

The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*)

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Abstract

American alligators *Alligator mississippiensis* undergo major transformations in morphology and ecology during development. These include several thousand-fold changes in body mass, modified snout and dental proportions, and shifts in diet from small, delicate foodstuffs to the inclusion of increasingly larger, more robust prey. How these changes in anatomical form contribute to actual physical performance and niche use is largely unknown. In the present study, bite-force measurements for 41 specimens of *A. mississippiensis*, were made throughout ontogeny (hatchling–older adults) using a series of precision force transducers. How this performance indicator scaled with respect to cranial and whole-body measurements was determined. Bite-force production throughout development was contrasted with ontogenetic changes in trophic ecology. The influences of this performance measure on these changes were then analysed. The results showed a 800-fold range (12–9452 N) of bite forces with values positively correlating with increases in body size. Scaling of biting forces through ontogeny showed positive allometry with respect to body mass, head length, jaw length, snout–vent length and total length. These patterns may be attributable to allometric growth of individual skeletal elements (and associated musculature), and/or progressive fusion and ossification of skull and jawbones during development. The overall pattern of force increase throughout ontogeny did not vary in association with major shifts in diet. Notably, the bite-force values for adult *A. mississippiensis* are the highest measured for any living animal and represent the first measures for a large crocodylian. Additionally, these data provide the first documentation of how bite force changes during ontogeny in a reptile. By bridging the rich morphological and ecological databases for these animals, this study opens the door to a comprehensive understanding of feeding in *A. mississippiensis*. Furthermore, it provides groundwork for standardized comparative studies of feeding among crocodylian, reptilian, or other gnathostome vertebrates.

Key words: Crocodylia, bite force, biomechanics, ecomorphology, scaling, *Alligator mississippiensis*

INTRODUCTION

A number of investigations of functional vertebrate morphology have sought an understanding of how the form and function of animal skulls, jaws, dentitions and associated musculature collectively contribute to feeding performance and the occupation of ecological niches (see recent reviews in Wainwright & Reilly, 1994; Schwenk, 2000). One group that has received such attention is the Crocodylia (Iordansky 1963, 1973; Dodson, 1975; Cleuren & De Vree, 1992, 2000; Busbey, 1994; Cleuren, Aerts & De Vree, 1995; Daniel & McHenry, 2001), an emphasis that partly stems from the intriguing suite of morphological and ecological

changes these animals undergo between hatching and adulthood (Mook, 1921; Kellogg, 1929; McIlhenny, 1935; Giles & Childs, 1949; Cott, 1961; Fogarty & Albury, 1968; Chabreck, 1971; Valentine *et al.*, 1972; Dodson, 1975; Hall, 1985; Delaney & Abercrombie, 1986; Pooley, 1989; Monteiro, 1997). Among the 23 species of crocodylians (King & Burke, 1989), the American alligator *Alligator mississippiensis* has been the focus of the majority of these anatomical investigations. At birth, alligators weigh *c.* 0.065 kg but can reach > 275 kg late in adulthood (Woodward, White & Linda, 1995). During this remarkable 4000-fold transformation, the short semi-broad snouts possessed by hatchlings elongate and become relatively more slender (Dodson, 1975). At the same time, the caniniform teeth of hatchlings progress from being delicate, needle-like implements to having a blunt and spike-like morphology in adulthood (Fig. 1). Similarly,

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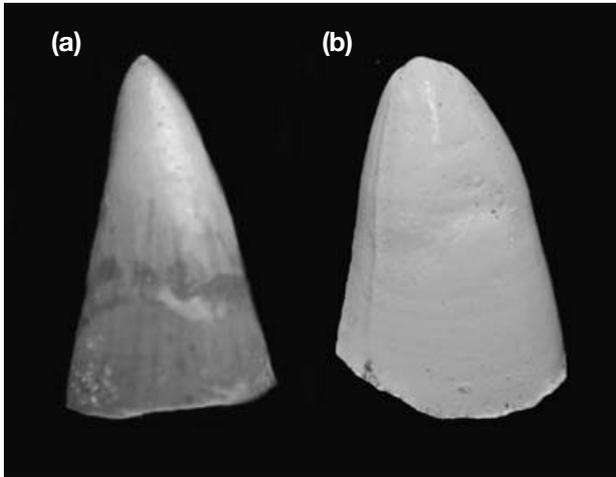


Fig. 1. Caniniform teeth of juvenile vs adult *Alligator mississippiensis* scaled to the same size to facilitate shape comparison. (a) Fourth maxillary tooth of a juvenile alligator (2.2 mm high). Juvenile alligators have slender, sharp teeth effective for piercing the integuments of insects, small fish, amphibians and reptiles. (b) Fourth maxillary tooth of an adult alligator (25 mm high). Adult alligators have robust, blunt teeth compared to juveniles. Blunt robust teeth are more resistant to damage from bending and shear stresses during hard impacts on materials like bone than sharper, more slender teeth with equal volume (Lucas & Luke, 1984).

the distal teeth (i.e. those toward the back of the jaws; see Hillson (1986) for oral biology terminology) which are initially sharp-edged and blade-like, become bulbous and molariform (Edmund, 1962). Interestingly, these modifications are paralleled by shifts in feeding ecology with each developmental stage effectively representing an ecological niche (Dodson, 1975). Hatchlings initially eat insects and tiny fish. Later, crustaceans and small to medium-sized vertebrates are added to the diet. The attainment of adulthood enables the consumption of large mammals and the crushing of large turtles. The latter behaviours are particularly common in the largest individuals, which are typically male in this highly dimorphic taxon (Neill, 1971; Dodson, 1975; Pooley, 1989).

Although many studies have documented the diets and functional morphology of crocodylians, virtually no data have been obtained on the biomechanical performance of the jaws (e.g. bite force) and teeth (e.g. strength, pressure generation). These measures provide some of the essential ties between these datasets and thus are critical for gaining a comprehensive understanding of how the phenotype of these animals relates to their realized ecological niche(s). Despite the inherent difficulties of working with large carnivorous reptiles, a few pioneering attempts to assess biting forces in crocodylians have taken place. Sinclair & Alexander (1987) included a 1-m TL sub-adult caiman *Caiman crocodilus* in their analysis of reptilian bite-force production. Following their lead, Vliet (pers. comm. cited in Erickson *et al.*, 1996) tested a prototype mechanical bite bar on much larger adults of

A. mississippiensis. Although a design flaw precluded ultimate implementation of the device, the experiment showed that powerful snapping bites could be elicited on adult members of the species. Finally, a study by Clueren *et al.* (1995) used electromyographic and morphological data to develop a sophisticated model for predicting bite-force production in *C. crocodilus*.

Building upon the findings from these efforts, bite forces were recorded throughout ontogeny in a complete growth series for *A. mississippiensis* using a series of precision, electronic bite-force transducers. Post-testing measurements of head and body lengths were then made on each specimen. How the performance measures compared with indices of body size was determined. The results were then contrasted with data from the literature on ontogenetic changes in cranial anatomy and feeding behaviour. From these analyses, whether *A. mississippiensis* bite forces scale with predictions of isometric scaling was documented for the first time. Specifically, muscle force generation is determined by the cross-sectional area of the muscles. Assuming isometry and maximum performance, bite force will scale isometrically to the sum of the cross-sectional areas of all of the jaw muscles contributing to a bite. Because areas scale to the square of linear measurements, bite force is also predicted to scale to the square of linear measurements (slope = 2.0). Because areas scale to the two-thirds power of volumes, and volume scales isometrically with mass, bite force is also predicted to scale to the two-thirds power (slope = 0.67) of body mass (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984).

Ancillary goals of our research included: (1) determining whether bite forces in *A. mississippiensis* drastically changed in relation to major dietary shifts during ontogeny; (2) assessing whether male and female alligators show similar performance measures at comparable sizes; (3) comparing *A. mississippiensis* bite forces with the few measures that have been made on other large animals.

MATERIALS AND METHODS

Specimen selection and husbandry

This research required access to an entire growth series (hatchling to large adult) of a large crocodylian that undergoes both major morphological and ecological modifications during development. The American alligator was deemed the ideal taxon for these purposes and was available for testing in large numbers through the St Augustine Alligator Farm and Zoological Park in St Augustine, Florida, U.S.A. Most animals in this facility were hatched from eggs collected in the field, although there were a few large, nuisance animals that were collected as adults in the field and had been maintained in captivity for many years. At the zoological park, the animals are free to range in large 'natural setting' enclosures or in a fenced-off, 0.5 ha natural buttonbush swamp. Shaded and natural light basking sites are accessible to all animals. Young animals are fed 'gator'

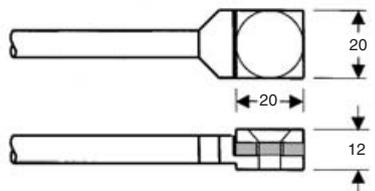
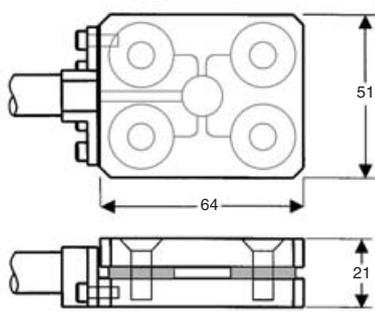
Transducer schematic	Mechanism	Range	Specimens
	Voltage / 4 strain gauges	0–200 N	TL > 90 cm mass > 2 kg
	Piezoelectric 1 load washer	0–4450 N	TL > 90 – 200 cm mass = 2–50 kg
	Piezoelectric / 4 load washers	0–22250 N	TL > 200 cm mass > 50 kg

Fig. 2. Design of the three transducers used to measure bite-force performance in *Alligator mississippiensis*. The general mechanism, measurement range and size range of animals tested are given for each transducer. Dimensions in mm.

pellets (Burriss Mill & Feed Inc., Franklinton, LA) along with minced nutria and beaver. Their diets are further supplemented with crickets, mice and rats as well as insects, fish, and lizards that they capture on their own. The staples of large animals include whole adult nutria and disarticulated beavers and occasionally parts from ostrich and emus. Some also manage to catch fish and birds on their own. A total of 53 animals ranging from hatchlings to adults 3.7 m long were selected for bite-force experimentation. Of these, 41 produced useable performance measures (see below). (Note: alligators with particularly broad snouts and protruding teeth (characteristics of unknown cause seen in some long-term captive animals; Neill, 1971; Guggisberg, 1972) were avoided in our testing. Preliminary testing on such animals showed a reluctance to bite with vigour. This behaviour was presumed to stem from the sensitive periosteal surfaces of the jaws coming into contact with the semi-rigid bite bars.)

Testing protocol

Equipment

Examining the ontogeny of bite-force performance in *A. mississippiensis* necessitated the capacity to obtain values from minute 0.30 m hatchlings to 3.7 m older

adult males. Furthermore, our testing required that these animals produce kinematically comparable, high-force snapping bites at the same location, to within a few degrees of complete jaw closure, and with a similar degree of precision.

To meet these specifications 3 different bite bars were used. A miniaturized force transducer was used in the testing of specimens < 90 cm total length (TL; < 2 kg) with low bite-force magnitude and small gape span. The basic design of this device is a double-cantilever beam made of metal plates that superficially resembles a tuning fork (Dechow & Carlson, 1983). The plates were constructed with 17-4PH stainless steel, a metal with excellent linear elastic properties suitable for accurate bite-force transduction (Dechow & Carlson, 1983). Uniaxial strain gauges were mounted on the surfaces of each beam (Dechow & Carlson, 1983; Fig. 2). Leather strips (2.5 mm thick × 3 mm wide × 20 mm long) were affixed with cyanoacrylate to the end of the outer surface of each beam as points of contact for the upper and lower teeth of the animals. These ensured that the potential for dental trauma from impacting the steel plates was minimized. Additionally, these fixed points for tooth contact served to eliminate error resulting from variation in bite positions along the length of the cantilever beams and allowed precise calculation of bite forces based on the calibration factor.

The strain gauges used on the small bite bar apparatus were uniaxial foil models (TML Tokyo Sokki Kendyujou

Co. Ltd, Tokyo, Japan, FLA-3-11-3L). These were bonded with cyanoacrylate to the top and bottom of the 2 beams at the base of each cantilever. The 4 gauges were wired in a full-bridge configuration such that the voltage output was proportional to the compressive force applied to the beams during biting. Analogue signals from the small transducer were amplified (National Instruments Inc., Austin, TX, SCXI Strain Isolation Amplifier), converted to a digital form (National Instruments Inc., PCMCIA-card), and acquired on a laptop computer (Apple Computer, Cupertino, CA, Macintosh G3 Powerbook) at a sampling rate of 1000 Hz using a customized virtual instrument run in LabView 5.1 (National Instruments Inc.).

The entire apparatus was calibrated by fixing the base of the transducer in a vice and hanging a series of weights from the ends of the beams (Dechow & Carlson, 1983). The mass of each weight and the voltage output for it was recorded and plotted. The transducer produced a nearly perfect linear relationship, and the slope of this line was calculated for each beam. The slope coefficients were used to calculate the calibration factor $[(\text{coefficient beam 1}) / (\text{coefficient beam 1} + \text{coefficient beam 2})]$ to convert raw bite-force data into Newtons of force (N). The transducer was calibrated before and after a series of bite-force trials and proved to be highly stable. Noise was < 1% of forces generated during actual bites. No data filtering was performed for either the calibrations or bite-force measurements.

The medium and large transducers were used to measure the bite forces of alligators ranging from 90 to 200 cm TL (2–50 kg) and > 200 cm TL (> 50 kg), respectively. The design of the medium and large transducers incorporated piezoelectric load washers sandwiched between 17-4PH stainless steel plates (Fig. 2). Leather pieces 6 mm (medium transducer) or 12 mm (large transducer) thick were affixed to the faces of the plates to meet each animal's teeth while biting. The size of animals for which the medium transducer was intended required a very slim and slender design to ensure standardized testing in which only the teeth of interest were engaged (see below). This model had 1 load washer with a 0–4450 N (1000 lb) range (Kistler Instrument Corp., Amherst, NY, Type 9000M057, $\leq 1\%$ error, pure DC analogue signal with a frequency of display of 10 KHz). The large transducer was designed for use with large alligators with much broader tooth spacing. As such, we used a sensor array of 4 larger load washers (Kistler Instrument Corp., Type 9000M056, $\leq 1\%$ error, pure DC analogue signal with frequency of display of 10 KHz) configured so that a bite anywhere on the steel plates would give a precise force measurement within a range of 0–22 250 N (5000 lbs). The piezoelectric transducers and bite bars were factory assembled, pre-loaded, and calibrated by the manufacturer (Kistler Instrument Corp.) and their accuracy verified following delivery and after testing using series of weights placed at various points on the contact plates. Charge output from the transducers was input into a DC-powered charge amplifier (Kistler Instrument Corp., Type 5995A) equipped with an LCD display and peak-detect and

peak-hold functions, so that maximal bite force could be read at the time of each trial.

Bite-force trials

Animals were restrained by 1 or more people during each testing run to ensure that axial rolling did not occur (Grenard, 1991), a source of signal not related to biting force. If necessary the animals were encouraged to gape by using taps to the top of the snout. The appropriate transducer was then placed unilaterally between the jaws and centred both mesio-distally and labio-lingually at the apex of the 11th maxillary tooth, the most prominent tooth at the back of the jaws. The sensing of the device upon the teeth typically elicited extremely aggressive, snapping bites. Kinematically, these bites were similar to those used by these animals during prey seizure and during intraspecific aggression where lateral thrusting of the head leads to unilateral seizure of the quarry (Pooley, 1989; Grenard, 1991; Erickson, 1996a) and high forces are generated owing to the necessity to deliver swift and injurious blows. The shattering of teeth often occurs during such bites in the wild and/or captivity as bones (Erickson, 1996a), wooden handling sticks (K. A. Vliet & G. M. Erickson, pers. obs.) or metal objects (McIlhenny, 1935) are seized. Obviously an animal's dentition is only functional within the range of stress which it can sustain and thus it is probable that the bites recorded approach the maximal possible for these animals.

During each trial, peak bite force was recorded from the computer (small transducer) or charge amplifier display (medium and large transducers). All trials were digitally videotaped at 30 frames/s with a Hi-8 digital camera recorder (Sony Inc., Tokyo Japan, DCR-TRV520) for post-testing analysis (see below).

At least 1 high-force snapping bite was elicited and recorded for each specimen and typically 3–5 were taken. The leather contacts were removed after each trial. Post-testing analysis of the bite marks and videos were used to verify that recorded bites had in fact occurred on the active surface of each transducer, in parallel with the jaw line, and directly centred about the 11th maxillary tooth. Trials for which these criteria were not met, for which the bites were not aggressive, or which were discontinuous from start to finish were not used in the post-testing analyses. The highest bite-force value that was recorded, which was almost invariably the first, was used in the subsequent regression analyses. (Note: how and why the biting forces of individuals decline during multiple bite sequences is not addressed in the present paper but will be a focus in a subsequent analysis.)

Morphometrics

Morphological measurements were taken after each bite-force trial. Body size measures included: total length (TL), snout–vent length (SVL) and body mass (M). Measures of head size included: head length (HL; snout tip to dorsal

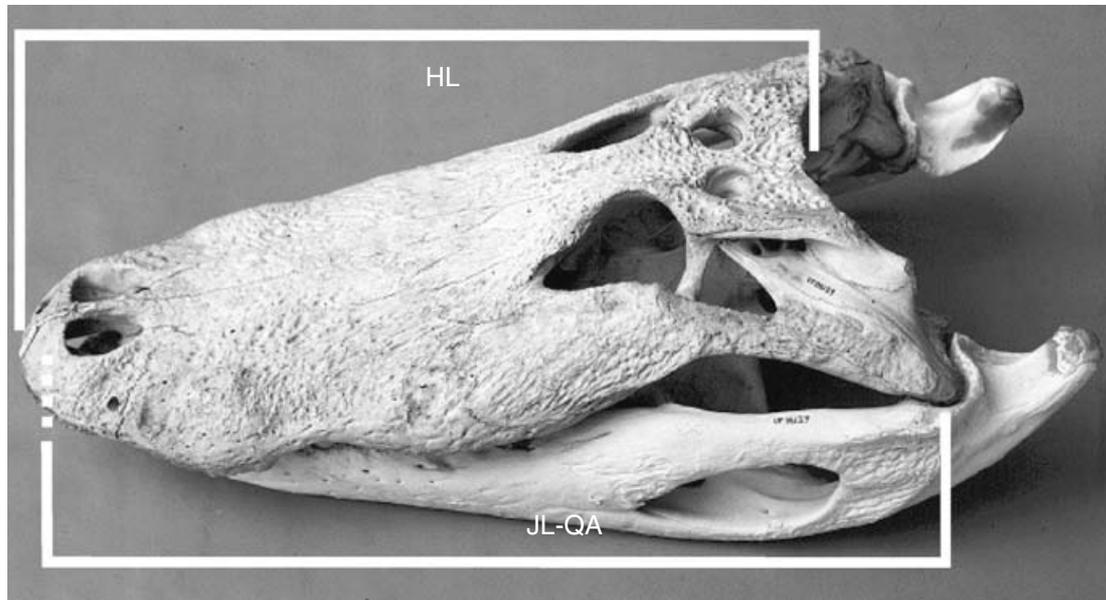


Fig. 3. Measures made on *Alligator mississippiensis* crania and jaws. HL, head length from tip of snout to dorsal supraoccipital margin; JL-QA, jaw length from rostral tip of dentary to center of quadrate-articular joint. These landmarks are readily apparent on specimens *in vivo*. Skull is from Florida Museum of Natural History, Spec. No. UF 35129.

supraoccipital border, a standard measure of crocodylian size; Fig. 3), and jaw length to quadrate/articular joint (JL-QA; rostral tip of lower jaw to centre of quadrate/articular joint, a measure of the jaw out-lever; Fig. 3).

Analysis

Raw bite-force data were plotted against each of the raw morphometric variables. The data were then log-transformed for further analysis. Simple linear regression was done with morphometric indices as the independent variables and bite force as the dependent variable. For each regression, 95% confidence intervals were calculated and plotted. The appropriate predicted linear relationship between each independent and the dependent variable was superimposed onto each plot. Theoretical lines were set to cross data lines at the mean values for each independent morphological variable. Regression coefficients were analysed for significant differences from isometric scaling predictions as well as from published information on the growth and dietary ontogeny of *A. mississippiensis*.

Males and females were compared for differences in body and head size as well as absolute bite force using a series of unpaired *t*-tests. *t*-tests were performed for all individuals and for sexually mature adults only (specimens ≥ 180 cm TL; Dodson, 1975; Joanen & McNease, 1975, 1980). Significance values were subjected to sequential Bonferroni tests to account for the potential non-independence of comparisons as well as the increased probability of type I errors associated with multiple comparisons. To test for a difference in bite-force performance between the sexes not resulting from size variation, a 1-way ANOVA was done using residuals calculated by regressing bite force against SVL. Statistical

Table 1. Summary statistics for raw morphological and bite-force data for *Alligator mississippiensis*

Variable	Minimum	Maximum
TL (cm)	31.5	371.5
SVL (cm)	15.5	189.0
Mass (kg)	0.077	296.7
HL (cm)	4.9	48.5
JL-QA (cm)	4.6	56.0
Bite Force (N)	12.0	9452.0

analyses were done using StatView v5 (SAS Institute Inc., Cary, NC) for Windows.

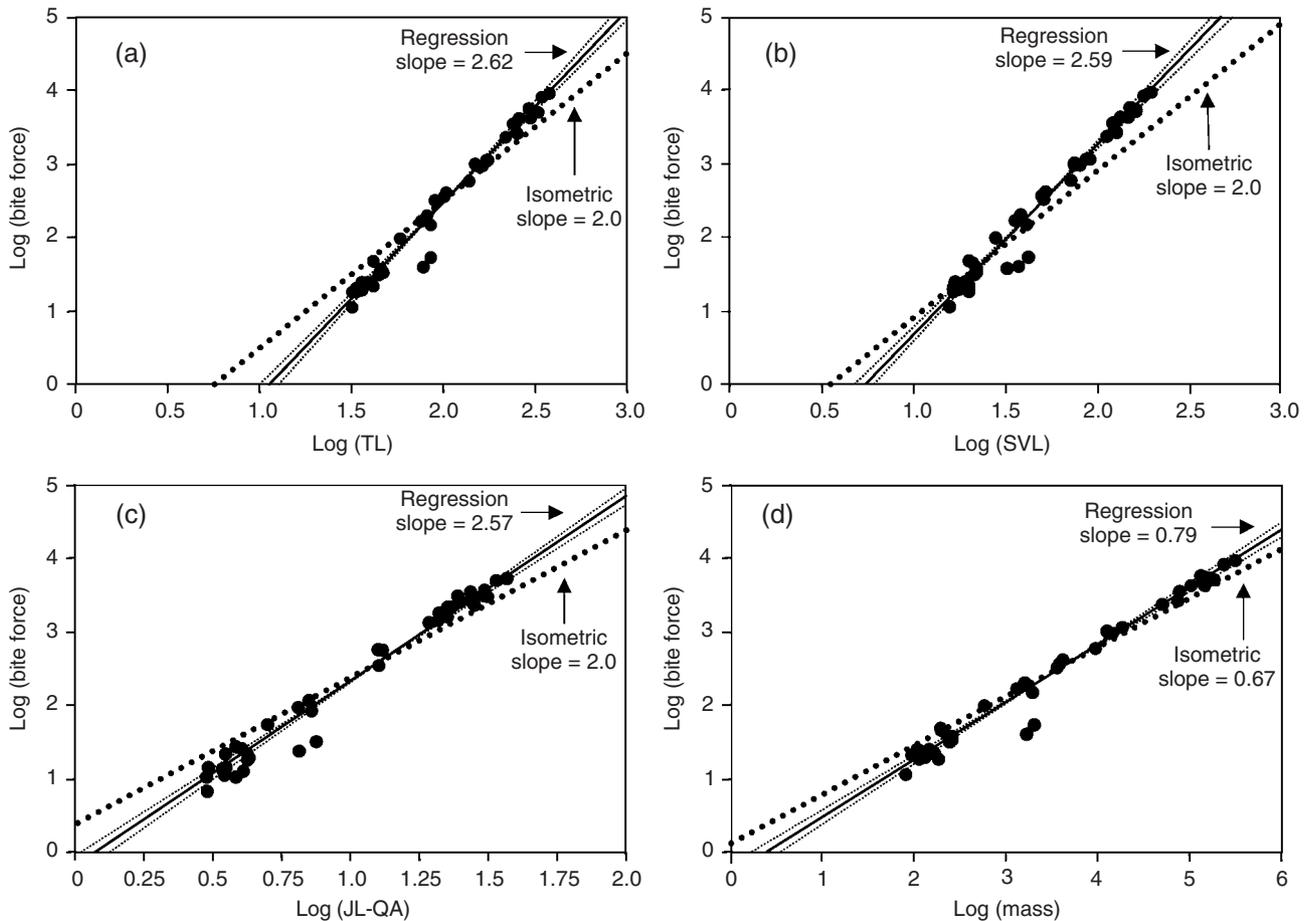
RESULTS

Aggressive bite-force readings were obtained from 41 specimens spanning a 12-fold range in linear measures of body size (TL, SVL), 10- to 12-fold range in head/jaw size (HL, JL-QA), and a > 3800-fold range in body mass (Table 1). Peak bite-force performance spanned nearly a 800-fold range (12-9452 N; Table 1).

Bite-force performance was significantly and highly correlated with all of the morphological variables that were considered (Table 2). Bite-force regressions scaled to body size (TL, SVL) showed coefficients (slopes) significantly greater than the logarithmic value of 2.0 predicted by isometry (Fig. 4a,b). Similarly, bite force scaled to head/jaw size (HL, JL-QA) showed coefficients significantly higher than the predicted value of 2.0 (Fig. 4c, Table 2). Regression of body mass vs biting force performance also showed a scaling coefficient that departed significantly from the predicted value of 0.67 (Fig. 4d).

Table 2. Summary of simple regression analysis for *Alligator mississippiensis*. Abbreviations for morphological variables are the same as used in the text. BF, bite force

Variables	r^2	Intercept	Slope	Confidence	Limits	F -value	P -value
BF vs TL	0.975	-2.76	2.62	2.48	2.76	1472	< 0.0001
BF vs SVL	0.972	-1.90	2.59	2.45	2.73	1337	< 0.0001
BF vs mass	0.975	-0.31	0.79	0.75	0.83	1491	< 0.0001
BF vs HL	0.973	-0.65	2.75	2.60	2.90	1419	< 0.0001
BF vs JL-QA	0.973	-0.46	2.57	2.42	2.72	1149	< 0.0001

**Fig. 4.** Log-log plots of peak bite-force performance on selected morphological measurements of *Alligator mississippiensis* body and head size. Solid lines, regressions for the data; light dashed lines, 95% confidence bands; heavy stippled lines, scaling predictions based on isometric growth together with respective slopes. (a) Bite force (N) as a function of: (a) TL (cm); (b) SVL (cm); (c) JL-QA (cm); (d) body mass (kg).

Based on the unpaired t -tests, no differences were detected between males and females for any morphometric variable or for absolute bite force when all individuals were examined. Conversely, when only sexually mature individuals were included in the t -tests, males were found to be significantly larger than females for all morphometric variables and for absolute bite force (Table 3). However, with the effect of size removed, bite-force performance did not differ between sexually mature males and females ($F_{1,8} = 0.402$, $P = 0.544$).

DISCUSSION

This study is the first to accurately measure bite forces in adults of a large crocodylian species and shows that such analyses are feasible throughout ontogeny. The findings open the door to a more comprehensive understanding of the form, function, performance and realized feeding niches of these animals. Furthermore, they show the potential for obtaining a similar understanding for all crocodylian taxa.

Table 3. *t*-tests comparing morphometrics and bite force between the sexes for sexually mature adults of *Alligator mississippiensis* only (TL \geq 180 cm). Males are absolutely larger than females in all morphometric dimensions and have greater bite force. The sequential Bonferroni test is for the five morphological measurements plus bite force

Variable	<i>t</i> -value	<i>P</i> -value
TL	5.280	0.0007
SVL	4.907	0.0012
Mass	4.767	0.0014
HL	5.675	0.0085
JL-QA	5.153	0.0013
Bite force	3.275	0.0113

Relationship between growth and bite-force performance

We found that *A. mississippiensis* bite-force performance did not scale to body or head size in the proportions predicted from isometric growth. Furthermore, the performance values did not show a discontinuous mixture of trajectories throughout development. Alternatively we found that the scaling coefficients showed an overlying continuous pattern of positive allometry that is present at all stages of development. It is probable that the disproportionate growth of the skulls, jaws and associated jaw adducting musculature that are manifest throughout development are collectively responsible for most of this pattern and their influence occurs gradually throughout ontogeny rather than sporadically. Notably, Dodson (1975) posited that the major allometric changes that occur to the skulls of *A. mississippiensis* would have their greatest bearing on the performance of jaw adduction. In Dodson's (1975) research the relative growth for 27 dimensions of the skull and jaws of alligators were documented throughout ontogeny. Fourteen of these features were mechanically tied to the closing of the jaws, because they represented cross-sectional areas for accommodating greater jaw adductor musculature, areas of muscle origin and insertion or lines of action. Variant scaling of each (six positive, three isometric and two negative) contributed to the resultant cranial and jaw allometry. Dodson (1975) pointed out that two of these variables in particular would positively contribute to biting performance, and may explain our empirical findings along these lines. The first of these was the relative width of the internal upper temporal fenestration (coefficient = 1.32) that changes from a narrow slit in young animals to a wider, rounded foramen in adults. Functionally this feature defines the cross-sectional area of the jaw closing m. adductor externus profundus (Dodson, 1975; Busbey, 1989). The second key measure related to jaw adduction was the distance from the posterolateral corner of the pterygoid to the medial condyle of the quadrate (coefficient = 1.10), a feature that serves as a proxy for size in the jaw closing m. pterygoideus posterior (Dodson, 1975; Busbey, 1989).

Other variables that might be partially responsible for the allometric pattern of bite force that were documented

include cranial and jaw element fusion and mineralization. During the testing of small alligators (TL < 60 cm), considerable flexion occurred on the balancing side relative to the working side of the jaws during bite-force trials. Conversely, no visually perceptible jaw flexion was observed in adults. It is plausible that this system compliance may be attributable to the unfused nature of juvenile skeletal elements involved with feeding (Romer, 1956; Iordansky, 1973; Dodson, 1975; Monteiro & Lessa, 2000) and/or the hypomineralized, low modulus characteristics of their newly formed skeleton (Currey, 1984). Regardless of the cause, flexion and displacement of the jaws and skull bones may have affected the transfer of force from the muscles to the bite point (particularly from balancing side jaw adductors to the bite point) and contributed to relatively lower resultant biting forces in these animals. This coupled with proportionally higher values in adults could have contributed to the overall positive allometry of biting forces through ontogeny.

The ultimate incorporation of the direct measures of force generation and system compliance with measures of lever mechanics into musculo-skeletal models for *A. mississippiensis* will be required to elucidate how the myriad of factors potentially responsible for the allometric patterns of force production actually contributed to the patterns observed.

Relationship between growth and diet and bite-force performance

Significant changes in the types and physical attributes of prey consumed by *A. mississippiensis* occur during ontogeny (Kellogg, 1929; McIlhenny, 1935; Giles & Childs, 1949; Fogarty & Albury, 1968; Chabreck, 1971; Valentine *et al.*, 1972; Dodson, 1975; Delaney & Abercrombie, 1986). Hatchling alligators eat primarily insects and small fish. At 40 cm TL, crustaceans, frogs and small reptiles are also added to the diet. When lengths approaching 90 cm TL are attained, birds and small mammals become primary constituents in the diet and reliance on small items greatly diminishes. After 150 cm TL is attained, medium-sized animals including mammals and turtles are regularly eaten, the latter of which are crushed using the molariform portion of the dentition. The staples of large alligators, those > 300 cm TL, include large mammals, such as deer and hogs and large turtles. Our research showed that these dietary shifts are achieved without modification to the single continuous allometric trajectory seen throughout life (Fig. 5). In other words, each shift in trophic ecology was not achieved using disproportionately more or less bite force than in the previous stage than would be expected from the overall continuous pattern of increase with size. As such, we do not anticipate that animals in the wild with different diets will deviate from the overall pattern seen in captivity. Nevertheless, the magnitude of their biting forces may vary. We are currently conducting a comparative study of bite forces in alligators in the field to address these considerations quantitatively.

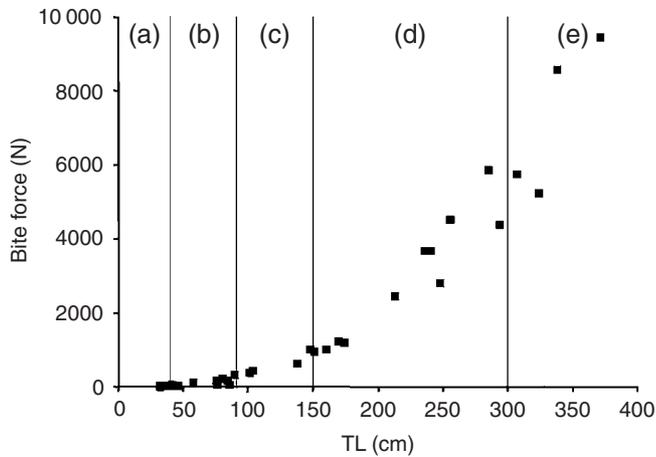


Fig. 5. Total length (TL) vs peak bite-force performance for *Alligator mississippiensis*. Vertical lines, TL at which major ontogenetic dietary shifts are known to occur. These data are based on the literature review by Dodson (1975). Note there are no precipitous changes in slope associated with major dietary shifts. Diet composed of: (a) insects, small fishes; (b) insects, small fishes, crustaceans, frogs, small reptiles; (c) medium-sized fishes, crustaceans, frogs, small reptiles, birds, small mammals; (d) medium to large fishes, snakes, large birds, medium to large mammals, turtles; (e) medium to large fishes, snakes, large birds, turtles, medium to very large mammals.

Why bite-force allometry?

It is difficult to say with certainty why *A. mississippiensis* shows continuous allometric increases in bite force throughout ontogeny. We are currently exploring the hypothesis that requirements for modified tooth morphology during development lead to teeth requiring allometrically greater bite forces to engage successively larger prey. We posit that the needle-like teeth of juveniles would experience higher absolute levels of tissue stress (lower safety factor—how overbuilt a structure is relative to typical loading; Currey, 1984) during use in isometrically scaled-up versions owing to bending moment considerations (Popov, 1968) and thus would be more prone to failure before replacement if such teeth were present in an adult alligator. The fact that the teeth in older individuals are required to function for absolutely longer periods of time due to slower replacement rates (Erickson, 1996b) and that alligators consume relatively larger and more robust prey later in ontogeny would further increase the chance of failure. To ensure a functioning dentition throughout development under such conditions requires morphological attributes to counter these factors. The larger, more robust teeth, with blunter tips seen in adult alligators are dental attributes that have been proven to provide excellent resistance to failure, particularly as hard objects such as bones are encountered (Lucas & Luke, 1984; Fig. 1). A trade-off stemming from the morphological shift away from both sharp and slender teeth is that relatively more force is required to penetrate prey fully. This may be the primary reason for the bite-force allometry seen in *A. mississippiensis*.

How do female and male alligator bite forces compare?

In Dodson's (1975) study on the cranial morphology of *A. mississippiensis*, the sex of the study animals was not known. As such it was indeterminable whether both sexes underwent similar changes over the range of sizes for which they overlap. In the present study, statistical similarity between the sexes at comparable sizes was found for the head and body length measures that were taken. These similarities contributed to comparable bite-force performance between the sexes. (Comparable findings were reported for the spotted hyena *Crocuta crocuta*, the only other animal that has been studied throughout development, Binder & Van Valkenburgh, 2000.) Our results suggest that female and male alligators have similar physical capacities to occupy the same feeding niches during the portion of ontogeny that they overlap in size.

How do bite forces of alligators compare to other taxa?

There have been only a few studies in which quantified measures of bite force have been made on animals. These include empirical analyses of maximal force production (e.g. Snodgrass & Gilbert, 1967; Dechow & Carlson, 1983; Strom & Holm, 1992; Herrel, Van Damme & De Vree, 1996; Herrel, Spithoven, *et al.*, 1999; Binder & Van Valkenburgh, 2000; Herrel, De Grauw & Lemos-Espinal, 2001; Herrel, Van Damee *et al.*, 2001), theoretical maximal values for both living and extinct taxa (Thomason, 1991; Cleuren *et al.*, 1995; Andrews & Bertram, 1997; Erickson, 2001; Rayfield *et al.*, 2001) and sub-maximal force measurements based on bite mark simulations (Erickson *et al.*, 1996). Unfortunately the data from most of these studies are incompatible owing to a lack of standardization for the design and accuracy of the devices, placement of the transducer, types of bites being studied, and morphological and ontogenetic information on the animals being studied. Consequently, the key characteristics that convey different levels of biomechanical performance between taxa cannot be identified at present. Nevertheless, gross generalizations can be made on how bite-force magnitude of *A. mississippiensis* compares absolutely, and in some cases relatively, with other gnathostome vertebrates. A survey of the higher bite forces from the literature (Fig. 6) reveals that adult *A. mississippiensis* show by far the highest bite forces measured for any living animal. Interestingly, the spotted hyena, today's bone crushing champion (Kruuk, 1972), although having the highest relative and absolute bite forces among carnivorans, pales in comparison to the much larger alligator (70 kg vs 371.5 kg; Estes, 1991; Table 1). Also, it seems that alligators can mechanically generate absolutely and relatively higher bite forces than some theropod dinosaurs such as the 1270 kg theropod *Allosaurus fragilis* (Rayfield *et al.*, 2001). This is not to say they were absolutely higher than all dinosaurs. The *A. mississippiensis* bite forces (9452 N) fall short of the sub-maximal bite-force estimates (conservatively

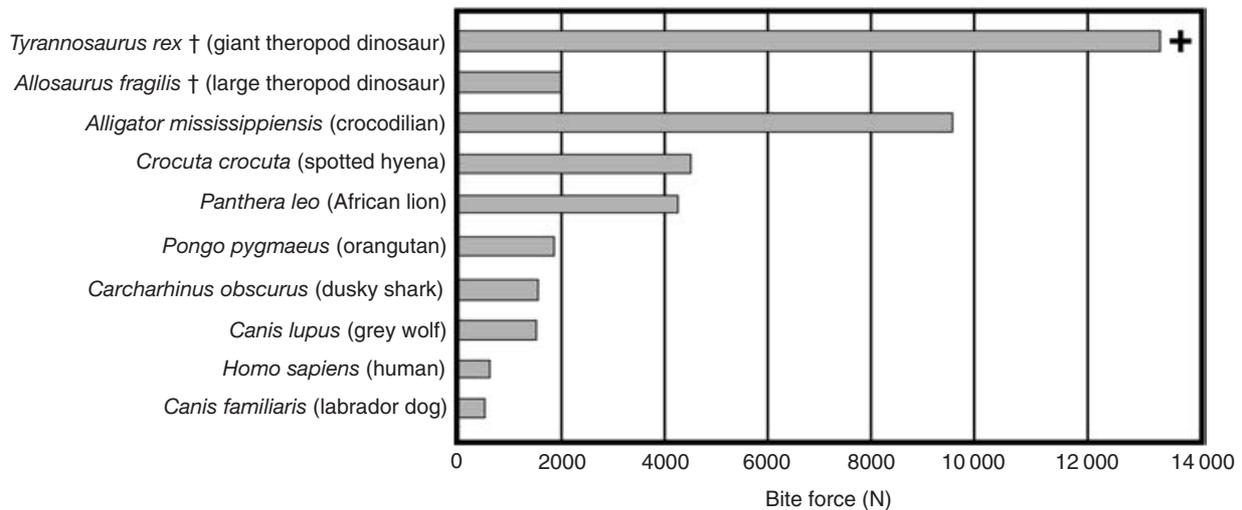


Fig. 6. Comparison of *Alligator mississippiensis* biting forces with some the largest values in the literature for other gnathostomes. These data include empirical measures of maximal biting force made using bite bars and theoretical measures using various modelling techniques (Snodgrass & Gilbert, 1967; Dechow & Carlson, 1983; Thomason, 1991; Strom & Holm, 1992; Binder & Van Valkenburgh, 2000). The data for *Tyrannosaurus rex* are derived from simulations of a single tooth mark that were probably made during sub-maximal biting and thus are considered conservative (Erickson *et al.*, 1996). Note that *A. mississippiensis* bite forces are the highest known for any living taxon and are much higher than those for the 1.4-ton *Allosaurus*. This suggests that crocodilians have relatively higher bite forces than theropod dinosaurs.

13 300 N) for the much larger 5000–7000 kg *Tyrannosaurus rex* (Erickson *et al.*, 1996). Nevertheless, it is probable that 9–11 m giant extinct crocodilians such as *Deinosuchus* (Erickson & Brochu, 1999), *Purussaurus* (Bocquetin *et al.*, 1991; Brochu, 1999), and *Rhamphosuchus* (Brochu, 1999; Head, 2001) did generate biting forces much greater than any theropod dinosaur. Testing this hypothesis will require bite-force measurements on a diversity of crocodilians since coefficients through ontogeny rarely reflect the same pattern seen across size interspecifically (Reiss, 1989).

Testing biomechanical models

Empirical biomechanical performance data are useful in that they can be used to develop or test predictive theoretical models. Cleuren *et al.* (1995) generated a model of the biting mechanics of *C. crocodilus* by integrating muscle force calculations from musculoskeletal anatomy with electromyographical data. Although the model was not based on *A. mississippiensis*, these two taxa show similar cranial morphology owing to their shared alligatoroid ancestry (Brochu, 1999). As such, it was decided to see how close their model came to predicting bite forces for *A. mississippiensis*. Using our regression equations, bite-force predictions were interpolated using the morphological parameters for the caiman specimen on which the model was based (TL = 0.65 m, mass = 1.0 kg) and compared them with the model predictions. Because the authors provide bite-force predictions for a bite point slightly anterior to that in our trials (Cleuren *et al.*, 1995: Fig. 4), a simple moment calculation was made to adjust the model predictions to reflect the 11th

maxillary tooth bite point used in our empirical study. Given these considerations, their model predicts that bite forces normal to the lower jawline should range between 58 and 119 N, with a mean of 92 N. Our regression shows that a comparable length alligator (0.65 m) typically generates a 95 N bite, and an animal of similar mass (1.0 kg), a 110 N bite. It is clear from this comparison that the model of Cleuren *et al.* (1995) agrees remarkably well with our empirical data. This is encouraging in that it indicates that empirically tested models of crocodilian biting may provide reasonable estimates of performance and that a viable model may already exist.

Future investigation

This research shows the potential for determining bite-force performance measures throughout ontogeny in large crocodilian taxa. These data form a vital bridge between anatomical potential and realized ecological niches. A comprehensive understanding of the form, function, performance, ecology and even evolution of crocodilian feeding will be gained from more investigations such as this in the future. Such standardized investigations on crocodilians and other taxa are encouraged.

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