into the other inlet. It was assumed that the lungs were the only compressible portion of the crocodile and that compliance of crocodiles was independent of body mass. The pressure rise following injection of water was converted into lung volume (ml BTPS at 25°C) by comparing these results to the plethysmograph calibration curve. For each crocodile, an average lung volume was estimated from at least six determinations taken from separate voluntary dives. To reduce errors in lung volume estimates due to lung shrinkage during submergence, the whole procedure was completed within 1 min of placing the crocodile into the plethysmograph.

Lung volumes of submerged crocodiles increased logarithmically with body mass (Fig. 1). The best fit least squares regression relating lung volume (VL ml BTPS) to body mass (M, g) is given by

$$\log VL = -1.048 + 0.906 \log M \quad (N = 24; r^2 = 0.96; s_b = 0.004).$$

The allometric exponent of 0.906 ± 0.008 (mean + 95% confidence limits) indicates that mass-specific lung volumes decreased with body mass from 52.8 ml kg^{-1} at 271 g to 41.3 ml kg^{-1} at the largest body mass of 3763 g.

Submerged lung volumes of *C. porosus* are approximately half the maximum lung volume reported for reptiles over the same body mass range (Tenney & Tenney, 1970; Wood & Lenfant, 1976). These low values are probably not due to intrinsic differences between lung morphology of *C. porosus* and other reptiles (Perry, 1983) but to buoyancy restrictions. Freely diving *C. porosus* are usually negatively buoyant, with an average specific gravity of 1.028 (Kirshner, 1985). To maintain this specific gravity, lung volume must be reduced considerably prior to submergence.

Mass-specific submergence lung volumes declined from 52.8 to 41.3 ml kg^{-1} in *C. porosus* over the range of body size examined and lie at the lower end of the range reported for submerged lung volumes of reptiles. The sea snake, *Pelamis platurus*, is

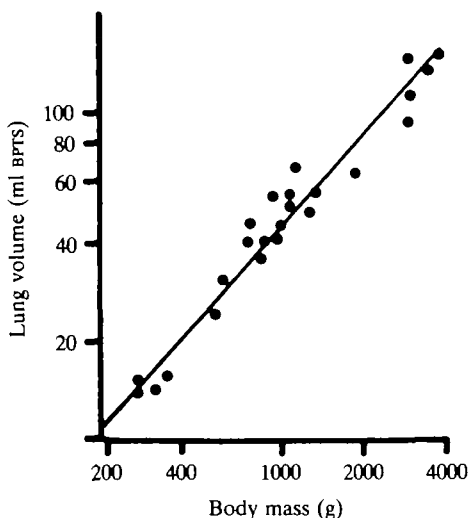


Fig. 1. The relationship between submerged lung volume ($\log V_L$) and body mass ($\log M$) in 24 juvenile *Crocodylus porosus*. The line represents the best fit least squares regression, see text for equation.

usually positively buoyant during submergence and dives with a mean lung volume of 88.2 ml kg^{-1} (Graham, Gee & Robinson, 1975). Negative buoyancy is achieved as the lungs compress during descent. The freshwater turtle, *Pseudemys* (now *Chrysemys*) *scripta*, has a submerged lung volume of between 100 and 120 ml kg^{-1} while resting on the bottom, giving it a specific gravity range of 1.021–1.040 (Jackson, 1969, 1971). Another freshwater chelonian, *Chelys fimbriata*, has a mean submerged lung volume of 81 ml kg^{-1} (Lenfant *et al.* 1970). Using similar methods for calculating lung volumes as in this study, Andersen (1961) reported lung volumes between 76 and 100 ml kg^{-1} in two juvenile *Alligator mississippiensis*. However, he may have overestimated submerged lung volume because alligators were not permitted to dive freely before being placed in the plethysmograph and may not have adjusted lung volumes to achieve neutral or negative buoyancy. The low mass-specific lung volume of *C. porosus* compared to other reptiles is probably due to several factors including different buoyancy requirements during submergence and differences in body density, particularly in comparison with chelonians (Kirshner, 1985).

A major finding here was that the allometric exponent of 0.906 ± 0.008 for submerged lung volume was significantly larger than the exponent of 0.75 reported for maximally inflated lungs in reptiles (t -test; $t = 39$; $df = 22$; $P < 0.01$) (Tenney & Tenney, 1970; Wood & Lenfant, 1976). It has been previously interpreted that a scaling factor of 0.75 for lung volume is in accordance with the decreased mass-specific energy requirements of larger reptiles (Tenney & Tenney, 1970). An allometric exponent of 0.906 indicates, however, that total mass-specific oxygen stores may have a scaling factor greater than resting aerobic metabolism. Assuming that the allometric exponent for the oxygen stored in the tissue and blood lies

between 0.75 and 1, then total oxygen store of a submerged *C. porosus* would have allometric exponents within the range 0.85–0.95. Resting metabolic rates of *C. porosus* are proportional to $M^{0.70}$ (Wright, 1986). Consequently, the duration of quiet aerobic dives should increase with body size with allometric exponents between 0.15 and 0.25. Aerobic dive duration of a 4-kg crocodile would be approximately 150–190 % longer than for a 0.3-kg animal. If the same relationship were to hold for extremely large crocodiles (>1000 kg), then these animals may be able to remain submerged for long periods (90–120 min) and still remain aerobic. There is evidence to support this idea as Cott (1961) reported that maximal submergence time increased with body size in the Nile crocodile, *Crocodylus niloticus*.

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REFERENCES

- ANDERSEN, H. T. (1961). Physiological adjustments to prolonged diving in the American Alligator *Alligator mississippiensis*. *Acta physiol. scand.* **53**, 23–45.
- BURGGREN, W. W. & SHELTON, G. (1979). Gas exchange and transport during intermittent breathing in chelonian reptiles. *J. exp. Biol.* **82**, 75–92.
- COTT, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29**, 211–356.
- GRAHAM, J. B., GEE, J. H. & ROBINSON, F. S. (1975). Hydrostatic and gas exchange functions of the lung of the sea snake *Pelamis platurus*. *Comp. Biochem. Physiol.* **50A**, 477–482.
- JACKSON, D. C. (1969). Buoyancy control in the freshwater turtle, *Pseudemys scripta elegans*. *Science* **166**, 1649–1651.
- JACKSON, D. C. (1971). Mechanical basis for lung volume variability in the turtle *Pseudemys scripta elegans*. *Am. J. Physiol.* **220**, 754–758.
- KIRSHNER, D. (1985). Buoyancy control in the Estuarine Crocodile, *Crocodylus porosus* Schnieder. Unpublished PhD thesis, University of Sydney. 165 pp.
- LENFANT, C., JOHANSEN, K., PETERSEN, J. A. & SCHMIDT-NIELSEN, K. (1970). Respiration in the fresh water turtle, *Chelys fimbriata*. *Respir. Physiol.* **8**, 261–275.
- MILSOM, W. K. (1974). Buoyancy control in the Atlantic loggerhead turtle, *Caretta caretta caretta* (Linne). Unpublished M.Sc. thesis, University of Washington, Seattle Washington. 117 pp.
- MILSOM, W. K. (1975). Development of bouyancy control in juvenile Atlantic loggerhead turtles, *Caretta caretta*. *Copeia* **1975**, 758–762.
- PERRY, S. F. (1983). Reptilian lungs. Functional anatomy and evolution. *Adv. Anat. Embryol. Cell Biol.* **79**, 1–81.
- SEYMOUR, R. S. (1982). Physiological adaptations to aquatic life. In *Biology of the Reptilia*, vol. 13 (ed. C. Gans & F. H. Pough), pp. 1–51. New York: Academic Press.
- TENNEY, S. M. & TENNEY, J. B. (1970). Quantitative morphology of cold blooded lungs: Amphibia and Reptilia. *Respir. Physiol.* **9**, 197–215.
- WOOD, S. C. & LENFANT, C. J. M. (1976). Respiration: mechanics, control and gas exchange. In *Biology of the Reptilia*, vol. 5 (ed. C. Gans & W. R. Dawson), pp. 225–274. New York: Academic Press.
- WRIGHT, J. C. (1986). Effects of body mass, temperature and activity on aerobic and anaerobic metabolism in the juvenile crocodile, *Crocodylus porosus*. *Physiol. Zool.* **59**, 505–513.