# THE RELATIONSHIP BETWEEN HEAD MORPHOLOGY AND BITE PERFORMANCE IN *ANOLIS* LIZARDS

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# CAN DIFFERENT SKULL MORPHOLOGIES YIELD SIMILAR BITE FORCES IN ANOLE LIZARDS

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# ABSTRACT

Bite force – the maximum strength exerted during biting – plays an important role in lizards behaviors with fitness consequences, such as foraging, territory defense, and mate competition. Stronger bites enable lizards to consume tougher prey and increase their likelihood of winning territorial disputes, potentially increasing survival and reproductive success. Despite this critical performance trait, the relationship between head morphology and bite force remains understudied in lizards, particularly in the genus *Anolis*, which is known for its ecological diversity and morphological specialization. This study investigates the correlation between head morphology and bite force in four Anolis species: *A. carolinensis*, *A. distichus*, *A. sagrei*, and *A. cristatellus*. I measured head morphology using geometric morphometrics on radiographs from 751 individual lizards. A linear discriminant analysis (LDA) revealed significant interspecific variation in head shape. My data demonstrated that species with substantially different shaped heads could generate similar peaks in bite performance. *Anolis carolinesis* (an arboreal specialist with long thin heads) and *A. cristatellus* (a semi-terrestrial species with a shorter, stockier head) achieve comparable bite force – an example of functional convergence despite morphological divergence. Additionally, I found differences in bite force and skull shape between two highly similar species, *A. sagrei* and *A. cristatellus*. These differences suggest the development of bite performance might be decoupled from morphological convergence. These findings enhance our understanding of morpholigcal evolution in lizards and highlight the complex relationship between form and function in *Anolis* lizards

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# Introduction

Fitness – an organism's ability to survive and successfully transfer material to subsequent generations – is a fundamental concept in the field of ecology and evolution. (Wadgymar et al, 2024). An individual's fitness is often determined by the interaction between its phenotype and the local environment: individuals that have advantageous phenotypic traits achieve higher reproductive success than those without such traits in their environment. One's ability to bite can be one of these adaptations witnessed within ecology. In lizards, biting is a performance trait that can determine an individual's success in many key fitness-related activities and behaviors, such as foraging and feeding, defense of territories, or competition for mates. Being able to produce a stronger bite force may enable a lizard to expand its range of prey items in its environment and increase their likelihood of success in agonistic interactions with reproductive competitors (Meyer et al, 2017). All these examples serve to demonstrate the importance of biting within the ecology of lizards.

With biting performance being important to all lizard species regardless of ecology, it remains unclear why species might evolve different head shapes which presumably confer different bite forces. A reasonable expectation would be that all species would evolve a head shape that maximizes bite force for its body size. In this study, I first investigated if different species – each with a distinct head morphology – produced differences in bite performances. Second, I explored which specific features of specie's head shape were strongly correlated with a high bite force.

Anoles, a diverse group of lizards distributed throughout the Americas and the Caribbean  (Losos, 2009). In the four large islands of the Greater Antilles in the northern

Caribbean, anoles have independently adaptively radiated to produce communities made up of the same set of six habitat specialist, referred to as “ecomorphs” in literature (Williams, 1972). Species in each ecomorph class all exhibit adaptations to the ecological niche they occupy in their environment: “trunk-ground” anoles occur on lower tree trunks and the ground, are brown, and possess relatively long limbs for running fast on flat surfaces; “trunk-crown” anoles occur on higher tree trunks and in leafy tree crowns, are green, and possess relatively long adhesive toepads that confer strong clinging ability (Losos, 2009). Many studies have explored the many different ecological differences amongst the species of anoles such as their limb length and body size, but head morphology tends to be ignored in the studies. Despite this, differences have been shown to exist amongst the ecomorphs. A study in 2019 found that head shape differs amongst the different anole ecomorphs, differing in their size, height, and length (De Meyer et al., 2019). Head morphology in relation to ecomorphs has been poorly investigated. My goal is to investigate how diversity in head morphology in the genus *Anolis* and the bite performance across these head morphologies.

To accomplish this, I collected lizards from four different anole species in the Fairchild Tropical Botanic Gardens: Cuban brown anole (*Anolis sagrei*) and Puerto Rican crested anole (*Anolis cristatellus*; both “trunk-ground” anoles), American green anole (*Anolis carolinensis*; “trunk-crown” anole), and Hispaniolan bark anole (*Anolis distichus*; “trunk” anole). All the species, expect *Anolis carolinesis,* are invasive within Florida, being from different islands within the Caribbean.

A many-to-one mapping of *Anolis* head morphology will be conducted within this study in order to understand the factors of head shape that play into an anole's ability to bite. In many-to-one mapping, many factors, skull dimensions, are associated with to a single entity, bite performance. I hypothesize that anoles in the community with wider skulls will have a stronger bite force than those with longer skulls, and that species of the same ecomorph, *A. cristatellus* and *A. sagrei*, will possess biting peaks of the same caliber.

# Material and Methods

## Specimen Collection

I collected 751 lizards from Fairchild Tropical Botanic Gardens in Miami, Florida (Miami-Dade County). After capture, individuals were quickly transferred to a field laboratory for bite force data collection. All procedures in this study were approved per Georgia Institute of Technology IACUC ID A100675

| Species | # of Individuals |
|---|---|
| *Anolis sagrei* | 57 |
| *Anolis cristatellus* | 627 |
| *Anolis distichus* | 16 |
| *Anolis carolinensis* | 51 |

**Table 1.** Number of individuals collected from each species out of the 751 in Fairchild Tropical Botanic Gardens.

## Bite Force Collection and Analysis

Bite force was quantified using a Kistler force transducer following the design in Herrel et al. (1999). Anoles were positioned in front of the transducer and encouraged to bite down on two plates attached to the transducer. Force measurements, recorded in Newtons, were logged in an Excel database for statistical analysis in R (version 4.4.0; R

Core Team 2020). Each individual underwent three consecutive bite force trials, and the maximum value across trials was extracted for all analyses. Bite force was analyzed and modeled as a function of head shape and body size (SVL). Anoles were kept at a constant temperature throughout data collection.

## Radiographic Imaging and Morphometric Analysis

To measure head morphology, I collected radiograph images of each lizard. Specifically, lizards were anesthetized and radiographed using a Vegaray-CL model of X-ray (Vegaray X-ray, 2021). Head morphological traits were extracted from radiographs using TPSdig, a geometric morphometric analysis software that enables morphological measurements to be done via the placement of landmarks on photos (TPSdig Version 2.16, Rohlf, F. J. 2006). These geometric morphometric 'landmarks' were exported into R using the package "geomorph" (Dean A, 2025) These measurements were analyzed to assess inter- and intraspecific variation and their correlation with bite force.

## Linear Discriminant Analysis in R

I used a linear discriminant analysis (LDA) to characterize the multivariate head shape of each individual lizard, using the R package "MASS" (Venables WN, 2002). First, I combines landmark coordinates from all species into a single array, selecting landmarks, and then performing a Generalized Procrustes Analysis (GPA) to align coordinates. Then, these GPA-aligned coordinates are used to perform the LDA. The LDA scores are plotted to visualize differences in head shape among both individuals and species in my data set. I tested if species exhibit significantly different head shapes using a MANOVA test.

# Results

*Species form distinct clusters based on head shape.* Species formed distinct clustered in the LDA plot, suggesting that each species exhibit different multivariate head shapes (Figure 1). From the MANOVA, an F value of 203.19 was given, suggesting that differences in head shape found in my LDA was significant. The first linear discriminant axis (LD1) accounted for over 90% of the variation in head morphology, with low LD1 values corresponding to short skulls, and high LD1 values indicating elongated skulls. The second linear discriminant axis (LD2) accounted for 7% of variation in head morphology, with low LD2 values corresponding to sharper heads and high LD2 values corresponding to wider heads. Notably, *A. carolinensis* and *A. distichus* exhibited well-separated clusters, with *A. carolinensis* possessing extremely long and thin skulls compared to every other species in the study and *A. distichus* possessing short and blunt skulls, characterizing two different extremes within skull length within the A*nolis* community on the island as shown through their LD values. In contrast, *A. cristatellus* and *A. sagrei* showed partial overlap in LD1, likely due to them belonging to the same ecomorph group, which suggests a high degree of morphological similarity in skull shape between these two species.

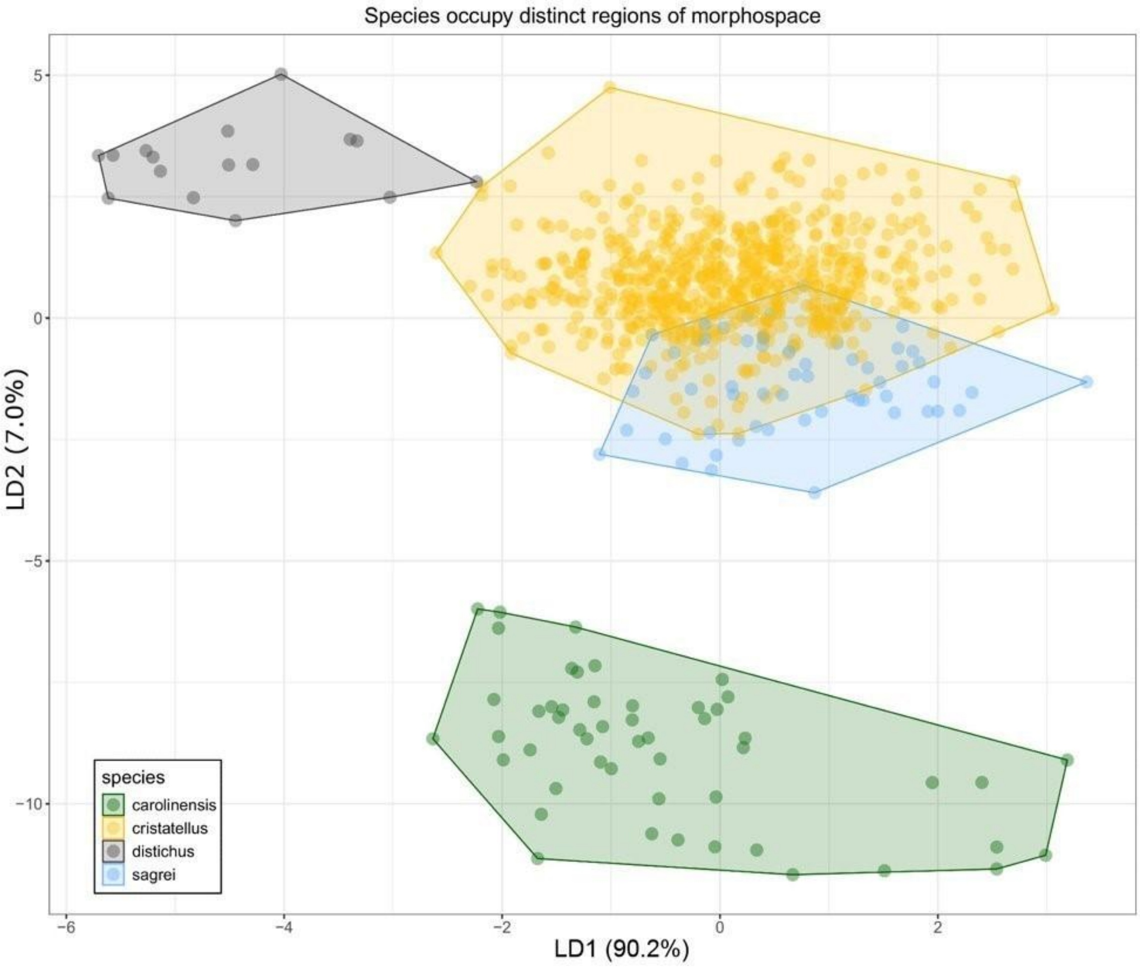

**Figure 1**. Species form distinct clusters based on the dimensions of their skulls. Individuals in *A. carolinensis* and *A. distichus* form more unique clusters while *A. sagrei* and *A. cristatellus* have some overlap in their clusters, mainly differing in LD2. All species differed significantly on LD1 and LD2 (Tukey's HSD, all species-species adjusted $p<0.05$)

*Divergent head shape clusters can occupy similar bite performance peaks.* Maximal bite performance surfaces on multivariate discriminant morphospace (i.e., LD1 vs. LD2) were visualized using the thin-plate spline (Tps) function in the fields package

(Nychka et al) in R. the Tps function fits thin-plate splines with smoothing penalties estimated by generalized cross-validation which minimizes prediction error (as in Stroud et al 2023). Using this approach, I estimated a maximal bite force surface for the entire community (Figure 2). This visualization identified two primary bite force peaks, one within the *A. cristatellus* cluster and another in the *A. carolinensis* cluster, both corresponding to high bite performance values. Despite their divergent morphologies, these species occupied distinct but similarly high-performance bite force peaks. *Anolis carolinensis* exhibited high LD1 values but relatively low LD2 values, distinguishing its bite performance profile from the other species examined.

A three-dimensional trait-space visualization (Figure 3) further delineated interspecific variation, with vertical markers denoting the mean head shape phenotype for each species. The analysis reaffirmed that *A. cristatellus* and *A. sagrei* possessed similar mean skull shapes, consistent with their shared ecomorph designation. In contrast, *A. distichus* and *A. carolinensis* exhibited unique head shape phenotypes, occupying distinct and non-overlapping regions within the morphological trait space.

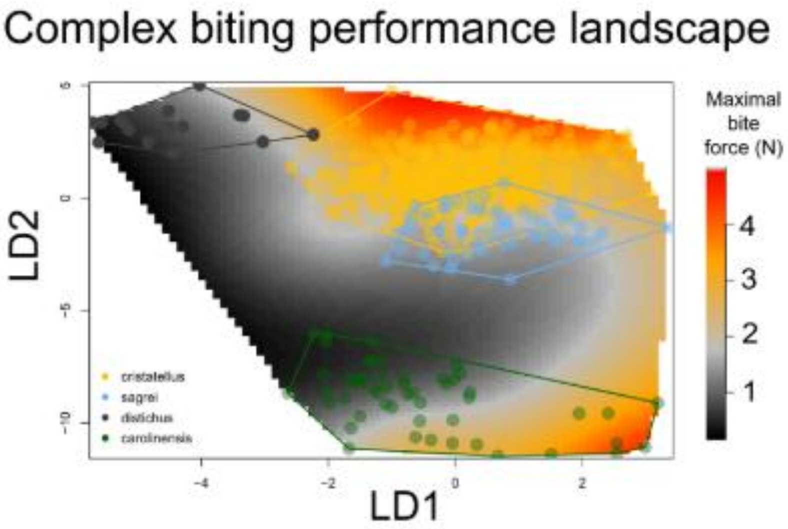

**Figure 2.** *Anolis carolinensis and A. cristatellus* occupy unique bite performance peaks in the trait space. Linear discriminant axis 1 and LD2 both represent different measurements of the anole's skull. A heat map representing the bite force is layered upon minimum convex polygons that represent the head shape distribution within the traitspace. Both peaks occupy a different extreme within skull values, with *A. cristatellus* occupying an extreme LD2 and *A. carolinensis* occupying an extreme LD1.

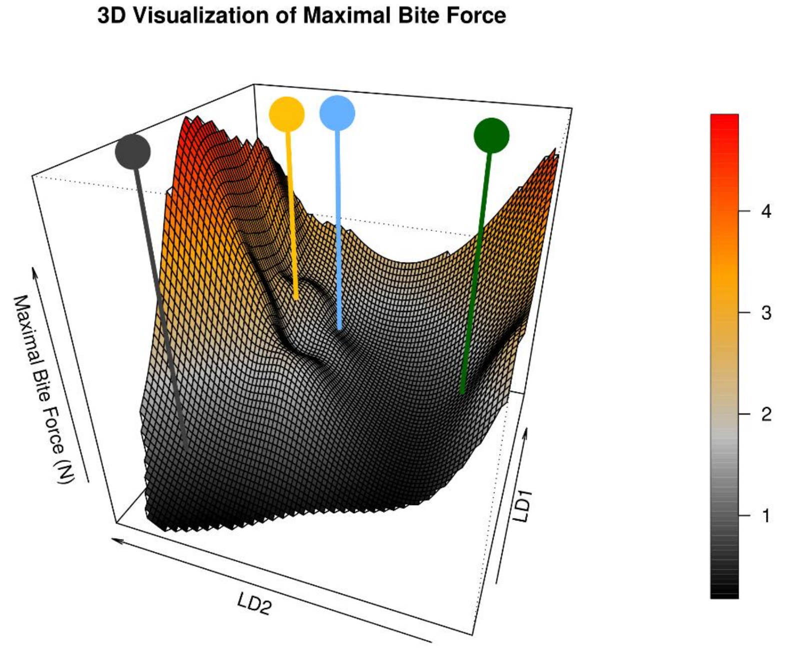

**Figure 3.** The vertical pins on top of the 3d map represent the mean head shape phenotype for each species of anole used within this study.

# Discussion and Conclusion

Trying to build a better understanding of how head morphology correlates with bite force helps construct a better understanding of their ecology. The study demonstrates interspecific variation in head morphology among *Anolis* spp., even among species of the same ecomorph. My results showed that two species belonging to the trunk-ground ecomorph, *A. cristatellus* and *A. sagrei*, had differently shaped heads. The sole native species, *Anolis carolinensis* differed from all other species in the study by having the longest and thinnest skull of any other species in the study from a ventral view, while *A. distichus* possess the shortest and bluntest heads of the species, as evident in the LDA plot (Fig. 1).

An interesting finding from the LDA bite force performance surface (Fig. 2) was that lizards that had shortest and bluntest head shapes were associated with weaker bite forces, as seen with the low bite force average found amongst the *A. distichus* population pool. The low bite force seen within this species could be due to their small size, because snout–vent length is also important when thinking about bite performance (Deeming, 2019).  In terms of highest bite force, I see that larger LD1 values in *Anolis carolinensis* are associated with stronger bite forces. A similar trend is seen within *Anolis cristatellus*, in which individuals with a higher LD2 scores are associated with achieving higher bite performances. A similar trend can be seen within LD1 and *Anolis cristatellus* but to a lesser degree. With the many-to-one mapping of head shapes via a linear discriminant analysis, I show that there are multiple factors in cranial morphology that determine the bite performance of anole.

The results suggest that similar bite performance peaks can be achieved between species despite having significantly different head shapes amongst *Anolis* spp. . Within the study, two species, *A. carolinensis* and *A. cristatellus*, despite having significantly different skulls, were able to occupy as seen within the LDA heat map, reaching similar peak in bite force (Fig. 2A). With both species being able to achieve similar bite performances while having big differences in their skull morphologies, I show that species are able to produce similar peak bite performances. The present study is one of the first to conduct a many-to-one analysis on the bite force of anoles by investigating the geometric morphological features of their skulls and investigating how they relate to an anoles' ability to bite. The present study helps construct a better understanding of the morphology dictating their bite performance. The study was able to showcase an example of convergent evolution within anole lizards, in that despite taking different evolutionary paths in skull morphology, were able to converge at a similar bite performance.

The present study sheds light on how the skull morphology of anoles plays into their ability to bite. The study showed that different species of anoles, despite their different head shapes, were able to produce similar peaks in bite performance. The many-to-one mapping analysis of bite force with head morphology helps construct a better understanding of how these morphologies relate to one's ability to bite. An interesting finding is the difference seen in *Anolis sagrei* and *A. cristatellus*, both species of the same ecomorph. Despite being of the same ecomorph, many individuals within figure 1 differ in their cranial morphology. This could be highlighting a possible decoupling of head shape from limbs and body morphology and functionality trends seen within species of the same ecomorph. A future study could investigate this possible separation in head morphology from ecomorph by looking into ecological implications of the relationship between head shape and bite force by looking into aspects like diet and habitat usage.

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