Ecomorphs of *Anolis* on Dominica: The Relationship of Morphology to Performance

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Abstract

Anoles, genus *Anolis*, represent a large part of the herpetofauna in the Eastern Caribbean. Over half of the genera are located in the Caribbean Islands. Each species has a different preferred microhabitat in which the anoles have evolved morphologies enabling them to be better adapted for locomotion. In this paper, I will discuss past studies that present evidence that anoles develop different morphologies and I will test their performance by racing the anole, *Anolis oculatus,* on race tracks designed to mimic the habitat of the primary and secondary rainforest of Dominica in which the anoles were observed most frequently.

Introduction

Anoles, genus *Anolis*, in the West Indies vary dramatically in external morphology on all islands. The genus *Anolis* is one of the most speciose vertebrate genera with greater than half of the species located on Caribbean islands. Morphology differs between species in tail length, body length (measured by snout vent length), thickness of hind limbs, length of hind limbs and forelimbs, length and width of head, and coloration (Losos 1995). The study of anole behavioral ecology is useful for understanding how morphology relates to movement patterns and habitat use. Anoles exhibit a wide range of specialized traits for the habitats that they occupy, and these forms are termed ecomorphs. Ecomorphs can be found both between and within species. Certain features of the environment pose different constraints on how they move through their habitat and consequently, how morphology and behavior coevolve (Irschick 2001, Losos 1995). There are studies that demonstrate how habitat structure causes the anoles to develop different life history strategies and physiological characteristics to avoid predation in their preferred microhabitat (Mattingly and Jayne 2003, Losos 1995). Other studies have theorized that the similarities in ecomorphs on each island are due to competitive exclusion, resource partitioning, and convergent phylogenetic radiation through evolutionary time as a part of natural selection (Moermond 1979, Losos 1995). The importance of these studies show that the evolution of communities represents multiple theories in which scientists reveal that adaptive radiations through time are intimately linked to the ecology and morphology of organisms. My study will provide a comparison of *Anolis oculatus* morphologies in two types of rainforest of Dominca that show morphological differences compatible with the ecomorphology theory, i.e. that behavioral patterns change with constraints in the microhabitat, which cause a predictable shift in specific morphologies for improved locomotion. My hypothesis is that anoles in the secondary forest will maneuver faster on a flat substrate and the anoles in a primary forest will maneuver faster on small perches. Therefore, the differences in morphological characteristics will correspond to the habitat in each forest.

Methods and Materials

To represent the secondary rainforest ecomorph I built a race track using 3 1X6 boards 2 meters long and galvanized hardware cloth. I installed doors by using U nails as hinges and attached a rope to the doors for a locking mechanism. I spaced the doors accordingly to deter anoles with my hand from stopping on the race track. I inserted a trap door at the end of the race track by cutting a piece of wood that would slide into one side of the track 8 inches from the end. Therefore, the anole was recaptured easily. For the second track I used the same track built for the secondary rainforest but placed a stick approximately 2 meters in length and 12 mm in diameter that ended just before the trap door. I inverted the track vertically to represent the primary rainforest habitat. Also, in order to induce jumping into the trap door I nailed a piece of wood that fit the width of the track that had some vegetation attached to it. I measured each anoles' jaw length, head length, head width, body length, tail length, hind limb length, forelimb length and thickness of hind limb by using a caliper measured in the nearest millimeter. In addition, I weighed each anole using a 30g Avinet balance. Jaw length was measured from tip of snout to the anterior eye socket, head length from ear hole to snout, head width from ear hole to ear hole, body length from snout to vent length (svl), tail length from vent to the end of tail, hind limb and forelimb length from attachment of limb to the longest toe, and thickness of hind limb at the thickest part of the thigh. Using a stopwatch I raced each anole on each race track once then rested for a minimum 30 minutes before racing again. I repeated this a minimum of two more times. When racing in the secondary rainforest race track I kept the anoles from jumping onto the hardware cloth by putting the track at an incline of approximately 30^o using a laser level to measure the angle from the ground. In the primary rainforest race track I placed the stick against the back board of the track using zip ties to deter the anoles from jumping onto the hardware cloth.

Results

After analyzing the measurements using SPSS and Microsoft Excel we performed principal component analysis (PCA) on all eight morphological variables measured. The first 2 factors from PCA capture 96.5% of the total variance in the data, therefore, we are justified in looking at the first 2 factors only (Table 1). As is commonly the case, the first factor from PCA represents the overall size of the animal studied. The second factor from PCA appears to capture strong differences between the lengths of tail from the two populations (Table 2). Head length, hind limb length, and forelimb length are strongly positive weighted in the second factor and tail length is strongly negative weighted (Table 2). Therefore, as the overall size increases or decrease the tail length varies between the anoles from both populations, with tail length proportionately smaller in larger body-sized animals. Table 3 shows individuals from Emerald Pool tend to have large positive values in the second factor and individuals from Springfield tend to have strongly negative values in the second factor. Also, Emerald pool anoles tend to be larger in overall body size while the Springfield anoles are more variable in body size. Therefore, the Emerald Pool anoles have lager bodies with shorter tails while the Springfield anoles have various sized bodies with longer tails.

The vertical races that were completed by each are represented in Table 4. Springfield anoles completed 31 of 45 total races, therefore, 31% failed to make it the finish line. Emerald Pool anoles completed 35 of 36 races, therefore, only 3% failed. A G-test was calculated to see if the proportions were equal. This test proved that the there was a highly significant difference in performance between the two populations ($G=12.7$, $df=1$). The average time on the vertical track between the two populations that completed the race was clearly different. The Springfield anoles had a mean time of 28.4 seconds and the Emerald Pool anoles was 13.65 (Table 5). To compare means I conducted a t-test for the two populations. The results were that these average performance times were significantly different, as shown in Table 6, (t-test for unequal variances, $t=4.204$, $df=19.3$, $p<0.0001$).

The 30^{o} degree races were fully completed by both populations. The average speed for the Springfield anoles was 8.9 seconds while the average speed for the Emerald Pool anoles was 8.1 seconds (Table 7). To compare means a test was performed that revealed that these times were not significantly different ($t=0.495$, $df=25$, $p=0.625$, Table 8).

Table 1. Total variance for Principal Components Factors from 8 morphological variables measured from Springfield and Emerald Pool anoles

Total Variance Explained

		Initial Eigenvalues[a]			Extraction Sums of Squared Loadings		
	Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
Raw	1	450.779	87.759	87.759	450.779	87.759	87.759
	2	45.011	8.763	96.522	45.011	8.763	96.522
	3	9.295	1.810	98.331	9.295	1.810	98.331
	4	4.610	.898	99.229			
	5	1.955	.381	99.609			
	6	1.664	.324	99.933			
	7	.241	.047	99.980			
	8	.101	.020	100.000			
Rescaled	1	450.779	87.759	87.759	4.658	58.224	58.224
	2	45.011	8.763	96.522	1.702	21.279	79.503
	3	9.295	1.810	98.331	.414	5.171	84.674
	4	4.610	.898	99.229			
	5	1.955	.381	99.609			
	6	1.664	.324	99.933			
	7	.241	.047	99.980			
	8	.101	.020	100.000			

Extraction Method: Principal Component Analysis.

a. When analyzing a covariance matrix, the initial eigenvalues are the same across the raw and rescaled solution.

Table 2. The component matrix for 8 morphological variables in factors 1, 2, and 3.

Component Matrix[a]

	Raw			Rescaled		
	Component			Component		
	1	2	3	1	2	3
Head L	2.488	1.398	1.141	.761	.427	.349
Head W	1.201	.621	.083	.790	.409	.054
Jaw L	.992	.871	.252	.526	.462	.134
SVL	5.225	3.670	1.935	.779	.547	.289
Tail L	19.448	-2.682	-.069	.991	-.137	-.004
F limb L	2.936	2.225	-1.007	.693	.525	-.238
H limb L	5.238	4.008	-1.757	.759	.581	-.254
H L Thick	.770	.481	.272	.731	.457	.258

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

Table 3. Plot of Springfield anoles as number 1 and Emerald Pool anoles as number 2 against the first two principal components.

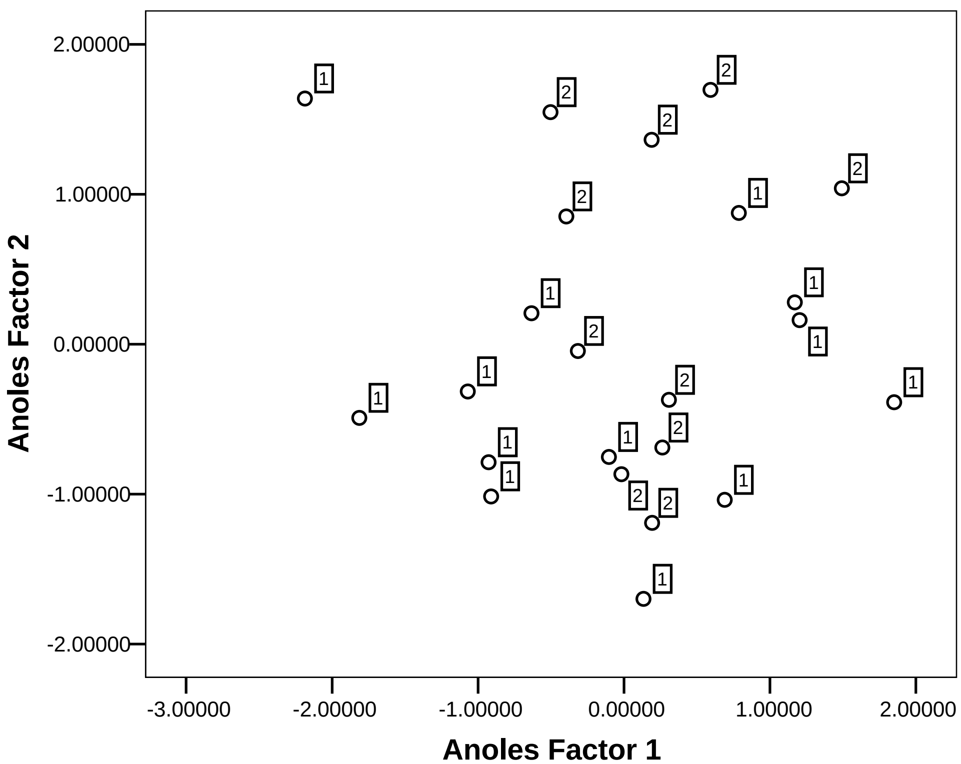

Table 4. Completed vertical races vs. failed races for each population of anoles

	complete	failed	total	% failed
Spring	31	14	45	31%
EP	35	1	36	3%
Total	66	15		

G=12.68, df=1, highly significant difference

Table 5. Vertical race tracks average speed for Springfield and Emerald Pool anoles

Group Statistics

	Site	N	Mean	Std. Deviation	Std. Error Mean
Avg Vertical	1	15	28.4360	12.41058	3.20440
	2	12	13.6546	5.01124	1.44662

Table 6. Vertical Race track T-test for Springfield and Emerald Pool anoles

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Avg Vertical	Equal variances assumed	6.841	.015	3.869	25	.001	14.78142	3.82038	6.91319	22.64964
	Equal variances not assumed			4.204	19.269	.000	14.78142	3.51580	7.42971	22.13312

Table 7. Race track with an incline of 30^{o} average speed for Springfield and Emerald Pool anoles

Group Statistics

	Site	N	Mean	Std. Deviation	Std. Error Mean
Avg 30	1	15	8.9389	5.24481	1.35420
	2	12	8.0917	3.05361	.88150

Table 8. Race track with an incline of 30^o T-test results for Springfield and Emerald Pool anoles

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Avg 30	Equal variances assumed	1.674	.208	.495	25	.625	.84722	1.71058	-2.67579	4.37023
	Equal variances not assumed			.524	23.099	.605	.84722	1.61583	-2.49459	4.18903

Discussion

The trends in morphological differences of the Springfield and Emerald Pool anoles suggest that the longer tails serve as another adaptation other than climbing vertically and shorter tails and bigger bodies are used better at climbing vertically. It has been suggested that anoles with longer tails will perform better on smaller perches in which they use the tails as a counter balance when jumping from perch to perch (Moermund, 1979 and Losos, 1990). Also, anoles with longer tails usually occupy an open vegetative area that can consist of grasses, bare ground, or rocks (Losos, 1990). Short tailed anoles have been suggested to be better adapted for running on flat surfaces such as the ground or large diameter trunks (Moermond 1979). Through observation the Springfield anoles where found usually in the early evening on the ground or behind vegetation. The Emerald Pool anoles were found on large surface rocks and on the base of trees near a pool of water in the early evening. Generally, the morphological trends in both sites where anoles where captured concur with previous studies predictions of longer tailed anoles maneuvering better in small perches and shorter tailed anoles maneuvering better on flat surfaces. Though both populations were virtually equivalent in the average time it took to finish on the 30^o race track there was an enormous difference in the time and completion on the vertical track. It could be suggested that through this study there are different ecomorphs for *Anolis oculatus*, in which the same species of anoles have changed morphologically through evolutionary time to become better adapted to maneuver through their environment.

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