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STUDY OF ADAPTIVE RADIATION EFFECTS ON SPRINT PERFORMANCE IN  
*ANOLIS* ECOMORPHS

by

Alexander Bergeson

A Thesis Submitted in Partial Fulfillment  
Of the Requirements for the  
University Honors Program

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Department of Biology  
The University of South Dakota  
May 2022

The members of the Honors Thesis Committee appointed  
to examine the thesis of Alexander Bergeson  
find it satisfactory and recommend that it be accepted.

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## ABSTRACT

Study of Adaptive Radiation Effects on Sprint Performance in *Anolis* Ecomorphs

Alexander Bergeson

Director Dr. Christopher Anderson

*Anolis* lizards have become model organisms for the study of adaptive radiation and convergent evolution due to repeated patterns of specialization that allow them to live in different environmental niches within the habitats they occur. As part of a suite of adaptations for living in specific habitats, many species have repeatedly evolved specific changes in anatomy and physiology that make them better able to perform and survive in their surroundings. These specialized forms are referred to as “ecomorphs” based on their preferred habitats and have been well documented among Caribbean anoles. Mainland species, on the other hand, are less studied. Here, focusing on two mainland species of anoles, *Anolis biporcatus*, a highly arboreal species, and *A. osa*, a more terrestrial species, I ask if differences in ecomorph type has led to changes in how incline impacts sprint performance. To do so, I analyzed sprint trials for individual of each species running on inclines from 0-60° and tested for effect differences. The results indicate that although the two species differ in their overall performance, they largely show similar effects of incline. *A. biporcatus*, however, exhibits a performance limit in their ability to generate sufficient power to elevate their body center of mass above 45° inclines, which is not observed in *A. osa*. This limit may be constrained by the increased habitat variability of the latter species with respect to incline.

KEYWORDS: *Anolis*, sprint performance, ecomorph, adaptive radiation

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## CHAPTER ONE

### Introduction

Highly diversified in both morphology and habitat use, *Anolis* lizards are excellent model organisms for biologists exploring adaptive radiation, or the diversification of a group of organisms to occupy a variety of ecological niches within their environment. Anoles are commonly found on Caribbean islands and mainland regions of Central and South America, as well as the southern US. Across repeated island colonization events in the Greater Antilles of the Caribbean, *Anolis* have diversified and adapted to live in different environmental niches within their habitats such that many of the niches are filled on each island, through its own colonization event. These range from species that live primarily on the ground to species that live primarily in the forest canopy, with many that reside on other parts of their structural habitat (Williams 1983). As part of a suite of adaptations for living in specific habitats, many species have repeatedly evolved specific changes in anatomy that make them better able to perform and survive in those surroundings (Herrel et. al 2008; Irschick and Losos 1999; Losos and Sinervo 1998; Vanhooydonck et. al 2006). These specialized forms are referred to as “ecomorphs” based on their preferred habitats. An ecomorph represents any species inhabiting the same portion of their structural habitat or niche that exhibits similar anatomical proportions and behavior, but that are not necessarily closely related phylogenetically (Williams 1972). As these ecomorphs have tended to evolve repeatedly across the Greater Antilles of the Caribbean, their convergent patterns suggest adaptive benefits. By comparing the consistent anatomical and physiological differences between

ecomorphs, one can better understand the mechanisms by which they have adapted to fit their environment.

A common area of study among anole ecomorphs involves examination of their sprint performance, as sprint performance is important for anoles as they move through their environment to search for and capture food as well as avoid predators. Numerous studies have examined how morphology and the typical perch diameter of an ecomorph's habitat each affect sprint performance (Vanhooydonck et. al 2006; Herrel et. al 2008). Losos and Sinervo (1998), for instance, found that species with longer legs have decreased sprint performance while running on narrow supports. Morphology among species is also known to vary in such a way so as to optimize performance on the substrate that is most like its habitat (Irschick and Losos, 1999). Within a species, however, the width of a running platform also affects sprint performance. In fact, sprint performance is maximized on wide surfaces and performance decreases when running on narrower substrates (Irschick and Losos 1999; Sathe and Husak 2015). While decreasing the diameter of the substrate an individual is running on leads to overall decreases in sprint performance, different ecomorphs are better able to perform on narrower substrates than others due to differences in their limb lengths.

Many studies of anoles have focused on Caribbean species for these comparisons, with fewer studies examining ecomorphs from mainland radiations. There are significant differences between mainland and island anoles, though, particularly in how they have adapted to best fit their habitats (Irschick et. al 1997). Species from these two different regions experience very different environmental pressures. For instance, because of a larger diversity of predators in mainland habitats, mainland anole populations see higher

rates of predation and mortality (Irschick et. al 1997). On islands, however, there is much more competition between different species due to a lower diversity of predators (Irschick et. al 1997). Those differences in predation and competitions serve as distinct pressures underlying natural selection and evolution that may result in differences in the patterns of adaptive radiation between the two regions. Indeed, striking differences in the relationship between morphology and ecology between these different regions have been documented (Irschick et. al 1997).

Although several studies have addressed the effect of perch diameter and morphology on sprint performance, how incline influences sprint performance in anoles is less studied. However, incline influenced sprint performance in both the western skink (*Eumeces skiltonianus*) and the western banded gecko (*Coleonyx variegatus*) (Farley 1997). First, increases in incline led to decreases in maximum speed (Farley 1997). Further, as incline increased, both species required more mechanical power to overcome gravity to accelerate and lift their center of mass during sprinting trials (Farley 1997). Similar findings seem likely to be observed in anoles, but how ecomorphs vary in how incline effects their performance is less clear.

Here, I examined how incline effected sprint performance in two mainland *Anolis* ecomorphs, *Anolis biporcatus* and *Anolis osa*. These two syntopic Costa Rican species are primarily associated with tree trunks and canopy foliage, and the ground, small branches, and root structures, respectively. This study, therefore, seeked to determine whether one species was better able to perform at higher inclines than the other. I hypothesized that, due to the habitat they inhabit, *A. biporcatus* would maintain sprint performance to a higher degree at increasing inclines when compared to *A. osa*.



Specifically, I predicted that living on more vertical tree trunks and branches would cause *A. biporcatus* to maximize performance under greater inclines. This study explores that hypothesis through thorough comparison of several sprint performance metrics across five different inclines. Through those comparisons, insight into the effect of incline, species, and their interaction on sprint performance is used to determine similarities and significant differences between the mainland ecomorphs.

## CHAPTER TWO

### Materials and Methods

#### Specimens

Ten adult males each of *A. biporcatus* and *A. osa* were collected from Costa Rica and brought into captivity for participation in experimental trials. Each specimen was individually housed in glass terrariums with basking bulbs and UVB lighting.

Additionally, each individual had access to *ad libitum* water, misting two to three times per day, and feeding two to three times per week during the data collection period.

During the collection of sprint performance, individuals were maintained at 30°C for *A. biporcatus* and 27.8 °C for *A. osa* by keeping the individuals in an incubator set to those temperatures prior to each trial for a period of at least one hour.

#### Sprint trials

Sprint performance trials took place on a 3m long, flat racetrack. The flat racetrack was used to elicit maximum sprint performance for each species and minimize the differential effect of substrate width on performance seen in previous studies (Sathe and Husak 2015; Irschick and Losos 1999). To provide adequate traction during trials, the running surface was covered in a texturized rubber, anti-slip tape. To begin each trial, the individual was released onto the surface on one end of the track. Once on the track surface, the animal was induced to run by the investigator clapping behind it. If clapping was not sufficient to induce running, the investigator would approach the animal from behind and lightly tap it on the tail. The animals were recorded from both a lateral and dorsal view by high-speed cameras filming at 500 frames per second. Prior to the trials,

each individual was marked with a white dot immediately anterior to the pelvic ilium on the dorsolateral side facing the lateral view camera during sprint trials. That dot acted as a point of reference for automatic point-tracking software during data analysis. The marking was placed so that it could be seen from both the lateral and overhead camera views. To determine differences in performance at varying slopes, 10 trials were performed with each individual at five inclines (0°, 15°, 30°, 45°, and 60°). During the trial periods, a maximum of five trials a day per individual were collected to increase the probability of obtaining trials with maximum performance (Losos et al. 2002).

#### Analysis of Sprint Performance

Sprint trials were calibrated using a reference frame with a calibration object in the view for each filming day in a digitizing tool for MATLAB (Hendrick 2008). Calibration reference frames for sprint trials with *A. osa* included a flat calibration mat, whereas reference frames for trials with *A. biporcatus* included a three dimensional cube. Following the camera calibrations, this digitizing tool was then used to track the white dot on each individual through every frame of each video, producing either  $x,y$  coordinates for *A. osa* or  $x,y,z$  coordinates for *A. biporcatus*. Position data were analyzed in IGOR Pro to calculate peak velocity, average constant velocity, peak acceleration, peak power, peak uphill power, average uphill power, and peak accelerative power for each trial. To calculate performance metrics from position data, a custom script was used to perform calculations within the IGOR Pro software. Peak velocity ( $\text{m s}^{-1}$ ) was calculated as the first derivative of position, acceleration ( $\text{m s}^{-2}$ ) was calculated as the second derivative of position and mass-specific power ( $\text{W kg}^{-1}$ ) was calculated as the

product of velocity and acceleration. Uphill power ( $\text{W kg}^{-1}$ ) was calculated as the mass-specific power component from the displacement in the z axis. Accelerative power ( $\text{W kg}^{-1}$ ), on the other hand, was calculated as the difference between uphill and total mass-specific power. Peak values were recorded as the highest value for each metric. Average values were calculated as an average of the metric over a period of relatively constant sprint performance, as visualized in sprint velocity traces for each trial. From these calculated performance metrics, the highest value for each was retained for statistical analysis as a measure of peak performance for each individual at each incline.

#### Morphological measurements

Morphological measurements were collected for body size and limb dimensions for each individual based on Lowie et al. (2019). A digital scale ( $\pm 0.001 \text{ g}$ ) was used for body mass and digital calipers ( $\pm 0.01 \text{ mm}$ ) were used for length values. Measurements for limb dimensions included: femur length (FL), tibia length (TL), metatarsus length (MTL), longest hind toe length (LHTL), humerus length (HumL), radius length (RL), metacarpus length (MCL), longest front toe length (LFTL). Measurements for body size included: body mass, snout vent length (SVL), tail length (TL), body length (BL), body width (BW), and body height (BH).

#### Statistical Analysis

To summarize morphological variation among individuals, a principal component analysis (PCA) was performed for inclusion in analyses of sprint performance. The resultant principal component (PC) scores represent a single dimension variable pooled

from the morphological measurements that explain the observed variation among individuals. The first set of PC score values (PC1) was the only PC score to account for more than 10% of the variation in morphology, so this score was used in later analyses of sprint performance as a metric of body size (Fig. 1).

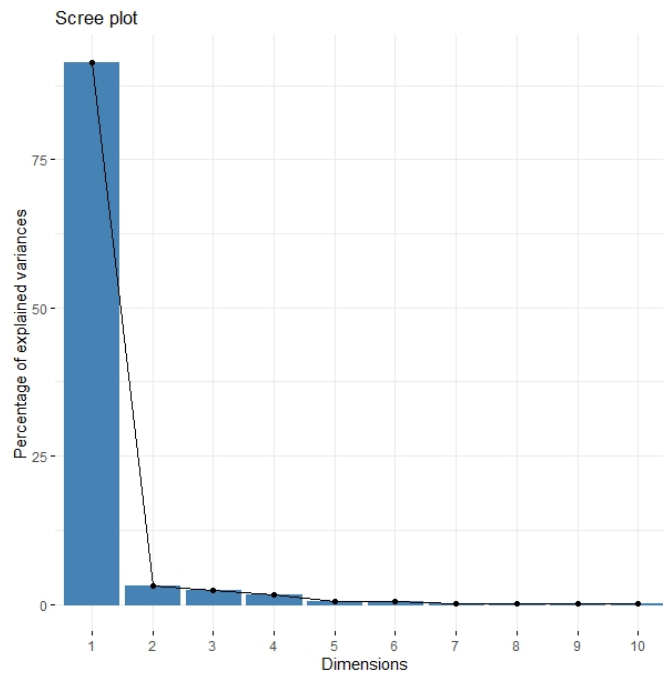


Figure 1. Principal component scores from PCA of all morphometric variables showing the percent variation explained by each.

Linear mixed models were then run to test for an effect of species, incline and their interaction on sprint performance variables with individual as a random effect and PC1 as a covariate. PC1 was used as a covariate to standardize morphology to control for its effect on sprint performance. For any performance parameter that yielded significant

differences in the interaction term between species and incline in this analysis, a post-hoc Tukey test was performed for each species individually with individual nested within incline as a random effect and incline as a categorical factor rather than a numerical integer, as required for post-hoc Tukey tests.

## CHAPTER THREE

### Results

#### Morphology

Of the 20 individuals originally collected, both morphological and sprint performance data was collected from seven *A. osa* and six *A. biporcatus*. *A. biporcatus* was larger than *A. osa* in all morphological measurements (Table 1; Fig. 2). *Anolis biporcatus* ranged from 86.96-89.72mm SVL, whereas *Anolis osa* ranged from 50.57-54.22mm. Additionally, *A. biporcatus* ranged from 10.772-18.431g in mass, whereas *A. osa* ranged from 2.204-2.668g.

Table 1. Summary of average morphometric measurements.

Variable	<i>Anolis osa</i>		<i>Anolis biporcatus</i>	
	Sample Size	Mean $\pm$ SEM	Sample Size	Mean $\pm$ SEM
Mass	7	2.42 $\pm$ 0.06	6	15.44 $\pm$ 1.15
Snout-Vent Length (mm)	7	52.75 $\pm$ 0.51	6	88.21 $\pm$ 0.42
Tail Length (mm)	7	101.61 $\pm$ 5.21	6	175.66 $\pm$ 19.55
Body Length (mm)	7	22.75 $\pm$ 0.35	6	42.66 $\pm$ 1.15
Body Width (mm)	7	7.46 $\pm$ 0.35	6	16.39 $\pm$ 1.56
Body Height (mm)	7	7.03 $\pm$ 0.19	6	16.20 $\pm$ 0.46
Femur Length (mm)	7	14.23 $\pm$ 0.25	6	19.61 $\pm$ 0.23
Tibia Length (mm)	7	14.54 $\pm$ 0.23	6	19.10 $\pm$ 0.19
Metatarsus Length (mm)	7	7.53 $\pm$ 0.12	6	10.52 $\pm$ 0.26
Longest Hind-Toe Length (mm)	7	10.08 $\pm$ 0.12	6	15.04 $\pm$ 0.11
Humerus Length (mm)	7	8.93 $\pm$ 0.22	6	13.36 $\pm$ 0.34
Radius Length (mm)	7	7.43 $\pm$ 0.25	6	11.53 $\pm$ 0.20
Metacarpus Length (mm)	7	2.43 $\pm$ 0.09	6	3.56 $\pm$ 0.18
Longest Front-Toe Length (mm)	7	6.25 $\pm$ 0.15	6	9.08 $\pm$ 0.29



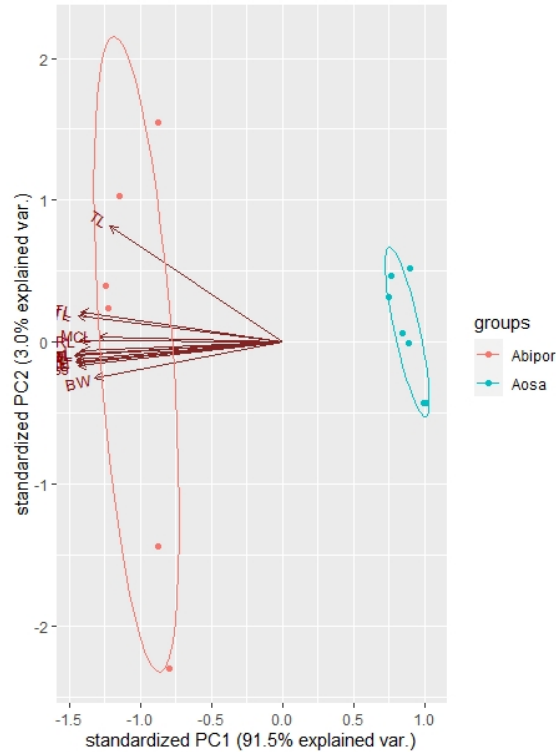


Figure 2. Results from a PCA of all morphometric variables showing PC2 graphed vs. PC1. The contributions of each morphological variable to each PC value are depicted as labeled vectors. Species are grouped by color. Body height (BH), body length (BL), body width (BW), femur length (FL), humerus length (HumL), longest front-toe length (LFTL), longest hind-toe length (LHTL), metacarpus length (MCL), metatarsus length (MTL), radius length (RL), snout length (SL), snout-vent length (SVL), tibia length (TibL), and tail length (TL).

The majority of the observed variation (91.45%) for all body morphological variables was accounted for by the first dimension of the principal component analysis (PC1; Fig. 1). No other dimension accounted for more than 5% of the observed variance. Principal component clustering shows no overlap in morphological dimensions between the two species (Fig. 2).

## Sprint performance

Sprint trials at all five inclines across the 0°-60° range were collected from each species. Maximum sprint performance ranges at each incline were relatively similar between the two species (Table 2).

Table 2. Summary of average performance measurements.

Variable	<i>Anolis osa</i>		<i>Anolis biporcatus</i>	
	Sample Size	Mean $\pm$ SEM	Sample Size	Mean $\pm$ SEM
0° Incline				
Peak Velocity	7	2.11 $\pm$ 0.17	6	2.23 $\pm$ 0.17
Constant Velocity Avg.	7	1.35 $\pm$ 0.13	6	1.32 $\pm$ 0.17
Peak Acceleration	7	52.26 $\pm$ 4.41	6	37.25 $\pm$ 2.14
Peak Power	7	59.22 $\pm$ 7.40	6	55.32 $\pm$ 4.75
Peak Uphill Power	7	0.00 $\pm$ 0.00	6	4.36 $\pm$ 0.90
Average Uphill Power	7	0.00 $\pm$ 0.00	6	0.61 $\pm$ 0.28
Peak Accelerative Power	7	59.22 $\pm$ 7.40	6	53.16 $\pm$ 4.51
15° Incline				
Peak Velocity	7	1.70 $\pm$ 0.13	6	1.90 $\pm$ 0.24
Constant Velocity Avg.	7	1.09 $\pm$ 0.15	6	1.12 $\pm$ 0.13
Peak Acceleration	7	65.32 $\pm$ 9.02	6	34.88 $\pm$ 4.82
Peak Power	7	76.83 $\pm$ 18.13	6	46.19 $\pm$ 7.68
Peak Uphill Power	7	3.87 $\pm$ 0.45	6	5.86 $\pm$ 0.59
Average Uphill Power	7	2.93 $\pm$ 0.41	6	2.76 $\pm$ 0.36
Peak Accelerative Power	7	74.53 $\pm$ 17.81	6	43.76 $\pm$ 7.33
30° Incline				
Peak Velocity	7	1.90 $\pm$ 0.15	6	1.89 $\pm$ 0.12
Constant Velocity Avg.	7	1.24 $\pm$ 0.11	6	1.12 $\pm$ 0.09
Peak Acceleration	7	53.98 $\pm$ 5.30	6	32.70 $\pm$ 3.81
Peak Power	7	63.68 $\pm$ 8.73	6	53.18 $\pm$ 6.86
Peak Uphill Power	7	8.00 $\pm$ 0.54	6	8.86 $\pm$ 0.63
Average Uphill Power	7	5.73 $\pm$ 0.59	6	5.60 $\pm$ 0.43
Peak Accelerative Power	7	57.08 $\pm$ 9.01	6	46.70 $\pm$ 7.05
45° Incline				
Peak Velocity	7	2.00 $\pm$ 0.07	6	2.02 $\pm$ 0.08
Constant Velocity Avg.	7	1.31 $\pm$ 0.07	6	1.38 $\pm$ 0.10
Peak Acceleration	7	54.37 $\pm$ 4.51	6	29.38 $\pm$ 1.50
Peak Power	7	75.58 $\pm$ 7.58	6	44.41 $\pm$ 2.02
Peak Uphill Power	7	10.88 $\pm$ 0.47	6	12.21 $\pm$ 0.18
Average Uphill Power	7	8.76 $\pm$ 0.63	6	9.46 $\pm$ 0.60
Peak Accelerative Power	7	67.97 $\pm$ 8.00	6	35.11 $\pm$ 2.00
60° Incline				
Peak Velocity	7	1.69 $\pm$ 0.05	6	1.64 $\pm$ 0.06
Constant Velocity Avg.	7	1.15 $\pm$ 0.04	6	1.02 $\pm$ 0.03
Peak Acceleration	7	46.90 $\pm$ 3.34	6	25.09 $\pm$ 4.07
Peak Power	7	57.47 $\pm$ 4.32	6	37.61 $\pm$ 4.39
Peak Uphill Power	7	12.39 $\pm$ 0.26	6	12.39 $\pm$ 0.43
Average Uphill Power	7	9.22 $\pm$ 0.52	6	8.23 $\pm$ 0.60
Peak Accelerative Power	7	47.80 $\pm$ 4.47	6	28.35 $\pm$ 4.43

Species had a significant effect on peak acceleration, peak uphill power, and peak accelerative power, whereas it had no significant effect on peak velocity, constant velocity average, peak power, and average uphill power (Table 3). With the exception of peak uphill power, *A. osa* had higher performance than *A. biporcatus* for all significantly different sprint performance metrics (Figs. 3,4,5). Incline had a significant effect on all tested variables except for constant velocity average (Table 3). Incline had a positive effect on peak uphill power and average uphill power (Figs. 4,6) and a negative effect on peak acceleration, peak accelerative power, peak velocity, and peak power (Figs. 3,5,7,8). PC1 was found to have no significant effect on any performance metric (Table 3). The interaction between species and incline degree had a significant effect on peak uphill power with the rest of the variables having not been significantly affected (Table 3; Fig. 4).

Table 3. Results of linear mixed model testing on sprint performance data.

Variable	Species			Incline			AllPC1			Species:Incline Degree		
	Df	F-Value	P-value	Df	F-Value	P-value	Df	F-Value	P-value	Df	F-Value	P-value
Peak Velocity	1,10	0.3753	0.5538	1,50	7.0961	<b>0.0104</b>	1,10	2.0669	0.1811	1,50	0.7825	0.3806
Constant Velocity Avg.	1,10	0.0907	0.7695	1,50	1.5081	0.2252	1,10	0.1074	0.7498	1,50	0.184	0.6698
Peak Acceleration	1,10	31.4787	<b>0.0002</b>	1,50	6.6637	<b>0.0128</b>	1,10	2.1154	0.1765	1,50	0.1702	0.6817
Peak Power	1,10	1.22612	0.2735	1,50	8.24789	<b>0.0166</b>	1,10	2.64771	0.1348	1,50	0.82493	0.3681
Peak Uphill Power	1,10	18.9035	<b>0.0014</b>	1,50	525.225	< <b>.0001</b>	1,10	1.4332	0.2589	1,50	15.2297	<b>0.0003</b>
Average Uphill Power	1,10	0.0001	0.9929	1,50	371.929	< <b>.0001</b>	1,10	0.3423	0.5715	1,50	0.9369	0.3377
Peak Accelerative Power	1,10	8.23372	<b>0.0167</b>	1,50	5.96963	<b>0.0181</b>	1,10	2.50711	0.1444	1,50	0.67905	0.4138

Bold P-Values indicate significant effects

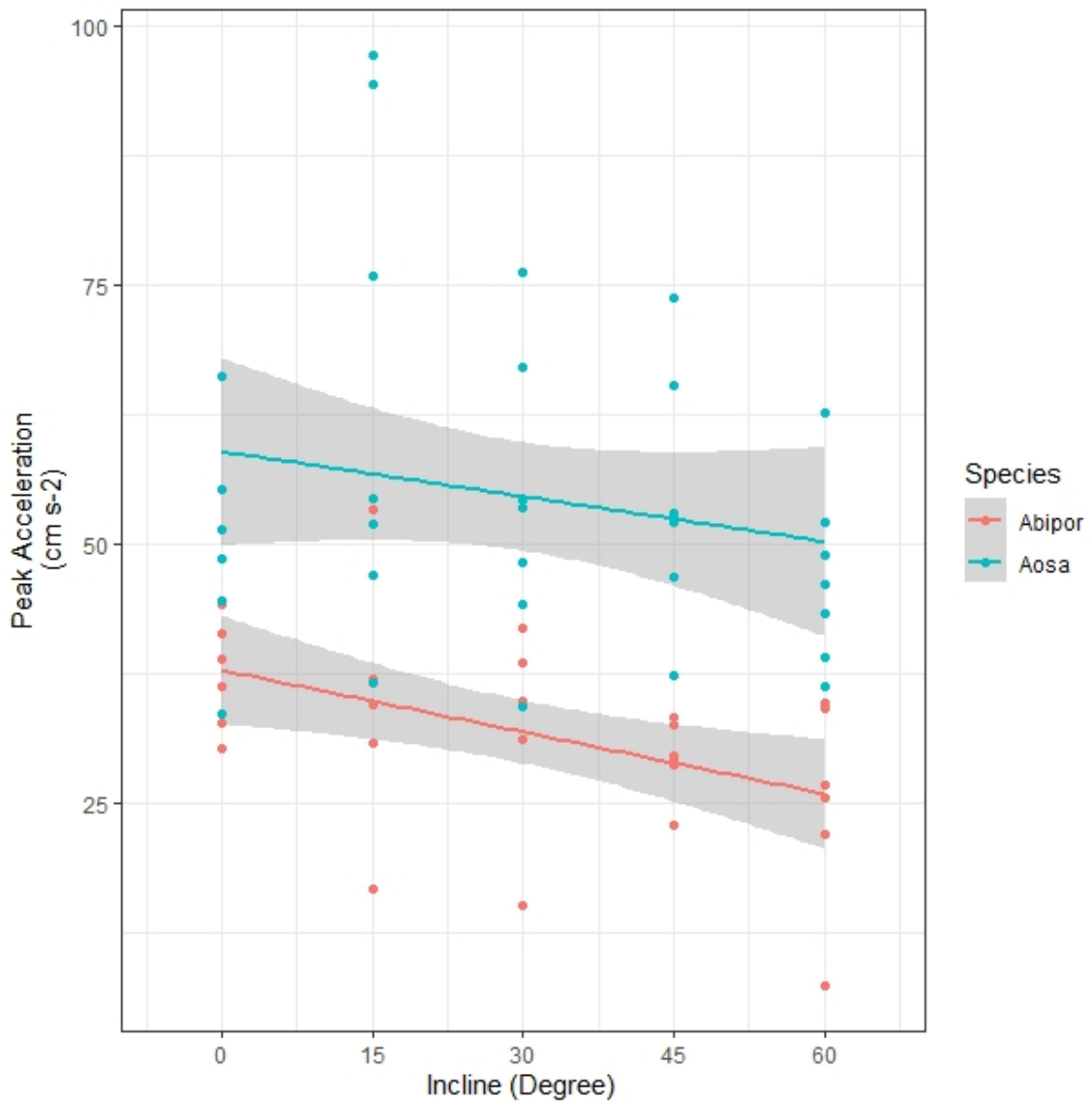


Figure 3. Relationship between incline and peak acceleration for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing a decline in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

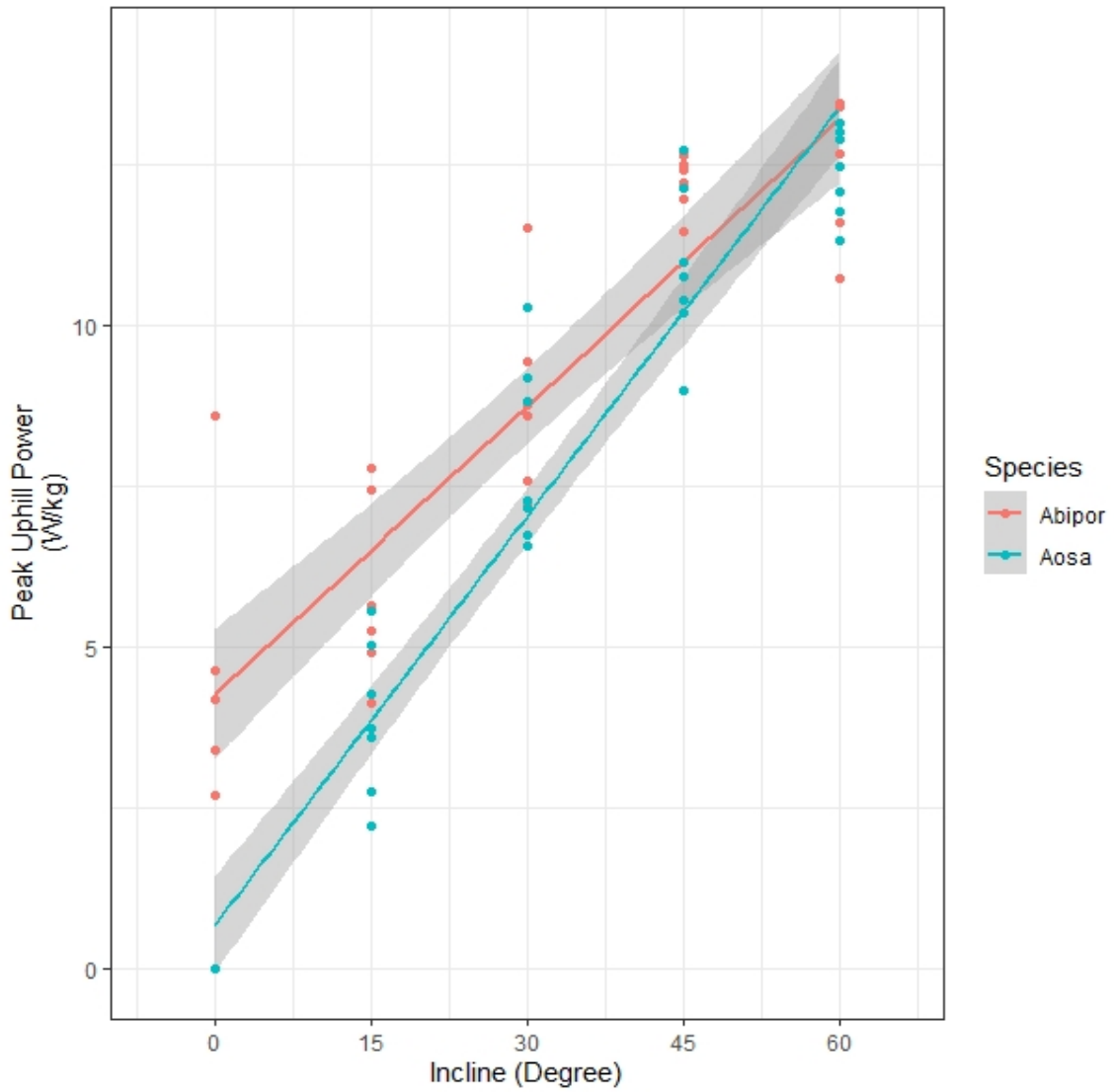


Figure 4. Relationship between incline and peak uphill power for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing an increase in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

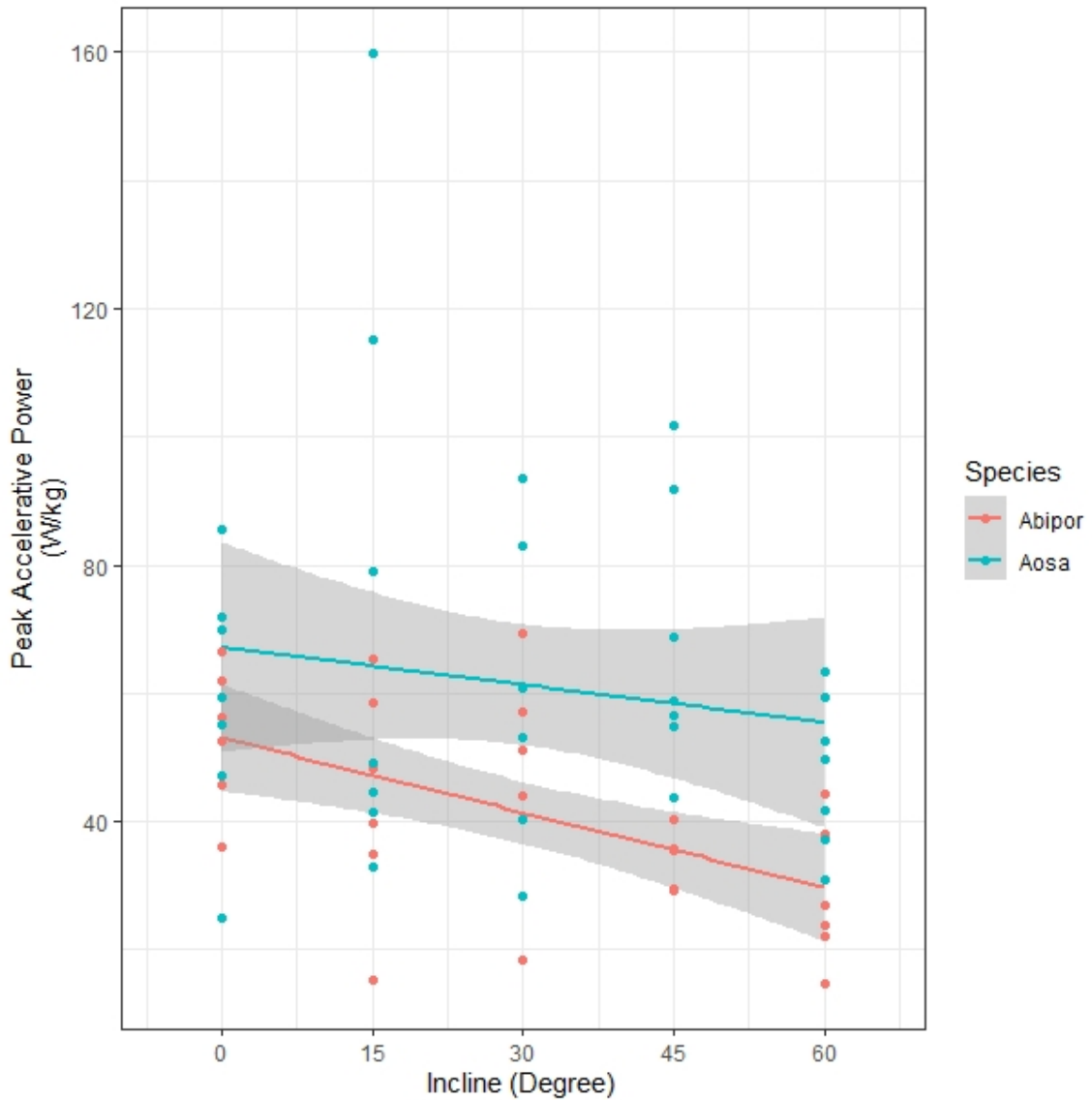


Figure 5. Relationship between incline and peak accelerative power for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing a decline in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.



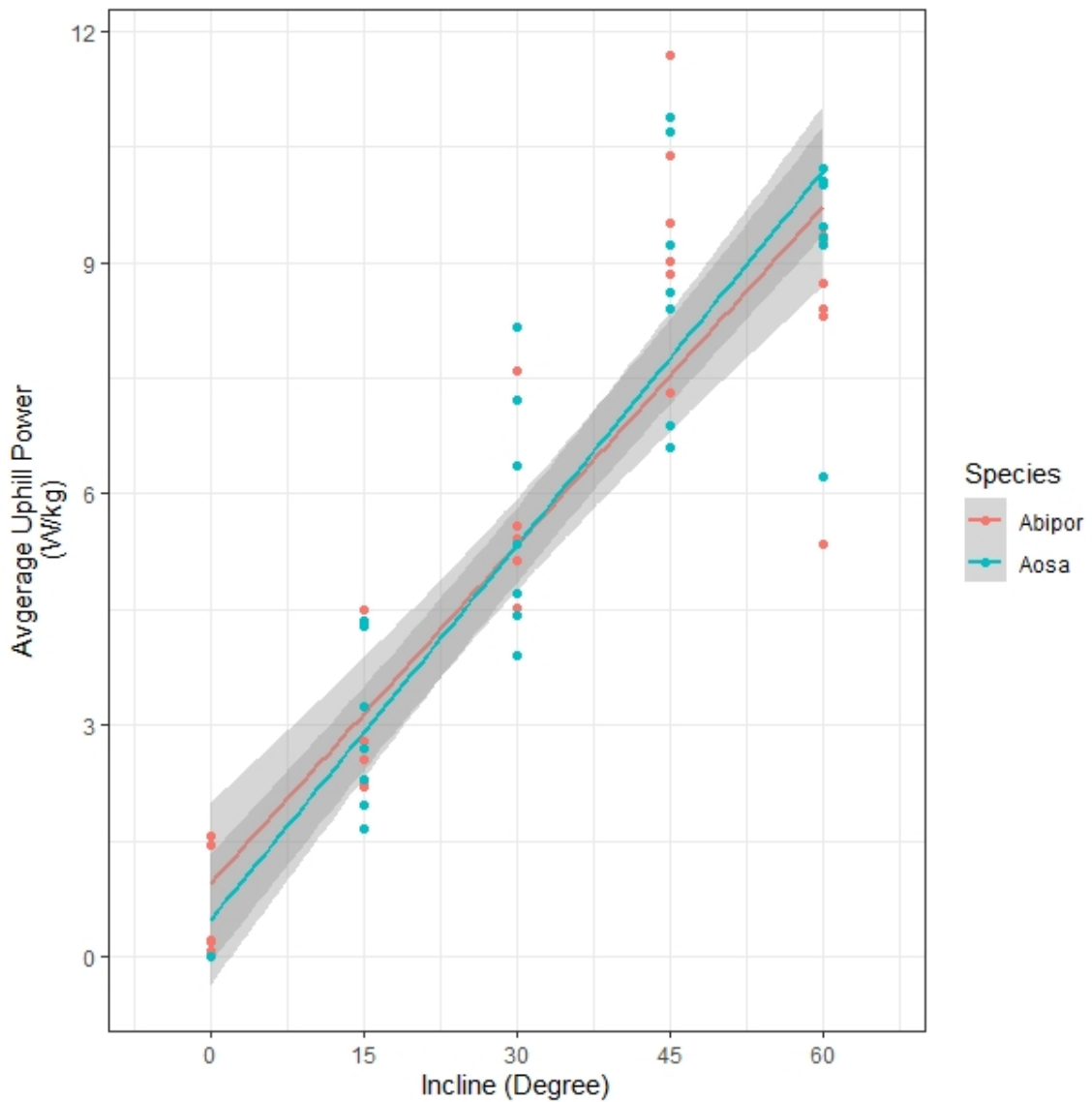


Figure 6. Relationship between incline and average uphill power for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing an increase in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

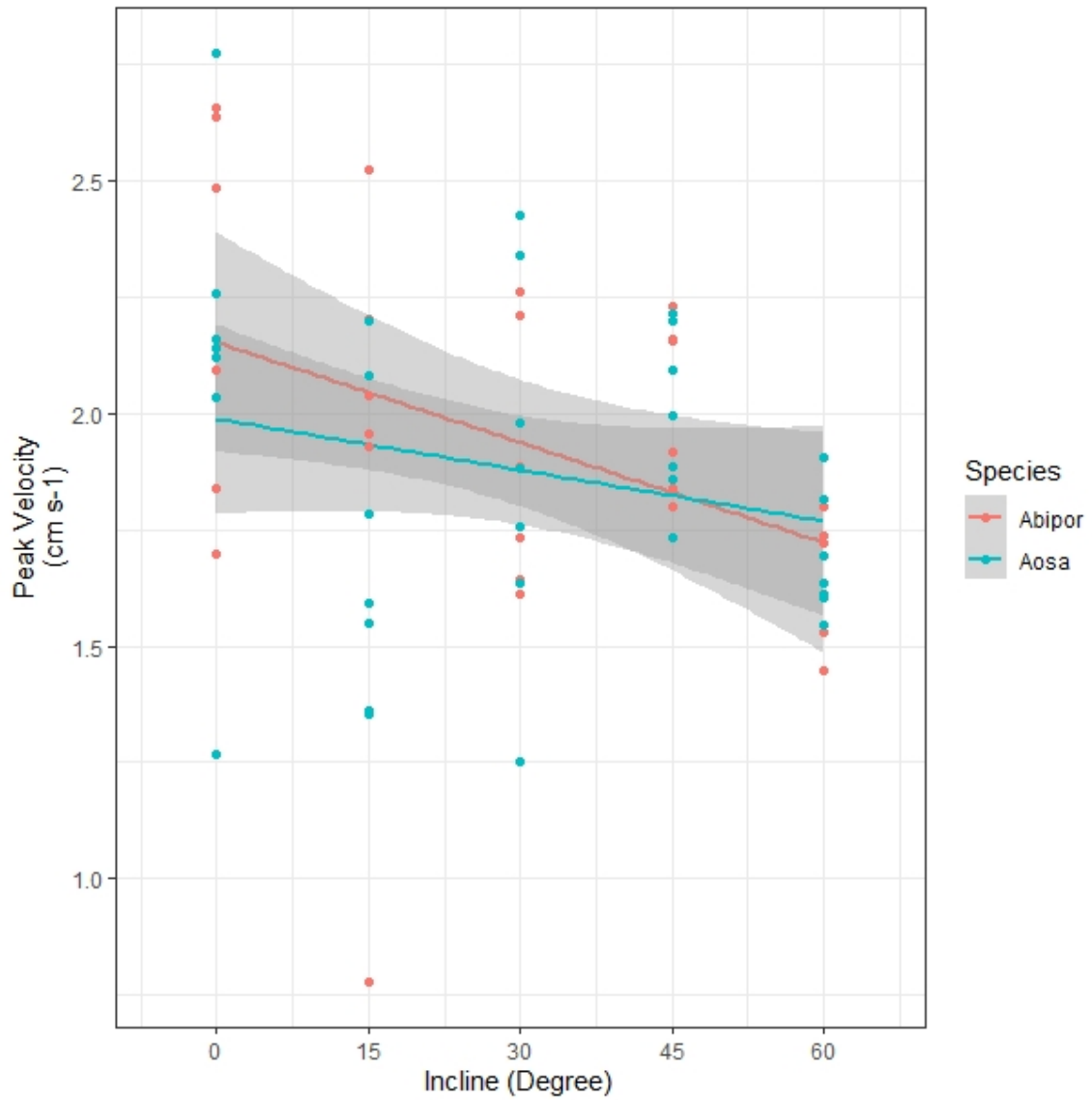


Figure 7. Relationship between incline and peak velocity for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing a decline in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

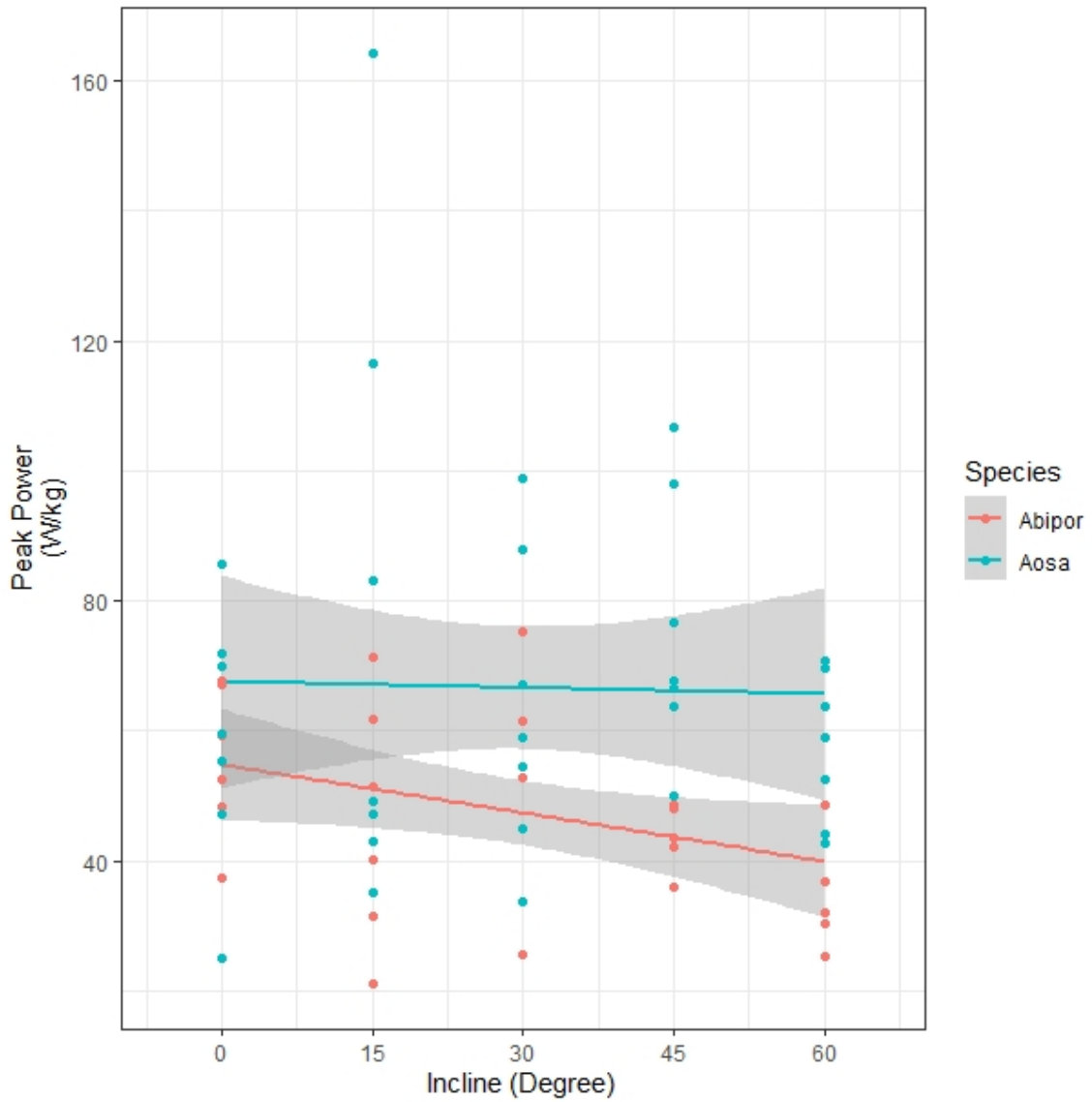


Figure 8. Relationship between incline and peak power for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing a decline in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

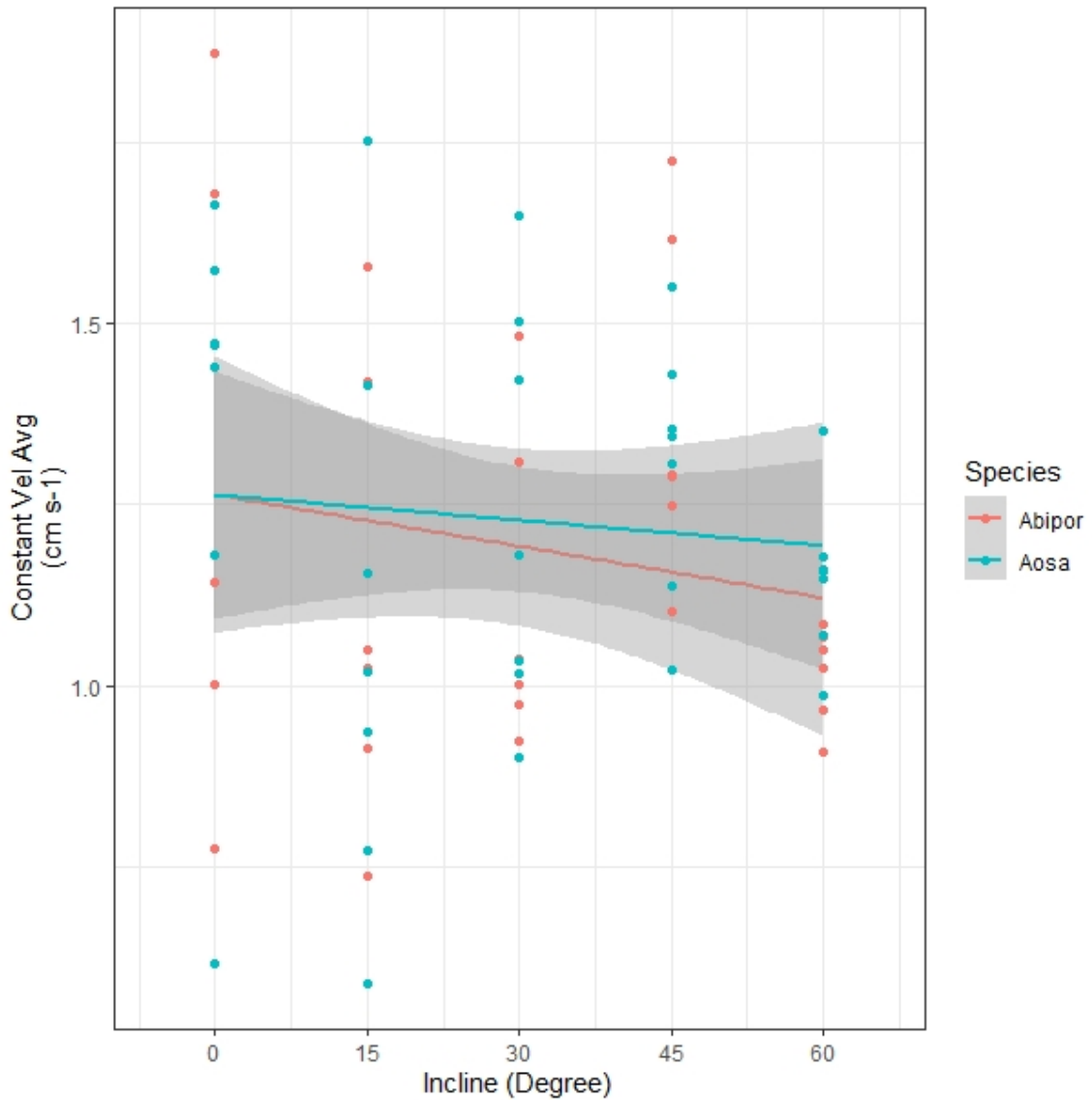


Figure 9. Relationship between incline and constant velocity average for *Anolis osa* (Aosa) and *Anolis biporcatus* (Abipor) showing no significant change in performance with increasing incline. Orange represents *A. biporcatus* and teal represents *A. osa* with each data point representing the performance of one individual. The shaded areas surrounding each trendline represents the 95% confidence interval.

For *Anolis biporcatus*, differences in peak uphill power output between 0° and 15°, and 45° and 60° incline pairs were found to not be statistically significant (Table 4; Fig. 10). Comparisons of all other combinations of incline pairs were found to have significantly different effects on peak uphill power output. For *Anolis osa*, differences between all pairings of inclines showed significant differences on its effect on peak uphill power output (Table 4; Fig. 11).

Table 4. Results of post-hoc Tukey test on effect of incline performance.

Incline	<i>A. biporcatus</i>		<i>A. osa</i>	
	Z-Value	P-value	Z-Value	P-value
0-15°	1.814	0.365497	8.1	<0.001
0-30	5.455	< 1e-04	16.117	<0.001
0-45	9.517	< 1e-05	23.515	<0.001
0-60	9.74	< 1e-06	26.442	<0.001
15-30	3.641	<b>0.002568</b>	8.017	<0.001
15-45	7.703	< 1e-04	15.262	<0.001
15-60	7.926	< 1e-04	18.19	<0.001
30-45	4.062	<b>0.000455</b>	7.094	<0.001
30-60	4.285	<b>0.000163</b>	10.022	<0.001
45-60	0.223	0.99945	3.048	<b>0.0195</b>

Bold P-Values indicate significant effects

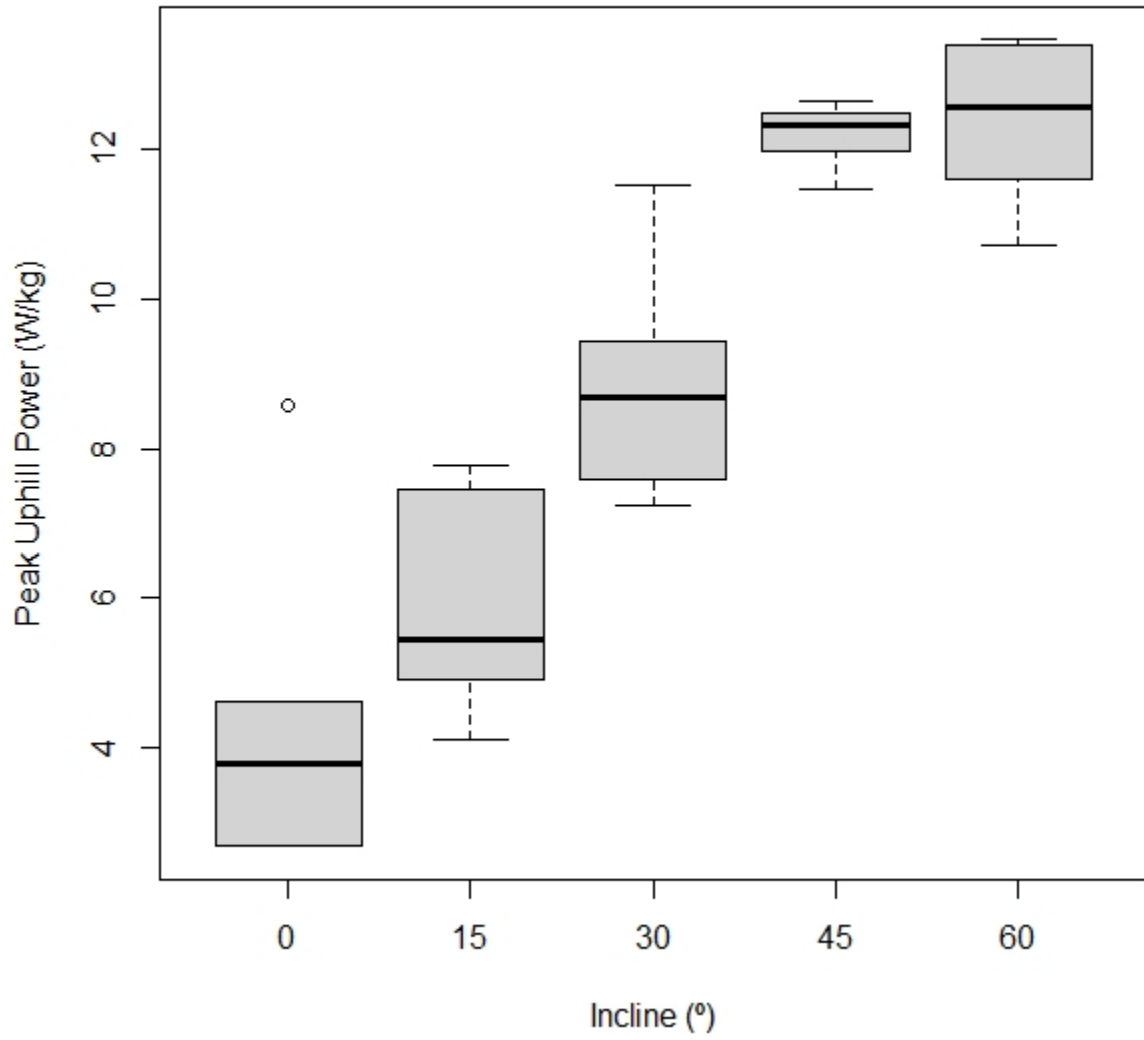


Figure 10. Boxplot showing peak uphill power performance values for *Anolis biporcatus*.

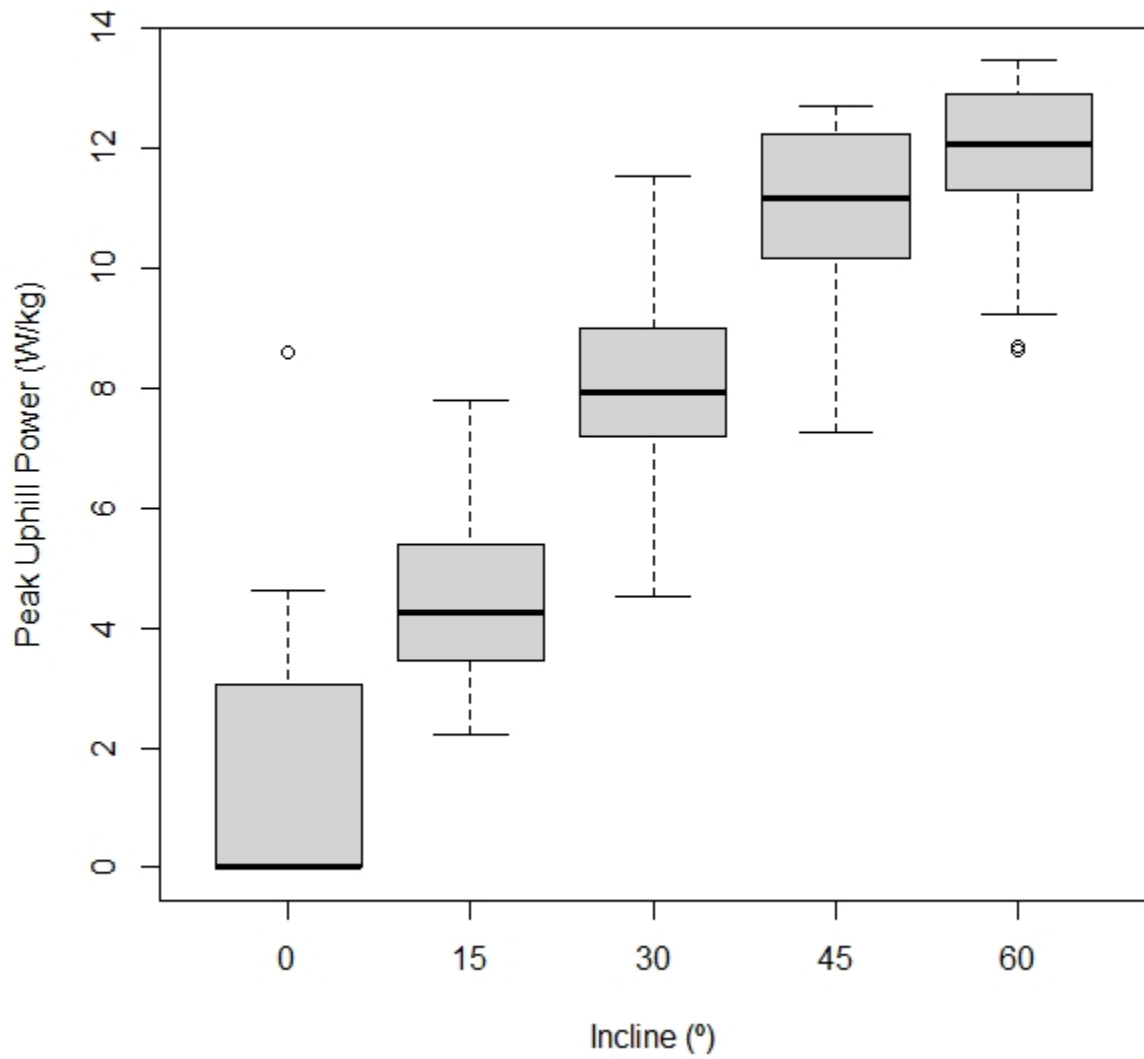


Figure 11. Boxplot showing peak uphill power performance values for *Anolis osa*.

## CHAPTER FOUR

### Discussion

These results illustrate that the sprint performance among two ecomorphs of mainland *Anolis* lizard running at different inclines is impacted in a number of ways. For both species, incline had a strong effect on various performance parameters. Despite large differences in morphology and habitat use between *Anolis biporcatus* and *Anolis osa*, much of their performance is quite similar across inclines, with surprisingly few differences. This was exemplified by the limited number of instances where performance was affected differently for each species as they ran at different inclines.

Incline alone predicted most sprint performance metrics. In fact, the only metric for which there was not a significant effect of incline was constant velocity average. A significant, negative effect of incline was observed for peak velocity, peak acceleration, peak power, and peak accelerative power, suggesting that increasing incline hindered these performance parameters. Peak uphill power and average uphill power, on the other hand, increased with incline, suggesting that, as incline increased, more mechanical power was needed to lift the center of gravity for individuals to move. These patterns were evident in both species, indicating that the effect of incline on performance was conserved between the two species. The directional effect of incline on both peak velocity and uphill power mirrors previous findings in the lizards *E. skiltonianus* and *C. variegatus* (Farley 1997). That uphill power increase with rising inclines suggests that the muscular systems of these species are capable of producing significantly more power (i.e. releasing energy more quickly) than they do while running on a level surface. Further, increases in uphill power output are met with declines in peak velocity, suggesting that



the capacity of these muscular systems to produce maximum mechanical power does not limit the maximum running speeds of these species (Farley 1997). Additionally, sprint performance trials in human sprinters also appears to show the same trend of non-maximal power output during running on level surfaces (Kyle and Caiozza 1986). That recurrence of mechanical power not limiting sprint performance may suggest a broader trend that may also be seen in species that utilize a bounding gait for sprinting.

The two species did differ in peak acceleration, peak accelerative power, and peak uphill power. Although all three performance parameters also showed an effect of incline, only one, peak uphill power, showed a significant effect of the interaction between species and incline. This indicates that, although *A. osa* had higher performance than *A. biporcatus*, incline affected peak acceleration and peak accelerative power in both species consistently (Figs. 3,5).

Similar effects of species on performance have been shown among island ecomorphs. In particular, the trunk-ground species, *Anolis sagrei*, exhibits higher sprint performance compared to the trunk-crown species, *Anolis carolinensis* and *Anolis evermanni* (Irschick and Losos 1999). Additionally, as the diameter of the running surface increased, all species saw similar increases in performance (Irschick and Losos 1999). Specifically, whereas *A. sagrei* had higher sprint performance for all diameters than other species, performance increased similarly for all species (Irschick and Losos 1999). Similarly, I found that the more terrestrial *A. osa* had higher sprint performance, at least in terms of peak acceleration and peak accelerative power, across all inclines than the more arboreal *A. biporcatus*.

Peak uphill power, on the other hand, showed a difference between species, incline, and the interaction between them, indicating that there is a difference in how the two species are affected by changes in incline. *Anolis biporcatus* had higher performance on average for all values except for at the 60° incline (Table 2), as the difference between the performance of the two species decreased as incline increased (Fig. 4). This pattern appears to be driven by the lack of significant difference in peak uphill power for *A. biporcatus* between 0° and 15° incline and between 45° and 60° incline (Table 4; Fig. 10), which would effectively reduce the slope of the regression line for this species (Fig. 4). The lack of significant differences between 45° and 60° inclines may indicate that *A. biporcatus* approaches its maximum performance for peak uphill power at 45° and could not increase further at higher inclines. The lack of a significant difference in peak uphill power between 0° and 15° inclines, on the other hand, may be related to the large size of *A. biporcatus* resulting in the center of mass for this species being elevated higher than in *A. osa* during level sprint trials, during which both species take a more upright, and occasionally bipedal stance, than observed at increasing inclines. *Anolis osa*, on the other hand, exhibited significant differences in peak uphill power between all incline combinations. This suggests that, unlike *A. biporcatus*, *A. osa* did not reach its peak performance at 45° inclines and may even continue to increase beyond 60° (Table 4).

The fact that *A. biporcatus* appears to reach a limit in its mechanical power production for uphill running at lower inclines than *A. osa* was surprising and contradicted my hypothesis based on the more arboreal nature of *A. biporcatus*. That such a limit for *A. osa* was not observed across the examined range of inclines suggests that *A. osa* was better suited to perform at high inclines, despite its terrestrial environment. A

possible explanation for these patterns may actually be derived from looking at the habitat variability of *A. osa*. Because the habitat of *A. osa* experiences rapid changes in incline as the species moves between the forest floor, root buttresses and low perches, it is possible that more flexibility in performance is needed to quickly match performance to the changes in inclines it encounters under normal circumstances.

Some potential limitations of this study relate to the limited number of species investigated, the differences in body size between the species, and escape behavior of anoles. Anytime one compares species in the hopes of broader application of their results, there can be issues that arise with the ability of the findings to be applied to a larger population. In the case of this study, by investigating two species there is the possibility that individual species variation, or even random chance, may be masking broader trends of performance (Garland and Adolph 1994). Increasing the total number of species examined in future studies will help to show if the trends observed here are more broadly observed among mainland *Anolis* in general. Additionally, the observed differences in body size between the two species examined may have confounded some comparisons. While utilizing PCA values to standardize the performance data, there is a possibility that at such different body sizes these two species experience differing constraints on their performance with incline, particularly as there was no overlap between the species. In future studies, consideration for using species with similar or overlapping body size may be beneficial to increase confidence in sprint performance trends. Finally, the differences in antipredator behavior of anoles may have an impact in the adaptation and subsequent performance of ecomorphs. How a species responds to a predator has a large impact in how they move within their environment. Some species may move in a vertical nature to

avoid capture, whereas others may tend to move more horizontally by running or moving to the opposite side of a trunk or branch (Vanhooydonck et al. 2006). Essentially, even though a species may be arboreal in nature, that does not mean that they necessarily frequently move vertically within their environment. Because an analysis of movement within the environment was not completed for the two species, it is possible that one or both of the species moves within their environment in an unexpected or different manner, therefore leading to adaptations that would not typically occur for their particular environment.

Similarities among how species varied and how incline impacted performance between this study and others suggest broader patterns of locomotor performance across inclines and ecomorphs. In particular, whereas increasing incline may reduce sprint speed, it seems increasingly clear that many lizards, and possibly even broader lineages, do not operate at the limit for their mechanical power production during maximal sprinting on level substrates. Further, more terrestrial *Anolis* ecomorphs, both from Caribbean and mainland lineages, appear to outperform more arboreal ecomorphs in many sprint performance characteristics, including as various aspects on their locomotor substrate are varied.

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