Comparison of locomotor performance & hind limb morphology between *Anolis carolinensis* and *Anolis sagrei*, related to the invasion of non-native *A. sagrei* in Florida

By

Kasey Buran

April, 2012



Allegheny College

Department of Biology

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A Senior Comprehensive Project in Partial Fulfillment of the Requirements
for a Bachelor of Science Degree from Allegheny College

I hereby recognize and pledge to fulfill my responsibilities as defined in the Honor Code and to maintain the integrity of both myself and the College community as a whole.

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Pledge

Approval by the Senior Thesis Committee:

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Dr. 1st Reader

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Dr. 2nd Reader

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ABSTRACT

While *Anolis* lizards have been extensively researched as the focus of many different topics, aspects of fitness as they relate to the biological invasion of *Anolis sagrei* in Florida have yet to be investigated. Much is known about both *A. sagrei* and its invasion into the native habitat of *A. carolinensis*, but little is known about exactly which aspects of *A. sagrei's* performance assisted in the success of its invasion. The objective of this study is to compare the ability of locomotor performance and a variable that influences locomotor performance, hind limb length, between *A. sagrei* and *Anolis carolinensis*, and then to expand on similar previous research by relating this comparison to the successful invasion of *A. sagrei* into Florida, the native habitat of *A. carolinensis*. The specific aspects of locomotor performance to be compared are sprint speed and climbing speed. Hind limb morphology was compared using the traits femur length, tibia length, metatarsus length, knee extensor muscle mass, and toepad area. Results show that there is no significant difference in sprint speed or climbing speed between *A. sagrei* and *A. carolinensis*. However, femur length and tibia length are significantly larger in *A. sagrei*. Results suggest that metatarsus length and knee extensor muscle mass are also larger in *A. sagrei*, but that toepad area is larger in *A. carolinensis*. As increased hind limb length has been correlated with increased sprint speed (Losos, 1990a; Losos, 1990b; Losos and Sinervo, 1989), the opposing results of this study to this trend suggests that sprint speed was not significantly instrumental to *A. sagrei's* invasion into Florida, and therefore may not be an ability that is substantially relevant to a species' survival or fitness.

INTRODUCTION

The unique relationship between the green anole, *Anolis carolinensis*, and the brown anole, *Anolis sagrei*, presents interesting topics for research related to biological invasions, habitat use, fitness, and a myriad of other subjects. *Anolis sagrei* has been reported to have successfully invaded the state of Florida, one of the native habitats of *A. carolinensis* (Kolbe et al., 2004; Lee, 1985). Fitness would be presumed to have played a major role in the ability of *A. sagrei* to achieve such establishment of populations in a previously uninhabited environment. Fitness can relate to many aspects of behavior, including predator escape, feeding, and intimidating rival males (Irschick and Garland, 2001) which could contribute to the success of a species in a non-native environment. This study concentrates more specifically on aspects of locomotor performance, sprint speed and climbing ability, and a variable that influences locomotor performance, hind limb length. This study expands on previous studies of similar concentration by comparing these characteristics between two specific species, *A. carolinensis* and *A. sagrei*. Such comparisons of hind limb length and locomotor performance can be related to the successful invasion of *A. sagrei* into Florida as possibly reflecting the superior performance, or fitness, of *A. sagrei* compared to *A. carolinensis* in the same habitat.

Anoles have been extensively studied by research scientists for decades with regard to mating (Jenssen et al., 2001; Ruby, 1984; Tokarz, 2002), discovery of new species (Hedges and Thomas, 1989; Nieto-Montes De Oca, 1994; Poe and Yañez-Miranda, 2007), predation (McLaughlin and Roughgarden, 1989; Paterson, 1999; Wunderle, 1981) and a vast amount of other subjects. Previous research has also expanded on the concept of ecomorphs among various species of anoles (Glor et al., 2003; Langerhans et al., 2006; Pounds, 1988). An “ecomorph” class contains species similar in morphology, ecology and behavior, and is named for the structural habitat that their species normally uses (Beuttell and Losos, 1999). Therefore, within a single geographic area there can be multiple different environments, each with an ecomorph requiring different characteristics or abilities to maximize fitness. *Anolis sagrei* and *A.*

carolinensis are both classified as belonging to different ecomorphs, suggesting that the two species have different abilities allowing them to be more fit in their respective environment. It is these different abilities, specifically sprint and climbing speed, which this study will compare between the two anole species in order to determine if they are instrumental to the success of one species' invasion into the habitat of the other. Superior ability of one species over the other would indicate that species' increased fitness. Fitness over other competing species is a necessary aspect of a successful biological invasion. Determining in which abilities or characteristics an invading species is more fit than another would enlighten scientists as to the reasons that a species, such as *A. sagrei*, could successfully invade a non-native habitat.

Anolis carolinensis

More commonly known as the green anole, *A. carolinensis* is one of the most prevalent and most well-known species of lizard in the United States (Smith, 1995). While most species of the genus *Anolis* inhabit the islands of the Caribbean, *A. carolinensis* is the only species of anole that is native to the United States (Vigil, 2006). In the U.S., populations of this species are known to inhabit North Carolina and southward through Georgia and Florida. They can also be seen along the Gulf Coast region, as far westward as the Rio Grande of Texas. As indicated by this species' preferred habitat, *A. carolinensis* enjoys warmer, tropical climates and increased humidity levels, relative to northern North America (Smith, 1995).

Anolis carolinensis is an arboreal lizard, inhabiting trees, shrubs, vines, and low vegetation (Smith, 1995). Based these observations and behaviors, studies evaluating the ecomorphs of different species of anoles have classified *A. carolinensis* as being of a "trunk-crown" ecomorph, categorizing such classified species by their structural habitat (Beuttell and Losos, 1999; Vanhooydonck, 2006).

Anolis sagrei

The brown anole, *A. sagrei*, is also a well-known type of anole and is becoming more widespread in the United States. *Anolis sagrei* is prevalent in its area of origin, throughout the Caribbean islands, most notably Cuba, the Bahamas, Jamaica, and the Cayman Islands. Similar to other species of anoles, *A. sagrei* prefers warmer temperatures and more humid environments (Vigil, 2006).

This species of anole has been classified as belonging to the "ground-trunk" ecomorph (Beuttell and Losos, 1999; Losos, 1990a; Vanhooydonck et al., 2006). *Anolis sagrei* can be found on the ground or close to it, in low vegetation and is rarely seen perching more than five feet above the ground surface (Vigil, 2006).

Unlike *A. carolinensis*, *A. sagrei* is not native to the United States. However, it now has established populations in the region, as it has been previously introduced (Vigil, 2006). *Anolis sagrei* has now been known to have colonized many new habitats throughout the southwestern United States (Campbell, 1999). The introduction of *A. sagrei* to southern Florida, a native habitat of *A. carolinensis*, created conditions now inviting one to look more closely into the possible means by which one species is able to invade the habitat of another.

Invasion of *A. sagrei*

The species *A. sagrei*, now prevalent in Florida, has its origins in Cuba where it has colonized a number of adjacent islands, including Jamaica and the Bahamas (Lee, 1985). Genetics reports reveal that the majority of *A. sagrei* populations have origins stemming from western, central, and eastern Cuba (Kolbe et al., 2004). The first report of the presence of *A. sagrei* in the Florida Keys was reported around 1880 (Kolbe et al., 2004; Lee, 1985; Vigil, 2006). There is evidence to support that there were multiple introductions of *A. sagrei* into the United States (Kolbe et al., 2004), introductions that were likely accidental, probably occurring during imports of cargo directly from Cuba (Kolbe et al., 2004; Lee, 1985).

Vigil (2006) reports that there were actually two species of brown anole introduced to Florida, the Cuban brown anole, *Anolis sagrei sagrei*, and a separate subspecies, the Bahamian brown anole, *Anolis sagrei ordinatus*. The two began to interbreed in Florida and the brown anoles of the United States today do not belong to either subspecies and are referred to only as *Anolis sagrei*.

After their presence was initially detected, reports of established populations of *A. sagrei* developed in the 1940s (Lee, 1985; Vigil, 2006), and establishment accelerated in the 1970s (Kolbe et al., 2004). Such a lag time between the initial introduction and establishment of populations is characteristic of biological invasions (Sakai et al., 2011). Since its introduction, *A. sagrei* has increased its range of habitat as well as number of populations (Vigil, 2006). Kolbe et al. (2004) found that the multiple introductions of this species "enhanced the ability of *A. sagrei* to occupy non-native areas by accelerating its geographic expansion over that possible by simple diffusion alone" (pg. 179).

Disturbingly, since the invasion of *A. sagrei* into Florida, populations of the native *A. carolinensis* have become more scarce (Campbell, 1999; Vigil, 2006). The cause of the population decrease of *A. carolinens*is, however, has been difficult to discern, as the decline following the introduction of *A. sagrei* is quite quick (Campbell, 1999). In some areas where *A. sagrei* has been introduced, *A. carolinensis* has shifted its habitat from vertical, including low vegetation, to strictly trunk and crown areas, while other times it has been forced from its habitat by the invading species altogether (Vigil, 2006). Campbell also observed this phenomenon in his 1999 study in which he introduced populations of *A. sagrei* to areas in which *A. carolinensis* populations had been established. Campbell recorded a decline in *A. carolinensis* populations *as A. sagrei* populations expanded, as well as the utilization of habitats different from those of the original *A. carolinensis* populations. *Anolis sagrei* also displays its invasive behavior under similar circumstances in the Grand Cayman Islands (Losos et al., 1993). In habitats where *A. sagrei* is now present, the Grand Cayman native, *A. consperus*, inhabits higher perches, whereas no change in perch height is detected in areas where *A. sagrei* is absent.

Similarly, Losos and Spiller (1999) observed small islands in the Bahamas which had not yet been populated by *A. carolinensis* or by *A. sagrei*. After placing both species on five different blocks of three islands each and observing the populations for three years, every population of *A. sagrei* was thriving, while many of the *A. carolinensis* populations had gone extinct or were very small in number. Losos and Spiller found that the *A. carolinensis* populations had little effect on those of *A. sagrei*. As *A. sagrei* has repeatedly proven to be more successful in regards to survival compared to *A. carolinensis*, a comparison of fitness between these two species is desired. This study takes such an initial step in comparing locomotor performance between these two species as well as related morphological characteristics, including hind limb length.

Hind Limb Morphology

Sprawling limbs characterize the majority of lizard species and require specializations of the vertebrae, pectoral girdle, and hind limbs to increase their function (Pough et al., 1998). Lizards' hind limbs are more robust and better developed than their forelimbs, as the hind limbs provide the majority of the propulsive force (Smith, 1995; Pough et al., 1998). Bipedal species tend to have longer hind limbs than forelimbs. Longer hind limbs are able to swing through a greater arc and therefore move further in a given interval of time. The lateral orientation of the femur, however, compromises propulsive force in the direction of movement, requiring a specialized knee joint that changes its orientation during the course of a single step. Hind limb specializations also include the condition of the tarsal bones and characteristic shape of the fifth metatarsal. The first four metatarsal bones are fused together, as the fifth is not attached and lies at an angle to the others. Among anoles, the fourth metatarsal is the longest digit (Pough et al., 1998).

Toepads are characteristic of anoles (Smith, 1995). The subdigital pad is divided into transverse scales or 'ridges,' called lamellae. Each lamella is covered with tens of thousands of microscopic, hair-

like structures called setae, with each containing hundreds of projections. These projections are instrumental in the ability of anoles to cling to smooth surfaces (Irschick et al., 1996). *Anolis* toepads differ in size and structure among species and researchers have observed that species that perch higher off the ground have more lamellae (Collette, 1961; Glossip and Losos, 1997; Williams, 1983).

Locomotor Performance

Locomotor performance can be related to overall organismal fitness as it affects a wide variety of behaviors basic to survival, including predator escape (Bennett and Huey, 1990), prey capture (Higham, 2007), and male-male interactions (Garland et al., 1990). The first focus of the two measurements of locomotor performance in this study is sprint speed. Sprint speed and all aspects of behavior with which it is correlated can be influential to the survival of the lizard, and therefore its ability to maintain establishment of its populations. As establishment of populations is crucial to the concept of biological invasions, be it on the part of the invading species or the native species of the invaded habitat (Sakai et al., 2001), sprint speed could be related to the overall success of an invasion, specifically of *A. sagrei* in Florida.

This study will compare overall sprint speed between *A. carolinensis* and *A. sagrei*. Specific morphological traits proven to be influential to this measurement of locomotor performance will be taken into account and compared. The first morphological trait to be studied is hind limb length. Previous studies have correlated increased hind limb length with increased sprint speed in both anoles (Losos, 1990a; Losos, 1990b; Losos and Sinervo, 1989) and other lizard species (Irschick and Garland, 2001; Irschick and Jayne, 1998). A second morphological trait of interest is that of knee extensor muscle mass. Of all muscles of the hind limb, the knee extensor muscle is the strongest determinant of sprint speed; all remaining muscles lack a significant correlation to sprint speed (Vanhooydonck et al., 2006).

The second of the two measurements of locomotor performance of focus in this study is climbing ability. Climbing ability can be evaluated in multiple ways, but in this study climbing ability will be evaluated based on climbing speed (Vanhooydonck and Van Damme, 2003; Vanhooydonck et al., 2000). As with sprint speed, along with overall climbing ability, two morphological traits correlated with climbing ability will also be compared between *A. carolinensis* and *A. sagrei*, the first being hind limb length. Previous studies have shown that lizards which inhabit terrestrial habitats and therefore run on broader surfaces have decreased speed on smaller perch diameters, among both anoles (Calsbeek and Irschick, 2007) and other species of lizards (Sinervo and Losos, 1991). Measurements of this aspect of locomotor performance relates to the ability of a species to establish populations in new environments and ecomorphs, crucial to the success of an attempted invasion of a new habitat. The second morphological trait related to climbing ability to be compared between species is toepad area. Toepad area is correlated with increased clinging ability among anoles (Glossip and Losos, 1997; Losos, 1990b) and has obvious effects on climbing ability, specifically the speed at which a specimen would be able to climb, which is this study's measurement of climbing ability.

METHODS

Anolis **Care**

I obtained 20 specimens, 10 *A. carolinensis* and 10 *A. sagrei*, through a distribution site based in Lakewood Ranch, Florida, ranging in size from about 49-64 mm and about 40-55 mm, respectively. 10 ten-gallon tanks were used to house all specimens, with 2 specimens inhabiting each tank, with a divider in the center.

All specimens' containers replicated the anoles' natural environment; mulch and dirt covered the ground of each container and vegetation was present such that the lizards had spaces of cover and something on which to climb. To simulate a warm environment, specimens were housed in a

temperature controlled room at 28° C. The containers were spritzed daily with water to maintain humidity.

The diet of anoles consists mainly of insects. Specimens were fed live crickets every 2 to 3 days. Sprint speed is relevant to many different aspects of performance, including prey capture. All specimens were fed live crickets to keep them from becoming "spoiled" or out of practice and less likely to reach high sprint speeds during trials. Each container had a small shallow bowl of water, although these lizards are not partial to drinking stagnant water. Instead, with the spritzing of each container daily, the specimens were able to lick water from the leaves of their vegetation.

Measurements of Hind limb and of Locomotor Performance

To measure sprint speed, I conducted time trials for each specimen on a track. The track was a flat, straight, horizontal surface made of cardboard, and was 1 m long. Transparent plexiglass barriers lined the sides of the track to ensure that the lizards ran straight through the track and not off to one side. A removable screen lid covered the top of the track during trials to keep the lizards from climbing over the barriers and escaping. I conducted 5 trials for each specimen, recorded by a Canon digital camera at 240 frames per second. The fastest speed attained over any 0.20 m interval in each trial was kept. This speed was found using the program Tracker. In this program, the 0.20 m interval over which the specimen sprinted the fastest could be determined and the time elapsed shown. Speed was then found using the simple formula, $d = v/t$, where d is distance (0.20 m), v is velocity, and t is time elapsed. Of the 5 fastest speeds recorded, 1 from each trial, the mean was taken for each specimen. Each lizard ran 1 trial per day to ensure that fatigue did not factor into performance. Specimens were persuaded to begin running with a clap of the hands or a slight touch of the tail by a small rod, and were influenced to run the length of the track by hand gestures or the presence of the small rod.

Measuring climbing ability was conducted similarly to measuring sprint speed. Specimens were encouraged to run up a straight tree branch. The branch was 1 m in length and raised to a 70° angle, following a study of similar focus performed by Vanhooydonck et al. (2000). 5 trials were conducted for each specimen, recorded by a Canon digital camera at 240 frames per second, and the fastest speed attained over any 0.20 m interval in each trial was recorded. Of the 5 fastest climbing speeds recorded, 1 from each trial, the mean was taken and each specimen's average climbing speed determined. Again, each lizard ran 1 trial per day. Specimens were persuaded to begin running with a clap of the hands or a slight touch of the tail by a small rod, and were influenced to run the length of the track by hand gestures or the presence of the small rod.

Following sprint speed and climbing trials, specimens were euthanized with MS-222 using a two-step procedure (Conroy et al., 2008). First, each specimen was injected intracoelomically with 250 mg/kg 1% MS-222 solution. As soon as the specimen lost response to a skin or toe pinch, each was then injected with 0.1 ml 50% (v/v) MS-222 solution. Cessation of respirations and palpable heartbeats were observed within 60 seconds of injection of 0.1 ml 50% (v/v) MS-222 solution.

Body and Hind Limb Measurements

The following body measurements were taken of each specimen with digital calipers: snout vent length (SVL, measured from snout to cloaca; mm), total length (measured from snout to end of tail; mm), and mass (g). The following external measurements were taken of the specimens' hind limb morphology with digital calipers: femur length (measured from hip to knee; mm), tibia length (measured from knee to ankle; mm), and metatarsus length (measured from the heel to the tip of the fourth toe; mm). External measurements of hind limb morphology also included the toepad area (cm^2), measured using the computer program Image J. Images of each specimen's toepads were viewed in Image J and area was calculated following determination of the boundaries of the toepad in the program. The area

of the toepads on toes 2 and 3 were measured from the fore limb, and the areas of the toepads on toes 3 and 4 were measured on the hind limb. All four toepad areas were combined to give a measurement of total toepad area, following procedures from previous research regarding toepad area (Beuttell and Losos, 1999; Glossip and Losos, 1997). As previously mentioned, this measurement has been correlated with clinging ability and can therefore contribute to climbing ability (Glossip and Losos, 1997; Losos, 1990b). The only internal measurement taken was knee extensor muscle mass, which has been shown to contribute to sprint speed (Vanhooydonck et al., 2006). The knee extensor muscles were dissected and removed from each specimen and immediately weighed to determine the total knee extensor muscle mass.

Statistical Analysis

The first objective of this study, to compare the differences in hind limb morphology and locomotor performance, evaluated by sprint speed and climbing ability, between *A. carolinensis* and *A. sagrei*, was broken down into three comparisons. The first comparison was between the hind limb morphology of *A. carolinensis* and the hind limb morphology of *A. sagrei*. Because the variables of hind limb morphology are not independent with respect to one another, they were compared between the two species using a MANCOVA. To account for the differences in body size among specimens, SVL was used as a covariate in this analysis, as mass and SVL have a strong correlation in *Anolis* lizards (Losos et al., 1994). This test was ran using the program SPSS. The second comparison was between the sprint speed of *A. carolinensis* and the sprint speed of *A. sagrei*. This comparison was analyzed using an ANCOVA, with SVL again used as a covariate. This test was performed using the program Past. The third comparison between the climbing ability of *A. carolinensis* and the climbing ability of *A. sagrei* was also analyzed using an ANCOVA, with SVL as a covariate. This test was also performed using the program Past.

A Shapiro-Wilk test for normality was performed with all characteristics measured (average sprint speed, average climbing speed, femur length, tibia length, metatarsus length, knee extensor muscle mass, and toepad area), and all results were significant ($p>0.05$).

RESULTS

Morphological data for all 20 specimens can be found in Table 1. One-way ANCOVA indicated that the populations of *A. carolinensis* and *A. sagrei* did not differ significantly in average sprint speed ($F=0.8852$, $p>0.05$; Table 2) or in average climbing speed ($F=0.02944$, $p>0.05$; Table 3), showing that *A. sagrei* does not sprint or climb faster than *A. carolinensis*.

Table 1. Morphological measurements of all specimens (B, brown- *A. sagrei*; G, green- *A. carolinensis*).

specimen	SVL (mm)	total length (mm)	femur length (mm)	tibia length (mm)	metatarsus length (mm)	knee extensor muscle mass (g)	toepad area (cm^2)
B1	48.62	140.73	11.65	11.30	16.50	0.021	0.073
B2	49.15	122.40	12.16	10.94	15.90	0.022	0.072
B3	51.55	155.94	13.43	12.28	16.87	0.041	0.084
B4	44.62	134.44	9.94	9.91	14.43	0.019	0.046
B5	36.04	86.11	8.98	8.28	11.83	0.011	0.034
B6	41.55	117.69	9.14	9.03	12.90	0.017	0.044
B7	42.40	115.98	9.64	8.93	12.33	0.015	0.047
B8	51.47	154.59	11.76	10.96	15.85	0.029	0.080
B9	53.12	156.48	13.24	12.62	18.15	0.047	0.104
B10	54.45	150.13	12.65	12.47	18.33	0.052	0.091
G1	49.46	140.89	9.01	8.92	12.63	0.006	0.078
G2	52.88	155.52	10.02	9.67	13.38	0.013	0.103
G3	51.55	155.86	10.23	10.01	14.04	0.014	0.096
G4	55.82	164.68	10.83	10.33	14.18	0.016	0.107
G5	57.55	170.90	11.82	11.37	14.72	0.016	0.132
G6	49.73	133.95	9.23	8.95	11.59	0.016	0.079
G7	51.86	153.05	11.61	10.63	12.78	0.016	0.100
G8	64.27	182.88	13.72	12.20	15.36	0.021	0.160
G9	60.44	183.85	11.83	11.25	15.13	0.022	0.157
G10	51.03	149.24	10.20	8.83	12.20	0.013	0.083

Table 2. Mean average sprint speeds and standard error for both *A. carolinensis* and *A. sagrei*.

Species	mean avg. sprint speed (cm/s)	standard error (cm/s)
A. carolinensis	78.4	± 7.1
A. sagrei	88.3	± 4.4

Table 3. Mean average climbing speeds and standard error for both *A. carolinensis* and *A. sagrei*.

Species	mean avg. climbing speed (cm/s)	standard error (cm/s)
A. carolinensis	80.4	± 3.9
A. sagrei	71.2	± 3.7

MANCOVA results comparing specimens' hind limb morphological traits (femur length, tibia length, metatarsus length, knee extensor muscle mass, and toepad area) and SVL yielded both significant and not significant results. The interaction between SVL and both femur and tibia were not determined to be significant ($p>0.05$), requiring ANCOVA's to be run on both traits. The ANCOVA's of both femur ($F=44.873$, $df=1$) and tibia length ($F=67.007$, $df=1$) of *A. sagrei* and *A. carolinensis* were determined to be significant ($p<0.05$), indicating that femur length and tibia length are significantly different between the two species. Both femur length and tibia length are larger in *A. sagrei* than in *A. carolinensis*.

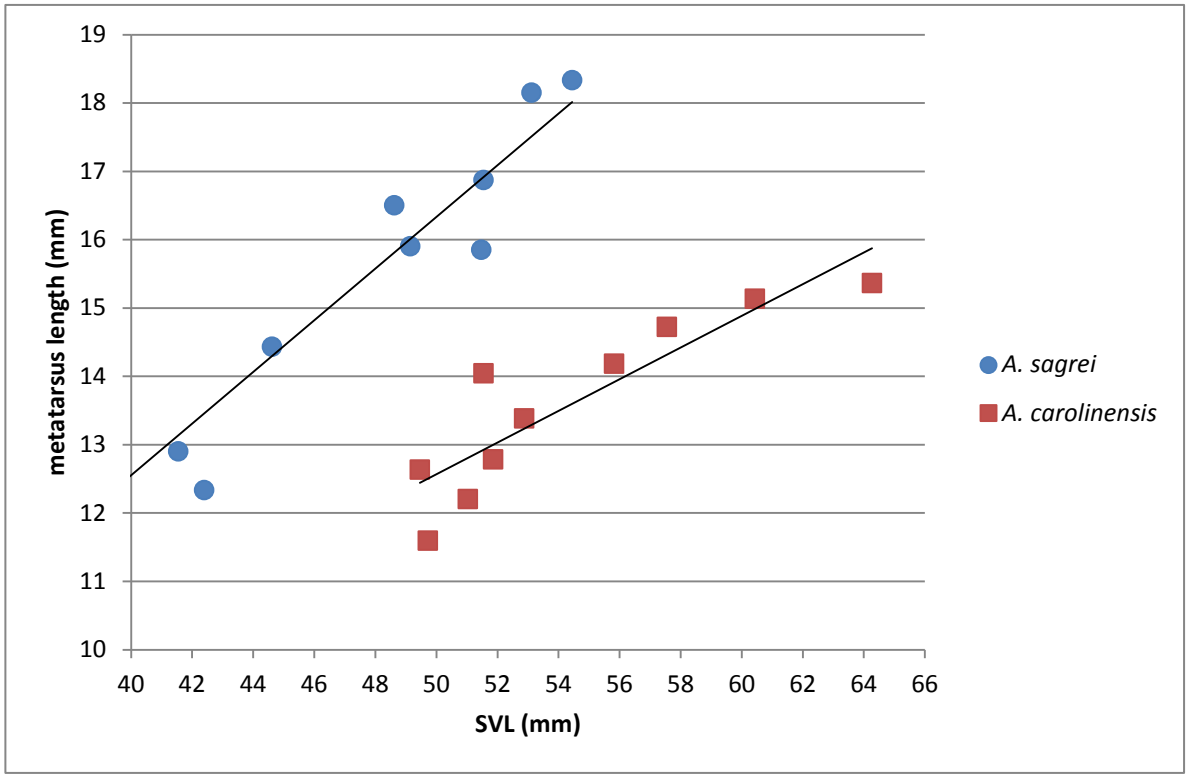
The MANCOVA results of the interaction between SVL and metatarsus length, knee extensor muscle mass, and toepad area were those found to be significant ($p<0.05$). Therefore, individual linear regressions of each of these traits against SVL were then performed (Table 4, Fig. 1). The linear regressions representing both metatarsus length and knee extensor muscle mass suggest that the metatarsus length and knee extensor muscle mass of *A. sagrei* is greater than *A. carolinensis*. The linear regression representing toepad suggests that the toepad area of *A. carolinensis* is greater than *A. sagrei*.

Table 4. Statistics drawn from linear regressions of three morphological characteristics, metatarsus length (mm), knee extensor muscle mass (g) and toepad area (cm^2), respectively, of both *A. sagrei* and *A. carolinensis* vs. SVL.

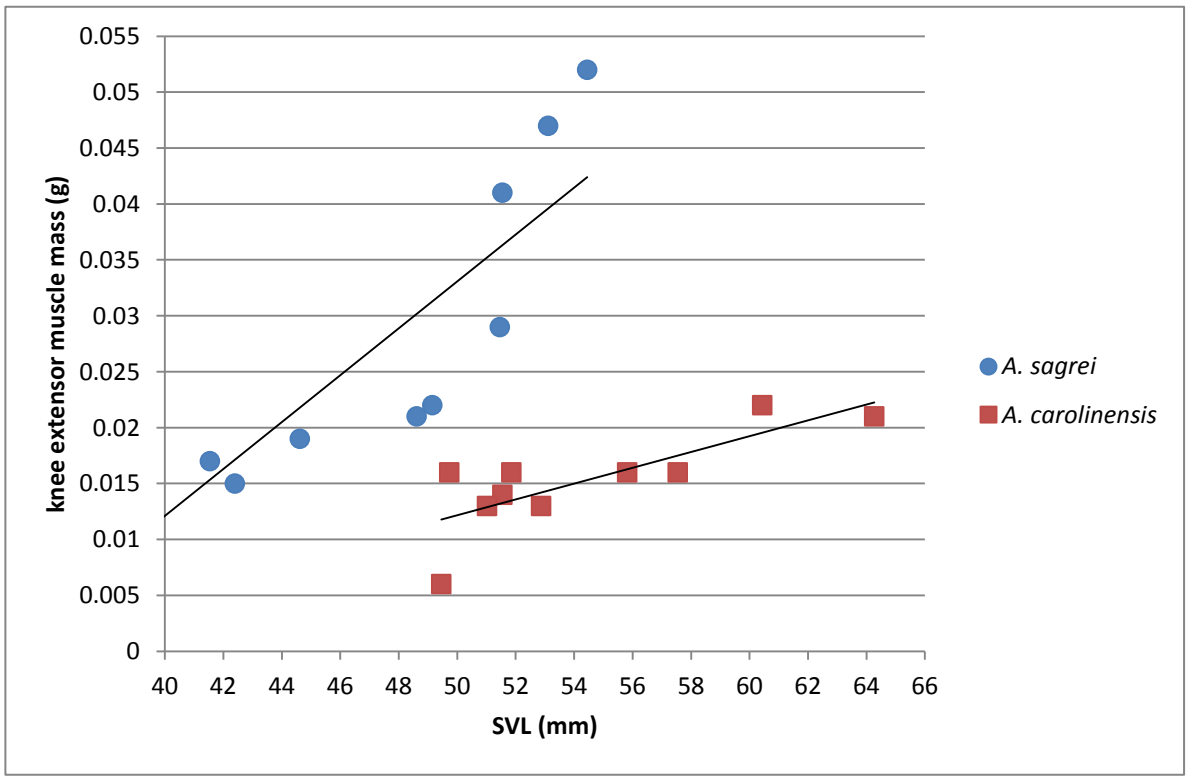
trait	species	y-intercept	b	r^2	t	p
metatarsus	*A. sagrei*	-2.5653	0.37792	0.91829	9.4821	<0.001
	A. carolinensis	0.9854	0.23165	0.79408	5.5543	<0.001
knee extensor	*A. sagrei*	-0.071738	0.0020961	0.75267	4.9341	0.001
muscle mass	*A. carolinensis*	-0.023215	0.00070723	0.61857	3.6019	0.007
toepad area	*A. sagrei*	-0.11005	0.0037539	0.90687	8.8264	<0.001
	A. carolinensis	-0.21502	0.0059589	0.94703	11.96	<0.001

Fig. 1. Linear regressions of morphological traits of both *A. sagrei* and *A. carolinensis* vs. SVL, represented on same graph. A) linear regression of SVL vs. metatarsus length, B) linear regression of SVL vs. knee extensor muscle mass, C) linear regression of SVL vs. toepad area.

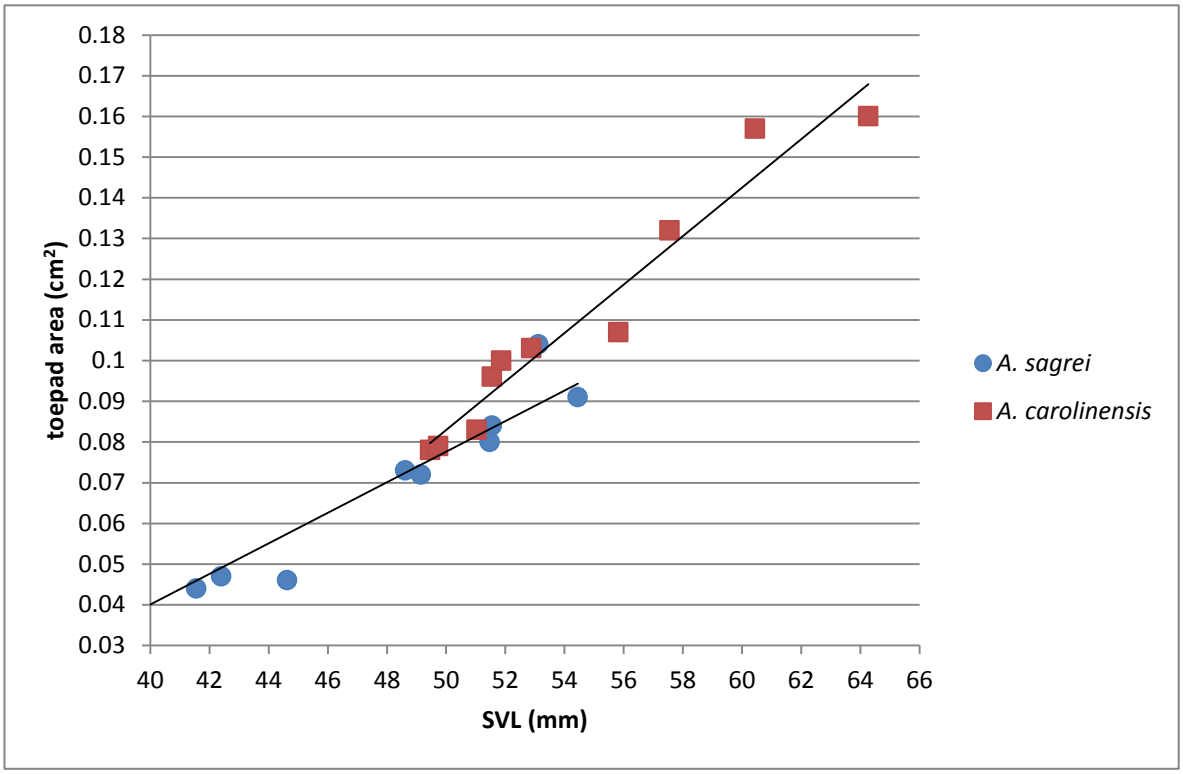
A)



B)



C)



DISCUSSION

The results of my study disconfirmed my hypotheses regarding sprint and climbing speed; *A. sagrei* did not sprint significantly faster than *A. carolinensis* and *A. carolinensis* did not climb significantly faster than *A. sagrei*. However, the hypotheses made in relation to hind limb morphology were supported, including those associated with both sprint and climbing speed, warranting closer inspection of the circumstances surrounding my measurements of both sprint and climbing speed.

The results suggest that *A. sagrei* possesses larger knee extensor muscles than *A. carolinensis*. As previously stated, knee extensor muscle mass is correlated with faster sprint speeds and is the only hind limb muscle to which sprint speed has been shown to be correlated in *Anolis* lizards (Vanhooydonck et al., 2006). Why the observed specimens did not follow this trend, then, should be explored further. Results also show that both femur and tibia length are longer in *A. sagrei* than in *A. carolinensis*, as well as suggests that metatarsus length is greater in *A. sagrei* than in *A. carolinensis*; combining for a longer

total hind limb length in *A. sagrei* than in *A. carolinensis*. Also as previously discussed, increased hind limb length has been correlated with increased sprint speed in lizards, including anoles (Irschick and Garland, 2001; Irschick and Jayne, 1998; Losos, 1990a; Losos, 1990b; Losos and Sinervo, 1989). This trend was also unexpectedly not detected among the observed specimens.

Similarly to the results surrounding sprint speed, the hind limb morphological trait correlated with climbing speed, toepad area (Glossip and Losos, 1997; Losos, 1990b), is suggested to be larger in *A. carolinensis* than in *A. sagrei*. However, results show that *A. carolinensis* does not climb significantly faster than *A. sagrei*. This study's results were expected to support these previously observed trends among lizards, including anoles, but they did not. The results, then, suggest that the measured average sprint and climbing speeds of the experimental specimens are not accurate representations of the specimens' sprinting or climbing capabilities or maximum speeds.

Inability to perform at maximum capacity could be a result of anything from physical to psychological distresses, especially fear among animals. A most apparent stressor in this study, while the specimens' living environment strove to mimic a natural anole habitat, the site and construction of both the sprint and climbing tracks did not. Contact with unfamiliar surfaces or lab environments may potentially have contributed to below maximal or sporadic sprint and climbing performances.

However, more pertinent to these species as a whole is the ecological relevance of the results of this study, regardless of the statistical significance. It is unknown whether these results are representative of the actual habits of the species in their true environments. This study strove to provide support for the idea that increased sprint speed in one species makes it more fit than another on the ground, therefore supporting the observations associated with the biological invasion of *A. sagrei* into Florida; since the introduction of the non-native *A. sagrei*, populations of *A. carolinensis* have been eliminated or have appeared to move to what is classified as the trunk-crown ecomorph, as opposed to inhabiting a lower, ground-trunk ecomorph. But if *A. sagrei* have not been shown to sprint faster than

A. carolinensis, it is unclear whether this study's measurements are flawed or biased, as discussed, or are, again, not an accurate reflection of these species' behaviors in their environments.

Irschick (2000) sheds light on this subject with an in-depth field study of eight species of *Anolis* lizards, including *A. sagrei* and *A. carolinensis*. *Anolis sagrei* was found to travel at 22.5 ± 3.4 cm/s on average, and *A. carolinensis*, 10.7 ± 1.6 cm/s. Still, the ranges of travelling speed were perhaps more telling; *A. sagrei* ranged from 2.0-133.8 cm/s while *A. carolinensis* ranged from 0.2-80.0 cm/s. With average traveling speeds so much lower than their measured maximums, these species clearly do not often perform at their maximum rate. This nearly suggests that the maximum rate at which an individual can travel is not unequivocally relevant to the daily activity nor, then, to the daily survival or fitness of that individual, and therefore to the population as a whole. However, this theory is unsubstantiated. An individual's survival may be minimally at risk, and therefore maximum sprint capacity rarely necessary, resulting in a lower measurement of average traveling speed.

Though, in further support of the insinuation of the lack of importance of travelling or sprint speed to the survival, and therefore to the success, of a species, Irschick (2000) determined that for all eight species of *Anolis* lizards in his study, at least 75% of their locomotor movements occurred between 0% and 40% of their maximum capacity. If only 25% of *A. sagrei's* and *A. carolinensis'* locomotor movements require speeds above only 40% of their maximum capacity, sprinting ability would not appear to be pertinent to the survival of an individual. Irschick's study, as well as this study's results, could suggest that a species' sprinting or climbing ability is not actually a significant determining factor in the success or fitness of these species, as was previously hypothesized. *A. sagrei* has successfully invaded the habitat of *A. carolinensis*, but that "superiority" is not reflected in this study's measurements of average sprint speed, perhaps because that is not the factor that is correlated most with the survival or success of a species in the environment of focus.

The question, then, that still remains pertains to why *A. sagrei* was in fact successful in invading the habitat of *A. carolinensis*. This study cannot conclude that it is due to *A. sagrei's* superior sprinting abilities. Though the species may have longer hind limbs than *A. carolinensis*, they did not prove to be significantly advantageous in regard to sprint speed. However, such morphological characteristics may be advantageous for other activities, which is an excellent basis for future study. Looking further into the morphological differences, specifically between *A. sagrei* and *A. carolinensis*, could shed light on the reasons behind the success of *A. sagrei's* invasion in Florida. Determining in which physical ways these two species differ could tell us in what survival- or fitness-related abilities *A. sagrei*, or *A. carolinensis*, is more skilled. Also, looking more closely at the environment in question, one may be able to determine which abilities are further advantageous in that specific habitat.

Another thought-provoking basis for further research can be drawn from a recent study conducted by Zalewski and Bartoszewics (2012). This study investigated the invasive American mink and its introduction into the Warta Mouth National Park in Poland, between 1996 and 2004. The two found that mink body mass significantly decreased during the period of population establishment within the area they studied; 13% decrease in males, 16% in females. Zalewski and Bartoszewics also monitored the mink's diet and determined that its diet changed seasonally, ultimately finding that the mink changed its body mass in relation to local conditions.

Following the idea behind Zalewski and Bartoszewics' study, perhaps it is not sufficient to be looking at morphological characteristics and abilities at the present time period, but reflecting on both during the time of population establishment. It may not necessarily be that one species is more fit to survive in an environment than another species, but rather that they more quickly, or were simply the only species able to adapt to the environment. *Anolis sagrei* could possibly have not arrived in Florida fit, but adapted to be more fit than the native *A. carolinensis* and successfully invaded its habitat. Learning

how a species such as *A. sagrei* was able to become fit and successfully invade Florida would be a breakthrough in the research surrounding this biological invasion.

There are countless traits, characteristics, and abilities that contribute to the capability of one species to invade the habitat of another, and certain abilities are only advantageous in a specific environment. Investigations down each path that leads to species survival or fitness, specifically of *A. sagrei*, would be cumbersome and challenging, but would give a world of insight into exactly why *A. sagrei* was successful in invading the Florida habitat of *A. carolinensis*. Further investigation into the pertinence of sprinting abilities to survival and fitness of *Anolis* lizards also appears to be valuable foundation of study, as this study found no significant difference in sprinting ability between a native and an invasive species. However, morphological differences between the two species were detected and determined to be significant. One could expand on these results and explore the advantages of these morphological differences, or any morphological difference, to perhaps determine why *A. sagrei* was successful in invading the habitat of *A. carolinensis*.

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