

Comparison of bite-force performance between long-term captive and wild American alligators (*Alligator mississippiensis*)

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Abstract

Nearly all animals show altered musculo-skeletal phenotypes when subjected to captive conditions. Whether such changes affect biomechanical performance is for the most part unknown. In American alligators *Alligator mississippiensis* such modifications include shortened jaws, more robust body form, and broadened heads. Bite-force performance was assessed for a variety of sizes of wild-captured alligator specimens and the results correlated with morphological indices. Bite forces ranged from 217 to 13 172 N, with the latter being the highest value ever measured for a living animal. These data were statistically compared with those for long-term captive specimens using ANCOVA. Bite-force performance showed similar patterns of increase between captive and wild-reared animals, and bite forces with respect to snout–vent length and body mass were statistically indistinguishable. Nevertheless, with respect to head size, captive alligators were found to bite more forcefully than their wild counterparts. These findings illustrate the importance of considering biomechanical performance differences between wild and captive individuals if meaningful ecological ties are to be made. Furthermore, before concluding that wild-reared or captive animals show similar or different biomechanical performances, it is important to understand that standardization to different morphological parameters can reveal conflicting results. Consideration as to which measures are the most germane to the question at hand is essential.

Key words: Crocodylia, biomechanics, bite-force performance, feeding, ecomorphology, phenotypic plasticity, *Alligator mississippiensis*

INTRODUCTION

The use of captive-raised live and/or museum specimens is commonplace in investigations of biomechanical form, function and performance (Dodson, 1975; Alexander, 1977; Carter *et al.*, 1980; Biewener *et al.*, 1983; Lanyon & Rubin, 1985). Because environmental conditions can exert a major influence on the development of the phenotype (Waddington, 1975; Travis, 1994; Schlichting & Pigliucci, 1998), there is overlying concern that these data may provide limited insight into how an organism's anatomy is truly adapted to its niche in the wild. In reptiles, environmentally induced changes in musculo-skeletal morphology have been linked to diet, lighting, enclosure sizes and thermal regimes that differ from natural conditions (Frye, 1981; Arnold & Peterson, 1990; Donoghue & Langenberg, 1996; Lane, 1996). Such variation is particularly manifest among long-lived

reptiles such as crocodylians. Captive individuals are invariably heavier than their wild counterparts and often exhibit relatively shorter jaws and broader heads (Neill, 1971; Grenard, 1991; Fig. 1). Also, in extreme cases (typically geriatric individuals), the alveoli and teeth may show buccal rotation and face outward from the jaws (Erickson, Lappin & Vliet, 2003). The cause(s) of these particular changes in crocodylians is unknown but may be related to dietary deficiencies, mechanical adaptation to atypical loading regimes while feeding, and/or prolonged contact with unnatural substrates (Meers, 1996).

In a previous study, bite-force performance was measured throughout a growth series of captive American alligators *Alligator mississippiensis* in an effort to understand how bite force, tooth morphology and dental pressures collectively contribute to the feeding ecology of these animals (Erickson *et al.*, 2003). The results showed a strong positive correlation of biting force with increase in animal size. The findings were then compared to data in the literature on size-dependent changes in wild-feeding ecology. One drawback to our research

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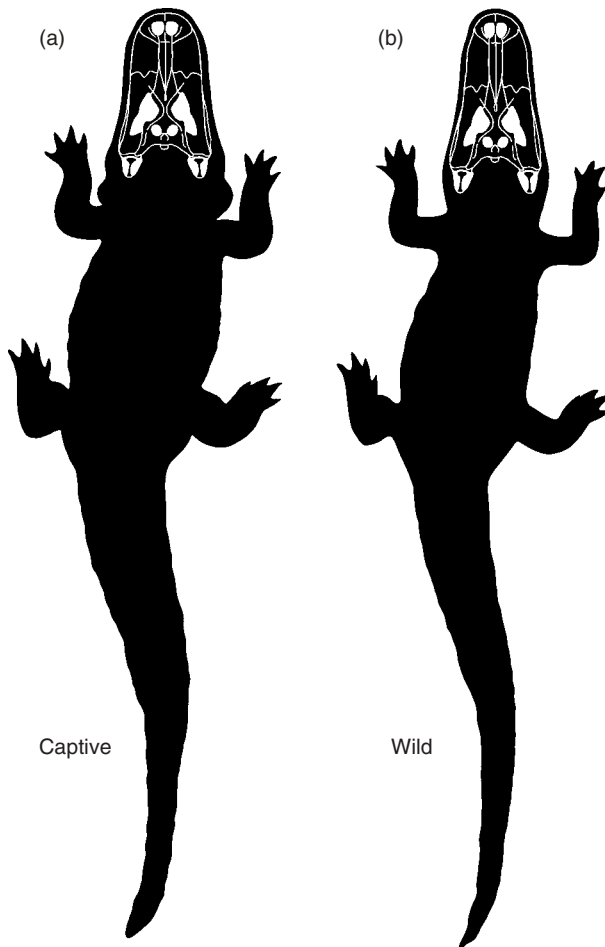


Fig. 1. Comparison of cranial vs body proportions between a typical wild *Alligator mississippiensis* and a long-term captive individual of comparable length. Short jaws, broad head shape, and obesity typify the phenotypically plastic changes that occur in crocodylians reared in captivity (a). Whole body silhouettes are based on photos and measures from a 3.38 m TL, captive specimen from the St Augustine Alligator Farm and Zoological Park, St Augustine, Florida that was used in the bite-force research by Erickson *et al.* (2003) and similar data from a comparable-sized 3.37 m wild-caught specimen from Lake Talquin, Gadsen County, Florida. Cranial outlines are based on a same-sized, long-term captive specimen (UF 61483) and a wild-raised individual (UF 10941). Note that the head width in the post-orbital region is equable when animals are standardized to body length suggesting similar potential for bite-force performance between these two particular animals. However, standardization to jaw length (not shown) would give the captive specimen an absolutely broader adductor region and greater potential for force generation.

was that it was not possible to verify whether the data could be tied to conditions in nature. The aforementioned differences in morphology between wild and captive alligators provided reason to suspect feeding performance might differ. Fortunately, the opportunity arose to test wild *A. mississippiensis* bite-force performance through most of ontogeny (including a fourfold range in snout-vent length (SVL) and nearly a 150-fold range of body masses).

From these data it was possible to compare performance values between animals reared in both environments. The following questions were then addressed. (1) Does bite-force performance differ between captive-reared and wild *A. mississippiensis*? (2) If performance differences exist, which morphological parameters, if any (e.g. body mass, SVL, jaw length) correlate with the differences? By providing answers to these questions, it was possible to ascertain for the first time how the captive-induced morphological abnormalities of crocodylians affect bite-force performance. Additionally it was shown how captive bite-force data can serve as a proxy for data garnered in the wild.

MATERIALS AND METHODS

Twenty-eight wild alligators from northern and central Florida, U.S.A., were used for bite-force experimentation. Specimens were made available for testing by the Florida Fish and Wildlife Conservation Commission, Florida Museum of Natural History (Gainesville), and a nuisance alligator control agent. The alligators were caught by these parties in lakes Griffin (Lake County), Woodruff (Volusia County), Talquin (Gadsen County), and Seminole (Seminole County/Jackson County) for their respective research and/or population control activities. The animals ranged from 44 to 191 cm SVL and 1.65 to 242.7 kg in body mass. The specimens were tested after post-capture rest periods ranging from 4 to 144 h. For our experiments 2 precision bite-force transducers were used (Fig. 2; Erickson *et al.*, 2003). A medium-sized transducer was used to test specimens < 65 cm SVL (< 5.75 kg), and a larger one was used for animals ranging from 65 to 191.5 cm SVL (5.75 to 242.7 kg). The design of both transducers incorporated piezoelectric load washers sandwiched between 17-4 PH stainless steel plates. Leather pieces 6-mm (medium-sized transducer) and 6-mm or 12-mm (large transducer) thick were affixed to the faces of the plates to meet each animal's teeth while it was biting (Fig. 3). The small transducer had a very 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 range (Kistler Instrument Corp., Amherst, NY, Type 9000M057). The large transducer was designed for use on large alligators with broader tooth spacing. We used a sensor array of 4 larger load washers (Kistler Instrument Corp., Type 9000M056) configured so that a bite anywhere on the steel plates would give a precise force measurement within a range of 0–22 250 N. Both load washer types have $\leq 1\%$ error and a pure DC analogue signal with a frequency of display of 10 kHz. The piezoelectric transducers were factory assembled, pre-loaded, and calibrated (Kistler Instrument Corp.) and the accuracy verified following delivery and testing using a 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 a LCD display and peak-detect and

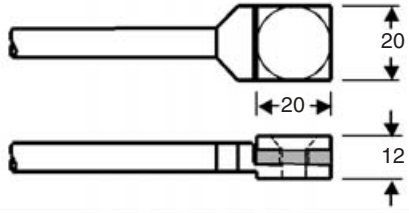
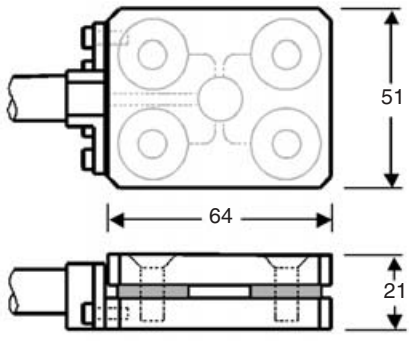
Transducer schematic	Mechanism	Range	Specimens
	Piezoelectric / 1 load washer	0–4450 N	TL = 90–200 cm Mass = 2–50 kg
	Piezoelectric / 4 load washers	0–22250 N	TL > 200 cm Mass > 50 kg

Fig. 2. Design of the two transducers used to measure bite-force performance in wild *Alligator mississippiensis*. The general mechanism, measurement range, and potential size range of animals that can be tested are given for each transducer. Dimensions provided on the transducer schematics are in mm.



Fig. 3. Bite-force trial on a wild-captured *Alligator mississippiensis*. The bite plates from the larger of the two transducers are about to be placed unilaterally between the jaws of this specimen. The placement of the device will be centred about the left, 11th maxillary tooth. Note the leather padding on the faces of the bite plates that protect the animal's teeth from damage during trials.

peak-hold functions. Maximal bite force could be read at the time of each trial.

Alligators were manually secured or strapped to a body-width platform during testing runs to ensure that axial rolling, a source of signal not related to biting force (Grenard, 1991; Busbey, 1994), did not occur. If necessary the animals were encouraged to gape with taps to the top of the snout. The appropriate transducer was then placed unilaterally between the jaws (i.e. between teeth on either the left or right side of the alligator) and centred at the apex of the 11th maxillary tooth, the most prominent tooth at

the back of the jaws (Fig. 3). The sensing of the device upon the teeth typically elicited extremely aggressive, snapping bites by each animal followed by crushing. Although these were defensive bites, kinematically they were similar to those used during prey seizure and processing, and in intraspecific aggression where lateral thrusting of the head is followed by the unilateral seizure of the quarry (Pooley, 1989; Grenard, 1991; G. M. Erickson & K. A. Vliet, pers. obs.), and high bite forces are generated to deliver injurious bites. The shattering of teeth often occurs during such bites in the wild and/or captivity as bones (Erickson, 1996), wooden handling sticks (G. M. Erickson & K. A. Vliet, pers. obs.), or metal objects (McIlhenny, 1935) are seized. Obviously an alligator's dentition is only functional within the range of stress that can be sustained and thus it is probable that the bites recorded approach the maximal possible for these animals. (Note: preliminary data on dental strength using teeth from some of these same wild specimens reveals that the stresses generated during the trials were within *c.* 20% of the rupture point of the crowns.)

During each trial, peak bite force was recorded using a charge-amplifier display. All trials were digitally videotaped for post-testing analysis at 30 frames/s using a Hi-8 digital camera recorder (Sony Inc., Tokyo Japan, DCR-TRV520) (see below). At least 1 high-force, bite was elicited and recorded for each alligator, and depending on their willingness to bite repetitively, 3–5 bites were typically measured. Post-testing analysis of the leather contacts and videos was conducted to verify that recorded bites had in fact occurred on the active surface of each transducer, in parallel with the jaw line, and directly centered about the 11th maxillary tooth. Trials for

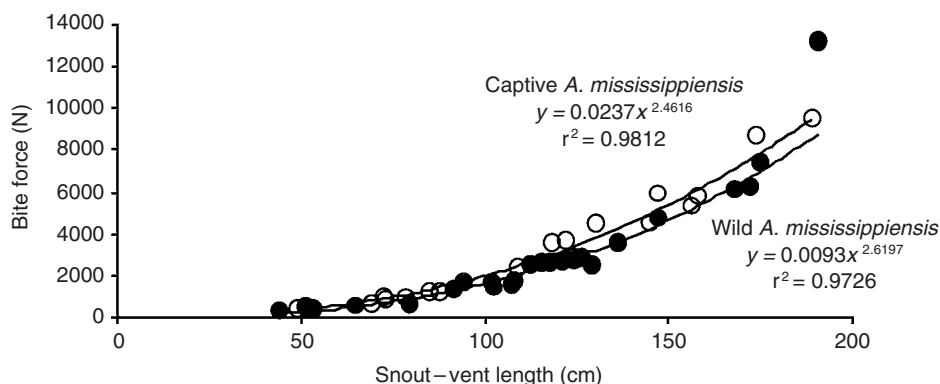


Fig. 4. Comparison of snout-vent length to bite-force performance in captive-reared *vs* wild-captured *Alligator mississippiensis*. Open circles, captive specimens; solid circles, wild animals. Note the similar patterns of increase during ontogeny suggesting that the overall patterns of ontogenetic change in bite force are not heavily affected by phenotypically plastic changes during captivity.

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 post-testing analyses. The highest recorded values were almost invariably made during the first bite. These were used in the subsequent regression analyses. Morphological measurements taken after each bite-force trial matched those taken on the previously tested captive animals. These included SVL (± 1 cm) and 3 measures related to the phenotypically plastic changes that occur during captivity: body mass (M , ± 0.01 kg), jaw length from the lower jaw tip to the quadrate-articular joint (JL-QA, ± 0.5 cm), and head length from snout tip to the dorsal supraoccipital border the (HL-SA, ± 0.5 cm). (There are other measures, e.g. snout-width, which may have usefully compared the captive and wild animals, but none of these were made on the captive sample in our initial bite-force study (Erickson *et al.*, 2003), so were unavailable for the present comparison.)

The bite-force data from the wild alligators in this study and same-length animals from our previous captive animal research ($n = 19$; Erickson *et al.*, 2003) were plotted against each of the raw morphometric variables. Power curves were then fitted so that post-hoc comparisons of bite force could be made for animals of any size (Microsoft Excel 2000, Microsoft Corp., Redmond, WA). The data were log-transformed and inspected for normality. Linear regressions were generated to enable analysis of covariance (ANCOVA). ANCOVA was performed with each continuous morphological parameter as the covariate to examine the effect of captive-rearing *vs* the wild condition on bite-force performance (StatView Version 5 for the PC, Abacus Concepts, Berkeley, CA).

To determine the degree of morphological variance between our wild and captive samples we compared mass, jaw length, and head length with respect to a standardized measure of body size (SVL). We plotted the raw data and made power curves from which relative comparisons were possible. For statistical comparisons we log-transformed the data and inspected them for normality. The residual values of each variable were calculated from regressions of each variable on SVL, and then were used in unpaired *t*-tests.

Table 1. Summary of ANCOVA results showing effect of captive *vs* wild rearing on bite-force performance of *Alligator mississippiensis*. Abbreviations for morphological variables as in text

Covariate	<i>F</i> value	<i>P</i> value
SVL	2.466	0.1244
Mass	1.360	0.2506
HL-SO (head length)	3.005	0.0909
HL-QA (jaw length)	7.175	0.0126

RESULTS

Twenty-four of the 28 wild alligators tested produced properly positioned, aggressive bites. Force values ranged from 216.6 (48 lbs) to 13 172 N (2,960 lbs), the latter being the highest bite force ever measured for a living animal (Erickson *et al.*, 1996). ANCOVAs showed a strong positive effect of size ($P < 0.0001$) upon all morphometric covariates. Comparisons of power curves between these data and those for captive alligators of comparable sizes revealed similar trajectories throughout ontogeny (Fig. 4). The effect of captive *vs* wild-rearing on bite-force performance was not significant ($P > 0.05$) with respect to SVL and body mass (Table 1; Fig. 5). Conversely, bite force significantly differed between captive-reared and wild alligators with respect to jaw length (HL-QA, $P = 0.013$, Table 1; Fig. 5) and nearly so with respect to head length (HL-SO, $P = 0.09$, Table 1; Fig. 5).

The comparison of cranial morphology between the wild and captive samples revealed that the latter have shorter jaws for a given SVL (unpaired *t*-test: *t*-value = 3.329, $P = 0.0021$; Fig. 6) and that captive alligators are considerably heavier than wild counterparts of equal size (unpaired *t*-test: *T*-value = 6.870, $P < 0.0001$, Fig. 6). Head lengths were on average slightly longer in the wild specimens but were statistically indistinguishable from the captive sample (unpaired *t*-test: *t* value = 0.831, $P = 0.411$).

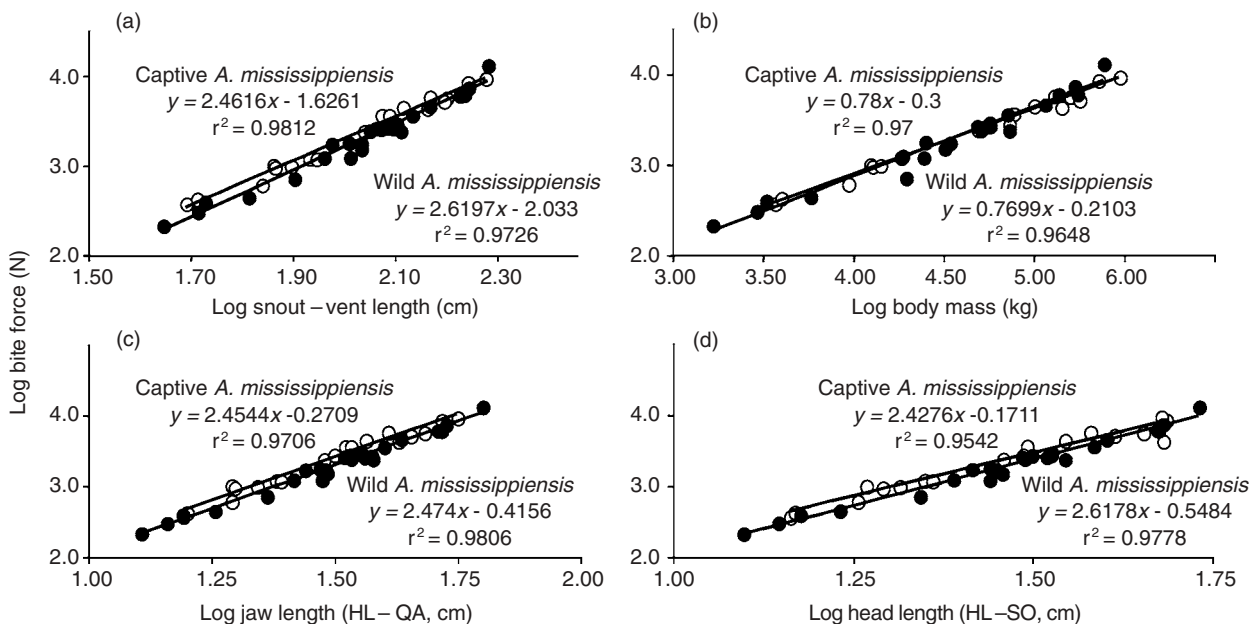


Fig. 5. Comparison of various morphological parameters vs bite-force performance between captive-reared and wild *Alligator mississippiensis*. Open circles, captive specimens; solid circles, wild animals. Comparisons of bite-force performance with respect to SVL (a) and body mass (b) revealed statistically indistinguishable results at a 0.05 level of significance. Comparison with respect to HL-QA (c) revealed significant differences, with captive alligators biting more forcefully for any given jaw length. Comparison with HL-SO (d) revealed nearly significant differences ($P = 0.09$; Table 1) with captive specimens biting more forcefully on average than wild counterparts for any given head length.

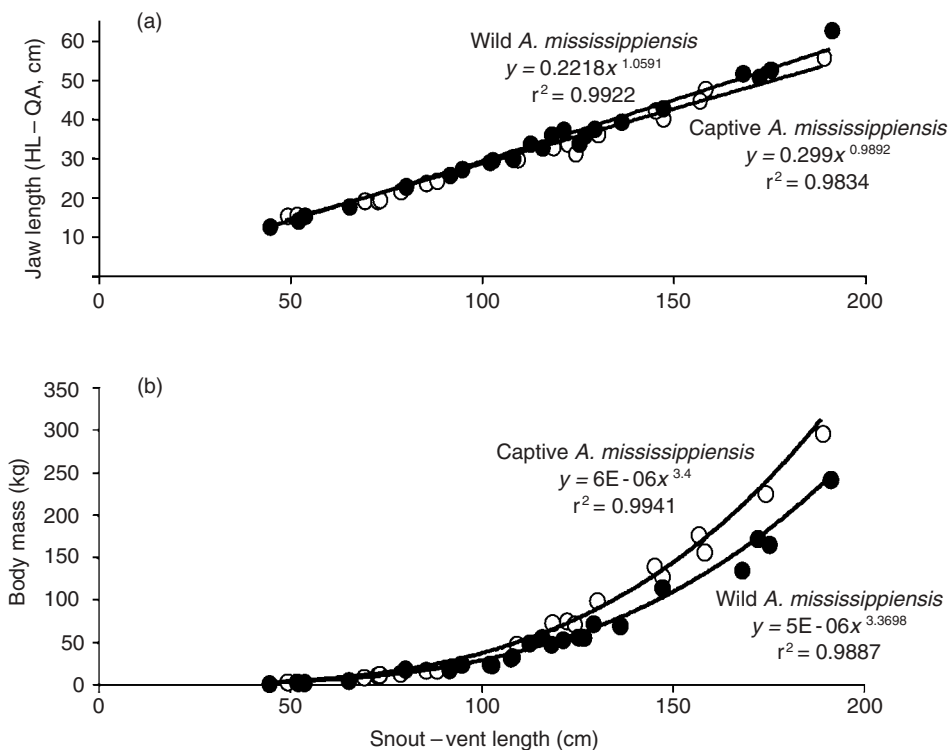


Fig. 6. Comparisons of jaw length and body mass with respect to SVL between captive-reared and wild *Alligator mississippiensis* showing phenotypically plastic modifications. Open circles, captive specimens; solid circles, wild animals. (a) Long-term captive-raised alligators from our previous research (Erickson *et al.*, 2003) have shorter jaws than wild individuals of comparable SVL from the present examination (unpaired t -test: t -value = 3.329, $P = 0.0021$). Large adults (SVL > 185 cm) in the wild have *c.* 7% longer jaws. (b) Captive alligators are considerably heavier than wild counterparts of equal length (unpaired t -test: t -value = 6.870, $P < 0.0001$). Large captive adult alligators (SVL > 185 cm) are *c.* 25% heavier than wild counterparts of equal length.

DISCUSSION

A broad diversity of animals, including insects (Bernays, 1986), fishes (Wainwright, Osenberg & Mittelbach, 1991), amphibians (Collins & Cheek, 1983), reptiles (Arnold & Peterson, 1990), birds (James, 1983), and mammals (Watt & Williams, 1951; Moore, 1965; Epstein, 1971; Patton & Brylski, 1987) can exhibit musculo-skeletal phenotypic plasticity when exposed to abnormal environmental conditions. As such, problems can arise when using captive-raised organisms as proxies for wild counterparts. The most famous example of this was the erroneous identification of 'new' carnivoran taxa (e.g. lions) on the basis of skeletal materials from zoo-reared specimens with unusual cranial and jaw proportions (Hollister, 1917, 1918). Hollister (1917) posited that the misshapen heads of these animals resulted from the unnatural combination of disuse of some muscles coupled with the continued use of others (also see Wolfgramm, 1894; Epstein, 1971). This promoted plasticity in which normal skeletal manifestations degraded or failed to develop, whereas others were maintained or showed proliferation. Besides confounding phylogenetic analyses, musculo-skeletal changes such as these can have the added downfall of altering normal performance during feeding (Hollister, 1918). Like captive carnivoran mammals (Wolfgramm, 1894; Hollister, 1918; Epstein, 1971), artificially-reared *A. mississippiensis* are often obese and show broad, shortened jaw proportions that may affect biomechanical capacities (Neill, 1971; Grenard, 1991; Meers, 1996). Our attempts to test this possibility revealed power equation trajectories (Fig. 4) and regression slopes (Fig. 5) for wild specimens nearly identical to those found in long-term captive specimens. This suggests that captive rearing of *A. mississippiensis*, does not substantially alter the patterns by which natural increases in bite force occur during development. In other words, the phenotypically plastic changes to the crania and bodies of *A. mississippiensis* during captivity, including up to 7% shorter jaws and 30% greater mass (Fig. 6), do not send bite-force trajectories down drastically different scaling pathways. Consequently any of the parameters studied in this examination (snout-vent length, body mass, jaw and head length) can be used as a rough proxy for the patterns of change through ontogeny that occur in the wild. This is not to say all values are identical in each comparison when animals of equal size are contrasted (see below), only that their proportional increases in biting force are similar as greater size is attained.

Although the patterns of increase in bite force between wild and captive-reared *A. mississippiensis* are similar throughout ontogeny, direct comparison of same-sized individuals reveals important differences between some morphological parameters. Statistically significant differences were found for the relationship between bite-force performance and jaw length (BF-QA). The relationship to head length (HL-SO) also approached significance ($P = 0.09$; Table 1). This suggests that captive alligators bite more forcefully than their wild counterparts with respect to jaw length and that phenotypic plasticity

stemming from captivity can and does affect biomechanical performance during feeding in *A. mississippiensis*. How does the shortening of jaws, acquisition of more robust bodies (Figs 1 & 6) and associated cranial broadening (Neill, 1971; Grenard, 1991, unquantified but observed in the present research), contribute to the greater biting capacities in captivity? At this juncture, we can only venture hypotheses to be tested. Nevertheless, both of the following are plausible explanations. First, the relatively broader heads of captive alligators may afford greater space for jaw-adducting muscles for any given jaw length relative to wild specimens (Fig. 1; Erickson *et al.*, 2003). Second, it is also feasible that the shortened jaws of captive alligators leaves the 11th maxillary teeth closer to the quadrate-articular joint, the fulcrum of this first-order lever system (Walker & Liem, 1994), thus providing greater mechanical advantage during biting (Cochran, 1982).

Unlike jaw length, comparisons of bite-force performance with respect to body mass and SVL showed comparable values between wild and captive-reared specimens (Fig. 5). This result shows the importance of parameter choice when comparing performance measures between wild and captive data sets. It is feasible in the same comparison to show superiority, equality, and inferiority in performance, depending on which variables are considered. As such, researchers need to be cognizant of these possibilities when designing experiments to compare performance between groups and may wish to use the present body of research as a guide in so far as the biomechanics of crocodylian feeding is concerned.

Why do these parameters (body mass, SVL) show similarity when jaw length measures showed captive animals to have superior bite-force performance? We suspect there are two independent reasons. First, the greater relative bite force of captives for a given jaw length is negated when standardized to body mass since captive individuals are almost invariably obese and thus have a greater relative volume of adipose tissue contributing to mass but not biting performance (Fig. 1).

The same effect occurs when standardization is made to SVL, but for a different reason. When standardized to SVL, and not jaw length, the relative width difference between skulls from wild and captive animals are largely negated and the aforementioned mechanical superiority of the feeding apparatus of the captive animals no longer manifests itself (Fig. 1). In other words the heads of the animals being compared are approximately equal in width and thus can both house similar volumes of jaw adductor musculature and achieve similar performance.

Implications

Even though almost our entire body of knowledge on musculo-skeletal biomechanics is based on captive animals, studies comparing wild vs captive-reared counterparts are virtually non-existent. The present research shows that phenotypic plasticity can lead to significant

biomechanical differences in performance that may confound extrapolations to wild animals and inferences of 'normal' performance. As such, more comparative analyses such as these are encouraged on other animals for which biomechanical performance has only been measured in captivity.

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