Does Bite-force Performance Follow the Law of the Lever?

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ABSTRACT

The Law of the Lever (Archimedes in antiquity), when applied to vertebrate jaws, predicts that bite force should be strongest towards the back of the jaws close to the jaw joint (fulcrum) and weaker farther from the joint. Using an empirical *in vivo* approach, we evaluated whether bite force in *Elgaria multicarinata* (Southern Alligator Lizard) follows a pattern based on the Law of the Lever. We measured bite force using a custom-built force transducer. Trials were video recorded, and for each trial we measured the bite out-lever, defined as the distance from the jaw joint to the point of bite force application. We then assessed the empirical data with a predictive model based on the Law of the Lever. Our results indicate that bite force in *E. multicarinata* is not consistent with model predictions. Surprisingly, bite force decreases more than predicted as bite out-lever increases (i.e., towards the jaw tips). This may be related to the unusual courtship behavior of alligator lizards, during which the male grips the female's head in his jaws, often for many hours. In ongoing research, we are testing additional species, including other lizards and alligators, which will shed light on whether *E. multicarinata* is an unusual case or representative of a broader pattern among at least some lizard lineages.

INTRODUCTION

Bite force is a measure of animal performance that is relevant to a variety of behaviors. In many species, bite force plays a role in feeding habits, as well as social interactions, including fighting, territoriality, dominance, and/or courtship (Lappin and Jones 2014). Quantifying bite-force performance can give insight into the facilitators and limiters of aspects of an animal's ecology and behavior. Bite force has been measured in a variety of animals, with lizards being one of the most studied groups, due largely to their reliance on biting for a variety of behaviors and their experimental tractability (Lappin and Jones 2014).

In vertebrate jaws, lever mechanics (i.e., Law of the Lever) indicate that bite force should be relatively low at bite points far from the jaw joint near the jaw tips, and be greater at positions closer to the jaw joint at the back of the jaws. Furthermore, the decrease in bite force with increasing bite out-lever should follow a predictable pattern (i.e., slope of relationship between bite force and bite out-lever). Using the Southern Alligator Lizard (*Elgaria multicarinata*), we tested the hypothesis that bite force in this species follows the Law of the Lever by comparing empirical measurements of *in vivo* voluntary bite force to a model based on the law.

METHODS

Model: An equation based on the Law of the Lever was used to produce a model predicting how bite force should vary with bite out-lever. At a bite out-lever of 50%, representing the posterior-most possible bite in the model, the standardized bite force is set at 1.0. As bite out-lever is increased, predicted standardized bite force decreases according to the equation (Fig. 1A). To remove size and produce a linear relationship for statistical comparison to empirical data, the inverse of bite out-lever was used in analyses and for illustration (Fig. 1B).

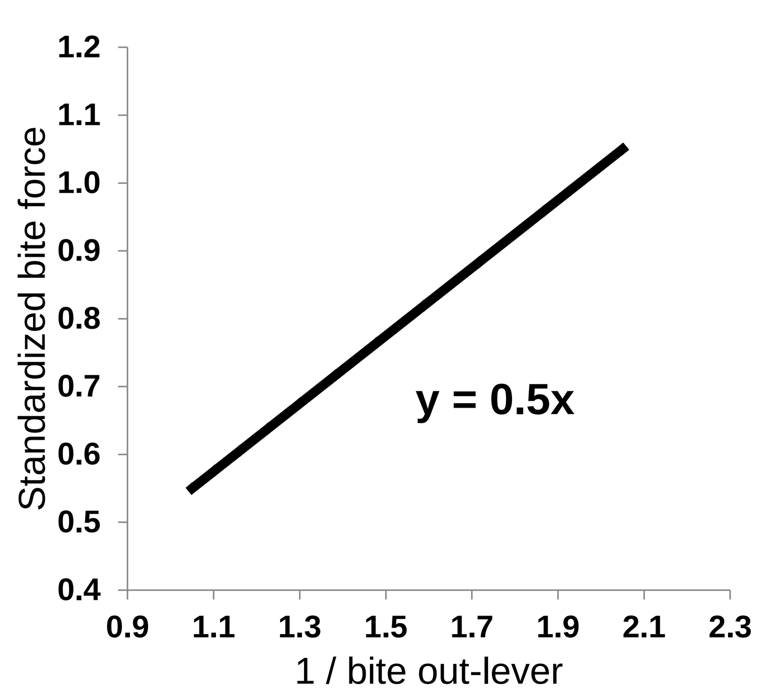
Figure 1. (A) Equation of Law of the Lever modified to represent bite force in most vertebrates (i.e., 3rd order lever). (B) Tabular and graphical representation of theoretical model representing predicted standardized bite force as a function of bite out-lever.

A

$$\text{bite force 2} = \frac{\text{(bite force 1) (bite out-lever 1)}}{\text{bite out-lever 2}}$$

B

Standardized bite force	Bite out-lever	1 / bite out-lever
1.00	50%	2.00
0.91	55%	1.82
0.83	60%	1.67
0.77	65%	1.54
0.71	70%	1.43
0.67	75%	1.33
0.63	80%	1.25
0.59	85%	1.18
0.56	90%	1.11
0.53	95%	1.05
0.50	100%	1.00



Specimens: We examined *Elgaria multicarinata* (Southern Alligator Lizards) for this study. We were able to acquire multiple measurements of bite force at various bite out-levers for six individuals. The specimens were wild-caught locally and maintained in the Cal Poly Pomona Vivarium. In addition to measuring bite force, we measured the body size (snout-vent length and body mass) and head size (length, width, depth) of each specimen.

Bite-force performance: Bite force was measured using a custom-built piezoelectric force transducer (Lappin and Husak 2005, Figure 2). We used leather strips as the biting substrate, to provide a naturalistic biting surface, to protect the teeth of the specimens, and to provide a discreet point for measuring the bite out-lever for each trial (Lappin and Jones 2014). The trials were recorded using a Sony DCR-SX45 video camera. Output from the transducer was displayed on a charge amplifier and recorded. We performed at least six trials for each individual. During the trials, we targeted both the anterior and posterior of the jaws in random order. We provided the specimens with one minute of rest between each trial.

Video Analysis: Using AVS Video Editor, we grabbed frames at the moment that bite force was applied to the transducer for each trial. From the frames, we used Image J to measure the bite out-lever as the distance from the ventral extent of the tympanum, a landmark for the quadrate-articular jaw joint, to the midpoint of the leather strip where the bite was applied.

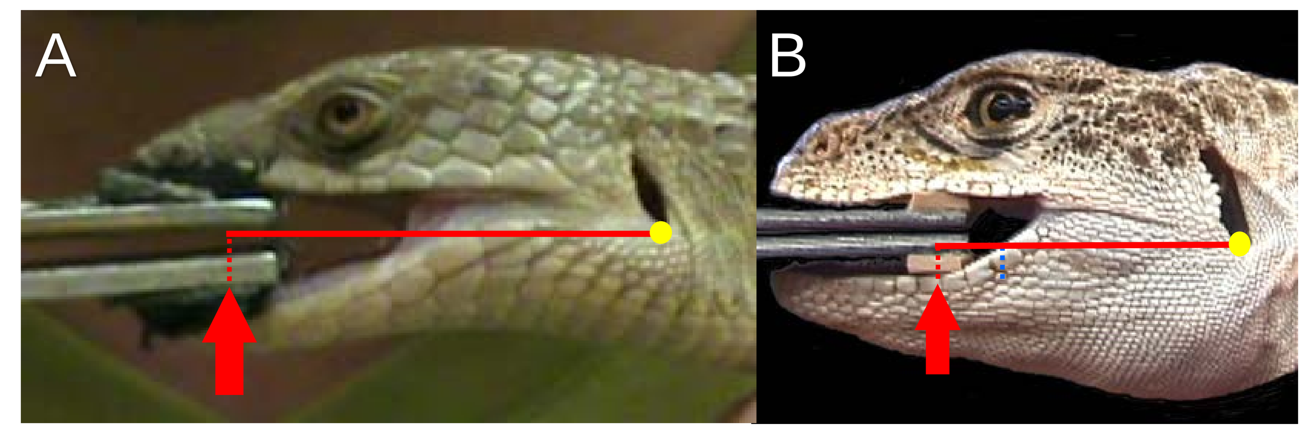


Figure 2. (A) *Elgaria multicarinata* and (B) *Gambelia wislizenii* biting force transducer. Red line indicates bite out-lever, and thick red arrow represents bite force vector.

Standardization: So that the empirical data could be directly compared to the model, we standardized *in vivo* bite force and bite out-lever for each trial for each specimen. Bite force was standardized, separately for each individual, by dividing the bite force for each trial by the strongest bite force measured among all trials. Bite out-lever was standardized by dividing the measured bite out-lever by head length. The inverse of the standardized bite out-lever data was used for graphical and statistical comparison to the model.

Statistical Analysis: For each specimen, we determined the slope ± 95% CL for the regression of standardized *in vivo* bite force on standardized bite out-lever (i.e., 1 / bite out-lever). If the slope of the modeled relationship (y = 0.5x) fell outside of the 95% CL, then that specimen was determined to exhibit a bite force profile that departs significantly from Law of the Lever model predictions.

RESULTS

The slope of the relationship between bite force and bite out-lever differed significantly from the model predictions for two of six of the specimens (Fig. 3, Table 1). For the two *E. multicarinata* specimens that departed from model predictions, the pattern was one of greater than predicted loss of bite force as bites were positioned increasingly farther from the jaw joint (i.e., greater bite out-lever). Notably, the two specimens that differed from model predictions exhibited by far the strongest predictive power of bite out-lever on bite force ($R^2 \geq 0.9$).

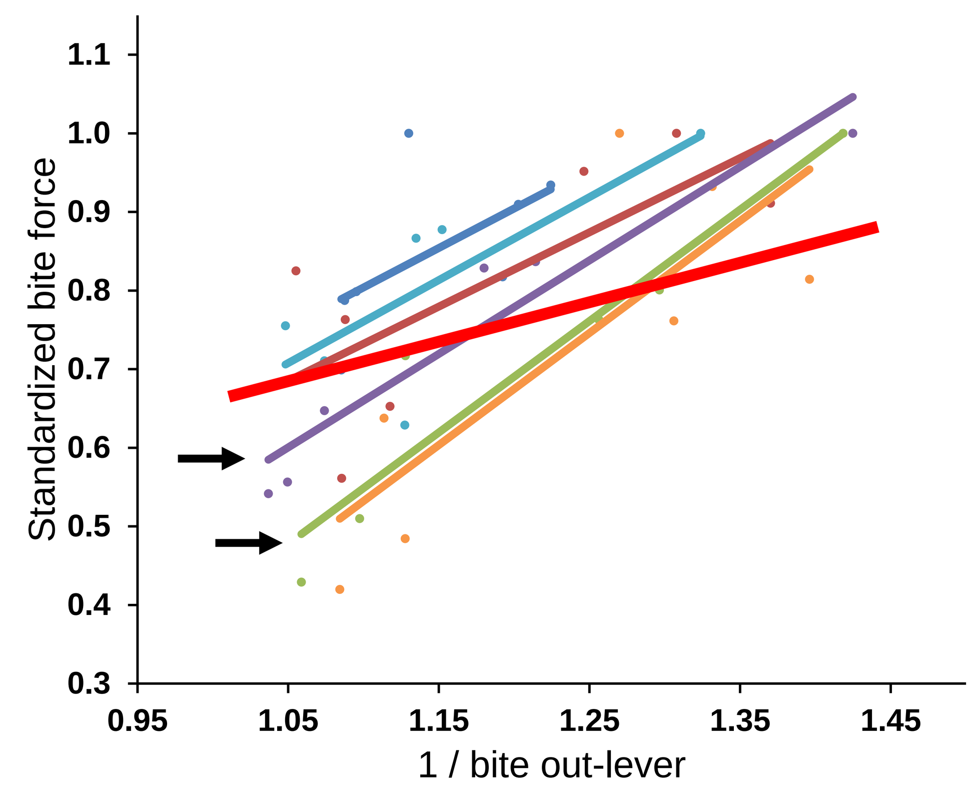


Figure 3. Regressions for six individual lizards (thin lines) and model predictions (thick red line). Black arrows indicate specimens that statistically differed from model predictions.

Table 1. Slope of standardized bite force as a function of bite out-lever. Specimens in bold significantly differed from model predictions (slope = 0.5).

Specimen	Slope	95% CL	R^2
0185-01	1.425	0.201 – 2.650	0.64
0186-01	1.004	-0.604 – 2.611	0.34
0186-03	0.946	-0.058 – 1.950	0.54
0188-03	1.055	-0.184 – 2.294	0.58
0189-01	**1.417**	**0.745 – 2.090***	**0.90**
0189-02	**1.189**	**0.703 – 1.676***	**0.92**

Figure 4. *E. multicarinata* courtship behavior.

DISCUSSION

Our results indicate that *E. multicarinata* may not follow the Law of the Lever, as the two specimens showing the strongest relationship between bite force and bite out-lever significantly differed from model predictions. For these cases, we were surprised to find that bite force decreased more than predicted as bite out-lever increases, meaning that these lizards disproportionately lost force closer to the tips of the jaw. In experiments with geckos, we found that they also do not follow the Law of the Lever, but they display the opposite pattern – as bite out-lever increases more force is retained than predicted by the model. We are testing additional lizard species, as well as alligators, in part to determine whether *E. multicarinata* represents an unusual case. We suspect that the pattern for *E. multicarinata* might be associated with its unusual courtship behavior, which involves the male gripping the head of the female with its jaws for many hours (Fig. 4).

Literature Cited

Lappin AK, Husak JF. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). American Naturalist 66: 426–436.

Lappin AK, Jones MEH. 2014. Reliable quantification of bite-force performance requires use of appropriate biting substrate and standardization of bite out-lever. The Journal of Experimental Biology 217: 4303-4312.

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