To Crush or to Engulf Your Victim

A Biomechanical Trade-off in Lizards versus Snakes

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ABSTRACT

Biological trade-offs among organisms are a fundamental part of organismal function. In this project, we examine the performance consequences of cranial kinesis by comparing bite force between snakes and lizards. Cranial kinesis is a biomechanical condition in which different components of the skull are mobile relative to each other, and snakes, which swallow their prey whole, exhibit the greatest degree of cranial kinesis among tetrapods. This allows them to swallow prey whole that is large relative to their head, with some able to swallow prey of greater mass than the snake itself. However, we hypothesize that this incredible and highly specialized behavior compromises snakes' ability to generate high bite forces. Lizards, which have far less kinetic skulls, are expected to show relatively great bite-force performance. Though the lesser degree of cranial kinesis of lizards reduces their ability to swallow large prey, it allows for greater bite force used to process prey into smaller pieces for swallowing. To test our kinesis versus force hypothesis, we used a piezoelectric force transducer to measure snake and lizard bite forces. Our results support the hypothesis that, for a given head size, lizards bite significantly harder than snakes. In addition, we found that vipers (venomous snakes including rattlesnakes and relatives [Viperidae]) and one death adder in our study have a significantly weaker bite than non-venomous snakes. This lends further support to our hypothesis, as vipers have the most kinetic skulls among snakes. Further research is warranted that (1) includes additional snake taxa exhibiting different degrees of cranial kinesis, and (2) integrates quantification of cranial kinesis, perhaps by surveying the natural history literature for maximum recorded size of prey ingested.

INTRODUCTION

A general principle in lever-based biomechanical systems (i.e., most musculo-skeletal systems) is that trade-offs exist between different aspects of performance. For example, consider the limb morphology of a deer versus a badger. The deer has long limbs bones with the major limb muscles concentrated close to its body. This results in a deer having high performance in terms of running speed, but it compromises its ability to generate high forces such as those needed for digging in hard soil. The badger, with short limbs and muscles extended well out from the body, is able to generate the high forces required for digging, but this compromises its ability to run quickly. Thus, comparing these two animals, we see a classic trade-off, namely that between force and speed.

Whereas lizards usually process their prey prior to ingesting it (Figure 1A), snakes are well known for their ability to swallow prey whole that are much larger than their own head (Figure 1B). This is possible because snakes exhibit an exceptional degree of cranial kinesis (Kardong, 2006; Figure 1C). Cranial kinesis refers to independent mobility among different parts of the skull, which is seen in many fish and reptiles (including birds), but not mammals. Although some lizards show a modest degree of cranial kinesis, it is extremely developed in snakes. Because cranial kinesis is typically associated with elongated, slender skeletal elements of the skull and jaws, as well as relatively loosely articulated skeletal elements, we predict that a trade-off exists between bite-force performance (i.e., force) and cranial kinesis (i.e., flexibility). Therefore, we expect that snakes have a significantly weaker bite than lizards .

In addition, there exists within snakes an appreciable range in the degree of cranial kinesis. Among all snakes, the venomous vipers (rattlesnakes and relatives) have the most kinetic skulls (Cundall, 1987), far more so than non-venomous snake species native to California (Figure 1D). Therefore, we also predicted that, among native California snakes, venomous species (i.e., rattlesnakes) would have a significantly weaker bite than non-venomous species.

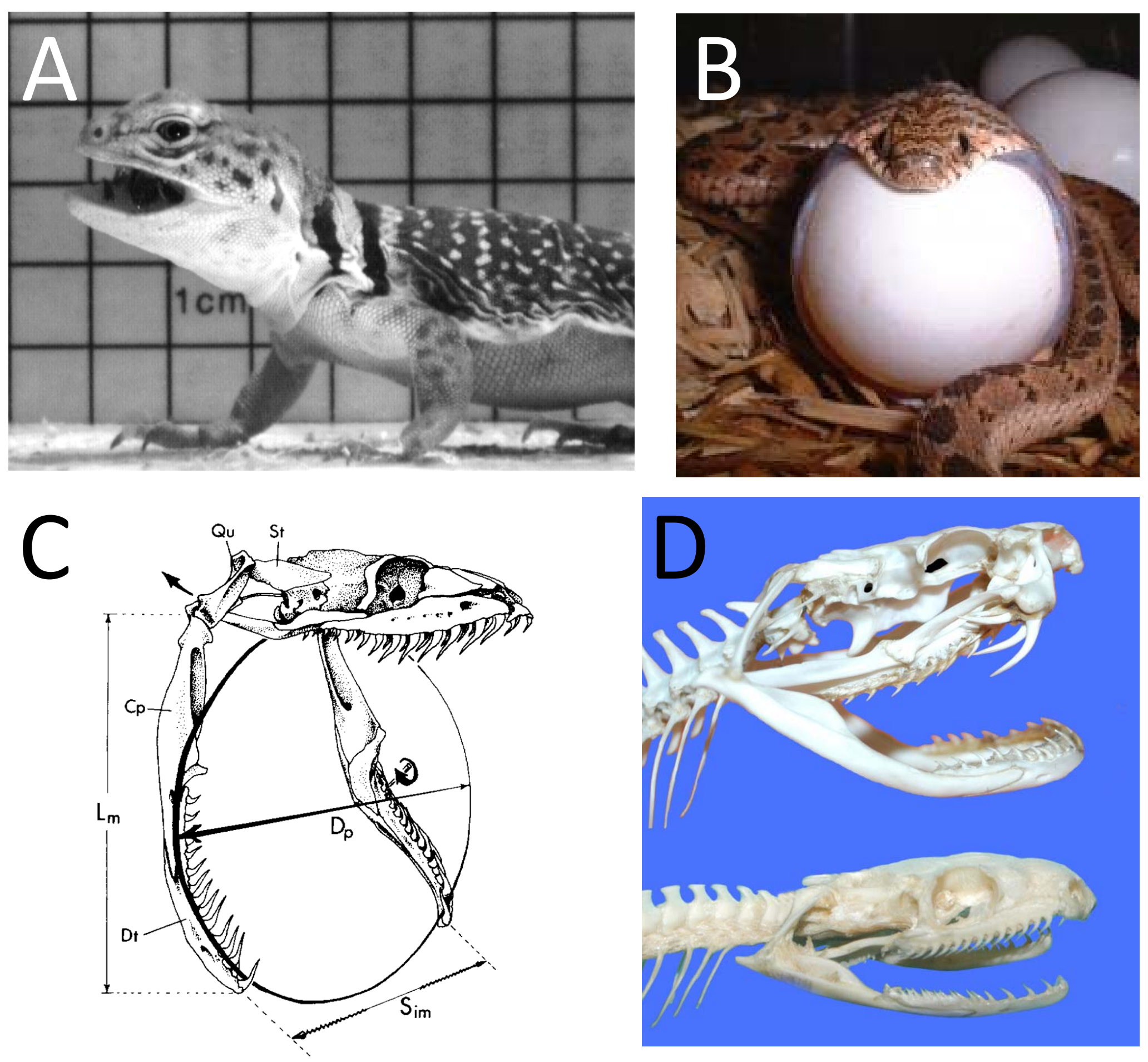

Figure 1. (A) Collared lizard (*Crotaphytus*) processing a beetle prior to ingesting it. (B) Egg-eating snake (*Dasypeltis*) swallowing a bird egg several times the size of its own head. (C) The swallowing ability of snakes is due to their well developed cranial kinesis. For example, in snakes the quadrate bones (Qu) are highly mobile, and there is no bony symphysis connecting two halves of the lower jaw. This allows the snake to move each side of its mandible independently, both antero-posteriorly and laterally. (D) Comparison between a venomous viperid (top) and non-venomous colubrid (bottom). Note relatively longer, more slender skeletal elements of the viperid, which can swallow larger prey than non-venomous snakes.

HYPOTHESES

- ➢ General Hypothesis – There is a trade-off between cranial kinesis and bite force.
- ➢Hypothesis 1 – For a given head size, snakes, which have far more kinetic skulls than lizards, will have lower bite-force performance than lizards.
- ➢Hypothesis 2 – Among different snake species, bite force is inversely related to the degree of cranial kinesis. Specifically, we predict that vipers, which have the most kinetic skulls of all snakes, have a weaker bite than non-venomous snakes.

METHODS

Specimens: We examined several species of lizards and snakes. Lizards included collared lizards (*Crotaphytus*), leopard lizards (*Gambelia*), alligator lizards (*Elgaria*), spiny lizards (*Sceloporus*), and geckos (*Gekko*). Snakes included king snakes (*Lampropeltis*), gopher snakes (*Pituophis*), rosy boas (*Charina*), as well as rattlesnakes (*Crotalus*) and a venomous death adder (*Acanthophis*). All of the lizards are native to California, except *Gecko*. And all of the snakes are native to California, except *Acanthophis*.

Morphometrics: To quantify body size, we measured snout-vent length, which is the distance from the tip of the snout the vent, the common opening of the waste and reproductive orifices. We also measured a series of head morphometrics using digital calipers (Lappin et al., 2006; Figure 2). For the analyses, we focused on head dimensions because the head is the functional unit that generates bite-force output.

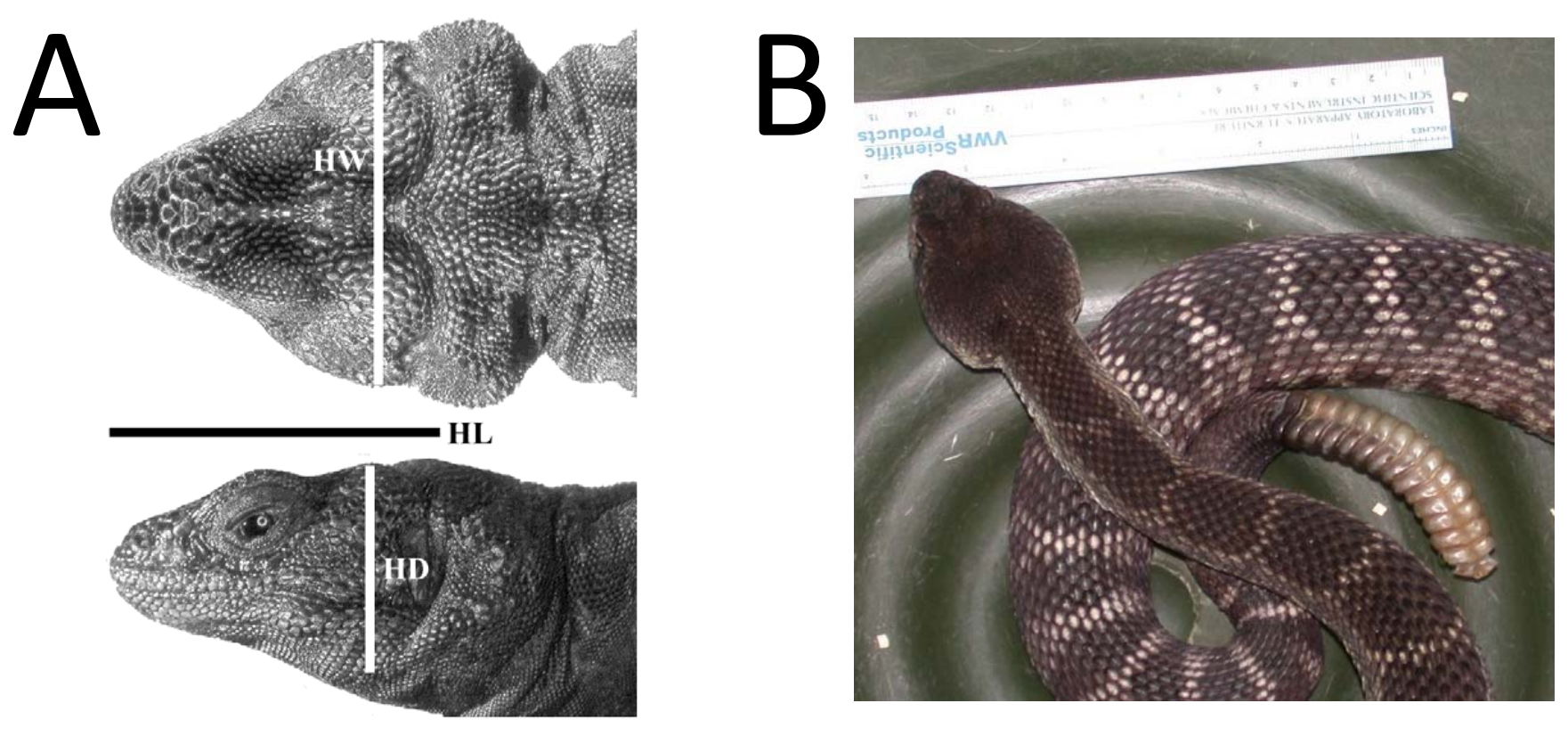

Figure 2. (A) Linear morphometrics measured include snout-vent length (not shown), head length (HL), head width (HW), and head depth (HD). (B) For venomous snakes, we took images of the snake together with a ruler and used ImageJ (v 1.43, NIH) to make the measurements.

Bite-force performance: Bite force was measured using two custom-built piezoelectric force transducers (Lappin and Husak, 2005; Figure 3). For lizards, leather was adhered to the biting surface, and specimens were encouraged to bite the transducer as a defensive response. For snakes, fresh mouse skin was placed over the biting surface, and snakes bit the transducer as a feeding response. Output from the transducer was displayed on a charge amplifier and recorded. We attempted to perform three trials per individual, though some individuals only would perform for one or two trials. For each individual, the greatest bite force measured among trials was used for analyses.

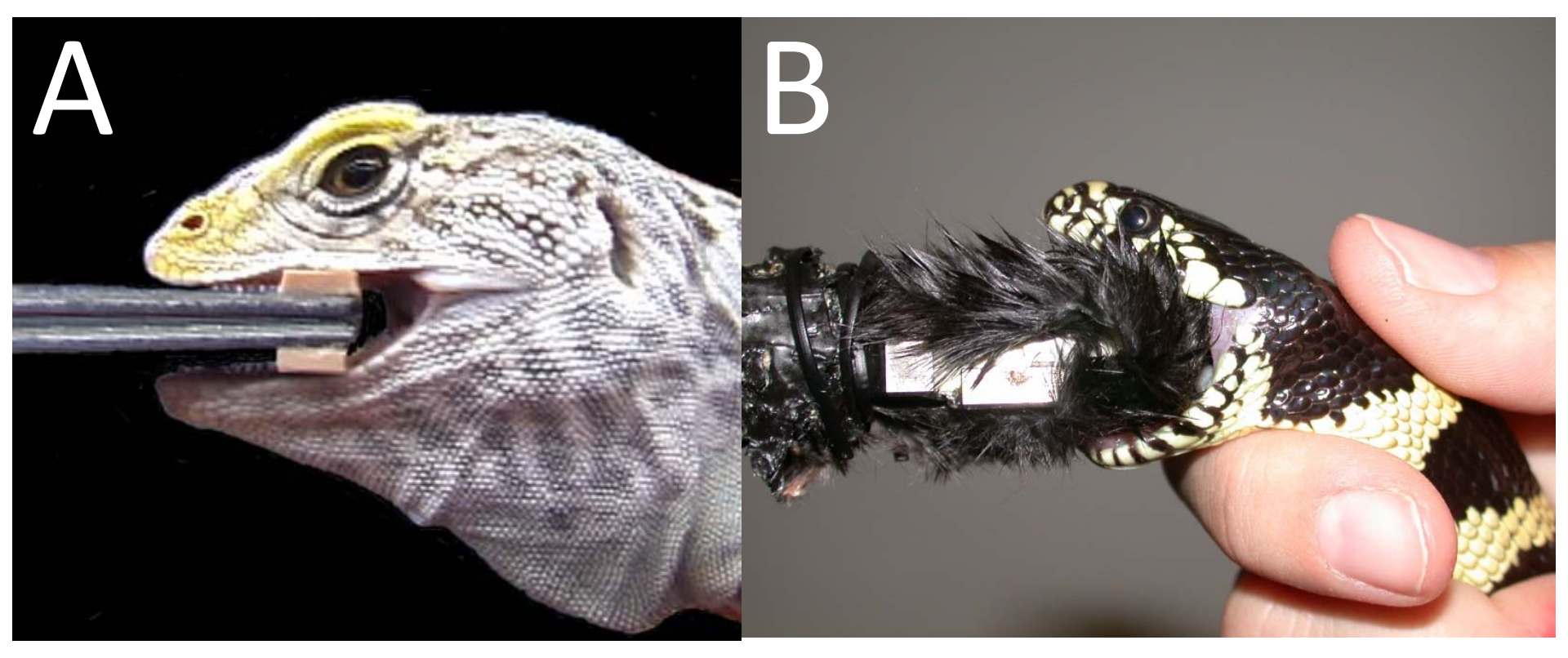

Figure 3. (A) Collared lizard (*Crotaphytus*) biting parallel bars of a custom-built piezoelectric force transducer. The lizard's bite generates force that produces an output on a digital charge amplifier. (B) King snake (*Lampropeltis*) biting stacked plates of custom-built piezoelectric force transducer designed with a handle so that venomous snakes can be tested. Note fresh mouse skin covering plates.

Statistical Analysis: We found that none of the variables were normally distributed. Therefore, we used the non-parametric Wilcoxon (Mann-Whitney) test to test for differences between groups.

To test the hypothesis that snakes cannot bite as hard as lizards, we performed a Wilcoxon rank-sum test comparing bite force between our sample of each group. To take into account variation among individuals in head size (i.e., head length), we ran a Wilcoxon rank-sum test on residuals of bite force on head length (calculated from entire sample of snakes and lizards).

To test the hypothesis that vipers cannot bite as hard as non-venomous snakes, we performed a Wilcoxon rank-sum test comparing bite force between our sample of each group. To take into account variation among individuals in head size (i.e., head length), we ran a Wilcoxon rank-sum test on residuals of bite force on head length (calculated from entire sample of snakes only).

RESULTS

We found that snakes cannot bite as hard as lizards, both in terms of absolute bite force (U = 62.63, df = 1, $p < 0.0001$; Figure 4) and bite force relative to head size (U = 66.40, df = 1, $p < 0.0001$).

We found that vipers cannot bite as hard as non-venomous snakes, both in terms of absolute bite force (U = 7.15, df = 1, $p = 0.0075$; Figure 5) and bite force relative to head size (U = 11.01, df = 1, $p = 0.0009$).

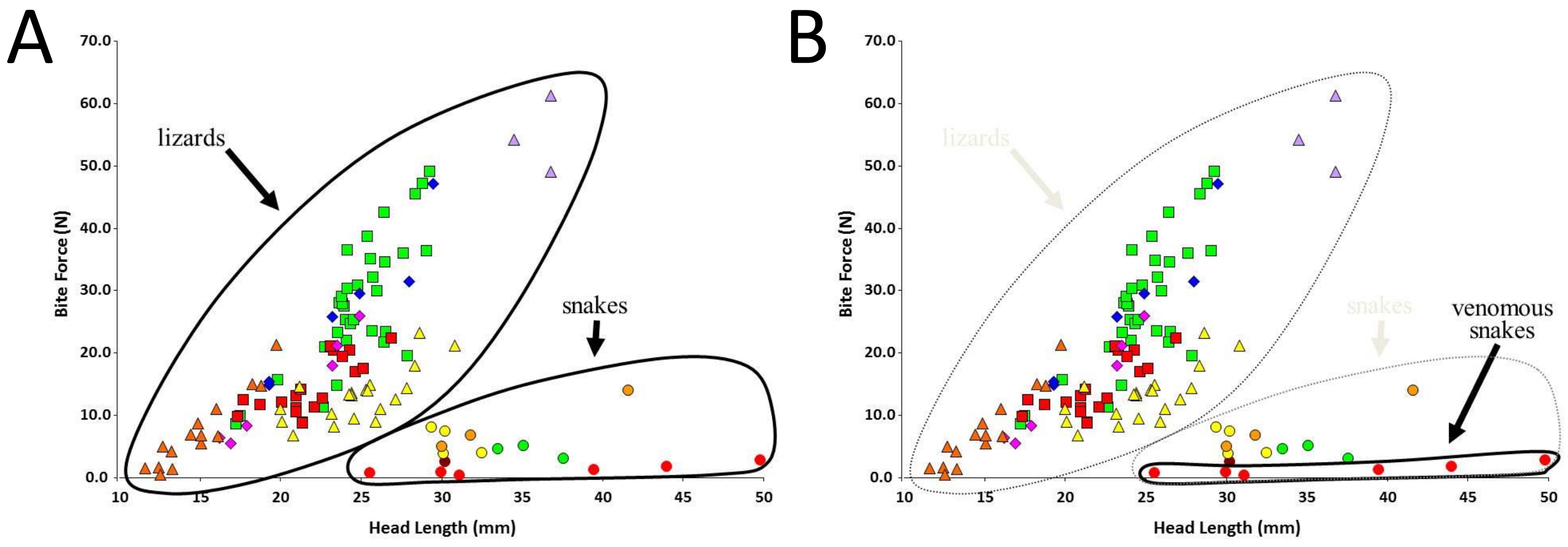

Figure 3. (A) Comparison of bite force relative to head length between lizards and snakes. For data points, each color represents a different species, separately for lizards and snakes. (B) Comparison of bite force relative to head length with focus on comparison between vipers (i.e., venomous snakes) and non-venomous snakes.

DISCUSSION

The ability of snakes to swallow large prey is a result of the evolution of a great degree of cranial kinesis, which is typically associated with elongated, slender, and loosely articulated skeletal elements (Cundall, 1987; Schwenk, 2000; Kardong, 2006; Figure 1C). We conclude that the extreme cranial kinesis exhibited by snakes compromises their capacity to generate bite forces comparable to lizards. Based on our results, this compromise is extreme, as we found that for a given head size, snakes bite with 3-20X less force than lizards. This represents a classic example of a biomechanical trade-off, in this case between force (i.e., bite force) and flexibility (i.e., cranial kinesis).

The considerably reduced capacity for a strong bite presents a challenge for snakes with respect to subduing prey. As such, snakes' lack of the ability to crush their prey may have driven the evolution of specialized mechanisms to kill prey. For example, constricting snakes, which are non-venomous, coil themselves tightly around their prey. This impairs circulatory system function such that the animal becomes unconscious due to a lack of blood flow in the major blood vessels. One example of a non-venomous snakes that uses constriction to kill prey is *Lampropeltis* (king snakes and relatives), a species of which we used in our study, which has been shown capable of swallowing prey greater than its own body mass (Jackson et al., 2004).

When we examine the dietary ecology of vipers (venomous snakes in family including rattlesnakes), records exist of individuals having swallowed bulky prey (i.e., mammals) over 2X their own body mass. The striking difference between vipers and non-venomous snakes in the capacity to swallow extremely large and bulky prey suggests that vipers have even greater cranial kinesis than non-venomous snakes (Cundall, 1987; Schwenk, 2000; Kardong, 2006; Figure 1D). Examination of the skulls of vipers shows that they possess even more lightly built skulls than non-venomous snakes, with particularly elongated skeletal elements key to swallowing large prey (Figure 1D). Our results show that non-venomous snakes are able to generate significantly greater bite forces than vipers, which lends further support to our hypothesis of a biomechanical trade-off, within snakes, between force and flexibility.

Vipers, like other venomous snakes, do not constrict their prey. Rather, they subdue prey via the injection of venom. The leading hypothesis for the driving force behind the evolution of the tissue-destructive venom of vipers is that it facilitates the digestion of the prey from the inside out, before it is even swallowed. Vipers have by far the longest fangs among venomous snakes, which allow them to deeply penetrate the body of the prey when injecting venom. As a result, vipers have evolved a unique jaw morphology that allows the fangs to be retracted and fit into the mouth when it is closed. Therefore, the extremely long fangs and biomechanics of fang erection in vipers allows them to swallow the largest and most bulky prey among all snakes, which reduces the frequency with which they must feed.

Further research is warranted that (1) includes additional snake taxa exhibiting a range of capacity for cranial kinesis, and (2) integrates quantification of cranial kinesis, perhaps directly with biomechanical analyses and indirectly by surveying the natural history literature for maximum recorded sizes of prey ingested.

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