

# PUBLISHED VERSION

C. M. Gienger, Matthew L. Brien, Christopher R. Tracy, S. Charlie Manolis, Grahame J. W. Webb, Roger S. Seymour, Keith A. Christian

**Ontogenetic comparisons of standard metabolism in three species of crocodylians**

PLoS ONE, 2017; 12(2):e0171082-1-e0171082-7

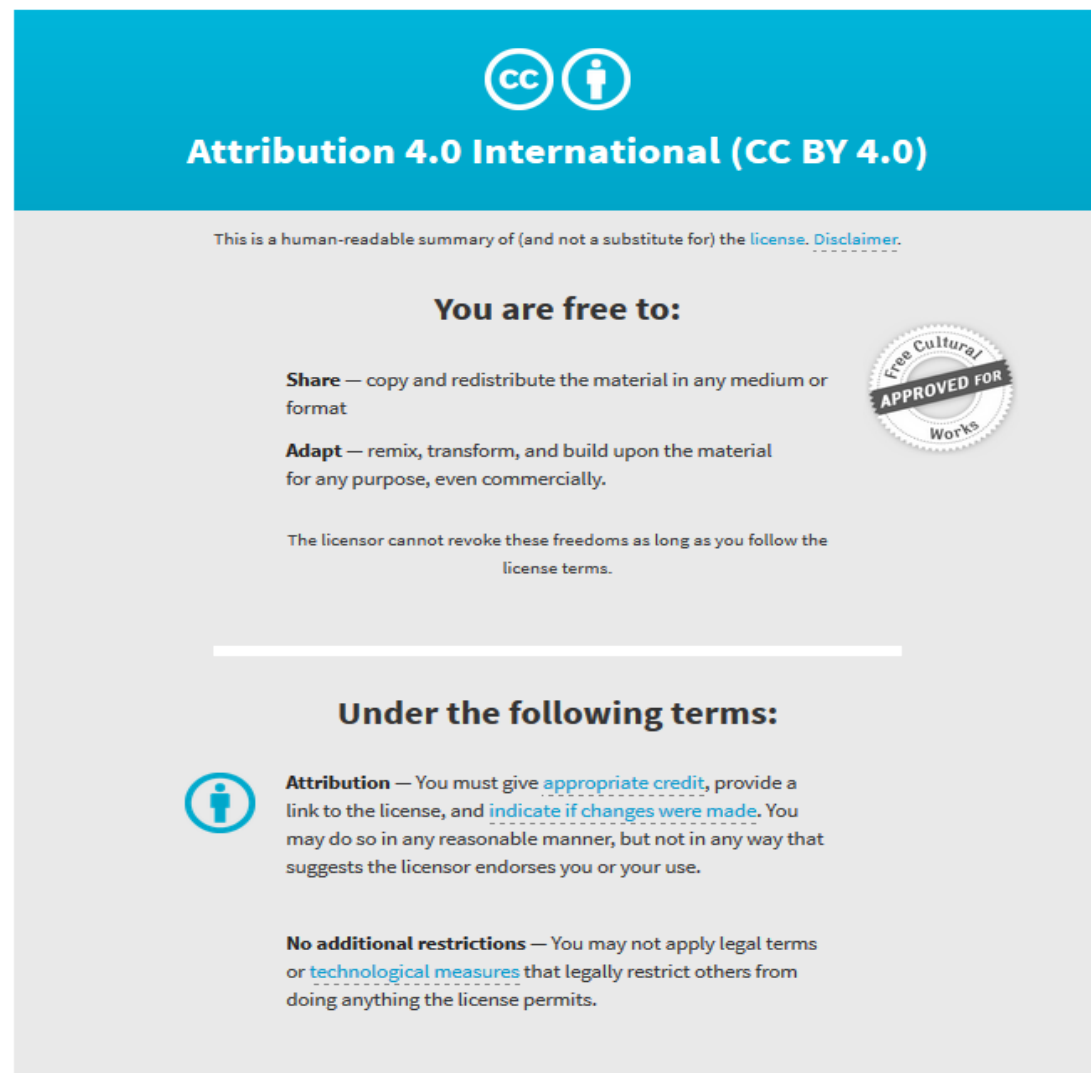
Copyright: © 2017 Gienger et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Originally published at:

<http://doi.org/10.1371/journal.pone.0171082>

## PERMISSIONS

<http://creativecommons.org/licenses/by/4.0/>



The graphic features a blue header with the CC BY 4.0 logo and the text "Attribution 4.0 International (CC BY 4.0)". Below this is a disclaimer: "This is a human-readable summary of (and not a substitute for) the [license](#). [Disclaimer](#)." The main content is divided into two sections: "You are free to:" and "Under the following terms:". The "You are free to:" section lists "Share" (copy and redistribute) and "Adapt" (remix, transform, and build upon), with a "Free Cultural Works APPROVED FOR" seal. The "Under the following terms:" section lists "Attribution" (give credit, link to license, indicate changes) and "No additional restrictions" (no legal terms or technological measures).

**Attribution 4.0 International (CC BY 4.0)**

This is a human-readable summary of (and not a substitute for) the [license](#). [Disclaimer](#).

**You are free to:**

**Share** — copy and redistribute the material in any medium or format

**Adapt** — remix, transform, and build upon the material for any purpose, even commercially.

The licensor cannot revoke these freedoms as long as you follow the [license terms](#).

**Under the following terms:**

**Attribution** — You must give [appropriate credit](#), provide a link to the license, and [indicate if changes were made](#). You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use.

**No additional restrictions** — You may not apply legal terms or [technological measures](#) that legally restrict others from doing anything the license permits.

28 June 2017

<http://hdl.handle.net/2440/104971>

RESEARCH ARTICLE

# Ontogenetic comparisons of standard metabolism in three species of crocodilians

C. M. Gienger<sup>1#a\*</sup>, Matthew L. Brien<sup>1,2#b</sup>, Christopher R. Tracy<sup>1#c</sup>, S. Charlie Manolis<sup>2</sup>, Grahame J. W. Webb<sup>1,2</sup>, Roger S. Seymour<sup>3</sup>, Keith A. Christian<sup>1</sup>

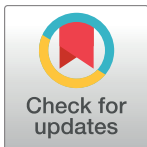
**1** Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, Australia, **2** Wildlife Management International and Crocodylus Park, Berrimah, Northern Territory, Australia, **3** School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia, Australia

#a Current address: Department of Biology and Center of Excellence for Field Biology, Austin Peay State University, Clarksville, Tennessee, United States of America

#b Current address: Department of Environment and Heritage Protection, Queensland Government, Cairns, Queensland, Australia

#c Current address: Department of Biological Science, California State University, Fullerton, California, United States of America

\* [giengerc@apsu.edu](mailto:giengerc@apsu.edu)



**OPEN ACCESS**

**Citation:** Gienger CM, Brien ML, Tracy CR, Manolis SC, Webb GJW, Seymour RS, et al. (2017) Ontogenetic comparisons of standard metabolism in three species of crocodilians. PLoS ONE 12(2): e0171082. doi:10.1371/journal.pone.0171082

**Editor:** Timothy Darren Clark, University of Tasmania, AUSTRALIA

**Received:** August 1, 2016

**Accepted:** January 16, 2017

**Published:** February 9, 2017

**Copyright:** © 2017 Gienger et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** Data are available from Figshare (DOI: [10.6084/m9.figshare.4585351](https://doi.org/10.6084/m9.figshare.4585351)).

**Funding:** Support was provided by the Australian Research Council ([www.arc.gov.au](http://www.arc.gov.au)); Linkage Grant LP0882478), the Rural Industries Research and Development Corporation ([www.rirdc.gov.au](http://www.rirdc.gov.au)); Project PRJ-000660), the Northern Territory Research and Innovation Fund, and Wildlife Management International ([www.wmi.com.au](http://www.wmi.com.au)).

**Competing interests:** The authors have declared that no competing interests exist.

## Abstract

Due in part to their large size, aggressive temperament, and difficulty in handling, there are few physiological studies of adult crocodilians in the literature. As a result, studies comparing individuals across an ontogenetic series and comparisons among species are also lacking. We addressed this gap in knowledge by measuring standard metabolic rates (SMR) of three species of crocodilians (*Crocodylus porosus*, *C. johnsoni*, and *Alligator mississippiensis*), and included individuals that ranged from 0.22 to 114 kg. Allometric scaling of SMR with body mass was similar among the species, but *C. porosus* had significantly higher SMR than did *C. johnsoni* or *A. mississippiensis*. Differences in SMR among species are potentially related to behavioural differences in levels of aggression; *C. porosus* are the most aggressive of the crocodilians measured, and have rates of standard metabolism that are approximately 36% higher at the grand mean body size than those measured for *C. johnsoni* or *A. mississippiensis*, which are among the least aggressive crocodilians.

## Introduction

Crocodilians (clade Crocodylia: Gavialidae, Alligatoridae, and Crocodylidae) have been an important group in our understanding of animal nutrition, growth, and physiology. As a result of their remarkable fecundity, rapid growth rates, and relative ease of captive propagation, crocodilians have long been a model for studies in reptilian nutritional physiology [1, 2]. However, a large majority of the published data regarding crocodilian physiology and metabolism has been collected from juveniles weighing less than ~3 kg, a size that is typically reached by most crocodilians within the first few years of life [3, 4]. The result is a potential demographic bias in the literature towards the study of young individuals that could yield a relatively myopic view of ontogenetic changes in physiological function that may accompany the extreme

growth and large body sizes achieved by crocodilians. For example, the largest of the extant crocodilians, the saltwater crocodile (*Crocodylus porosus*), changes in body mass by more than four orders of magnitude across a lifetime from a ~60 g hatchling [5] to just over 1,000 kg in the very largest of adults [6].

Because physiological data for larger crocodilians are relatively scarce and because there are considerable logistic and safety justifications for focusing research efforts on smaller crocodilians rather than large, ontogenetic comparisons among species are largely lacking from the literature. This study was undertaken to partially address this deficiency by comparing how standard metabolic rate (SMR) changes with ontogeny in three species of crocodilians, *C. porosus*, *C. johnsoni*, and *Alligator mississippiensis*. These species are all among the largest of the extant crocodilians, but differ appreciably in temperament; *A. mississippiensis* and *C. johnsoni* are considered among the least aggressive of the crocodilians, where *C. porosus* is thought to be the most aggressive [7, 8]. There is a growing body of literature linking variation in rates of energy use (both intra and interspecifically) to differences in behavioral phenotype and temperament [9–12], and we explore how potential differences in energy use among crocodilians may be related to temperament and aggressive behavior.

## Materials and methods

Our methods for measuring standard metabolic rates are described in detail in two previous studies [13, 14], but we briefly summarize them here. Crocodiles and alligators in this study (*C. porosus*, *C. johnsoni*, and *A. mississippiensis*) were from captive populations maintained by Crocodylus Park, Darwin, Northern Territory, Australia. Animals were housed in outdoor enclosures and were divided into conspecific groups containing other similar-sized individuals. Each enclosure had a pond area with water deep enough for swimming and retreat, and a dry-land area for basking. Body mass ranged from 0.22 to 114 kg. Animals less than 1 kg were weighed to  $\pm 1$  g using a laboratory scale, those between 1 and 25 kg were weighed to  $\pm 10$  g using a postal scale, and those above 25 kg were weighed to  $\pm 1$  kg using a crane scale.

For individuals less than 25 kg body mass, we used metabolic chambers made from opaque PVC pipes (250–400 mm diameter; 30–200 L) matched to body size. Chambers were filled approximately half full with water [15] and temperature was maintained at 30°C by submersed 100 W aquarium heaters. For the larger individuals (> 25 kg), we used a single chamber, 4 m long, 1.5 m wide, and 1 m tall. The chamber was constructed from 6 mm plate steel, sealed at one end, and access was through a removable air-tight door bolted to a flange at the opposite end. Four 250 mm circular access portals on the top and sealed ends of the chamber allowed for filling of the tank and for visual inspection of crocodiles. The chamber was filled about two-thirds full with water and temperature was maintained at 30°C by four 500 W submersed aquarium heaters. The steel metabolic chamber and associated gas sampling equipment were housed inside a 6 m insulated and temperature controlled (25°C) commercial steel shipping container.

For safety reasons, it was necessary to incapacitate the larger crocodiles (> 10 kg) temporarily while they were transferred to and from respirometry chambers. We subdued larger individuals with electro-stunning, and a 12V charge was applied to the dorsal surface of the neck for 3 to 10 s (Graham Electrical Stunners, Atherton, QLD, Australia). Stunning temporarily incapacitates the animal so that the jaws can be secured shut and the eyes covered before the animal has a chance to struggle. Individuals typically remain immobilized for 5 to 10 min after stunning and usually return to normal activities (e.g. swimming and basking) soon after being released. Electro-stunning is a common handling practice in the alligator and crocodile farming industries [16] and is less stressful to the animals than using the alternative of manual

restraint with ropes or webbing [17]. All experimental protocols were approved by the Charles Darwin University Animal Ethics Committee (project reference number A09015).

Rates of oxygen consumption were measured using flow-through respirometry [18, 19]. Room air was pulled through a drying column (silica gel) and passed through a mass flow meter (Sierra Instruments) and respirometry chamber. Flow rates were adjusted from 0.2 to 10 L min<sup>-1</sup> according to the size of the animal. A subsample of excurrent chamber air was drawn through a drying column (Drierite; Hammond Co.) and into an oxygen analyzer (Fox Box, Sable Systems International or Ametek S-3AI, AEI Technologies). A gas flow switching system was programmed to alternate sampling between the excurrent chamber air stream (sampled for 45 min each hour) and a baseline stream of dry room air (15 min each hour). Oxygen concentration was recorded every 3 s on a laptop computer using LabHelper software (Warthog Systems).

Individuals were fasted for 3–4 days before being moved into respirometry chambers, and after a settling-in period of 6–12 h, each was measured for 3–4 days. Rates of oxygen consumption were calculated using standard equations [20], implemented in LabAnalyst (Warthog Systems) that used the most level 15 min section (300 samples) of each 45 min interval. The lowest recorded value during the entire run was taken as the standard metabolic rate (SMR).

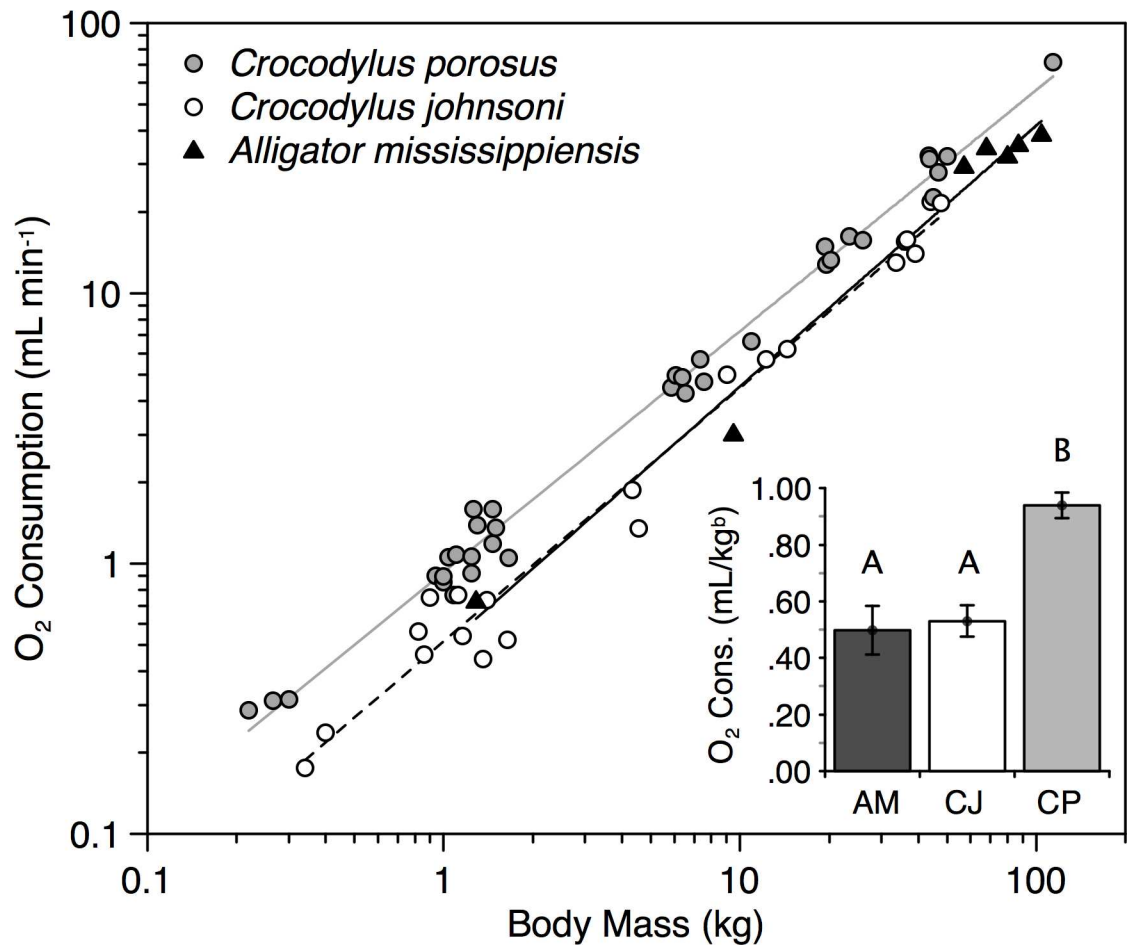
We attempted to use animals of similar size ranges for each of the three species measured (Fig 1). However, this was complicated by two factors: that adult *C. porosus* grow much larger than *C. johnsoni* and *A. mississippiensis*, and that we did not have access to individual *A. mississippiensis* < 9.5 kg. In order to balance the ranges of body sizes used to compare species we limited measurements to individuals ≤ 114 kg, and supplemented the dataset with published values from the literature. We used data from Lewis and Gatten (1985) for four juvenile *A. mississippiensis*, and data in that study were collected in a similar fashion as our measurements (standard metabolism at 30°C using metabolic chambers partially filled with water). Data from Lewis and Gatten [21] were reported in mass-specific units, and we calculated mean whole-animal rate from the reported mean body mass (1.29 kg).

Rates of oxygen consumption (SMR) and body mass data were log<sub>10</sub>-transformed so that conventional allometric equations could be derived from ordinary least squares regressions [22]. The equations have the form  $SMR = aM^b$ , where  $a$  is the scaling coefficient (intercept),  $M$  is body mass, and  $b$  is the exponent (slope of the regression line). Differences in scaling coefficients and exponents were tested with analysis of covariance (ANCOVA), according to Zar [23]. Log<sub>10</sub> body mass was used as a continuous covariate in comparison of log<sub>10</sub> SMR among species (categorical predictor variable).

Because the range and distributions of body sizes differ among species, we also compare mass-independent SMR among species using ANOVA. We divided whole-animal metabolic rate by the body mass of each individual raised to its species-specific scaling exponent (mass-independent SMR = whole-animal SMR/ $M^b$ ). This removes the allometric effect of body mass on SMR allowing a mass-independent comparison [24]. Pairwise differences in whole-animal SMR and mass-independent SMR between species were made using Scheffé post-hoc contrasts.

## Results

Standard metabolic rate (ml O<sub>2</sub> min<sup>-1</sup>) was measured in 63 individuals: 35 *C. porosus* ranging in size from 0.22 to 114 kg, 21 *C. johnsoni* ranging from 0.34 to 48 kg, and 7 *A. mississippiensis* ranging from 1.29 to 104 kg (Fig 1). Standard allometric equations relating body mass to SMR at 30°C are  $SMR = 0.931M^{0.892}$  for *C. porosus* (standard error of exponent = 0.015),  $0.516M^{0.937}$  for *C. johnsoni* (s.e. = 0.032), and  $0.491M^{0.965}$  for *A. mississippiensis* (s.e. = 0.054). The slopes of the allometric relationships between body mass and SMR did not differ among species (no



**Fig 1. Scaling of standard metabolism ( $O_2$  consumption) for three species of crocodylians measured at  $30^\circ\text{C}$ .** The highly aggressive *Crocodylus porosus* has significantly higher standard metabolism than the less aggressive *Crocodylus johnsoni* and *Alligator mississippiensis*. Inset figure shows mass-independent means (bars) and standard errors (error bars) of  $O_2$  consumption. Species not connected by same letter are significantly different.

doi:10.1371/journal.pone.0171082.g001

significant interaction;  $F_{2,59} = 1.7$ ,  $P = 0.19$ ), but there was a significant difference in intercepts among species (ANCOVA  $F_{2,59} = 51.8$ ,  $P < 0.001$ ). Least square means of SMR were  $4.26$  (s.e. =  $0.033$ )  $\text{mL } O_2 \text{ min}^{-1}$  for *C. porosus*,  $2.53$  (s.e. =  $0.042$ )  $\text{mL } O_2 \text{ min}^{-1}$  for *C. johnsoni*, and  $2.77$  (s.e. =  $0.077$ )  $\text{mL } O_2 \text{ min}^{-1}$  for *A. mississippiensis*. On a pairwise basis, *C. porosus* had a higher SMR than both *C. johnsoni* and *A. mississippiensis* (Scheffé  $S = 95.7$  and  $25.5$  respectively, and  $P < 0.001$  for both), but *C. johnsoni* and *A. mississippiensis* did not differ from one another ( $S = 1.1$ ,  $P > 0.5$ ).

Mass-independent means of SMR were  $0.94$  (s.e. =  $0.021$ )  $\text{mL } O_2/\text{kg}^b$  for *C. porosus*,  $0.53$  (s.e. =  $0.027$ )  $\text{mL } O_2/\text{kg}^b$  for *C. johnsoni*, and  $0.50$  (s.e. =  $0.047$ )  $\text{mL } O_2/\text{kg}^b$  for *A. mississippiensis*. On a pairwise basis, *C. porosus* had a higher mass-independent SMR than both *C. johnsoni* and *A. mississippiensis* (Scheffé  $S = 11.6$  and  $8.4$  respectively, and  $P < 0.001$  for both), but *C. johnsoni* and *A. mississippiensis* did not differ from one another ( $S = 0.5$ ,  $P = 0.85$ ).

## Discussion

There is much variability in rates of crocodylian metabolism, even under standard conditions [13, 21]. The majority of variation in SMR can be explained by body size, but behavioural and

ecological differences among species likely also contribute [25–28]. Our results are consistent with general physiological and behavioural hypotheses that link variation in animal temperament to variation in energy use [9–12]. Our data support the notion that SMR is correlated with temperament in crocodilians, interspecifically, and we propose it as a general hypothesis that is in need of testing.

The species measured in this study are at opposite ends of the spectrum in relative levels of aggression and in tolerance of conspecifics. While *A. mississippiensis* and *C. johnsoni* are among the least aggressive of the crocodilians, *C. porosus* is arguably the most aggressive [7, 8]. More measurements are needed, and we suggest some key species that should be measured to address the hypothesis; *C. mindorensis* (Philippine Crocodile) and *C. rhombifer* (Cuban Crocodile) are also considered very aggressive (G.J.W. Webb personal observation) while *C. siamensis* (Siamese Crocodile) and *Gavialis gangeticus* (Gharial) are thought to be among the least aggressive [8].

The correspondence between aggressive-dominance behaviour and energy use has been demonstrated intraspecifically in other species, including Atlantic salmon [29, 30], brown trout [31], and giant freshwater prawns [32]. Lizards that had levels of aggression experimentally increased by testosterone implants showed rates of field metabolism that were elevated compared to control individuals (Marler and Moore 1989). However, increased energy expenditures were primarily the result of increased aggression and territory defence rather than elevated SMR alone [33]. Thus, the energetic costs of increased aggression may be manifested in both elevated SMR and through increased energy expenditure due to behavioural interactions.

The differences in SMR among *C. porosus*, *C. johnsoni*, and *A. mississippiensis* are considerable, and at a body mass of 20 kg (the approximate mean body size of all measured individuals) differences amount to a 36% higher standard metabolic requirement for *C. porosus* relative to the other species. However, comparison of SMR at the mean body size is somewhat confounded by ontogenetic effects, and at 20 kg the three species are at different life stages; *C. johnsoni*, and *A. mississippiensis* are near or at sexual maturity, whereas *C. porosus* is not sexually mature until reaching a much larger size [34, 35]. Therefore, higher SMR in *C. porosus* over the size range examined here might be partially explained by higher than expected metabolic rates that frequently accompany rapid juvenile growth in reptiles [36–38].

This report fills an important gap in the literature, and is the first report to detail comparative energetics of crocodilians across a significant portion of their natural size range. Because SMRs of the majority of crocodilian species (>23) have not been examined, the analyses presented here should provide a good foundation for additional studies that consider the energetic consequences of behavioural and ecological differences among the crocodilians.

## Supporting information

**S1 File. Raw data used to calculate standard metabolism in three species of crocodilians.** (XLSX)

## Acknowledgments

Support was provided by the Australian Research Council (Linkage Grant LP0882478), the Rural Industries Research and Development Corporation (Project PRJ-000660), the Northern Territory Research and Innovation Fund, and Wildlife Management International. We thank the staff at WMI for logistical support, including Jemeema Brien, Steve Coulson, Dave Ottway and John Pomeroy, who helped construct the respirometry chambers and provided animal care and maintenance during experiments. We also thank Doug Glazier and Shaun Killen for

their review and for providing several helpful suggestions and relevant citations that improved the manuscript.

## Author Contributions

**Conceptualization:** CMG MLB CRT SCM GJWW RSS KAC.

**Data curation:** CMG.

**Formal analysis:** CMG MLB CRT RSS KAC.

**Funding acquisition:** CRT GJWW RSS KAC.

**Investigation:** CMG MLB.

**Methodology:** CMG MLB CRT SCM GJWW RSS KAC.

**Project administration:** CMG.

**Resources:** SCM GJWW RSS KAC.

**Supervision:** GJWW KAC.

**Validation:** CMG MLB CRT RSS KAC.

**Visualization:** CMG.

**Writing – original draft:** CMG MLB CRT SCM GJWW RSS KAC.

**Writing – review & editing:** CMG MLB CRT SCM GJWW RSS KAC.

## References

1. Coulson RA, Hernandez T. Alligator metabolism, studies on chemical reactions in vivo. *Comparative Biochemistry and Physiology*. 1983; 74(1):1–182. PMID: [6831860](#)
2. Coulson RA, Herbert JD, Coulson TD. Biochemistry and physiology of alligator metabolism *in vivo*. *Am Zool*. 1989; 29(3):921–34.
3. Coulson TD, Coulson RA, Hernandez T. Some observations on the growth of captive alligators. *Zoologica*. 1973; 58(2):47–52.
4. Garnett ST, Murray RM. Parameters affecting the growth of the estuarine crocodile, *Crocodylus porosus*, in captivity. *Aust J Zool*. 1986; 34(2):211–23.
5. Webb GJW, Cooper-Preston H. Effects of incubation temperature on crocodiles and the evolution of reptilian oviparity. *Am Zool*. 1989; 29(3):953–71.
6. Britton ARC, Whitaker R, Whitaker N. Here be a dragon: exceptional size in a saltwater crocodile (*Crocodylus porosus*) from the Philippines. *Herpetol Rev*. 2012; 43(4):541–6.
7. Lang JW. Crocodilian Behaviour: Implications for Management. In: Webb GJW, Manolis SC, Whitehead PJ, editors. *Wildlife Management: Crocodiles and Alligators*. New South Wales, AU: Surrey Beatty and Sons; 1987. p. 273–94.
8. Brien ML, Lang JW, Webb GJ, Stevenson C, Christian KA. The good, the bad, and the ugly: Agonistic behaviour in juvenile crocodilians. *PLoS ONE*. 2013; 8(12):e80872. doi: [10.1371/journal.pone.0080872](#) PMID: [24349018](#)
9. Biro PA, Stamps JA. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol Evol*. 2010; 25(11):653–9. doi: [10.1016/j.tree.2010.08.003](#) PMID: [20832898](#)
10. Careau V, Garland T Jr. Performance, personality, and energetics: correlation, causation, and mechanism. *Physiol Biochem Zool*. 2012; 85(6):543–71. doi: [10.1086/666970](#) PMID: [23099454](#)
11. Careau V, Reale D, Humphries MM, Thomas DW. Of voles, mice, chipmunks and dogs: the energetics of animal personality. *Integr Comp Biol*. 2010; 50:E24.
12. Careau V, Thomas D, Humphries MM, Reale D. Energy metabolism and animal personality. *Oikos*. 2008; 117(5):641–53.

13. Seymour RS, Gienger CM, Brien ML, Tracy CR, Manolis SC, Webb GJW, et al. Scaling of standard metabolic rate in estuarine crocodiles *Crocodylus porosus*. *J Comp Physiol B*. 2013; 183(4):491–500. doi: [10.1007/s00360-012-0732-1](https://doi.org/10.1007/s00360-012-0732-1) PMID: [23233168](https://pubmed.ncbi.nlm.nih.gov/23233168/)
14. Gienger CM, Tracy CR, Brien ML, Manolis SC, Webb GJW, Seymour RS, et al. Energetic costs of digestion in Australian crocodiles. *Aust J Zool*. 2012; 59(6):416–21.
15. Grigg GC. Metabolic rate, Q10 and respiratory quotient (RQ) in *Crocodylus porosus*, and some generalizations about low RQ in reptiles. *Physiol Zool*. 1978; 51(4):354–60.
16. Peucker SKJ, Davis BM, van Barneveld RJ. Crocodile Farming Research: Hatching to Harvest. Kingston, ACT: Australia: Rural Industries Research and Development Corporation; 2005. 111 p.
17. Franklin CE, Davis BM, Peucker SKJ, Stephenson H, Mayer R, Whittier J, et al. Comparison of stress induced by manual restraint and immobilisation in the estuarine crocodile, *Crocodylus porosus*. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*. 2003; 298A(2):86–92.
18. Lighton JRB. Measuring Metabolic Rates: A Manual for Scientists. Oxford: Oxford University Press; 2008.
19. Withers PC. Design, calibration and calculation for flow-through respirometry systems. *Aust J Zool*. 2001; 49:445–61.
20. Withers PC. Measurement of  $VO_2$ ,  $VCO_2$ , and evaporative water loss with a flow-through mask. *J Appl Physiol*. 1977; 42(1):120–3. PMID: [833070](https://pubmed.ncbi.nlm.nih.gov/833070/)
21. Lewis LY, Gatten RE Jr. Aerobic metabolism of american alligators, *Alligator mississippiensis*, under standard conditions and during voluntary activity. *Comparative Biochemistry and Physiology Part A: Physiology*. 1985; 80(3):441–7.
22. Schmidt-Nielsen K. Scaling: Why is Animal Size So Important? Cambridge: Cambridge University Press; 1984. 241 p.
23. Zar JH. Biostatistical Analysis. Upper Saddle River, N.J.: Prentice Hall; 1999.
24. Heusner AA. Body size and energy metabolism. *Annu Rev Nutr*. 1985; 5:267–93. doi: [10.1146/annurev.nu.05.070185.001411](https://doi.org/10.1146/annurev.nu.05.070185.001411) PMID: [3896270](https://pubmed.ncbi.nlm.nih.gov/3896270/)
25. Killen SS, Atkinson D, Glazier DS. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol Lett*. 2010; 13(2):184–93. doi: [10.1111/j.1461-0248.2009.01415.x](https://doi.org/10.1111/j.1461-0248.2009.01415.x) PMID: [20059525](https://pubmed.ncbi.nlm.nih.gov/20059525/)
26. Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AST, et al. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *The American Naturalist*. 2016; 187(5):592–606. doi: [10.1086/685893](https://doi.org/10.1086/685893) PMID: [27104992](https://pubmed.ncbi.nlm.nih.gov/27104992/)
27. Reinhold K. Energetically costly behaviour and the evolution of resting metabolic rate in insects. *Funct Ecol*. 1999; 13(2):217–24.
28. Andrews RM, Pough FH. Metabolism of squamate reptiles: allometric and ecological relationships. *Physiol Zool*. 1985; 58(2):214–31.
29. Cutts CJ, Metcalfe NB, Taylor AC. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *J Fish Biol*. 1998; 52(5):1026–37.
30. Cutts CJ, Metcalfe NB, Taylor AC. Fish may fight rather than feed in a novel environment: metabolic rate and feeding motivation in juvenile Atlantic salmon. *J Fish Biol*. 2002; 61(6):1540–8.
31. Hoogenboom MO, Armstrong JD, Groothuis TGG, Metcalfe NB. The growth benefits of aggressive behavior vary with individual metabolism and resource predictability. *Behav Ecol*. 2013; 24(1):253–61.
32. Brown JH, Ross B, McCauley S, Dance S, Taylor AC, Huntingford FA. Resting metabolic rate and social status in juvenile giant freshwater prawns, *Macrobrachium rosenbergii*. *Mar Freshwat Behav Physiol*. 2003; 36(1):31–40.
33. Marler CA, Walsberg G, White ML, Moore M. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behav Ecol Sociobiol*. 1995; 37:225–31.
34. Ferguson MWJ. Reproductive Biology and Embryology of the Crocodilians. In: Gans C, editor. *Biology of the Reptilia*. 14 Development A. New York: Wiley; 1985. p. 329–491.
35. Webb GJW, Crawford J, Yerbury MJ, Messel H. Growth rates of *Crocodylus porosus* (Reptilia: Crocodylia) from Arnhem Land, Northern Australia. *Australian Wildlife Research*. 1978; 5(3):385–99.
36. Wieser W. A distinction must be made between the ontogeny and the phylogeny of metabolism in order to understand the mass exponent of energy metabolism. *Respiration Physiology*. 1984; 55(1):1–9. PMID: [6709979](https://pubmed.ncbi.nlm.nih.gov/6709979/)
37. Nagy KA. Energy costs of growth in neonate reptiles. *Herpetol Monogr*. 2000; 14:378–87.
38. Beaupre SJ, Zaidan F III. Scaling of  $CO_2$  production in the timber rattlesnake (*Crotalus horridus*), with comments on cost of growth in neonates and comparative patterns. *Physiol Biochem Zool*. 2001; 74(5):757–68. doi: [10.1086/322965](https://doi.org/10.1086/322965) PMID: [11517461](https://pubmed.ncbi.nlm.nih.gov/11517461/)