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 connected by mobile joints, which allow for increased flexibility of the jaw. In lizards, this trait is seen in the ability to swallow prey whole, whereas in snakes, this trait is seen in the ability to swallow prey in a more elongated form. We predict that a trade-off exists between bite-force performance (i.e., force) and flexibility (i.e., cranial kinesis). For example, in snakes the quadrate bones (Qu) are highly mobile, and there is no bony synapsis connecting two halves of the lower jaw. This allows the snake to move each side of its mandible independently, both antero-posteriorly and laterally. We compare bite force to cranial kinesis in snakes and lizards. 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). We found that snakes cannot bite as hard as 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, 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 directly with biomechanical analyses and indirectly by natural history literature for maximum recorded size of prey ingested.

INTRODUCTION

A general principle in lever-based biomechanical systems (i.e., most muscle-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 limbs 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 the 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, these two animals, we see a classic trade-off, namely that between force and performance.

In addition, there exists within snakes an appreciable range in the degree of cranial kinesis. Among all snakes, the 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.

HYPOTHESES

Hypothesis 1 – 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), python snakes (Python), corn snakes (Pantherophis), as well as rattlesnakes (Crotalus) and a venomous death adder (Acanthophis). All of the lizards are native to California, except Geckos. 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 to the vent. We measured bite-force performance using digital calipers (Lappin et al., 2006; Figure 2). For the analyses, we focused on head dimensions included king snakes (Crotaphytus) and a venomous death adder (Acanthophis) 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 to accommodate a handle so that venomous snakes can be tested. Note fresh mouse skin covering plates.

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 to accommodate a handle so that venomous snakes can be tested. Note fresh mouse skin covering plates.

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 1D). 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, snake bite with 3-2.5X 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, constriction, 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 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 tightly 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 higher 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 venoms 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 a unique evolutionary advantage of being able to swallows 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 different degrees of 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.

LITERATURE CITED

KELLOGG HONORS COLLEGE CONVOCATION 2013

Mentor: Dr. A. Kristopher Lappin

Biomechanical Trade-off in Lizards versus Snakes

Gabrielle Barton and Cassandra Stepp-Bolling, Biology – Zoology

To Crush or to Engulf Your Victim?

Figure 2. (A) Linear morphometrics of prey. For Figure 1A and 1B, height (HL), width (HW), and head depth (HD). (B) For venomous snakes, we took images of the jaw along the snake together with a ruler and used Inkscape 1.4.3, NIH to make the measurements.