

March 2019

The effects of social and physical interactions on lizard morphology, behavior, and ecology

Casey Gilman

Follow this and additional works at: https://scholarworks.umass.edu/dissertations_2



Part of the [Other Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Gilman, Casey, "The effects of social and physical interactions on lizard morphology, behavior, and ecology" (2019). *Doctoral Dissertations*. 1498.

https://scholarworks.umass.edu/dissertations_2/1498

This Open Access Dissertation is brought to you for free and open access by the Dissertations and Theses at ScholarWorks@UMass Amherst. It has been accepted for inclusion in Doctoral Dissertations by an authorized administrator of ScholarWorks@UMass Amherst. For more information, please contact scholarworks@library.umass.edu.

**THE EFFECTS OF SOCIAL AND PHYSICAL INTERACTIONS ON LIZARD
MORPHOLOGY, BEHAVIOR, AND ECOLOGY**

A Dissertation Presented

by

CASEY A. GILMAN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

FEBRUARY 2019

Organismic and Evolutionary Biology

© Copyright by Casey A. Gilman 2019

All Rights Reserved

**THE EFFECTS OF SOCIAL AND PHYSICAL INTERACTIONS ON LIZARD
MORPHOLOGY, BEHAVIOR, AND ECOLOGY**

A Dissertation Presented

by

CASEY A. GILMAN

Approved as to style and content by:

Duncan J. Irschick, Chair

Elizabeth M. Jakob, Member

Diane A. Kelly, Member

Jonathan B. Losos, Member

Patricia Wadsworth, Director
Interdepartmental Graduate Programs

DEDICATION

To:

My mother, whom I miss terribly; and Toni, who supported me through it all.

ACKNOWLEDGEMENTS

I am grateful to the many delightful people I met and worked with while at UMass. Their kindness and humor were the twinkling lights in the sometimes amorphous mist that is graduate school. First, my fellow students. These include, but are by no means limited to, Teri Orr, Sarah Goodwin, Chi-Yun Kuo, Justin Henningsen, Tom Eiting, Skye Long, Michael Rosario, Dan King, Scott Schneider, and many joyous undergrads.

I would also like to thank a few of the former UMass faculty and staff who provided scientific and general support: Betsy Dumont, Patty Brennan, and Penny Jaques (we love you, Penny). Thank you to the Organismic and Evolutionary Biology Graduate Operations Committee who worked their hardest to uplift and guide students. Although the meetings were a tad terrifying, I always left feeling better about my place in the world. Thanks to Maggie DeGregorio, who remotely guided me through the last legs of this journey.

Thanks to Duncan Irschick. You inspired me to reach for something uncomfortable. Thank you to my committee members, Beth Jakob, Diane Kelly, and Jonathan Losos. This has been a long and meandering journey. I appreciate you sticking with me through all of it and supporting my somewhat unconventional tactics.

Thank you to Craig Albertson and members of his lab for their warmth and generosity. Thanks also to Beth Jakob, Diane Kelly, and Skye Long for sharing their knowledge, skills, and lab space. Robbie Cairl was helpful whenever I needed random materials or a laugh. A big thank you to my collaborators, Michael Bartlett, Ariel Kahrl, Ammon Corl, Julia Klaczko, Michael Imburgia, Robert Cox, Gary Gillis, Barry Sinervo, and Al Crosby. Thanks to Brett DeGregorio, who tried in vain to help me find viable green anole populations after a terrible winter.

I'd also like to thank the many individuals and organizations who have provided support and encouragement during my journey to pursue a career outside academia: Gary Gillis, Diane Kelly, Norman Johnson, Penny Jaques, Betsy Dumont, Jeff Podos, Ed Blaguszewski, Janet Lathrop, Shana Passonno, UMass Amherst News & Media Relations, UMass Office of Professional Development, Society for Integrative and Comparative Biology, Journal of Experimental Biology, ComSciCon, AAAS Mass Media Science & Engineering Fellows program, and New England Public Radio. To my science communication students, thanks to those of you who enthusiastically tolerated my foray into scicomm instruction. I learned an immense amount from the experience.

Toni Maestas and my mother: You know what you did.

And, lastly, a shout out to two of the best editors I've worked with outside academia. You provided support and inspiration and gave me hope for a future I thought might never happen. Kathryn Knight is the most cheerful, insightful, and prompt editor I've ever had. Sam Hudzik, I fear and admire you tremendously.

ABSTRACT

THE EFFECTS OF SOCIAL AND PHYSICAL INTERACTIONS ON LIZARD MORPHOLOGY, BEHAVIOR, AND ECOLOGY

FEBRUARY 2019

CASEY A. GILMAN, B.S., UNIVERSITY OF NEW MEXICO

M.S., UNIVERSITY OF NEW MEXICO

Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Duncan J. Irschick

Interactions with the physical and social aspects of an animal's surroundings direct the trajectory of local adaptation and can lead to tremendous diversity within and across taxa. In my dissertation, I explored how interactions between lizards and their environment lead to morphological, behavioral, and ecological diversity. First, I examined how a common, but unexplored habitat characteristic, perch flexibility, affects jumping performance of an arboreal lizard. I found that in the lab, green anole lizards (*Anolis carolinensis*) did not take advantage of the natural recoil of the flexible perches, and suffered decreased jump distance and takeoff speed as a consequence. Next, I extended my inquiry into how this habitat characteristic affects multiple aspects of behavior and morphology of the lizards in nature, given the potential performance costs associated with flexible perches. Most strikingly, I found that while green anoles used a range of perches in their habitat for most activities, they selectively jumped from relatively non-flexible perches. Then, I sought to more broadly understand the effects of habitat on the whole organism. I examined associations between habitat structure and complexity on male and female sexual and non-sexual traits, as these would reflect habitat effects on locomotion, foraging ecology, and social interactions. I found that while there was no association between habitat structure and variation in most traits I examined, male body condition decreased with decreasing vertical vegetative complexity. Finally, I focused on the role of social interactions in increasing morphological diversity. I examined the association between genital morphology and male mating type in an alternative mating strategy population of the terrestrial lizard *Uta stansburiana*. I found that male mating types differed in genital length and complexity, suggesting that strong sexual selection may drive morphological differentiation within populations. Together, my work shows the importance of animal-environment interactions as drivers of diversity and contributes to the broader fields of sexual selection, behavior and evolutionary ecology.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS.....	v
ABSTRACT.....	vi
LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
CHAPTER	
I. TOTAL RECOIL: PERCH COMPLIANCE ALTERS JUMPING PERFORMANCE AND KINEMATICS IN GREEN ANOLE LIZARDS (<i>ANOLIS CAROLINENSIS</i>)	
A. Introduction.....	1
B. Materials and Methods.....	4
1. Perch characteristics in the wild.....	4
2. Laboratory trials.....	5
3. Statistical analyses.....	7
C. Results.....	8
1. Perch characteristics in the wild.....	8
2. Laboratory trials.....	9
D. Discussion.....	12
II. FOILS OF FLEXION: THE EFFECTS OF PERCH COMPLIANCE ON LIZARD LOCOMOTION AND PERCH CHOICE IN THE WILD	
A. Introduction.....	21
B. Materials and Methods.....	24
1. Available habitat and general-use perch measurements.....	24
2. Jump perch measurements.....	26

3. Data analysis.....	27
C. Results.....	29
D. Discussion.....	31
III. SEXUALLY DIMORPHIC RESPONSES TO HABITAT COMPLEXITY IN THE GREEN ANOLE LIZARD, <i>ANOLIS CAROLINENSIS</i>	
A. Introduction.....	42
B. Methods.....	46
1. Habitat structure.....	46
2. Lizard traits.....	49
3. Statistical analyses.....	51
C. Results.....	53
1. Habitat structure.....	53
2. Lizard traits and ecology.....	53
D. Discussion.....	56
IV. GENITAL MORPHOLOGY ASSOCIATED WITH MATING STRATEGY IN THE POLYMORPHIC LIZARD, <i>UTA STANSBURIANA</i>	
A. Introduction.....	65
B. Methods.....	70
1. Taxon sampling.....	70
2. Hemipenis preparation.....	71
3. Genital and non-genital trait measurements.....	72
4. Hemipenis shape analysis.....	72
5. Statistical analyses.....	73
C. Results.....	74
D. Discussion.....	76
BIBLIOGRAPHY.....	88

LIST OF TABLES

Table		Page
1.1	One-way repeated-measures ANCOVA $F_{2,26}$ -values (with associated significance levels) for jump variables across three treatments: rigid perch, flexible perch, and most flexible perch. $N = 11$ for each treatment. Asterisks indicate significance with the sequential Bonferroni test.....	18
2.1	Results from principal component analysis of jump perch characteristics. Substantial loadings are in bold.....	41
3.1	Structural characteristics of the habitat along 50 meter transects at each site.....	62
3.2	ANCOVA results for trait differences across sites, F -statistics, and P -values for each trait.....	63
3.3	Summary statistics for ordinary least square regression of traits on body size (b , r^2 , t -value), significance from test of deviation from a slope of one (P), coefficient of variation (CV), coefficient of variation with body size held constant (CV'), and trait measurement repeatability (ICC).....	64
4.1	Sexual and non-sexual trait comparisons across the three morphs. ICC coefficients (repeatability of measurements), ANCOVA results for differences in traits across morphs and interaction between morph and body size (SVL), and post-hoc comparisons between morphs. Significant results are shown in bold with asterisks.....	83

LIST OF FIGURES

Figure		Page
1.1	<p>The effects of three levels of perch compliance on the jump variables jump distance (A & B) and takeoff velocity (C & D). Increased compliance significantly affected both variables in larger lizards (> 3g, B, D) but not smaller lizards (< 3g, A, C). Each point represents the mean and s.e.m. of two jumps for an individual from one perch type (< 3g, $N = 7$; > 3g, $N = 4$). Lines connect each individual's value across the three perch types. F and P values shown are from one-way repeated measures ANOVA for each group. Asterisks indicate significance with the sequential Bonferroni test.....</p>	17
1.2	<p>The effects of three levels of perch compliance on A) takeoff angle, B) takeoff duration, and C) landing angle. Of the three jump variables, only landing angle was significantly affected by increased perch compliance. F and P values shown are from one-way repeated measures ANOVA ($N = 11$). Asterisks indicate significance using the sequential Bonferroni test.....</p>	19
1.3	<p>Perch interference effects on takeoff, flight and landing angle. A) Movie stills of the same lizard (6g) jumping from a compliant (i-iv) and most flexible (v-viii) perch types. White lines show body and tail base angles throughout the jump. This lizard had a positive takeoff and landing angles from the rigid and compliant perch types (i, v), but the rebound of the most compliant perch hit the middle of the tail and caused the body to pitch forward (vi, vii), resulting in a negative landing angle (viii). B) Relationship between mass, compliance and landing angle. Note that landing angles decrease as compliance increases, largely due to the pitching caused by perch and tail interactions (rigid perch: straight line, flexible perch: dashed line, most flexible perch: dotted line, longest jumps of $N=11$ lizards per perch type). C) Relationship between mass, compliance, and perch velocity as the perch contacts the tail. Note the greater velocities for the larger lizards... </p>	20
2.1	<p><i>Anolis carolinensis</i> individuals and the study site. A) Green anole male on a relatively inflexible tree trunk, B) Green anole female on a more flexible leaf, and C) Our study site in Volusia County, FL. This site was dominated by low-lying cabbage palm plants, with few larger palms and other trees.....</p>	36

2.2	Frequency distributions of perch compliance and diameter in Riverbreeze County, FL. A&D) Perches available in the habitat ($N=112$), B&E) Perches generally occupied by <i>Anolis carolinensis</i> ($N=80$), C&F) Perches used for jumping by <i>A. carolinensis</i> ($N=80$). Compliance is shown here as the log transformed values to aid in visualization of the data. Significant differences ($P<0.005$) between frequency distributions within a variable are shown as with asterisks.....	37
2.3	Relationship between angle-to-landing perch and distance-to-landing perch. A) Angle and distance to new perch for downward jumps B) Angle and distance to new perch for upward jumps. Although the relationships were not significant, green anoles jumped the largest range of distances at the least extreme angles.....	38
2.4	Relationship between perch diameter and compliance in the wild. There was a significant relationship between the diameter of a perch and its compliance for palm leaflets (slope=-1.26, $P<0.001$, $N=180$) and petioles, branches and trunks (slope=-2.43, $P<0.001$, $N=116$), but not palm leaves (slope=-0.28, $P=0.3$, $N=24$).....	39
2.5	Relationship between perch compliance (on a log scale) and lizard jump distance. Open circles are data from our previous lab study (Gilman et al. 2012) and closed circles are field data from this study. In both the lab and field, the longest jumps tended to occur from the least compliant perches.....	40
3.1	Three transect areas in Spruce Creek Park. A) A heterogeneous northern corridor along a dirt road, B) A continuously vegetated eastern corridor along a dirt road, and C) A relatively sparsely vegetated interior southern corridor with low palms and a few tall trees.....	61
4.1	One hemipenis from each morph (bb:mate-guarding, oo:usurper, yy:sneaker) shown in three views. From the left: apical, with the horn (h); sulcal, with the sulcus spermaticus running up the midline (s), and lateral, with the trunk (t), and apex (a).....	82
4.2	Static allometry of the tibia and hemipenis of all males in the study. While the tibia (A) scaled significantly lower than one in the males in our study, the hemipenis (B) did not scale significantly different from one. The morphs are color and shape coded as orange circle: (oo) usurper, blue square: (bb) mate-guarding, and yellow triangle: (yy) sneaker.....	84

4.3	<p>Relationship between the first two principal components of the harmonics from the elliptical Fourier analysis of the hemipenis lateral outlines. PC1 explained 73% of the variation in shape, with hemipenes becoming less curved with increasing values of PC1. PC2 explained 12% of the variation, with hemipenes becoming squatter and more bulbous with increasing values of PC2. There was no significant different in lateral shape across morphs ($P=0.89$).....</p>	85
4.4	<p>Relationship between the first two principal components of the harmonics from the elliptical Fourier analysis of the hemipenis sulcal outlines. PC1 explained 53% of the variation in shape, with hemipenes becoming slimmer with increasing values of PC1. PC2 explained 18% of the variation, with hemipenes becoming shorter and squatter with increasing values of PC2. There was no significant different in sulcal shape across morphs ($P=0.64$).....</p>	86
4.S1	<p>Outlines of hemipenes of 23 individuals generated by Momocs from digital images. These outlines were used for elliptical Fourier analysis of A) lateral shape, and B) sulcal shape. Sample IDs are given within the outlines.....</p>	87

CHAPTER I

TOTAL RECOIL: PERCH COMPLIANCE ALTERS JUMPING PERFORMANCE AND KINEMATICS IN GREEN ANOLE LIZARDS (*ANOLIS CAROLINENSIS*)

A. Introduction

The ability of an animal to move effectively through its habitat is often essential for survival (Turchin, 1998), and adaptations of animals to locomotor challenges have provided insights into the evolution of many taxa (Biewener, 2003). Because of its general importance, many studies have examined locomotion from a variety of perspectives, including physiological (Ricciardella et al., 2010; Zhong et al., 2011), anatomical (Schoenfuss et al., 2010; van Casteren and Codd, 2010) and kinematic (Hugel et al., 2011; Larson and Demes, 2011), among others. Although these studies are representative of aspects of locomotion of many animals, few studies have directly addressed the locomotor challenges of animals that inhabit structurally complex arboreal habitats, with some exceptions (e.g. Bonser, 1999; Spezzano and Jayne, 2004; Vanhooydonck et al., 2006). For arboreal animals, the interaction between individuals and their habitat can be complex because of the variability in perch characteristics, such as diameter, length, angle and compliance (Irschick and Losos, 1999; Mattingly and Jayne, 2004). Perch compliance may be of particular concern for arboreal animals that use jumping as a means of moving through their habitat because of the high forces generated during takeoff (Crompton et al., 1993). The mass of the animal and the forces generated during takeoff cause compliant perches to bend, resulting in both potential and kinetic energy being lost to the perch (Alexander, 1991; Bonser, 1999; Demes et al., 1995). If an animal is able to take advantage of the kinetic energy stored in the perch, the

animal could use the perch as a springboard to propel itself, offsetting the initial energy loss. However, the use of perches as a springboard during jumping has thus far only been seen in humans (Channon et al., 2011). If a compliant perch is not used as a springboard, loss of energy to the perch could have marked effects on an animal's locomotion and behavior by decreasing the distance or speed at which the animal is able to jump. Therefore, perch compliance could ultimately affect an arboreal animal's ability to reach its intended target (the perch), which might have fitness consequences.

Thus far, research on the effects of perch compliance on jumping has been restricted to a few studies of primates and birds (Bonser et al., 1999; Channon et al., 2011; Crompton et al., 1993). These authors found that in laboratory jumping trials, common starlings (*Sturnus vulgaris*) do not compensate for the loss of energy due to a compliant perch, whereas in contrast, white-cheeked gibbons [*Hylobates (Nomascus) leucogenys*] minimize the effects of compliance by using low-power jumps to limit perch deflection. In the wild, bush babies (*Galago moholi*) chose larger-diameter (therefore less compliant and more energy efficient) perches for maximal jumps. Although these studies have been extremely valuable, the behavior and locomotor kinematics of birds and primates may inadequately represent the large number and wide range of small animals that use compliant perches, such as frogs, lizards, small mammals and invertebrates. There may be other strategies that smaller animals employ, which would be useful to explore. Additionally, the effects of perch compliance on jumping across individuals of different size and age classes within a species have hardly been considered (but see Crompton et al., 2003). Finally, because of dramatic differences in morphology among

taxonomic groups, it is possible that the effects of compliance could differ because of interactions of some body parts (e.g. the tail, such as in lizards) with the compliant perch.

One clear prediction and finding based on theory and empirical data is that if a small animal jumps from a compliant perch before the perch recoils, some kinetic energy of the jump will be lost to the bending of the perch, as seen with larger animals. Therefore, we predict that arboreal lizards will jump before the perch recoils, as observed in larger animals (Demes et al., 1995), and that increased perch compliance will negatively impact key aspects of jumping, particularly jump distance and takeoff speed, likely because of the loss of kinetic energy to the perch. We also predict that because jump distance in lizards is determined largely by takeoff speed and takeoff angle, lizards will increase takeoff angles from compliant perches to offset the negative effect on takeoff speed (Toro et al., 2004). Lastly, we anticipate that within a species, as mass increases, the negative effects of compliance on jump distance and takeoff speed for the same perch will increase. Larger animals cause greater displacement of compliant perches and generate greater absolute forces during takeoff than smaller animals, and therefore will lose more potential and kinetic energy of the jump (Alexander, 2003; Toro et al., 2003).

Arboreal lizards present an exceptional system in which to test the effects of perch compliance on behavior and jumping performance. For example, there are 400+ species of *Anolis* lizards, the majority of which use a variety of arboreal habitats and regularly use jumping to move around (Irschick and Losos, 1999). Anole ecology and locomotion has been widely studied (Calsbeek and Irschick, 2007; Irschick and Losos, 1999; Losos and Sinervo, 1989; Spezzano and Jayne, 2004; Vanhooydonck et al., 2006),

although one anole species has been particularly well studied in terms of jumping, namely the green anole, *A. carolinensis* Voigt 1832 (Bels et al., 1992; Gillis et al., 2009; Kuo et al., 2011; Losos and Irschick, 1996; Toro et al., 2003; Vanhooydonck et al., 2005). However, the effect of perch compliance on this species, or any small (<65 g) species, is unknown. This species inhabits complex three-dimensional habitats, jumping between adjacent branches, from branches or tree trunks to the ground, and to branches, leaves and trunks above the original perch (Irschick and Losos, 1998) (D.J.I., unpublished). The green anole occupies a wide variety of perch types, from leaves and narrow branches to trunks, and therefore encounters a range of compliances that may affect performance (Irschick et al., 2005a; Irschick et al., 2005b) (C.A.G., unpublished). In this study we investigated how perch compliance affects several key jumping variables, including jump distance, takeoff duration, takeoff angle, landing angle and takeoff speed, across a range of body sizes in the arboreal green anole, *A. carolinensis*.

B. Materials and Methods

1. Perch characteristics in the wild

Studies of animal performance capacity are only valuable if they are performed in an ecologically relevant context (Irschick and Garland, 2001). To date, there are no published data on the compliance of the perches that anole lizards use in natural settings. To determine whether the compliances of the flexible perches used in our study fall within the natural range found in the wild, we conducted a small survey of perch compliance in *A. carolinensis* at Riverbreeze County Park, Oak Hill, FL, USA. We walked through the park until we encountered an adult male or female *A.*

carolinensis, and then noted the substrate type (leaf, vine, branch or trunk), and measured the perch diameter and compliance ($N=54$). To determine compliance, we measured the height of the perch, hung a fishing sinker of known mass from the perch at the exact spot where the individual was found, and measured the height of the perch again. We then calculated the compliance using the relationship between displacement and force:

$$C = \frac{d\delta}{dF},$$

where C is compliance, F is force [mass in kg * 9.81, (gravitational acceleration)], and δ is the displacement of an object due to the force (Halliday et al, 2005).

2. Laboratory trials

We used five females (2.02 ± 0.57 g, mean \pm s.d.) and six males (4.30 ± 1.79) of *A. carolinensis* for our jumping trials, which we acquired through the pet trade. All individuals were in good health with intact original tails. We marked each individual on its ventral surface with a permanent marker and housed them individually in plastic aquaria (42.9x15.2x21.6 cm) supplied with wood mulch and a wood basking perch. The cages were sprayed with water daily, and the lizards were fed calcium-dusted crickets twice a week and provided with a 12 h:12 h light:dark cycle using an aluminum clamp work light and a 65 W incandescent bulb.

We conducted jumping trials in a large glass aquarium (182x62x64 cm) that prevented lizards from escaping during the trials. Before trials commenced, we marked each lizard with Wite-Out® (BIC Corporation, Shelton, CT, USA) at six locations (three dorsal and three lateral: pelvis, mid-body and shoulder) to use as landmarks during analysis. To elicit maximal jump performance, we heated lizards to close to their preferred body temperature, 31°C (Lailvaux and Irschick, 2007), for approximately 1 h

by placing them in individual cloth bags in a small Styrofoam cooler (30x30x30 cm) heated by an aluminum work lamp with a 65 W incandescent bulb. Each lizard was placed at the end of a horizontal balsa wood plank at one of three levels of compliance (rigid, flexible and most flexible) and was encouraged to jump by rapid hand gestures towards the lizard. Perch compliance was calculated by first measuring the flexural modulus of the balsa wood ($N=5$) in a three-point bend configuration (span length=75 mm) using an Instron 5500R (Instron, Norwood, MA, USA), and then using the formula:

$$C = \frac{4l^3}{Ewt^3},$$

where E is the measured flexural modulus of the wood, and l , w and t are the length, width and thickness of the wood, respectively. All planks measured 2 mm thick by 25 mm wide, with a 25x25 mm strip of fiberglass screen glued to one end for traction. Compliance was altered by changing the length of the wood. The rigid perch was fully supported by a steel file (3x16x150 mm) underneath the board that prevented flexion but did not interfere with the size characteristics of the board. The other two perches were 30 cm (flexible, $C=0.27 \text{ mN}^{-1}$) and 40 cm (most flexible, $C=0.64 \text{ mN}^{-1}$) long. All perches were placed 11 cm above the landing surface, which extended from below the perch to ~60 cm past the perch to allow lizards to jump at a natural range of distances. We presented the lizards with a perch (wooden dowel, 1.24x10 cm diameter x length) at approximately the same height as the jump perch, though slightly farther than their known maximal jump distance [$\sim 40\text{--}45$ cm away (Bels et al., 1992)], to provide an incentive for jumping. This perch system, which was also used in Kuo et al. (Kuo et al., 2011), was designed to elicit maximal jumps, as it mimics the natural tendency of this species to jump from perch to perch in the wild. Lizards jumped from one perch type one

to two times a week (one to two jumps per trial), and perch types were determined randomly before each set of trials. We filmed each jump at 500 frames s^{-1} with a Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA). The glass aquarium contained a large mirror positioned on one side of the aquarium at a 45 deg angle to the perch and landing area, which allowed simultaneous recording of the lateral and ventral views of each jump.

We used the average of the two longest and straightest jumps per individual per perch type for kinematic analysis, and used ImageJ (Rasband, 1997–2009) to calculate the following variables: (1) jump distance, the distance traveled of a clearly visible mark on the lizard from rest to landing; (2) takeoff angle, the angle between a line from the pelvis to the shoulder girdle and the horizon just after the feet left the perch; (3) landing angle, the angle between the same line and the horizon when any of the lizard's feet first contacted the landing surface; and (4) takeoff duration, the time between the start of the jump to just after the lizard's feet left the perch. With these data, we also calculated takeoff speed as the average speed traveled during the last five frames of takeoff (Kuo et al., 2011).

All experimental procedures were conducted under the permission of University of Massachusetts Amherst Institutional Animal Care and Use Committee (protocol number 2011-0051).

3. Statistical analyses

We began our analyses by testing for the combined effects of compliance and mass on the dependent variables jump distance, takeoff duration, takeoff speed, takeoff angle and

landing angle, using one-way repeated-measures analyses of covariance (ANCOVAs). Individual masses of some of the animals changed slightly over the course of the study (mean=-0.004 g), so we used mass at the time of the jump as a covariate, compliance level (rigid, flexible and most flexible) as a fixed factor and individual as a random factor. To better understand the effects of the interaction between compliance and mass on jump variables, we followed these analyses with one-way repeated-measures ANOVAs using either the full data set of the average of the best two jumps per individual per perch type ($N=33$), or with the data set separated by lizard mass (lizards <3 g, $N=21$; lizards >3 g, $N=12$). There were both males and females in the group of smaller individuals, so we tested for the effects of sex on the dependent variables using one-way repeated measures ANOVAs. There were no differences between the sexes for any dependent variable in the small group, so the sexes were pooled (distance: $F_{1,18}=2.01$, $P=0.17$; takeoff duration: $F_{1,18}=0.90$, $P=0.36$; takeoff speed: $F_{1,18}=1.03$, $P=0.33$; takeoff angle $F_{1,18}=0.77$, $P=0.39$; landing angle: $F_{1,18}=0.75$, $P=0.40$). We separated the individuals into these two categories based on our observation that the size data naturally fell into these two distinct groupings (small lizards: mean=2.05 g, range=1.43–2.92 g, $N=7$; large lizards: mean=5.43 g, range=3.81–6.05 g, $N=4$). To account for multiple ANOVAs, a sequential Bonferroni test was used for each set of tests (Rice, 1989). To test for differences in jump distance and takeoff speed between the size groups we used Mann–Whitney–Wilcoxon tests for the rigid and most compliant perches.

C. Results

1. Perch characteristics in the wild

Perch diameter and compliance of the perches measured at Riverbreeze County Park ranged from 0.2 to 1.0 cm and 0.01 to 1.67 mN⁻¹ for branches, 0.3 to 1.0 cm and 0.01 to 0.53 mN⁻¹ for vines, 1.4 to 13.0 cm and 0.01 to 0.17 mN⁻¹ for palm fronds, 0.4 to 5.1 cm and 0.03 to 1.43 mN⁻¹ for leaves, and 3.5 to 5 cm and 0.12 to 0.83 mN⁻¹ for terminal branch leaf clumps, respectively.

2. Laboratory trials

Lizards jumped from the rigid perch with the same general kinematics as seen in other studies (Bels et al., 1992; Gillis et al., 2009): the jump started with placement of the hind feet towards the front of the body; lizards then used their hind limbs to propel themselves forward with a mean positive body angle of 12.1±1.7 deg and a mean speed and duration of 130.4±2.6 cm s⁻¹ and 0.1±0 s. After the takeoff phase, the aerial phase followed with the forelimbs limbs tucked close to the body, and lizards landed with the body angled so that the hind feet contacted the landing substrate first (26.7±4.2 deg), at a mean distance of 34.4±0.9 cm.

When jumping from compliant perches, lizards began their jumps by placing their hind feet forward in a manner similar to that from the rigid perch. However, during the takeoff phase, extension of the hind limbs resulted in a downward deflection of the perch. The lizards continued to push against the perch through takeoff, and the perch began to recoil after the lizards lost contact with it. No lizards remained on the perch during recoil.

From the rigid perches, large lizards had significantly greater jump distances than small lizards, and takeoff speeds similar to those of small lizards (Mann–Whitney test, distance: $W=120.5$, $P=0.006$; speed: $W=132.0$, $P=0.05$; Fig. 1). However, with increased

compliance, large lizards jumped significantly shorter distances and had lower takeoff speeds than smaller lizards (distance: $W=193.0$, $P=0.03$; speed: $W=193.0$, $P=0.03$; Fig. 1). The ANCOVAs revealed significant interaction effects between animal mass and perch compliance for two of the jump variables, jump distance and takeoff speed (Table 1). Increased compliance resulted in significantly shorter jump distance in large lizards (23% decrease from rigid to most flexible perch types), but did not result in significant changes in jump distance in small lizards (large: $F_{2,8}=10.22$, $P=0.01$; small: $F_{2,17}=0.37$, $P=0.70$; Fig. 1A,B). Similarly, increased compliance had a negative effect on takeoff speed, but only for the large lizards (large: $F_{2,8}=9.71$, $P=0.01$; small: $F_{2,17}=2.69$, $P=0.10$; Fig. 1C,D). There was no significant interaction effect between animal mass and perch compliance for takeoff angle or duration (takeoff angle: $F_{2,26}=0.82$, $P=0.45$; duration: $F_{2,26}=1.27$, $P=0.30$; Table 1), and increased compliance did not significantly affect either variable (takeoff angle: $F_{2,29}=2.07$, $P=0.14$; duration: $F_{2,29}=0.20$, $P=0.82$; Fig. 2A,B).

Increased compliance resulted in significantly decreased landing angles for both small and large lizards ($F_{2,29}=6.55$, $P=0.004$; Fig. 2C). The negative landing angles appeared to be caused by the perch striking the lizard tail upon recoil. We observed that when lizards jumped from rigid perches, they often dragged their tail along the perch during takeoff, as also noted in a previous study (Gillis et al., 2009). When jumping from compliant perches, the part of the tail that was still in contact with (or sometimes above) the perch was struck when the perch recoiled, thus lifting the tail and ultimately changing the body position of the lizard during flight and landing (Fig. 3A). This interaction resulted in the lizards, particularly the large ones, landing horizontally or with a negative angle to the horizon (Fig. 3B). We also observed an effect of mass in general on landing

angle, with larger lizards having lower landing angles from every perch type (mass: $F_{2,26}=43.79$, $P<0.001$; Table 1, Fig. 3B).

Because we observed an interaction between the recoiling perch and the lizard tail, we also analyzed the perch speed just before the perch contacted the tail to determine whether perch speed contributed to the negative landing angles of the larger lizards. The perch speed from the rigid perch was 0 cm s^{-1} , so we removed it from the analysis. Perch speed was not significantly different between compliant perch types for either group of lizards (paired t-test; small lizards: $t=1.18$, $P=0.26$; large lizards: $t=0.93$, $P=0.39$), but the tails of larger lizards were hit with significantly greater perch speeds than the small lizards for both perch types (flexible: $W=122$, $P=0.009$; most flexible: $W=116.0$, $P=0.002$; Fig. 3C).

We considered the possibility that the width of the perch we chose for our study may have contributed to the extreme perch–tail interactions, i.e. a compliant perch wider than the perch the lizards choose to jump from in the wild may result in abnormal interactions between the lizard and the perch. Although we did not formally test this possibility, we performed some preliminary trials to determine whether perch width was a confounding factor. We repeated jumping trials with three males (1.50, 4.75 and 5.90 g) using a compliant perch half the width of our original perch (13x3 mm, $C=0.30 \text{ mN}^{-1}$), using a similar setup as our other trials. We oriented the perch parallel to the landing pad, as before, and also angled the perch 45 deg to the landing pad. We were unable to set the perch perpendicular to the landing pad, but wanted to account for lizard orientation as another factor leading to non-typical jumps in our lizards. Regardless of perch orientation, perch–tail interactions resulted in forward pitching of all lizards from this

narrow perch. The smallest lizard, however, was able to right itself mid-flight and land horizontally from both perch orientations. This mid-flight readjustment was typical of smaller lizards in our original set of trials.

D. Discussion

Despite the frequent use of compliant perches by *A. carolinensis* in the wild, perch compliance negatively affected several aspects of jumping performance in this species during our laboratory trials. Because lizards lost contact with the compliant perches before the perches recoiled (i.e. they did not use the recoil like a springboard to propel themselves), they lost energy to the perch, resulting in decreased jump distances and takeoff speeds in large lizards. In addition, perch recoil following takeoff resulted in the perches striking the lizards on the tail, which pitched the lizards forward and resulted in significantly altered landing angles for all lizards. The perches used in the wild by *A. carolinensis* at our site span a large range of diameters and compliances. However, the perches we used in our study were similar in compliance (0.27 and 0.64 mN^{-1}) to those of many of the branches, vines and leaves. Therefore, although it is necessary to use caution when attempting to extrapolate laboratory-based performance results to performance in the wild, our results show that perch compliance could affect both performance and behavior in *A. carolinensis* in the wild, particularly in larger individuals.

Environmental perturbations, such as changes in substrate compliance or terrain height, and air or water flow speed and direction, are well known to influence locomotion in various animal taxa (Alexander, 2003; Biewener, 2003; Hildebrand et al., 1985; Hill et al., 2008). Because these perturbations can be energetically challenging and cause

locomotor instability, their effects have been studied across a range of taxa, including cockroaches (Sponberg and Full, 2008), lizards (Korff and McHenry, 2011), turkeys (Gabaldón et al., 2004), fish (Webb and Cotel, 2010), gibbons (Channon et al., 2011) and humans (Moritz and Farley, 2003). In environments where these perturbations are common, animals often evolve behavioral means of compensating for the impacts on locomotion. For example, cockroaches run more quickly to offset the effects of rough terrain (Sponberg and Full, 2008) and, as mentioned above, gibbons use low-power jumps to compensate for the effects of perch compliance (Channon et al., 2011). Indeed, one of the themes from this body of work is the remarkable ability of animals to overcome quite formidable natural obstacles through morphological and behavioral specializations.

In this regard, it is notable that *A. carolinensis* did not compensate for changes in perch compliance by altering their kinematics or behavior, and individuals were affected quite dramatically. The largest lizards suffered a substantial loss of speed, distance and potentially accuracy (which was not measured but implied from the unstable jumps) when induced to jump from compliant perches. This lack of compensation has also been observed in common starlings, which Bonser et al. (1999) posited might lead to decreased initial leap distance and an inability to escape from predators. This suggests that these two animals do not necessarily strive for locomotor efficiency when choosing perches. Given these results, the use of compliant perches by green anoles in the wild, with its resultant diminished locomotor performance, might ultimately impact fitness in the wild by decreasing an animal's ability to catch prey or avoid predators, although this needs to be tested empirically. A recent review (Irschick et al., 2008) showed that poor

locomotor performance can negatively impact fitness in a variety of lizard and snake species. Our results clearly show costs associated with compliant perch use in green anoles; however, it remains to be seen whether these costs do indeed affect fitness, and how this species is impacted by perch compliance in the wild.

The independent radiation of the genus *Anolis* into distinct ecomorphs has led to extensive study of the relationship between the morphology, ecology and behavior of these species (Losos, 1990; Losos, 2009; Williams, 1972; Williams, 1983). Although the preferred perch diameter, height and even length of the perches used by these species are well documented, the compliance of the perches used in the wild is unknown. The compliance of a structure depends on the material's modulus and the structure's geometry, and, as a general rule, as branches get thinner they become more compliant (Bonser et al., 1999). Although the degree of compliance will vary by substrate type (e.g. wood versus leaf), many of the small-diameter branches *Anolis* lizards jump from are somewhat compliant. The use of narrow, and likely compliant, perches is common in several of the *Anolis* ecomorphs. In particular, the truck-crown, twig and grass-bush ecomorphs, including *A. carolinensis*, often use perches that are 0.5 cm or less in diameter (Irschick et al., 2005a; Losos, 1990; Losos, 2009). Given the negative effects of perch compliance seen in the present study, it is likely that this habitat variable could be an important and underappreciated aspect of anole ecology and behavior, and potentially help explain some of the less well-understood morphological and habitat-use correlations. As an example, *Anolis* ecomorphs that use broader perches tend to have

longer legs and jump more frequently than ecomorphs that use smaller-diameter perches (Losos, 2009). However, some anoles use extremely narrow perches, but have long limbs and jump regularly. This latter group is often composed of small lizards, suggesting that size is a factor in determining compliant perch use.

The results from our preliminary tests of the effects of compliance using narrow perches suggest that perch–tail interactions may occur regardless of perch width or orientation. However, the structures of perches in nature are complex, and how they recoil depends on several factors, such as material properties and to what extent recoil is damped, for example by air drag if leaves are present on the branch. Additionally, green anoles jump at a variety of angles to and from a range of perch types in their three-dimensional habitat and perch–tail interactions may only occur under specific circumstances (Irschick and Losos, 1998) (D.J.I., unpublished). Therefore, more data are needed to test the importance of perch–tail interactions in the wild. In addition, more research is necessary to determine whether these lizards are able to sense the compliance of perches used in the wild, and, if so, whether their locomotor strategy changes to potentially compensate for this compliance. In our study we found that large lizards were generally more reluctant to jump from the most compliant perch, indicating that although they were forced to jump from these perches, they did have some sense of the compliance of the perch before jumping and perhaps were aware of potential costs of jumping from compliant perches. They often hopped down to the substrate below them as opposed to jumping forward with a positive takeoff angle. After sufficient coercion, however, large animals jumped from compliant perches using the same takeoff angle and duration as they did from more rigid perch types, and as small lizards did from all perch types.

Because all individuals we used for the trials were obtained through the pet trade, it is unclear whether this reluctance is due to an innate or learned response to this particular perch characteristic. Additionally, although our results support the prediction that large lizards would be affected to a greater degree than small lizards, more data are needed to understand whether this effect is stepwise or gradual.

Recent work has shown the value of examining locomotion in nature, and how animals interact with habitat structure (Fulton et al., 2001; Irschick and Losos, 1999; Johansen et al., 2007; Mattingly and Jayne, 2004; Youlatos and Samaras, 2011). Green anoles in the wild segregate perches across age or sex classes based on perch diameter: smaller animals use narrow perches, and larger animals use larger perches (Irschick et al., 2005a). Although laboratory trials have shown that perch diameter influences maximum running speed (Irschick and Losos, 1999) but not jump distance from noncompliant perches (Losos and Irschick, 1996), both jump distance and jump speed are reduced by compliant perches for larger animals. Therefore, perch segregation may reflect the constraints imposed by small-diameter compliant perches, alone or in conjunction with other factors such as intraspecific competition. However, it is possible that larger individuals of *A. carolinensis* in the wild may occasionally choose compliant perches when the costs of jumping from these perches do not outweigh the gains, e.g. from better resources or for territorial defense. Understanding how this particular habitat characteristic affects the way animals move, and their ability to navigate their habitat, would provide greater insight into an important yet understudied aspect of locomotion.

Figure 1.1: The effects of three levels of perch compliance on the jump variables jump distance (A & B) and takeoff velocity (C & D). Increased compliance significantly affected both variables in larger lizards (> 3g, B, D) but not smaller lizards (< 3g, A, C). Each point represents the mean and s.e.m. of two jumps for an individual from one perch type (< 3g, $N = 7$; > 3g, $N = 4$). Lines connect each individual's value across the three perch types. F and P values shown are from one-way repeated measures ANOVA for each group. Asterisks indicate significance with the sequential Bonferroni test.

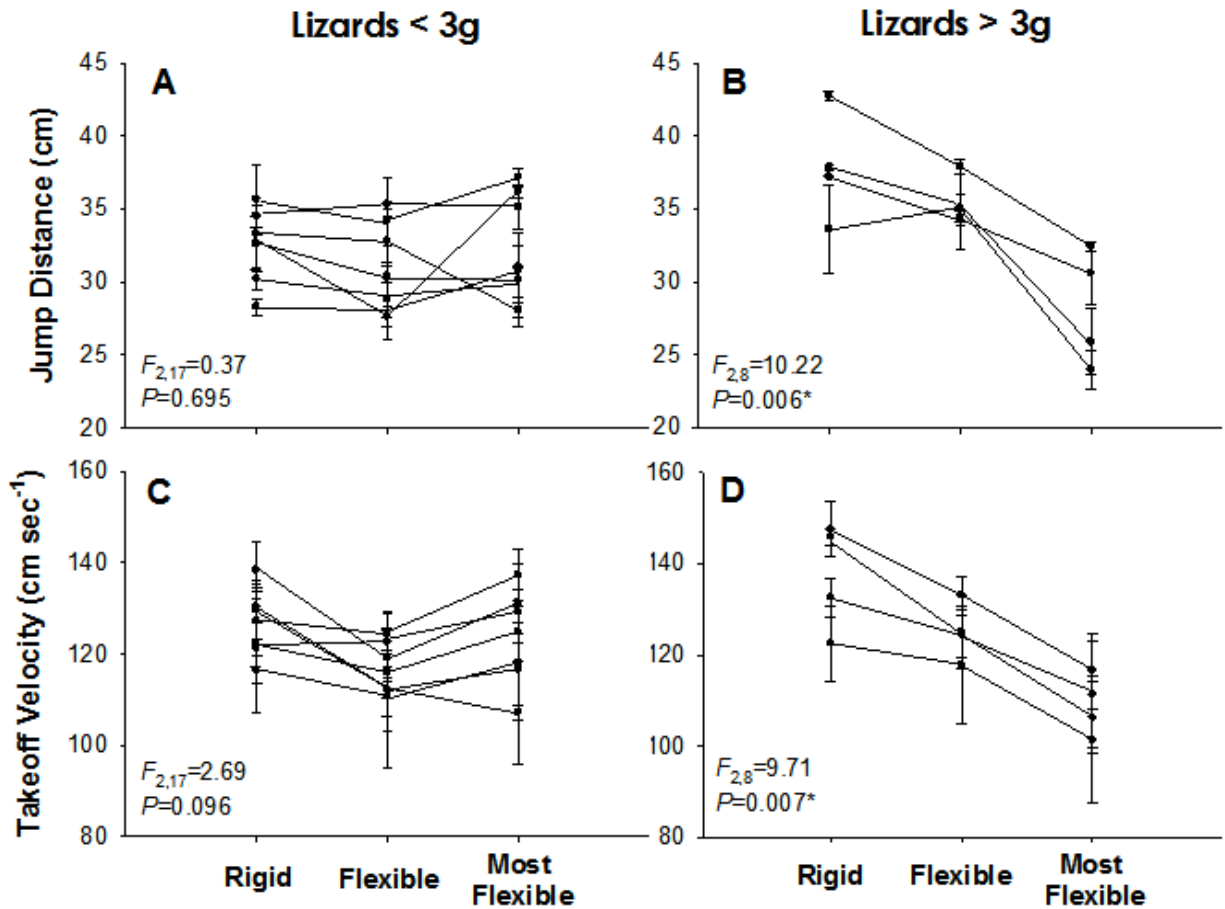


Table 1.1: One-way repeated-measures ANCOVA $F_{2,26}$ -values (with associated significance levels) for jump variables across three treatments: rigid perch, flexible perch, and most flexible perch. $N = 11$ for each treatment. Asterisks indicate significance with the sequential Bonferroni test.

Variable	Compliance	Mass	Compliance x Mass
Jump distance	3.35 (0.051)	2.59 (0.120)	8.08 (0.002)*
Takeoff duration	0.26 (0.770)	9.86 (0.004)*	1.27 (0.297)
Takeoff velocity	7.95 (0.002)*	0.14 (0.708)	9.76 (<0.001)*
Takeoff angle	2.14 (0.138)	2.34 (0.138)	0.82 (0.450)
Landing angle	16.79 (<0.001)*	43.79 (<0.001)*	2.25 (0.126)

Figure 1.2: The effects of three levels of perch compliance on A) takeoff angle, B) takeoff duration, and C) landing angle. Of the three jump variables, only landing angle was significantly affected by increased perch compliance. *F* and *P* values shown are from one-way repeated measures ANOVA (*N* = 11). Asterisks indicate significance using the sequential Bonferroni test.

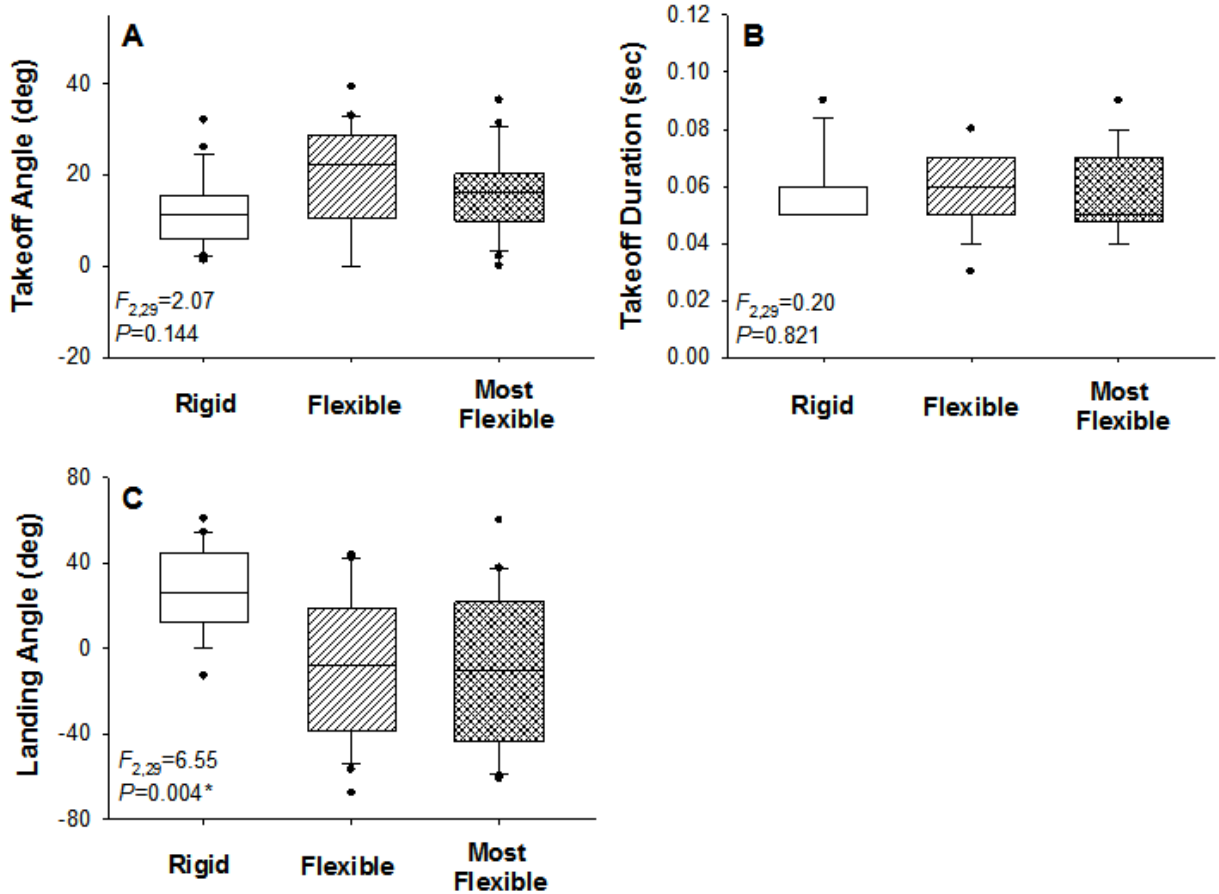
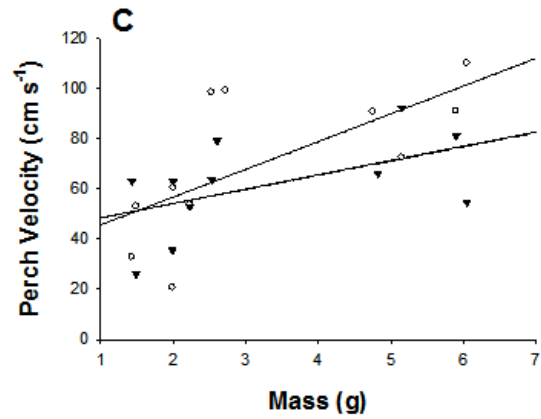
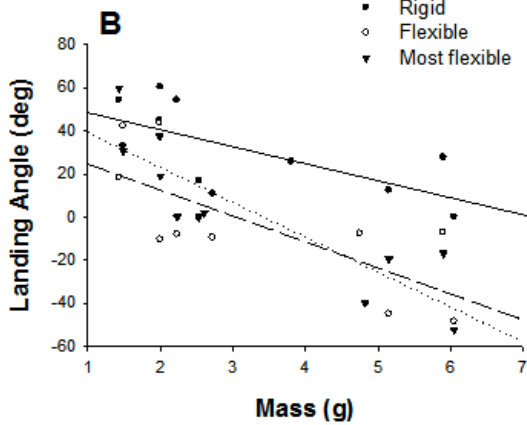
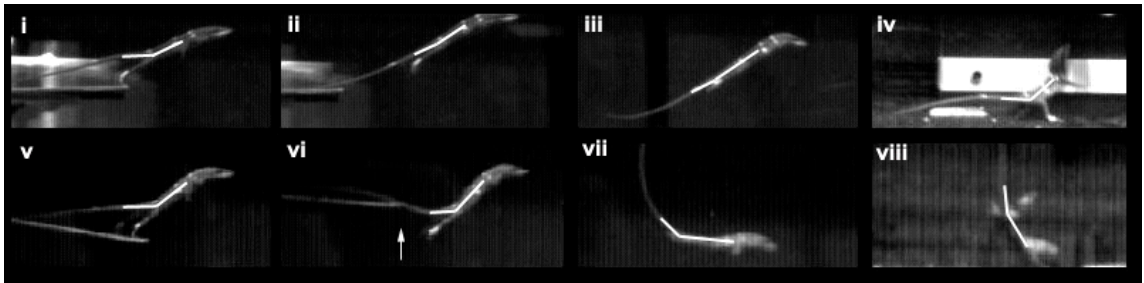


Figure 1.3: Perch interference effects on takeoff, flight and landing angle. A) Movie stills of the same lizard (6g) jumping from a compliant (i-iv) and most flexible (v-viii) perch types. White lines show body and tail base angles throughout the jump. This lizard had a positive takeoff and landing angles from the rigid and compliant perch types (i, v), but the rebound of the most compliant perch hit the middle of the tail and caused the body to pitch forward (vi, vii), resulting in a negative landing angle (viii). B) Relationship between mass, compliance and landing angle. Note that landing angles decrease as compliance increases, largely due to the pitching caused by perch and tail interactions (rigid perch: straight line, flexible perch: dashed line, most flexible perch: dotted line, longest jumps of $N=11$ lizards per perch type). C) Relationship between mass, compliance, and perch velocity as the perch contacts the tail. Note the greater velocities for the larger lizards.

A



CHAPTER II

FOILS OF FLEXION: THE EFFECTS OF PERCH COMPLIANCE ON LIZARD LOCOMOTION AND PERCH CHOICE IN THE WILD

A. Introduction

Habitat variation may pose a challenge for animal locomotion, and can lead to the evolution of morphological, behavioral and ecological adaptations. The variation in structural characteristics within the habitat, such as substrate type, size and incline, influences locomotion across a wide range of animal taxa (Hildebrand et al. 1985; Alexander 2003; Biewener 2003; Hill, Wyse & Anderson 2008; Peattie 2009; Flaherty, Ben-David & Smith 2010; Ellerby & Gerry 2011). Arboreal habitats present challenges for locomotion because of their complex three-dimensional nature, and the perches and supports used by arboreal animals during locomotion often vary in diameter, length, angle, compliance (flexibility), and the size of the gaps between structures (King 1998; Mattingly & Jayne 2004). Larger and more stable perches such as trunks and wide branches are often surrounded by smaller branches and foliage, which can bend and become unsteady underneath an animal's weight. Arboreal animals must either balance and move along both the stable and more compliant structures, or may have to travel greater distances to move around their habitat.

Structural compliance may be important for arboreal animals that use jumping. Jumping is a highly power-intensive form of movement (Crompton, Sellers & Gunther 1993; Lailvaux & Irschick 2007; Kuo, Gillis & Irschick 2011). When an animal jumps from a compliant perch, the forces generated during the jump bend the perch away from the animal. Unless the animal is able to use the recoil of the perch to propel itself

forward, the perch absorbs part of the energy of the jump and less energy is available for the jump itself (Alexander 1991; Gilman et al. 2012). Jumping from compliant perches is not only challenging, but it can also be dangerous, particularly for larger animals. When these supports are high off the ground, animals are at risk of falling when supports give way, or if they are unable to reach their intended support due to loss of jump energy to the perch (Bonser 1999). Because of the potential risks associated with using compliant perches, variable perch compliance within a habitat may have striking effects on arboreal animal locomotion and behavior by affecting perch and path choice, and locomotor performance.

Thus far, research on the effects of perch compliance on arboreal behavior in the wild has been restricted to a few studies of primates. These studies show that primates such as the western woolly lemur (*Avahi occidentalis*, ~ 1 kg) and the white-faced saki (*Pithecia pithecia*, ~ 1.6 kg) use larger, sturdier branches for longer jumps (Warren & Crompton 1997; Walker 2005); the Sumatran orangutan (*Pongo abelii*, 45-90 kg) has been shown to use multiple supports and alter jumping posture to minimize the effects of perch flexibility (Thorpe, Holder & Crompton 2009). Although this work provides insights to the locomotor behavior of these animals, the researchers did not directly measure compliance of the perches that were used, or that were generally available in the environment.

Arboreal lizards present an excellent system with which to employ an integrative view of locomotion and how it is influenced by habitat variables such as compliance. The genus *Anolis* includes almost 400 species of arboreal lizards, ranging in size from ~1-200 g. These lizards vary greatly in morphology, ecology, and locomotor ability, and they

frequently use jumping to move around their habitat (Irschick & Losos 1999). One particularly well-studied species, the green anole (*Anolis carolinensis* Voigt 1832) often occupies compliant perches such as narrow branches, twigs, grass, and leaves and is generally found on perches less than 2 meters high (Irschick et al. 2005a; Irschick et al. 2005b; Gilman et al. 2012) (Fig. 1). This proximity to the ground allows for direct quantification of habitat characteristics, and determination of how locomotion is influenced by compliance and other habitat variables.

Recently, we performed lab trials on the effects of perch compliance on jumping kinematics and performance in *A. carolinensis*, and we found that increased compliance resulted in significantly shorter jump distances and lower take-off velocities (Gilman et al. 2012). Because these lizards occupy habitats in which they must jump to and from compliant perches, our results suggest that perch compliance may be an important structural variable that influences how this species negotiates its habitat. A substantial body of work has examined how perch diameter and substrate type influence locomotion in *Anolis* lizards (Losos & Sinervo 1989; Macrini & Irschick 1998; Losos & Irschick 1996; Irschick & Losos 1999; Spezzano & Jayne 2004; Vanhooydonck, Herrel & Irschick 2006), and perch diameter in particular has been cited as a driver of the anoline adaptive radiation (Losos 2009). However, the lack of field data on compliance, and its influence on locomotion, leave open the question as to how this variable might also play a key role in the ecology of these or other animals. This question has general implications because compliance is a ubiquitous habitat feature that could affect species across many groups (e.g., lizards, snakes, frogs, mammals, birds and primates).

In this study we addressed three questions: 1) Do green anoles chose perches at random, or do they select perches with specific qualities for general use and jumping? Alternatively, is there a disconnect between which perches green anoles generally move on and which they decide to jump from? If true, this would suggest deliberate choice of perches for certain movements. 2) What are the effects of perch compliance on the locomotor behavior of green anoles? Does perch compliance negatively affect jump distance in nature as in the lab? 3) What is the relationship between perch diameter and compliance for natural structures that green anoles use (i.e., can perch diameter be used as a proxy for compliance in this system, as is common in studies of primates (Warren & Crompton 1997; Walker 2005; Thorpe et al. 2009))?

B. Materials and Methods

1. Available habitat and general-use perch measurements

We conducted our field study in May and June 2011 at the River Breeze Park in Volusia County, FL, USA at a site dominated by small and medium cabbage palms (*Sabal palmetto*), generally less than 3 m high. We explored the relationship between perch use by green anoles and perch compliance. We quantified the available structural habitat of this site by measuring perches at 0.5, 1 and 1.5 m heights every 5 m along two 50 m transects located 7 m apart and running the length of the longest stretch of palm-dominated habitat where individuals were found. We did not include measurements at 2 m, because few individuals jumped from 2 m or above (5%), and the structural habitat is relatively homogeneous above 1.5 m heights. We placed 1 m rods horizontally and perpendicularly to the transect at 0.5, 1 and 1.5 m. For any vegetative structure within 5

cm of any point on this pole, we measured perch diameter (width) (± 1 mm), perch angle of inclination ($\pm 0.1^\circ$, Digi-Pas DWL-80E digital angle electronic angle gauge, Digi-Pas USA, Avon, CT), length to proximal node (any branching point proximal to the perch point) (± 1 mm), distance to nearest perch (± 1 mm), diameter of nearest perch (± 1 mm), angle of nearest perch ($\pm 0.1^\circ$), and compliance of the point closest to the pole, resulting in a total of 112 perches (following Irschick et al. 2005a; Irschick et al. 2005b). Because we had observed anoles perching on all parts of each type of vegetation throughout the habitat, we treated these measured points as potential perch sites for the anoles. We measured compliance in one of two ways. For generally horizontal and compliant perches (or perches that could be made close to horizontal by bending large supporting branches), we measured the height of the perch, hung one of five fishing sinkers of known mass (3.75, 5.37, 10.68, 14.32, or 28.61 ± 0.01 g) from the perch at the exact spot where the individual was found, and measured the height of the perch again (displacement), as in Gilman et al. (2012). For less compliant, vertical perches, such as palm branches and tree trunks, we used a push-pull tension gauge (GPP-8, Jonard Industries Corp., Tuckahoe, NY) to displace the perch, and recorded the mass required for displacement (± 5 g) and displacement. We then calculated the compliance using the relationship between displacement and force:

$$C = \frac{d\delta}{dF},$$

where C is compliance, F is force (mass in kg * 9.81, gravitational acceleration) and δ is the displacement of an object due to the force (Halliday, Resnick & Walker 2005).

Higher values of C indicate greater compliance. To determine if green anoles chose

compliant perches randomly for general use (basking, running), we walked through the park and noted the perch site of any lizard we sighted, as long as the lizard did not jump from the perch. We then measured perch height, perch diameter, and compliance of these perches ($N=80$).

2. Jump perch measurements

To determine if green anoles chose jump perches at random, or with regard to compliance, we did the following. We walked through the park daily between 0800 and 1200, 1600 and 1930, and scanned all potential perches (i.e., leaves, leaflets, petioles, trunks, branches) for the presence of adult lizards. Once spotted, we used a Sony DCR-SR100 digital camcorder (Sony, Tokyo, Japan) to videotape undisturbed behavior of individuals for a period between 5 and 35 minutes. We recorded one to three jumps per individual for 17 females (2.01 ± 0.3 g, mean s.d.) and 37 males (3.35 ± 0.6 g) for a total of 80 jumps. We then captured each individual and recorded its mass (± 0.1 g) using a Pesola Micro-Line 20010 spring scale (Pesola AG, Baar, Switzerland). We measured snout-vent and tail length, and we estimated humerus, radius, forelimb metatarsal, longest forelimb toe, femur, tibia, hind limb metatarsal, and hind limb longest toe lengths (± 1 mm) using a clear plastic ruler. Females in this study were determined by having greater than 42 mm snout-vent length, reduced dewlaps, and narrow tail bases. Males were greater than 46 mm snout-vent length and had enlarged dewlaps and tail bases. We used video playback to locate the sites the individual jumped from (P_1) and to (P_2) and measured perch height (± 1 mm), diameter, angle of inclination, distance to nearest perch, nearest perch diameter, angle, angle between P_1 and P_2 ($\pm 0.1^\circ$), and straight line distance

between P_1 and P_2 (± 1 mm). We also used frame-by-frame video playback of each jump to determine if lizards jumped before, during, or after perches recoiled.

3. Data Analysis

To determine the relationship between perch diameter and compliance in natural structures, we combined data for similar structures (live and dead palm leaflets; live and dead palm leaves; or live and dead branches, palm petioles, and trunks) from all perches measured (jump perches (P_1), landing perches (P_2), available habitat, non-jump perches, $N=320$) and performed linear regression analysis on each structure type. We did not include vines in the analyses because vines at the site were supported by other structures and we did not expect to see a relationship between diameter and compliance.

We compared available habitat, general use perch, and jump perch variables using bootstrap Kolmogorov-Smirnov tests (1000 runs) and used a conservative significance cut-off ($P < 0.005$) (see also Mattingly & Jayne 2004 and McElroy et al. 2007). We also compared available habitat, general use perch, and jump perch variables for just palm plants, as plant species may differ in compliance, and therefore any correlation between perch variables and perch choice may be an artifact of the use of a particular species of plant for specific behaviors (e.g., jumping) ($N=63$ jump perches, $N=67$ general use perches, $N=98$ available habitat perches). There were no significant differences between males and females for jump perch compliance ($P=0.39$), diameter ($P=0.91$), height ($P=0.34$), distance to nearest perch ($P=0.16$), or jump distance ($P=0.06$) (bootstrap Kolmogorov-Smirnov) so males and females were pooled for all analyses. Because habitat use is tightly linked to morphology in this species, we tested for morphological

differences between the sexes by conducting a correlation-based principal component analysis of the ln-transformed morphological estimates, and then used a t-test to compare male and female principal component scores.

In addition to our three primary questions (above) we also wanted to determine if there was a relationship between jump angle (angle between P_1 and P_2) and jump distance. We performed linear and nonlinear regressions of log-transformed jump distance against jump angle, and then also arbitrarily divided jump angle into categories (-90 to -61°, -60 to -31°, -30 to 0°, 0 to 30°, 31-60°, 61-90°) to evaluate jump distance ranges.

The results of our previous lab study showed that compliance has a negative effect on jump distance (Gilman et al. 2012). Therefore, we wanted to test whether this also occurred in the wild. However, because habitat variability can be complex and multiple habitat characteristics may influence jump distance, we used correlation-based principal component analysis to reduce dimensionality in the following perch variables: perch height, perch diameter, perch angle, distance to nearest perch, angle to P_2 , and compliance. We log-transformed perch diameter, distance to nearest perch, and compliance to normalize these variables before conducting the PCA. For components with eigenvalues greater than 1.0, we conducted a Monte Carlo test of the significance of the eigenvalues using 1000 permutations of the data matrix to compare the original eigenvalues to the distribution of eigenvalues under a null hypothesis of no real correlation structure, and we retained components with significant eigenvalues ($P < 0.005$). We then used linear regression of jump distance against the PCA scores of the retained components to examine the effects of habitat variability on jump distance. We

continued our use of a conservative significance value ($P < 0.005$) as our cut-off for the regression analysis, but because the resulting regression was not significant we did not conduct additional analyses.

C. Results

We observed that green anoles in our study lost contact with compliant perches prior to recoil, and did not use the perch to propel themselves forward. Green anoles jumped from their perches to other substrates at a range of angles from their perches (see below), and occasionally dropped to the ground to capture prey. Lizards did not appear to be disturbed by our presence, as noted in other studies (Mattingly & Jayne 2004).

There were significant differences in perch use distributions compared to available habitat distributions for both perch compliance and diameter, though the trend was different between the two variables (Fig. 2). Lizards jumped from perches that were significantly less compliant than those they generally occupied, as well as those available in the habitat, for all plants combined and palms alone ($P < 0.005$ for all). However, the distribution of the diameter of the perches they jumped from was similar to the distribution of perches they generally occupied ($P = 0.81$ all plants, $P = 0.71$ palms), but significantly different from those available in the habitat ($P < 0.005$ all plants and palms alone). The distribution of compliance of perches they generally occupied was similar to available habitat distributions ($P = 0.21$ all plants, $P = 0.43$ palms), while the distribution of diameters was significantly different between the two ($P < 0.005$ for all).

We were unable to find a significant best fit model for the relationship between jump angle and log-transformed jump distance, likely because lizards do not jump

maximally at all times as they navigate their habitat. At all angles, lizards jumped short and mid-range distances. However, there was a trend toward shorter jump distances at more extreme jump angles (Fig. 3). Lizards jumped from 5 to 21 cm at the most extreme angles (61-90°), from 6 to 30 cm at 31-60°, and from 5 to 41 cm at the shallowest angles (0-30°), and therefore jumped the greatest range of jump distances at angles closer to horizontal.

Principal component analysis of the jump perch variables resulted in eigenvalues greater than one for both PC1 and PC2 (Table 1), but only PC1 had a significant eigenvalue ($P < 0.005$). PC1 had high and positive loadings for perch angle (0.70), distance to nearest perch (0.58), and negative loading for perch height (-0.74) and compliance (-0.84). The relationship between jump distance and PC1 scores was not significant, but it showed a trend toward longer jump distances with increasing PC1 scores (i.e., low compliance, low height, increased distance to the nearest perch, and increased jump perch angle) (slope=0.04, $P=0.02$).

Similar to the lack of habitat specialization between sexes in this population (see above), there was little morphological differentiation between males and females. Only the first principal component, which is an indicator of overall size, had an eigenvalue greater than 1.0 (5.41, compared to 0.81, 0.50, 0.43, 0.29, 0.25, 0.20, 0.11 for PC2-PC8) and explained 68% of the variance. There were significant differences in the principal component scores between males and females for PC1 ($P < 0.005$), but no significant differences for any other component (P2-P8, $P > 0.35$) indicating that males and females differed significantly only in size.

There was a significant negative relationship between perch diameter and perch compliance for some, but not all perch types at the River Breeze Park field site (Fig 4). Increased perch diameter resulted in decreased perch compliance for trunks, branches and palm petioles (slope = -2.43, $P < 0.005$, $R^2 = 0.64$), and palm leaflets (slope = -1.26, $P < 0.005$, $R^2 = 0.23$), but not palm leaves (slope = -1.18, $P = 0.306$, $R^2 = 0.05$).

D. Discussion

We found that perch compliance had significant effects on perch choice and locomotor performance in green anoles. Although green anoles used perches with a range of compliance, they jumped from relatively less compliant perches, and jumped the farthest distances from the least compliant perches. We also found that, as in our lab study, green anoles jumped from compliant perches prior to recoil, and did not use the energy stored in the perch for their jump (Gilman et al. 2012). Lastly, we found a significant negative relationship between perch diameter and compliance in most natural structures in the habitat; however, variability in compliance for a given diameter generally precludes the use of diameter as a proxy for compliance in this system.

Habitat characteristics have direct effects on animal locomotion and performance, and the ability of organisms to perform maximally in their natural habitat often has fitness benefits (Arnold 1983; Garland & Losos 1994). For example, optimal performance such as maximal sprint speed in ectotherms is dramatically affected by microhabitat temperature (Huey 1991). In addition to temperature, the structural characteristics of the habitat can also directly affect animal performance (Irschick & Losos 1999; Toro, Herrel & Irschick 2004). For jumping animals such as *Anolis* lizards,

there are three primary ways of optimizing jumping performance that help their ability to escape predators: increasing jump distance, jump speed, and jump accuracy (Irschick et al. 2008; Toro et al. 2004). The first index of performance, jump distance, was negatively affected by increased compliance in both our lab and field studies (Fig. 5) (Gilman et al. 2012). It is reasonable to argue that it would be beneficial for *Anolis* lizards, as well as many other animals, to choose habitats where at least one of these performance traits would be maximized, although determining which one is most relevant is challenging (Toro et al. 2004). However, our lab study revealed that increased compliance resulted in decreases in all three aspects of jump performance (Gilman et al. 2012), indicating that any usage of compliant perches decreases performance in all three. Although many perches used by green anoles in our study population are highly compliant ($\geq 0.64 \text{ mN}^{-1}$), green anoles appear to jump off perches on which jumping performance is maximized. Green anoles jumped from rigid to moderately compliant perches (up to the compliance that reduced maximal jump distance in the lab by 5%) 74% of the time in the wild, and jumped from more compliant perches (greater than or equal in compliance to those that reduced maximal jump distance in the lab by 22%) only 15% of the time, even though these more compliant perches make up 38% of the available habitat. The tendency to choose relatively sturdier perches to jump from has also been observed in some primates, and appears to be a necessary compensation in many arboreal habitats (Warren & Crompton 1997; Walker 2005). For example, *Pithecia pithecia* (~1.6 kg) is a primate that uses leaping to navigate its habitat frequently (~40% of the time), and does so from perches that range from < 2 to >15 cm, but only leaps from perches of < 2 cm 4% of the time, a behavior that may maximize leap distance (Walker 2005).

Although green anoles and primates appear to use similar ways of minimizing the negative effects of perch compliance on jumping, animals of different sizes experience a given habitat in different ways. For example, gaps that are large and prohibitive for crossing to a small animal may be inconsequential to a much larger species (Fleagle & Mittermeier 1980; Walker 2005). In that respect, variability within the diameter-compliance relationship is important when attempting to determine the effects of compliance on small animal locomotion, as small animals are sensitive to minor changes in compliance (Demes et al. 1995). In our lab study, we found that a 137% increase in compliance (from 0.27 to 0.64 mN^{-1} or -0.57 and -0.19 respectively, on a log scale) resulted in a 22% decrease in jump distance in our larger animals (Gilman et al. 2012) (note that as seen in Figure 4, these compliance values are clearly within the values for a range of branch and palm leaflet diameters). Therefore, while using diameter as a proxy for compliance may be appropriate for larger animals like primates, it could easily mask the effects of compliance on behavior in smaller animals, given the high variability in the diameter-compliance relationship we observed at our study site. Additionally, comparisons of the compliance and diameter distributions (Fig. 2) show that these two habitat variables tell very different stories regarding perch use. While green anoles jump from and perch on supports within similar diameter ranges, they are more selective when jumping with regard to compliance and choose less compliant perches when jumping than for general use.

Species that occupy different habitats with varying structural layouts or physical attributes may exhibit behavioral and locomotor adaptations to the local habitat (Dagosto 1994; Krajewski et al. 2011). For example, Dagosto and Yamashita (1998) found that

three species of lemurs leap less, climb more, and move quadrupedally more often at a site with larger, taller trees compared to a site with smaller trees, and Krajewski et al. (2011) found that the amount of wave exposure at different sites affected the activity budget and location of activity in four species of reef fishes. Although we found a trend toward longer jumps from perches at low heights and low compliances at our site, this may not be typical of green anoles in all habitats they occupy. Our study site was dominated by relatively low cabbage palm plants, and few larger trees (Fig. 1). Perches low to the ground tended to be mostly trunks and palm petioles, which are generally less compliant than palm leaves and leaflets, and the majority of perches higher off the ground were relatively compliant palm leaflets. Principal component analysis and the relationship between PC1 and jump distance showed a trend toward longer jump distances from low-lying, low compliance, close-to-vertical perches, which were generally palm petioles and trunks. Because the more rigid structures at our study site are lower to the ground, it is difficult to disentangle the effects of perch height and compliance on jump distance. It is possible that green anoles are more inclined to jump farther at lower heights in general, to avoid the risk of falling from greater heights and expending energy regaining their original position, or encountering conspecifics or predators. Replication of this study at field sites with different types of dominant vegetation (e.g., mostly trees, where low compliance perches are available at a range of heights) would help to determine whether or not green anoles (and potentially small animals in general) are more cautious about jumping from high perches, regardless of compliance. In addition, further studies are needed to determine which aspects of

jumping (e.g., speed, distance, accuracy) are most critical for fitness in small animals, and whether this changes across habitats.

In conclusion, we found that compliance is a structural characteristic that has dramatic effects on the behavior and performance of green anole lizards. Lizards in our study avoided jumping from highly compliant perches, even though they were often found on them, basking, foraging or during other forms of locomotion. Although the effects of perch height and perch diameter have been well-studied in this species, this is the first study to shed light on the effects of compliance. In addition to directly affecting jumping performance, perch compliance may also cause physical instability during the jump, particularly in small animals, and further biomechanical studies are needed to reveal additional effects of compliance in jumping animals. Many small animals use jumping as a means to navigate their habitat, and we hope that our results will inspire other researchers to examine this variable more broadly.

Figure 2.1: *Anolis carolinensis* individuals and the study site. A) Green anole male on a relatively inflexible tree trunk, B) Green anole female on a more flexible leaf, and C) Our study site in Volusia County, FL. This site was dominated by low-lying cabbage palm plants, with few larger palms and other trees.



Figure 2.2: Frequency distributions of perch compliance and diameter in Riverbreeze County, FL. A&D) Perches available in the habitat ($N=112$), B&E) Perches generally occupied by *Anolis carolinensis* ($N=80$), C&F) Perches used for jumping by *A. carolinensis* ($N=80$). Compliance is shown here as the log transformed values to aid in visualization of the data. Significant differences ($P<0.005$) between frequency distributions within a variable are shown as with asterisks.

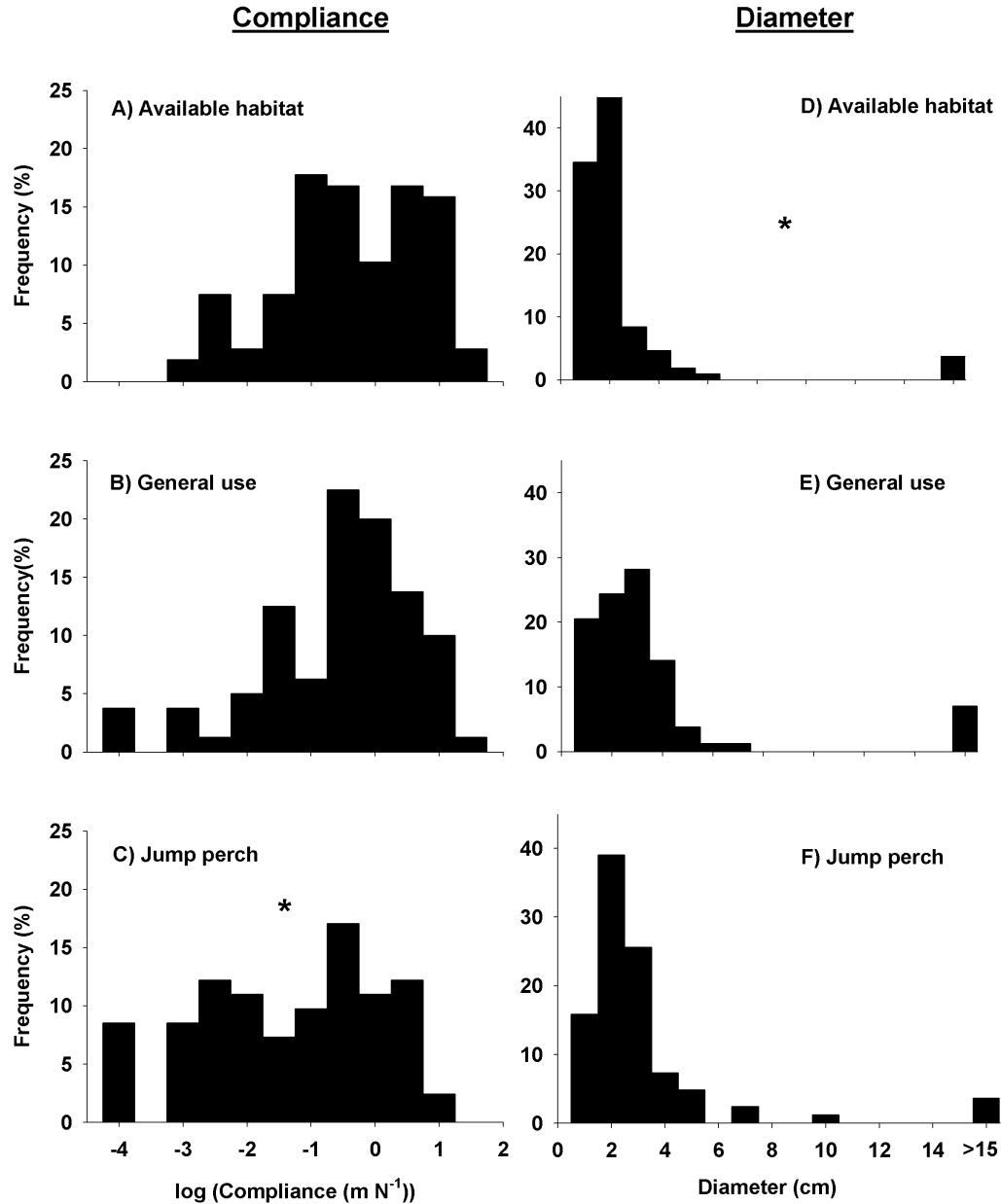


Figure 2.3: Relationship between angle-to-landing perch and distance-to-landing perch. A) Angle and distance to new perch for downward jumps B) Angle and distance to new perch for upward jumps. Although the relationships were not significant, green anoles jumped the largest range of distances at the least extreme angles.

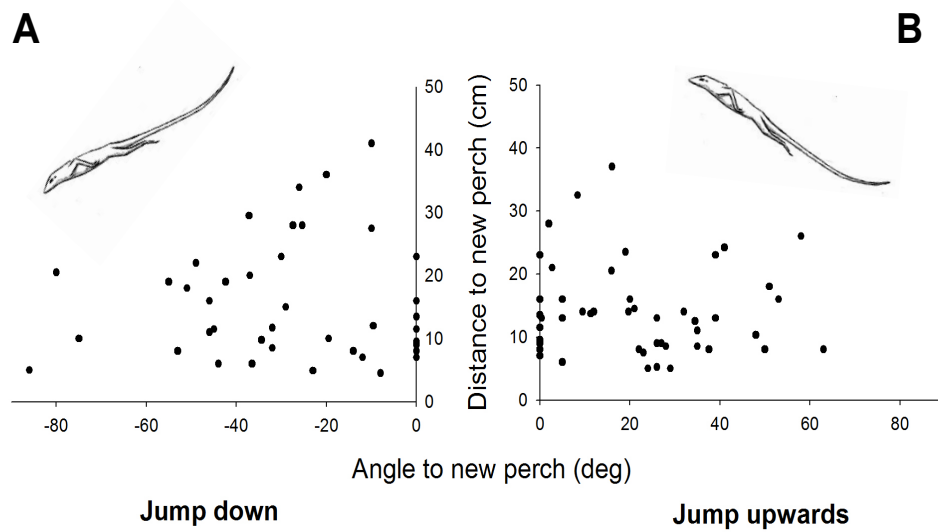


Figure 2.4: Relationship between perch diameter and compliance in the wild. There was a significant relationship between the diameter of a perch and its compliance for palm leaflets (slope=-1.26, $P<0.001$, $N=180$) and petioles, branches and trunks (slope=-2.43, $P<0.001$, $N=116$), but not palm leaves (slope=-0.28, $P=0.3$, $N=24$).

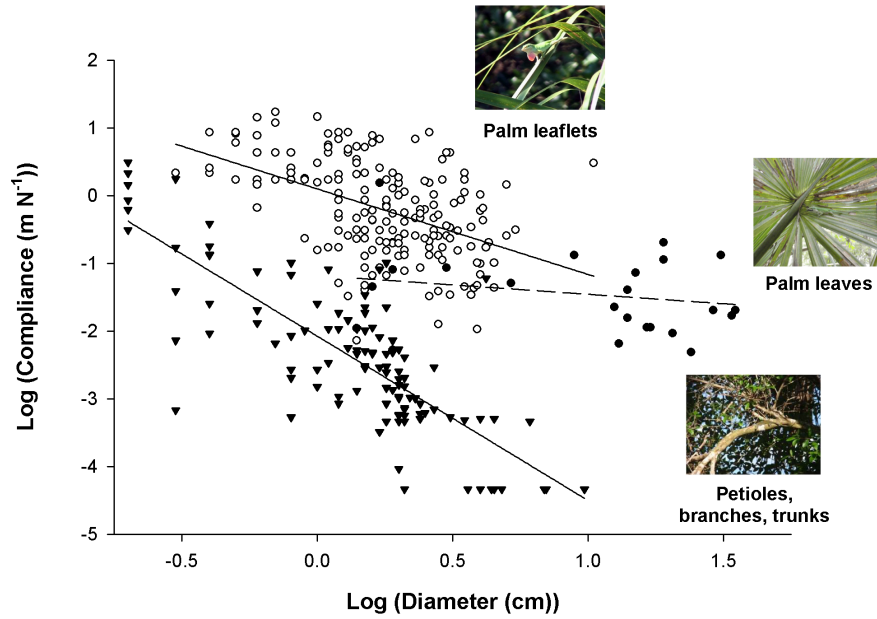


Figure 2.5: Relationship between perch compliance (on a log scale) and lizard jump distance. Open circles are data from our previous lab study (Gilman et al. 2012) and closed circles are field data from this study. In both the lab and field, the longest jumps tended to occur from the least compliant perches.

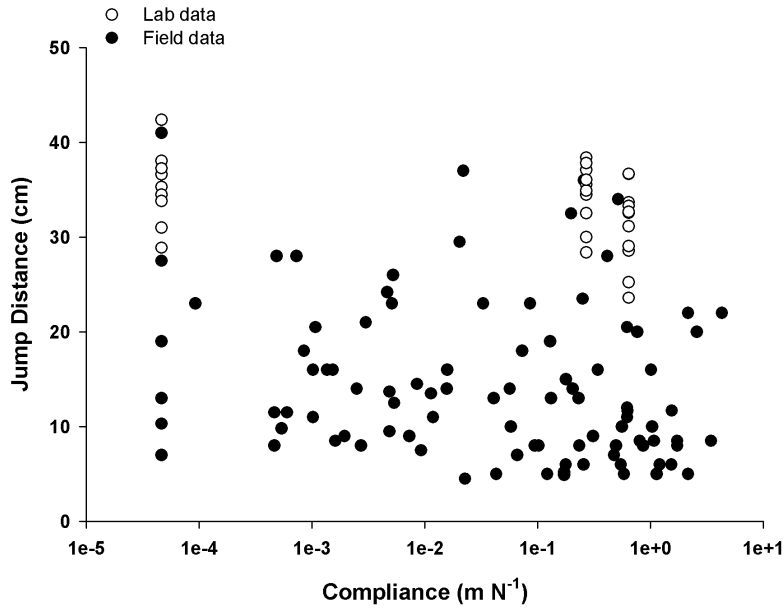


Table 2.1: Results from principal component analysis of jump perch characteristics. Substantial loadings are in bold.

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>	<i>PC6</i>
Variance	2.33	1.05	0.93	0.70	0.62	0.38
Proportion of Variance	0.39	0.17	0.15	0.12	0.10	0.06
Cumulative Proportion	0.39	0.56	0.72	0.83	0.94	1.00
<i>Perch Characteristics</i>			<i>Eigenvectors</i>			
Jump perch height	-0.49	0.16	-0.06	0.41	-0.61	-0.44
Jump perch diameter	0.23	0.68	-0.53	0.33	0.3	-0.05
Jump perch angle	0.46	0.14	-0.27	-0.35	-0.72	0.25
Jump perch compliance	-0.55	0.08	-0.17	0.1	-0.04	0.81
Angle to landing perch	0.23	-0.68	-0.48	0.49	-0.03	0.06
Distance to nearest perch	0.38	0.15	0.61	0.59	-0.14	0.29
<i>PC1 Loadings</i>						
Jump perch height	-0.74					
Jump perch diameter	0.35					
Jump perch angle	0.70					
Jump perch compliance	-0.84					
Angle to landing perch	0.35					
Distance to nearest perch	0.58					

CHAPTER III

SEXUALLY DIMORPHIC RESPONSES TO HABITAT COMPLEXITY IN THE GREEN ANOLE LIZARD, *ANOLIS CAROLINENSIS*

A. Introduction

Animals necessarily interact with the structural characteristics of their habitat. These interactions have multifaceted consequences for the animal. Variation in the structural characteristics of the habitat can lead to site-specific adaptation in body proportions, locomotion, foraging ecology, social signaling, and mating strategy (Petren and Case 1998, Pounds 1988, Boughman 2001, Badyaev 2008, Losos 2009). Additionally, these adaptations can be plastic or fixed, and can occur in one or both sexes (Shine 1991, Butler et al. 2000, Hollander et al. 2006). These complex effects are often studied as single traits or aspects, but many of the effects occur in concert.

Limb length and locomotor ecology has been shown to differ within species of lizards occupying habitats of varying structural characteristics, such as perch width and vegetative complexity (Kohlsdorf et al. 2001, Irschick et al. 2005a, Dill et al. 2013, Winchell et al. 2018). Lizards that live in variable habitats must run and jump from a variety of surfaces, and limb length and locomotor adaptations have direct fitness consequences as animal performance can affect prey capture and predator avoidance (Miles 2004). Additionally, males and females can be dimorphic with one or more of these characteristics within habitats as a result of sexual selection and reproductive and ecological requirements (Butler and Losos 2002, Irschick et al. 2005a). Because males and females can be dimorphic in body and gape width, differences in body condition

within species have also been observed, possibly due to differences in prey size associated with habitats (Stehle et al. 2017).

Habitat distribution across space, how continuous or clumped the vegetation is, has been shown to affect male-male competition in lizards across populations (Emlen and Oring 1977, McCoy et al. 2003, Zamudio and Sinervo 2003, Bloch and Irschick 2006, McMillan and Irschick 2010). In promiscuous species, where males defend territories and attempt to control access to multiple females, continuous habitats have more evenly distributed resources, which results in relatively low competition between males (Zamudio and Sinervo 2003). In contrast, habitats where resources or structures are clumped can result in high male competition, as females become closely aggregated and despotic males aggressively defend these prime territories, while other males are left to compete or lose out on mates (Zamudio and Sinervo 2003). This habitat structure variability sometimes affects the intensity of male-male interactions while concurrently causing adaptations in limb morphology and ecology (Irschick et al. 2005a).

Sexual traits are affected by habitat as a result of changes in the intensity of social interactions. Precopulatory traits, such as ornaments, weapons and body size, and postcopulatory traits, such as testis size, sperm traits and genitalia can both respond to changes in the magnitude of male-male competition. However, the degree of the effect on pre and postcopulatory traits depends on a number of factors, including relative importance of the traits and their costs (Lüpold et al. 2014). For example, in taxa where males physically compete for access to females, precopulatory traits, like body size, have shown to garner greater investment than postcopulatory traits like testis size. This is true across taxa, as well as within lizards (Lüpold 2014, Kahrl et al. 2016). Sperm traits also

respond to male-male competition intensity (Morrow and Gage 2001, Gomendio et al. 2007, Crean and Marshall 2008, Immler et al. 2010, Calhim et al. 2011, Bakker et al. 2014), and they are sensitive to changes in body condition, as sperm is energetically expensive to produce (Rowe and Houle 1996, Alavi et al. 2009, Merrells et al. 2009, Immler et al. 2010, Kahrl and Cox 2015). Genitalia respond to the intensity of competition between males as they evolve to displace sperm from other males within the female reproductive tract, reach closer to the oviducts to ensure insemination, or to provide stimulus to females (Hosken and Stockley 2004, Brennan et al. 2010, Eberhard 2010). Additionally, testis, sperm, and genitalia have all shown seasonal changes associated with increases in testosterone, which increases with increasing male competition (Yang and Wilczynski 2002, Holmes and Wade 2005, Beck and Wade 2008, Immler et al. 2010). Together these studies show the potential direct and indirect effects of habitat variability on many aspects of animal social structure, behavior, and morphology. While some of these effects been studied across taxa, there are no studies to date that have examined multiple associations between habitat and sexual and non-sexual traits in an effort to understand environmental effects on the organism as a whole. Additionally, although the effects of habitat variability on limb morphology is well-documented, there are few studies examining habitat associations with postcopulatory traits. And while sexual selection literature continues to expand in focus, less is known about squamate postcopulatory evolution (though see Johnson et al. 2014). To that end, we chose to study habitat effects on multiple traits in a small arboreal lizard, *Anolis carolinensis*.

Anolis carolinensis is a small lizard that occurs in southern North America as far west as Texas, and as far north as Tennessee and southeastern Virginia. This arboreal species has a highly visual communication system, and is generally found in its habitat on perches less than two meters high, making the interactions between the dimorphic males and females easy to observe (Irschick et al. 2005a, 2005b, Edwards and Lailvaux 2012, Kamath et al. 2013). These lizards are generalist insectivores, eating insects encountered on the ground and on vegetation (Jenssen et al. 1995, Nunez et al. 1997). A great deal is known about the mating system and ecology of *A. carolinensis*; however, few studies have investigated postcopulatory sexual selection in this species (but see Passek et al. 2002). *A. carolinensis*, like most reptiles, is promiscuous, with males and females mating multiply (Passek et al. 2002, Uller and Olsson 2008, Kamath and Losos 2017).

A. carolinensis has been used extensively as a model in studies of behavior, physiology, morphology, ecology, and evolution (e.g., Lovern et al. 2004, Losos 2009, Johnson et al. 2011, Kerver and Wade 2011). And while recent work is beginning to examine the tradeoffs between pre and postcopulatory sexual selection in other *Anolis* lizards (Kahrl and Cox 2015, 2017) and the effects of habitat on body condition, morphology and social structure on *A. carolinensis* (Battles et al. 2013, Dill et al. 2013, Stehle et al. 2017), continued efforts to unify these ideas are needed. In this study we sought to take a whole-organism approach to examine the role of habitat structure and complexity on the ecology, morphology, and behavior of *A. carolinensis*. We measured sexual and non-sexual traits in male and female *A. carolinensis* at three sites within a park that varied in vegetation density and composition. We measured five characteristics of the habitat, as well as male and female body condition, tibia length, genital size and

shape, and sperm and testis size in males. We predicted that increasing habitat patchiness, or clumping of resources, would increase male-male competition. This increase would be reflected in smaller testis size and longer and possibly more elaborate hemipenes in males, as male testis size has been shown to decrease as male-male competition increases in lizards (Kahrl et al. 2016), and genital length and complexity may confer reproductive advantages (King et al. 2009, Eberhard 2010, Johnson et al. 2014). We also predicted that females may show correlated changes in genital shape across sites (male-female coevolution: Hosken and Stockley 2004). However, this is the first study to examine the genitalia of a natural male and female lizard population, so these data are largely exploratory. We predicted that male and female limb length and body condition will vary across sites, as seen in other studies, and males and females will show sex-specific ecological requirements. Lastly, we predicted that body condition would be affected by differences in habitat structure, as seen in other studies, and may affect sperm traits.

B. Methods

1. Habitat structure

We conducted our study in Spruce Creek Park, Port Orange, FL in May and early June 2014 during the *Anolis carolinensis* breeding season with permission from the county park Director. Spruce Creek Park is a ~1 km long (north-south) by ~0.3 km wide (east-west) nature park and campground bordered on the east side by a highway, swamp on the west, and bays on north and south sides. To determine the areas most populated within the park, as well as perch heights used by *A. carolinensis*, we began by taking a survey of the height of perches used by *A. carolinensis* males and females. We walked through the

park between 0800 and 1900, when lizards were active, and scanned all potential perches (leaves, leaflets, petioles, branches, trunks, vines) for adult lizards. Once spotted, we used a laser pointer to mark the perch until within reach (if necessary) and measured perch height (± 1 mm), substrate type (i.e., leaf, branch, trunk), and GPS coordinates ($N=54$ active perches). We walked through all accessible areas of the park to eliminate the potential bias for searching for lizards in human-preferred areas.

We found that the areas of the park most populated by lizards were a northern corridor along a dirt road (Fig. 1A), a continuously vegetated eastern corridor along a dirt road (Fig. 1B), and a relatively sparsely vegetated interior southern corridor (Fig. 1C). These corridors varied in the amount and density of species of vegetation, but they were all generally dominated by longleaf pine (*Pinus palustris*), saw palmetto (*Serenoa repens*), slash pine (*Pinus elliotii*), turkey oak (*Quercus laevis*), cabbage palm (*Sabal palmetto*), and other small scrubs and vines. We chose to focus on these three corridors for vegetation transects and to capture lizards. The southern and eastern corridor were at the southern end of the park, ~ 50 m apart, and the northern corridor was at the north end, ~ 850 m from the eastern site and 1 k from the southern site. The southern and eastern site were within a continuous patch of forest separated by a walking path, and the northern site was separated from the other two sites by a shallow bay inlet with a continuous forest corridor connecting the sites along the eastern border of the park.

In each of the three corridors (north, south, east), we quantified the available structural habitat by measuring perches every 5 m along 50 m transects at the edge of the road (north and east corridors) and within the southern corridor, as these were the most populated areas within the corridors. At every 5 m along the 50 m transect, we ran a 5m

sub-transect perpendicular to the original transect. At every 1 m along the sub-transects, we extended a 2 m vertical rod and recorded the number of contacts with vegetation (and type of vegetation) along the stick up to 2 m. We did not measure above 2 m as 81% of perches used by lizards during our survey were 2 m or lower (methods modified from Wiens and Rotenberry 1981 and Gilman and Irschick 2013). We only included perch data for perches likely to be used by *A. carolinensis*, based on observations at this site and previous studies (i.e., no branch perches smaller than 0.5 cm diameter, no small or highly flexible leaves; Gilman et al. 2012, Gilman and Irschick 2013).

To evaluate the structural characteristics at each site, we calculated five measures of vegetative physiognomy. We measured relative horizontal openness (devoid of vegetative structures above 0.5 m), horizontal heterogeneity, and the total number of available perches, as these measures relate to habitat patchiness and could influence male-male interactions (August 1983, Bloch and Irschick 2006). We also measured vertical heterogeneity and vertical openness, as these have been shown to affect arthropod biomass and richness (González-Megías et al. 2007). For horizontal openness, or patchiness, we summed the total contacted points at each one-meter sampling point ($N=50$) along the transect and counted the total sampling points that lacked vegetation above 0.5 M. We calculated vertical openness by summing all the vegetation contacted between each 10 cm height interval across the entire site transect ($N=100$) and counting the number each 10 M height lacked vegetation across the site. We calculated total perches as the total number of contacts with vegetation at each site. We measured horizontal heterogeneity by calculating the variation in total perches at each 5 meter sub-transect using the equation:

$$HI = \frac{\sum \text{Max} - \text{Min}}{\sum x},$$

where Max=maximum number of contacts recorded among the 10 sub-transects, Min=minimum number of contacts recorded among the 10 sub-transects, N =the total number of sub-transects, and \bar{x} =the mean number of contacts within the set of sub-transects (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). This index provides insight into how variable the sub-transects are across the site. For vertical heterogeneity, we summed all the contact points between each 20 cm height interval across the entire site transect ($N=100$ points per 20 cm, 10 sample points per site). We used the heterogeneity equation above with HI indexing the variation in vegetation structure across each 20 cm height. We used 20 cm as our small-scale vertical heterogeneity index because of its biological relevance for *A. carolinensis*. In the lab and field, *A. carolinensis* jump from ~10 to 40 cm between a range of flexible perch types (Gilman et al. 2012, Gilman and Irschick 2013). Therefore, 20 cm is an attainable distance for these lizards to move from perch to perch for food, mates, and when avoiding predators.

2. Lizard traits

We collected 15 female and 17 male *A. carolinensis* and measured snout-vent length (SVL \pm 1 mm), body mass (\pm 0.1 g), perch characteristics and location (as above). Females were euthanized post-capture for dissection, and males were euthanized following sperm collection. We collected sperm from males by gently applying pressure posterior to the cloaca and pipetting up ejaculate that collected at the cloaca. We stored sperm from each male in 50 μ l 10% formalin for measurement later. In the lab, the fixative was removed and the cells were air-dried on slides. We stained the sperm with

Sperm Blue™ (Microptic SL, Barcelona, Spain) and then imaged them with an Olympus Magnafire camera (Olympus America, Melville, NY) at \times ~100 magnification using differential interference contrast microscopy. We measured the length of the head, midpiece, and tail for 6-13 sperm per male using ImageJ (NIH, Bethesda, MD), then calculated the length means for each male. Although all males were reproductive and sperm was present when we applied pressure to the cloaca, we were only able to successfully prepare slides for 13 males (south=3, east=4, north=6). For testis volume, we measured testis linear dimensions to the nearest 0.01 mm and calculated the volume using the formula for spheroid volume:

$$vol = \left(\frac{4}{3}\right) \pi * \frac{\text{length}}{2} * \frac{\text{width}}{2} * \frac{\text{height}}{2}.$$

We measured both testes for each male twice and used the mean of four measurements per male. We calculated the repeatability of the measurements as the intraclass correlation coefficient (ICC), using the ICC package (Wolak, Fairbairn, & Paulsen 2012) in R version 3.1.0 (R Core Team 2014).

Genital preparation and measurements - We dissected the females and noted the presence of eggs/enlarged follicles. This ensured all females in the study were reproductive. We removed the cloaca and clipped the oviduct 2-4 mm from the cloacal/oviduct junction. We imaged the ventral, dorsal, and lateral views of each cloaca with a Leica DFC450 C digital microscope camera mounted to a Leica M165 FC microscope. We then used ImageJ (Rasband, 1997–2012) to measure linear dimensions of the length and width of the ventral view, and the height of the lateral view of the cloaca. For males, we dissected and prepared one hemipenis per male (whichever side

everted more fully during preservation) following Zaher & Prudente (2003) and Gilman et al. (*in press*). We then imaged the lateral, apical (distal), and sulcal (side along where the sulcus spermaticus, or sperm channel, runs) hemipenis to obtain linear dimensions of the trunk, lobe (or apex), the fleshy ‘horn’ at the distal tip of the hemipenis, and the area of the apex. We did not include one male from the southern site in our analyses because we were not able to obtain a fully inflated hemipenis.

We also measured one non-genital trait, the right tibia, of all specimens. After digitally imaging each tibia, we used ImageJ to measure from the joint with the femur (knee) to the articulation with the metatarsus (ankle). We measured each specimen twice (using the same digital image for each pair of measurements), and used the mean value for each individual in our analyses. We calculated the repeatability of the measurements as the intraclass correlation coefficient (ICC).

3. Statistical analyses

We conducted our statistical and shape analyses using R version 3.1.0. We tested for differences in genital dimensions and tibia length (all \log_{10} transformed) in males and females, as well as testis volume in males, across sites using analysis of covariance (ANCOVA) with the trait as the dependent variable, site as the independent variable, and \log_{10} SVL as a covariate (after confirming homogeneity of slopes). We then estimated body condition for each individual two ways: 1) Residuals from ordinary least squares linear regressions of log-transformed body mass on \log_{10} transformed body length (OLS) and 2) as a scaled mass index (SMI), using the smart package in R (Warton, Wright, Falster, & Westoby 2006, Warton, Duursma, Falster, & Taskinen 2012) (Peig and Green

2009, 2010, Kahrl and Cox 2015, Falk et al. 2017). We tested for differences in the two body condition indices across sites in the two sexes using ANOVAs. We followed significant findings with Tukey's honest significant difference post hoc tests to determine which sites were significantly different from each other. We calculated an index of sexual size dimorphism at each site as SVL males/SVL females as a simple comparison.

Because we were not able to obtain equal sample sizes of sperm from each site, and because body condition has been shown to affect sperm traits in *Anolis* lizards (Kahrl and Cox 2015, 2017), we examined the relationship between the body condition indices and sperm sizes on all males as a group using linear regression models.

Male and female scaling relationships and variance - We examined the relationship between sexual and non-sexual traits (genital size, testis volume, and tibia length) and body size (snout-vent length, SVL) in males and females using OLS regression of the \log_{10} transformed data. Although there is disagreement in evolutionary biology literature on the best regression method for allometry, OLS regression has been recommended as a descriptor of functional scaling relationships when measurement error is low (Kilmer and Rodríguez 2017, Eberhard 2018). We tested the resulting slopes against isometry ($b_{OLS}=1$), to determine if the scaling relationships were isometric or allometric (greater than 1 showing positive allometry, less than 1 showing negative allometry) using the *smatr* package in R. We then examined the variation of these traits using the coefficient of variation (CV, ratio of the standard deviation to the mean) and coefficient of variation with body size held constant (CV') (Eberhard 1998, Bertin and Fairbairn 2007, Klaczko and Stuart 2015).

We used elliptical Fourier analysis (EFA) to compare the general shape of male and female genitalia across sites. We imported the cloacal and hemipenal images used for the linear data into R and tested for differences using the R software package Momocs (Bonhomme, Picq, Gaucherel, & Claude 2014). Once we imported the outlines into R, we processed the outlines so they retained shape but were invariant to size, rotation, and starting point. This ensured we compared genital shape, but not size. We chose to use 9 harmonics for males and 7 for females, which gathered ≥ 99 % of the total harmonic power. To determine if genital shape was similar or dissimilar across sites in each sex, we first conducted a principal component analysis using the harmonic coefficients from the EFA. We then conducted a multivariate analysis of variance using the EFA harmonic coefficients.

C. Results

1. Habitat structure

The five physiognomic measures we calculated for the three sites are shown in Table 1. In general, the southern site was the patchiest site. It had the greatest number of horizontal open areas and fewest perches. The eastern site was the most continuous. It had the greatest number of perches, and was low in horizontal openness and horizontal heterogeneity. The northern site was the most complex, having the highest heterogeneity, both horizontally and vertically.

2. Lizard traits and ecology

Although the three sites differed in their structural characteristics, these differences did not affect most traits we measured (Table 2). However, body condition varied significantly across sites in males. These results were robust to both body condition indices (OLS: $F_{2,14}=6.438$, $P=0.010$; SMI: $F_{2,14}=5.795$, $P=0.015$). With both indices, males at the northern site had significantly higher body condition than those at the southern site (north-south: OLS: $P=0.008$; SMI: $P=0.013$; north-east: OLS: $P=0.121$; SMI: $P=0.101$; east-south: OLS: $P=0.435$; SMI: $P=0.624$). In contrast, females did not vary significantly across sites in body condition (OLS: $F_{2,12}=1.264$, $P=0.318$; SMI: $F_{2,12}=2.255$, $P=0.147$). Unlike males, both body condition indices showed the highest values of body condition in females at the eastern site, as opposed to the northern site (SMI: north: 1.810 ± 0.046 mean, SE; east: 1.915 ± 0.063 ; south 1.759 ± 0.049 ; OLS: north: -0.003 ± 0.011 ; east: 0.016 ± 0.015 ; south -0.013 ± 0.012). The sexual size dimorphism index was greatest at the eastern site (1.24), intermediate at the northern site (1.19), and lowest at the southern site (1.17).

To further examine the relationship between body condition and structural characteristics, we performed stepwise multiple linear regression. We set each of the two body condition indices separately as dependent variable, and set our five measures of vegetative physiognomy as independent variables, using the MASS package in R (Venables and Ripley 2002). The resulting model from our stepwise multiple regression model revealed a significant positive relationship between vertical heterogeneity and body condition in males, robust to both body condition indices (OLS: $F_{1,15}=13.66$, $P=0.002$; SMI: $F_{1,15}=11.90$, $P=0.004$). Body condition and vertical heterogeneity were highest at the northern site and lowest at the southern site.

Although there was a significant effect of body condition across sites, there was no relationship between body condition and sperm traits on all males as a group (head length: OLS: $F_{1,11}=2.355$, $P=0.153$; SMI: $F_{1,11}=0.412$, $P=0.534$; midpiece length: OLS: $F_{1,11}=2.01$, $P=0.184$; SMI: $F_{1,11}=0.955$, $P=0.350$; tail length: OLS: $F_{1,11}=0.268$, $P=0.615$; SMI: $F_{1,11}=0.018$, $P=0.895$).

Genital shape - There were no significant differences in genital shape across sites for males or females. The three principal components were significant and explained 77.9% of the variation in lateral hemipenis shape. PC1 explained 39.3%, PC2 26.0%, and PC3 7.8% of the variation. There was no significant difference across sites in lateral shape (MANOVA: $F_{2,13}=4.233$, $P=0.209$). Following sulcal view PCA analysis of hemipenis shape, PC1 significantly explained 50% of the variation in shape. There was no significant difference in sulcal shape across sites (MANOVA: $F_{2,13}=0.695$, $P=0.406$). Female cloacal shape analyses revealed PC1 significantly explained 61.7% of the variation in shape, while PC2 explained 17.9% of the variation. There was no significant difference in cloacal shape across sites (MANOVA: $F_{2,12}=1.055$, $P=0.494$).

Male and female scaling relationships and variance - The relationship between sexual and non-sexual traits and body size, trait variability, and repeatability of measurements are shown in Table 3. Male and female genital length and width scaled isometrically, as did female tibia to body size, while male tibia to body size showed a weakly isometric relationship. Trait variability was higher in sexual traits than non-sexual traits, for both males and females.

D. Discussion

Variability in the physical dimensions and complexity of an animal's habitat can have a broad range of effects on its feeding ecology, morphology, and social interactions. In this study we sought to investigate the effects of variability in habitat structure on sexual and non-sexual traits in male and female green anole lizards, *Anolis carolinensis*. We found that body condition in males increased significantly with vertical heterogeneity. Body condition was highest at our northern study site, which was generally the most structurally complex site of the three we studied. Body condition in males was intermediate at the eastern site, which had the most homogeneous vegetation, and lowest at the site with the patchiest habitat: the southern site. Interestingly, female body condition was statistically consistent across sites. Although habitat variation has also been shown to affect morphology and physiology, there were no significant differences across sites in any other trait we measured (genital shape and size, tibia length, and testis volume in males), and there was no relationship between body condition and sperm size. Lastly, we found that genital traits scaled isometrically in both males and females, as did female tibia length, while male tibia length showed a weak trend toward negative allometry. We also found that trait variability was higher in sexual traits than non-sexual traits, for both males and females. Although our sample sizes were small, our results support previous studies showing sexually dimorphic responses to habitat in *Anolis* lizards.

We predicted that body condition would vary across sites, as habitat structure determines arthropod biomass and diversity (Greenstone 1984, Davidowitz & Rosenzweig 1998, Halaj et al. 2000, Romero-Alcaraz & Avila 2000, Tanabe et al. 2001).

However, as males, but not females, were affected, it is possible that intraspecific competition and male signaling costs were responsible for low body condition at the southern site, as it was the patchiest site, and we expected this would increase male-male competition (Brandt 2003, Irschick et al. 2005a, Lailvaux et al. 2012). Yet, we did not find any secondary evidence of male-male competition variability across sites, as none of the postcopulatory traits we studied in males differed (testis size, genital shape or size), and the sexual size dimorphism index values did not correspond with body condition. These results are not entirely surprising. Differential male-male competition for mates and territory requiring selection on precopulatory traits, such as body size and aggressive behavior, can result in corresponding tradeoffs in allocation to postcopulatory traits, but the intensity of competition has been shown to determine the degree of tradeoff (Fitzpatrick et al. 2012, Lüpold 2014, Blengini 2016, Kahrl et al. 2016, Naretto et al. 2016). It is possible that habitat structure at the southern site, relative to the northern site, is associated with lower body condition because of differences in predation pressure associated with each habitat. Open habitats increase visibility to predators and provide fewer refuge sites from predation (Kie and Bowyer 1999, Denno et al. 2005, Shepard 2007). Therefore, the southern males may have lower body condition than the northern males because of increased predator avoidance (Martin and Lopez, 1999, 2000, Moore et al. 2000, Pérez-Tris et al. 2004, Amo et al., 2007, Rodrigues-Prieto et al. 2010, Sinervo et al. 2010, Gallego-Carmona et al 2016). As male *A. carolinensis* signal more and move more than females, they likely would be more conspicuous to predators than females (Nunez et al. 1997, Bloch and Irschick 2006, Dill et al. 2013). In this way, male body condition may be more influenced by habitat than females across our sites.

Additionally, open habitats may affect body condition via dehydration, as open habitats provide less shade and decrease relative humidity (Chen et al. 1999, Losos 2009). Kattan and Lillywhite (1989) found that *A. carolinensis* lizards exposed to a dehydrating environment for 8 days suffered decreased mass relative to the hydrated lizards, even though the dehydrated lizards compensated by increasing lipid deposition in their skin to decrease water loss. Males that move more than females may also be at greater risk of dehydration than females at sites where water is limited or temperatures are higher (Dupoué et al. 2017).

Habitat heterogeneity and complexity, especially on small scales, has been shown to be important for arthropod abundance and diversity (Greenstone 1984, Davidowitz & Rosenzweig 1998, Halaj et al. 2000, Romero-Alcaraz & Avila 2000, Tanabe et al. 2001). Therefore, we might expect the differences in body condition in males to be linked to arthropod abundance, though we did not gather these data. However, combined results from studies of body condition in *A. carolinensis* across sites within a park in Texas found females had lower body condition at the site with the greatest arthropod biomass (Battles et al. 2013, Dill et al. 2013, Stehle et al. 2017). The authors suggest that this may be due to the greater proportion of larger arthropods at this site, which would have been more difficult for the females to eat, and that arthropod nutritional value may vary across sites (Battles et al. 2013, Stehle et al. 2017). Additionally, Battles et al. (2013) proposed that the high arthropod biomass may have increased competition at this site. It is possible that a combination of factors is involved in determining the cause of lower body condition at our southern site in males.

Although our sites varied in structural characteristics and male body condition varied across sites, we did not find differences across sites in relative tibia length. Males and females also had similar isometric tibia scaling relationships with body size, though male slopes were lower and verged on allometric. *A. carolinensis* morphology has shown plastic responses to perch width in the lab (Kolbe and Losos 2005), and sex-specific limb and perch associations in the field (Irschick et al. 2005b, Dill et al. 2013). However, populations do not always respond morphologically to perch dimensions as predicted, and lack of ecological and morphological differentiation between the sexes also exists across populations in this species (Irschick et al. 2005a, Gilman and Irschick 2013). As male and female tibia to body size relationships were similar, this suggests that, in general, there was little morphological differentiation between the sexes. However, we only measured one limb dimension. Other studies have found that while one limb, or part of the limb, did not differ between the sexes, other limbs did (Irschick et al 2005a, 2005b). Therefore, it is possible that the sexes do differ morphologically, but the tibia is not the limb element that is being selected on across habitats.

We found no effect of habitat on postcopulatory traits across sites, however our study did provide some valuable sexual trait data. First, sexual trait dimensions had higher variability than non-sexual traits. Similar results have been found in other studies (Pomiankowski and Møller 1995, Eberhard 2009, Klaczko and Stuart 2015), and Pomiankowski and Møller (1995) suggest the high variability in sexual traits is due to strong sexual selection for this variability, as opposed to directional selection for an ideal trait. Interestingly, hemipenis length had relatively low variability, compared to the other sexual traits. This was also true in a previous study of two subspecies of *A. grahmi*

(Klaczko and Stuart 2015). However, because there is so little data on the variability of hemipenis dimensions within and across populations, and because hemipenis shape and length function is largely unexplored (though see King et al. 2009, Johnson et al. 2014), it is difficult to speculate on the meaning of the different levels of variability. Second, hemipenis and cloacal dimensions scaled isometrically in our study. The data for the allometry of squamate genitalia is sparse, but a handful of studies are beginning to show a pattern. Hemipenis length in two other studies of lizards also scaled isometrically (Klaczko and Stuart 2015, Gilman et al. *in press*), though another subspecies of the same lizard studied in Klaczko and Stuart (2015) showed negative allometry with body size. Although scaling patterns vary across taxa, these results contrast starkly with the vast majority of studies, which have been done on arthropods, showing negative allometry in genitalia (Hosken & Stockley 2004, Eberhard 2009, Voje, 2016). Our study is unique in the small subset of squamate data because we examined the relationships between genitalia and body size for both sexes. As both sexes scaled isometrically, either both sexes are under the same selective pressures, or these traits are evolving in unison (Voje and Hansen 2013, Voje et al. 2014).

Here we provide the first examination of genital and non-genital traits in the lizard *A. carolinensis* across habitats of varying complexity and density. We found that although this species has been shown to respond in multiple ways to habitat variability, across our sites, habitat characteristics had limited ecological effects on the lizard. Our results did show, however, that the habitat effects were sexually dimorphic in nature. While these data add to a growing body of work examining whole body effects of habitat on animals, further work examining the whole-animal effects of habitat are needed.

Figure 3.1: Three transect areas in Spruce Creek Park. A) A heterogeneous northern corridor along a dirt road, B) A continuously vegetated eastern corridor along a dirt road, and C) A relatively sparsely vegetated interior southern corridor with low palms and a few tall trees.

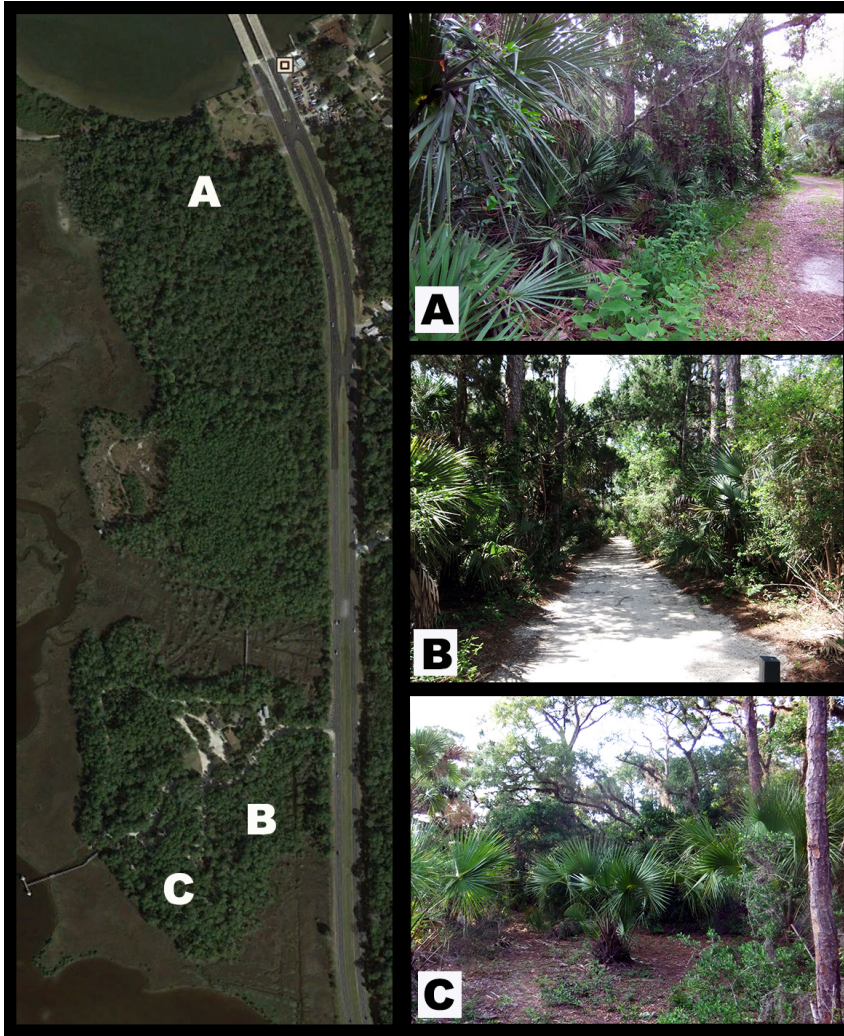


Table 3.1: Structural characteristics of the habitat along 50 meter transects at each site.

	South	East	North
Vertical openness	2	4	2
Vertical heterogeneity	1.58	1.88	2.25
Total perches	101	165	111
Horizontal openness	25	10	16
Horizontal heterogeneity	1.98	1.76	2.25

Table 3.2: ANCOVA results for trait differences across sites, *F*-statistics, and *P*-values for each trait.

	<i>F</i>	<i>P</i>
Males		
Hemipenis length	0.367	0.702
Hemipenis body width	0.472	0.637
Hemipenis lobe width	0.538	0.600
Hemipenis horn length	1.031	0.392
Hemipenis horn height	1.799	0.215
Testis volume	0.109	0.898
Tibia length	0.019	0.981
Females		
Cloaca length	0.214	0.811
Cloaca width	2.065	0.183
Cloaca height	0.222	0.805
Tibia length	1.105	0.372

Table 3.3: Summary statistics for ordinary least square regression of traits on body size (b , r^2 , t -value), significance from test of deviation from a slope of one (P), coefficient of variation (CV), coefficient of variation with body size held constant (CV'), and trait measurement repeatability (ICC).

	b	r^2	t -value	P	CV	CV'	ICC
Males							
Hemipenis length	0.679	0.126	1.423	0.512	4.480	4.188	0.999
Hemipenis body width	0.673	0.064	0.976	0.643	14.560	14.086	0.987
Hemipenis lobe width	1.402	0.096	1.219	0.732	15.269	14.518	0.901
Hemipenis horn length	-0.786	0.038	-0.739	0.115	33.271	32.633	0.995
Hemipenis horn height	-1.378	0.096	-1.221	0.054	38.192	36.308	0.984
Tibia length	0.639	0.487	3.771	0.050	1.690	1.210	0.940
Testis volume	0.693	0.021	0.561	0.807	7.762	7.680	0.947
Females							
Cloaca length	0.935	0.042	0.751	0.959	15.050	14.731	0.997
Cloaca width	0.733	0.053	0.855	0.760	11.452	11.144	0.996
Cloaca height	1.118	0.106	1.240	0.898	23.021	21.769	0.980
Tibia length	0.944	0.581	4.248	0.804	2.512	1.626	0.930

CHAPTER IV

GENITAL MORPHOLOGY ASSOCIATED WITH MATING STRATEGY IN THE POLYMORPHIC LIZARD, *UTA STANSBURIANA*

A. Introduction

Animal mating strategies range from monogamous to highly promiscuous, and are often determined by environmental factors and social pressures (Emlen & Oring, 1977; Rowe, Arnqvist, Sih, & Krupa, 1994; Kokko & Rankin, 2006). In species that have alternative male mating strategies, males within a population will often specialize in two or more different mating strategies (Gross, 1996; Moczek & Emlen, 2000; Taborsky, 2008). These alternative strategies are found across taxa and evolve when competition for fertilization is strong (Dominey, 1984; Fleming, 1996; Miller, 2013). Examples of common behavioral strategies in these systems are dominant territoriality to mate with multiple females; mate-guarding one or a few females; and sneaking copulations from other males' females (Sinervo & Lively, 1986; Gross, 1996; Shuster, 1989; Emlen, 1997; Widemo, 1998). These strategies are often associated with distinct morphological, behavioral, and physiological phenotypes (Taborsky, 2008).

Populations with alternative mating strategies typically have strong sexual selection and therefore offer excellent opportunities to test hypotheses regarding the effects of male-male competition on reproductive traits, such as testes, sperm, and genital size and shape. For example, studies of alternative mating strategies have been used to address the hypothesis that dominant males will spend more somatic resources on mate guarding and territory defense than on investment to their gonads, relative to other male mating types (Gage, Stockley, & Parker, 1995). Testis size has been shown to be larger in

sneaker males, relative to dominant males, in primates (Setchell & Dixson, 2001), fish (Gage et al., 1995; Oliveira, Ros, & Gonçalves, 2005), birds (Jukema & Piersma, 2006), lizards (Olsson, Schwartz, Uller, & Healey, 2009), and dung beetles (Reynolds & Byrne, 2013). The strong selective pressure of sperm competition—the competition between sperm from two or more males to fertilize the same egg or set of eggs—in alternative mating strategy systems has also resulted in differences in sperm traits across male morphs (Gage et al., 1995; Alonzo & Warner, 2000; Uglem, Galloway, Rosenqvist, & Folstad, 2001; Smith & Ryan, 2010). Sneaker males have significantly longer sperm than territorial males in *Onthopagus binodis* dung beetles (Simmons, Tomkins, & Hunt, 1999) and partnered males in *Loligo bleekeri* squid (Iwata et al., 2011). In a study of *Lepomis macrochirus* bluegill sunfish, parental males had longer-lived sperm than sneaker and satellite males, though sperm density was highest in sneakers, suggesting a tradeoff between morph-specific sperm competition risk and resource allocation options (Neff, Fu, & Gross, 2003). Genitalia have been shown to be morph-specific in polymorphic snails, with euphallic individuals being able to self-fertilize and cross-fertilize as both males and females, and hemiphallic and aphyallic individuals only being able to self-fertilize and cross-fertilize as females (Schrag & Read, 1996; Doums, Viard, & Jarne, 1998). Genital polymorphism also occurs across morphs in arthropods (Mound, Crespi, & Tucker, 1998; Mutanen & Kaitala, 2006). However, to our knowledge, the published examples of vertebrates with morph-specific differences in genitalia have been limited to fish (Oliveira, Canario, & Grober, 2001a; Marentette, Fitzpatrick, Berger, & Balshine, 2009, with caveats; Hernandez-Jimenez & Rios-Cardenas, 2017).

Compared to other physical traits, genitalia can evolve rapidly and show remarkable diversity within and across taxa (Hosken & Stockley, 2004; Böhme & Ziegler, 2009; Eberhard, 2010; Rowe & Arnqvist, 2012; Klaczko, Ingram, & Losos 2015). Sexual selection is often cited as the likely cause driving this relatively rapid evolution (Arnqvist, 1998; Eberhard, 2010; Hosken & Stockley, 2004; Simmons, 2014). Genital shape and length may evolve under sexual selection pressure in several ways: to aid sperm transfer or remove competing males' sperm (sperm competition), to stimulate the female and gain a fertilization advantage or to alert the female of some male 'cues' (cryptic female choice), or in an evolutionary arms race between the sexes (antagonistic coevolution) (Cordoba-Aguilar, 1999; Arnqvist & Rowe, 2002; Rivera, Andres, Cordoba-Aguilar, & Utzeri, 2004; Eberhard, 2009a; Simmons & Garcia-Gonzalez, 2011; Eberhard, 2010). Most studies examining the effects of sexual selection on genital evolution have been on insects (Simmons, 2014). While there is a growing body of literature on vertebrates, the relationship between sexual selection and genital evolution has only just begun to be examined empirically in lizards and snakes (King et al., 2009, Johnson et al., 2014, Friesen, Uhrig, Mason, & Brennan, 2016; Klackzo, Gilman, & Irschick, 2017).

Lizards and snakes have paired intromittent organs that are held inverted in the base of the tail until everted for copulation. These organs, termed hemipenes, can be single or bi-lobed, and sometimes have fleshy extensions at various points on the distal (apical) end (see Böhme & Ziegler, 2009). Each hemipenis has an open groove (sulcus spermaticus, or sperm channel) running through the ventral side whose function is to transfer sperm when the hemipenis is everted during copulation. Hemipenes can be

simple or have a range of external ornamentations (e.g., pits, ridges, papillae, horns) (Savage, 1997; Böhme & Ziegler, 2009). Hemipene morphology evolves relatively rapidly compared to other external traits, and is commonly used as a taxonomic character in lizards because it can be used to distinguish otherwise cryptic species (Köhler & Sunyer, 2008; Böhme & Ziegler, 2009; Köhler & Vesely, 2010; Klaczko et al., 2015). Given sexual selection's role in driving the evolution of genitalia in closely related species across taxa, we were interested whether genital morphology could be differentiated within a vertebrate species with high levels of sexual selection. We therefore studied side-blotched lizard, *Uta stansburiana*, males within an alternative mating strategy population known to experience high levels of male-male competition (Sinervo & Lively, 1996; Zamudio & Sinervo, 2000).

Uta stansburiana is a small terrestrial lizard that exhibits an alternative mating strategy polymorphism, with three genetically-determined male mating strategies (Sinervo and Lively, 1996; Sinervo, 2001; Corl, Davis, Kuchta, & Sinervo, 2010). Males with orange throats control large territories with many females; blue-throated males closely mate-guard females and cooperatively defend smaller territories; and yellow-throated males sneak on to other males' territories to copulate with females (Sinervo & Lively, 1996; Zamudio & Sinervo, 2000; Sinervo, 2001; Sinervo & Clobert, 2003; Sinervo et al., 2006). Male-male competition in this system can be intense; large and aggressive orange-throated males can usurp territories and mates from less-aggressive blue-throated males, but are at risk of mating competition from yellow-throated sneaker males (Sinervo & Lively, 1996). Females mate with multiple males, across more than one morph, and up to 81% of all clutches are fertilized by multiple males (Zamudio &

Sinervo, 2000). Mate-guarding blue-throated males have been shown to sire significantly more singly-sired clutches than the other two males, while yellow-throated sneaker males are significantly more likely to sire offspring in multi-sired clutches (Zamudio & Sinervo, 2000). Yellow sneaker males also more frequently sire progeny on later clutches well after they have died (posthumous fertilizations) suggesting morph-specific sperm competition strategies (Zamudio & Sinervo, 2000).

The males of polymorphic *U. stansburiana* populations have distinct precopulatory behavioral strategies and morphologies, but thus far there have been no studies detailing this lizard's reproductive anatomy. Our goals were to 1) provide a morphological description of the hemipenis of the three *U. stansburiana* morphs, and 2) test for differences in hemipenis morphology across the morphs. We hypothesized that sneaker male genitalia will have the most distinct morphology relative to the other two morphs. A previous study suggests *U. stansburiana* sneaker morphs have the highest level of sperm competition in this system (i.e., father the most multi-sired clutches, Zamudio and Sinervo, 2000), and sneaker morph postcopulatory traits have been shown to differ from territorial morphs in other systems (e.g., Simmons, Tomkins, & Hunt, 1999; Neff, Fu, & Gross, 2003; Iwata et al., 2011 (above)). However, because the majority of studies of sexual selection and genital evolution have been on invertebrates, and comparisons across morphs within terrestrial vertebrate populations have not been studied, it is unclear precisely how the genitalia will differ. We compared genital size and shape using multiple linear measurements and geometric morphometric techniques. We also examined the relationship between body size and genital and non-genital traits

(hemipenis and tibia), for all males, as these data for squamates are currently rare in the literature.

B. Methods

1. Taxon sampling

We captured male lizards from our long-term study population of *U. stansburiana* (Baird and Girard, 1852) at Los Baños Grandes, Merced County, California, USA. We collected the animals during the peak of breeding season, and within three weeks of each other, to minimize seasonal effects on morphology. Our methods of collecting the animals were approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee (#Sineb1404). We measured the body mass and snout-vent length (SVL), and visually scored the morph phenotype of each lizard based on throat color. We assigned morphs according to the intensity and location of the orange, blue, and yellow coloration on the throat of the lizard. We have previously documented that the male and female strategies and associated throat colors are genetically determined and are hypothesized to arise from the OBY locus, which is likely a single gene with three alleles, or two tightly linked genes (Sinervo, Svensson, & Comendant, 2000b; Sinervo, Bleay, & Adamopoulou, 2001; Sinervo et al. 2006). We focused our study on individuals with the greatest throat color differences, to maximize our chances of detecting other phenotypic differences among the morphs. Therefore, we conducted our study on individuals with all orange on their throats (n=8; putative *oo* genotypes), all blue on their throats (n=8; putative *bb* genotypes), and all yellow on their throats (n=7; putative *yy* genotypes). Individuals with multiple colors on their throat (e.g. blue and orange) were not used.

2. Hemipenis preparation

We prepared one hemipenis per male (generally the left, unless the right was easier to access) for morphometric analysis by dissecting out, everting, and then inflating each hemipenis with warm, pigmented Vaseline, following Zaher & Prudente (2003). To achieve this, we thawed each lizard specimen until still cold but pliable, to maintain tissue integrity. We then made an incision to the midline of the tail, from the cloaca to well past the hemipenis bulge, and removed the skin to expose the hemipenis and associated muscles. We removed the transversus penis (a muscle) from the surface of the hemipenis, and cut the tendon of the retractor penis magnus muscle, just below the hemipenis. To evert the hemipenis, we grasped the severed retractor muscle tendon with small forceps, just below the distal end of the hemipenis, and gently pushed the hemipenis until it began to bulge outward from the cloaca. Then, while holding the tendon with one hand, we gently pressed the hemipenis where it was visible protruding from the cloaca, and slowly everted the hemipenis. We repeated this motion until the tip of the hemipenis was visible. Then we dissected the hemipenis from the animal by cutting along the cloaca, along the outer basal ridge of the hemipenis, so just a small portion of scale tissue was left at the base of the hemipenis. We removed all associated muscle tissue that remained protruding from inside the hemipenis to ensure that we would be able to fill the hemipenis without obstruction. We then filled the everted hemipenis with pink-pigmented Vaseline (warmed until just fluid consistency with a hot plate) using a glass syringe and a small, dulled-tip needle. The pink-pigmented Vaseline allowed us to gauge inflation while in process and visualize the hemipenis ornamentation in contrast once we completed inflation; the flesh of the hemipenes was light colored, and

the Vaseline was visible through the flesh (see Fig. 1). Once the hemipenis was filled completely (as determined by the Vaseline pigment showing clearly through all areas of the hemipenis tissue, and by examining the tissue to determine whether there was still additional tissue that could be expanded), we tied off the end of the hemipenis just above the scale line to keep it filled. Once cool, the Vaseline ensured hemipenes retained their inflated shape.

3. Genital and non-genital trait measurements

We imaged the lateral, apical (distal), and sulcal (side along where the sulcus spermaticus, or sperm channel, runs) views of each hemipenis with a Leica DFC450 C digital microscope camera mounted to a Leica M165 FC microscope. We then used ImageJ (Rasband, 1997–2012) to measure linear dimensions of the trunk, lobe (or apex), the fleshy ‘horn’ at the distal tip of the hemipenis, and to measure the area of the apex (see Fig.1 and Table 1). We measured one non-genital trait, the right tibia, of the same specimens. We used a digital caliper to measure from the joint with the femur (knee) to the articulation with the metatarsus (ankle). We measured each specimen twice (using the same digital image for each pair of hemipenal measurements), and used the mean value for each individual in our analyses. We calculated the repeatability of the measurements as the intraclass correlation coefficient (ICC), using the ICC package (Wolak, Fairbairn, & Paulsen, 2012) in R version 3.1.0 (R Core Team 2014).

4. Hemipenis shape analysis

We conducted our shape and statistical analyses using R version 3.1.0. To compare the general shape of the hemipenis across morphs, we imported the lateral and sulcal images used for the linear data into R and tested for differences in shape across the three morphs using elliptical Fourier analysis (EFA) in the R software package Momocs (Bonhomme, Picq, Gaucherel, & Claude, 2014, also see <http://vbonhomme.github.io/Momocs>, and <https://CRAN.R-project.org/package=Momocs> for detailed instructions). Once we imported the outlines into R, we processed the outlines so they retained shape but were invariant to size, rotation, and starting point. This ensured we compared hemipenis shape, but not size. In elliptic Fourier analysis, x and y coordinates along an outline are decomposed into harmonic sums of a cosine curve and a sine curve defining an ellipse in a plane, and four coefficients per harmonic are obtained, two for x and two for y . We chose to use 15 harmonics, which gathered 99 % of the total harmonic power. See Figure S1 for the outlines of the hemipenes of the 23 individuals generated by Momocs from our digital images.

5. Statistical analyses

Following a test for homogeneity of variances across groups using Bartlett's test, we tested for differences in hemipenis linear dimensions and apical area, lateral and sulcal aspect ratios, as well as tibia length, and body mass using one-way analyses of covariance (ANCOVAs). We set animal size (SVL) as a covariate and morph as the fixed factor. We followed significant results from the ANCOVAs with post-hoc Tukey HSD tests. To analyze shape variation across individuals, we conducted a principal component analysis using the harmonic coefficients from the EFA. Following the principal

component analysis we conducted a multivariate analysis of variance using the EFA harmonic coefficients to test for shape differences across the morphs.

We examined the relationship between body size (snout-vent length, SVL) and genital (hemipenis) and non-genital (tibia) traits and across the three morphs using ordinary least squares regression of the \log_{10} transformed data. We then tested the resulting slopes against isometry ($b_{OLS}=1$), to determine if the scaling relationships were isometric or allometric (greater than 1 showing positive allometry, less than 1 showing negative allometry) using the *smatr* package in R (Warton, Wright, Falster, & Westoby, 2006; Warton, Duursma, Falster, & Taskinen, 2012).

C. Results

The fully everted hemipenes of all three alternative mating strategy morph phenotypes were qualitatively similar (Fig. 1). Each unilobed hemipenis had a narrow, smooth trunk with no ornamentation. The single sulcal spermaticus terminated at the center of the apical lobe and was bordered by sulcal lips. The apical lobe was bulbous, capitate, and covered in calyces. The lobe protruded out from sulcal side in an L-shape with the trunk, had fleshy ridges along the lateral-sulcal proximal border, and had a well-developed, fleshy, apical horn.

The relationships between body size (SVL) and hemipenis and tibia length across the three morphs is shown in Figure 2. The slope of the hemipenis length to SVL was not different from 1.0 (slope=1.16, $P=0.635$), but the slope of tibia length to SVL was just significantly less than 1.0 (slope=0.65, $P=0.047$), indicating that while genitalia increased

proportionally with animal size, tibia in smaller animals were slightly larger relative to size than in bigger animals.

There was a significant global difference in hemipenis length across morphs, with the yellow sneaker males having significantly shorter hemipenes than the other two morphs (orange usurper= 7.62 ± 0.26 mm mean \pm SE, blue mate-guarder= 7.63 ± 0.24 mm, yellow sneaker= 6.70 ± 0.25 mm, Table 1; ICC coefficients are listed in Table 1). We found few other differences across morphs in dimensions descriptive of overall hemipenis size. However, the ANCOVAs revealed significant differences across morphs in apical horn dimensions. There was a significant difference in horn base width across morphs, with the orange usurper males having greater horn base widths than the sneaker males. Horn tip width was also significantly different across morphs, with the usurper males again having greater horn tip widths than the sneaker males. Yellow sneaker males also had significantly smaller body masses than the other two morphs, and significantly shorter tibia than the orange usurpers. There were no significant interaction effects between animal size (SVL) and morph for any of the variables we tested (Table 1). The principal component analysis of lateral shape revealed that PC1 explained 73% of the variation in shape, with hemipenes becoming less curved with increasing values of PC1 (Fig. 3). PC2 explained 12% of the variation, with hemipenes becoming squatter and more bulbous with increasing values of PC2. There was no significant difference in overall lateral shape across morphs ($P=0.885$). Following sulcal view PCA analysis of hemipenis shape, PC1 explained 53% of the variation in shape, with hemipenes becoming slimmer with increasing values of PC1 (Fig. 4). PC2 explained 18% of the variation, with

hemipenes becoming shorter and squatter with increasing values of PC2. There was no significant difference in overall sulcal shape across morphs ($P=0.640$).

D. Discussion

Alternative male mating strategies can have intense male-male competition, often resulting in striking differences in behavioral, morphological, and postcopulatory traits across morphs (Simmons et al., 1999; Oliviera, Taborsky, & Brockman, 2008; Miller, 2013). We tested for evidence of morphological differences in a postcopulatory trait, the genitalia, and in body mass and tibia length in the lizard *U. stansburiana*. We found that generally, the two territorial morphs were broadly similar while the sneaker males were distinct from the territorial males. While we found no differences across morphs in the overall shape of the hemipenis, the isometrically-scaling hemipenis was shortest relative to body size in the sneaker males, and the usurper males had significantly greater relative apical horn widths than the sneaker males. The sneaker males also had significantly smaller relative body masses than the other two morphs and shorter relative tibia lengths than the usurper males. Our results support previous findings of morphological differentiation across morphotypes and provide new evidence of morph-specific genital morphology in a vertebrate population with alternative reproductive strategies.

We found significant differences across morphs in relative hemipenis length and relative apical horn widths. These differences might arise simply as a byproduct of disparities in testosterone levels across morphs, they may serve a postcopulatory function, or perhaps, a combination of both. In our study, usurper males had significantly longer hemipenes with wider apical horns than sneaker males. Although not the rule, the

influence of androgen level on the development of differential morphology across morphs in alternative reproductive systems is common (Oliveira et al., 2008). For example, in two species of blennies, an external fertilizing fish with flexible alternative reproductive tactics, the large, nest-defending dominant morph has higher androgen levels than the sneaker males; these nest-defenders also have larger genital papilla than the sneakers (Oliveira, Carneiro, Gonçalves, & Canario, 2001a, Oliveira et al., 2001a). However, when sneakers are supplemented with androgens, their genital papilla size increased, confirming the role of androgens in the development of genital morphology in dominant males (Oliveira et al., 2001a, 2001b). Additionally, in rats and hamsters, penis morphology and genital spine development is dependent on androgen levels (Sachs, Glater, & Ohanlon, 1984; Arteaga-Silva et al. 2008). For lizards, steroid hormones play a role in sexual differentiation of the copulatory organs during development and testosterone has been shown to increase hemipenis size in adult geckos (Beck & Wade, 2008; Holmes & Wade, 2005). Usurper *U. stansburiana* males have the highest levels of testosterone of the three morphs (Sinervo, Miles, Frankino, Klukowski, & DeNardo, 2000a). Therefore, it is possible that increased testosterone, or other factors influencing development, are responsible for longer hemipenes and wider apical horns in the usurper morph. Alternatively, it is possible that developmental requirements of other structures create tradeoffs resulting in relative hemipene size differences across morphs (Emlen 2001).

Although differences in genital length across alternative mating morphs has been documented in snails and fish, evidence of subtle differences in genital ornamentation is less well-documented (Doums et al., 1998; Greven, 2005; Oliveira et al., 2008). In

species with intromittent copulation, complex male genital ornamentation is widespread in vertebrates (Kelly, 2016) including lizards and snakes (Dowling & Savage, 1960; Bohme & Zeigler, 2009). In *U. stansburiana*, the enlarged apical lobe of the hemipenis spines is covered in calyces. These and other forms of hemipenal ornamentation (e.g., fleshy horn on *U. stansburiana* and some *Anolis* lizards (Gilman, *pers. obs.*), pendunculi on Chamealeonid hemipenes (Klaver & Böhme, 1986)) may have important roles in sexual selection. For example, in other taxa, male genital ornamentation, such as epidermal spines, has been shown to induce ovulation (in mammals such as Carnivora (Zarrow & Clark, 1968) and rodents (Altuna & Lessa, 1985; Bennett, Faulkes, & Molteno, 2000; Katandukila & Bennett, 2016)). Orr & Brennan (2016) showed that penile spines across all mammalian orders were associated with larger testes sizes, suggesting that sexual selection may drive the presence of spines, though some mammals in their data set showed induced ovulation without the presence of spines. In garter snakes, hemipenis spines have been shown to increase copulation duration (Friesen, Uhrig, Squire, Mason, & Brennan, 2014).

Male and female genitalia mechanically interact during copulation; this sets the stage for selection on genital morphology (Eberhard, 1990). Connor & Crews (1980) showed that the calyces on the apical lobe of the hemipenis of *Anolis carolinensis* were in direct contact with the epithelium of the cloaca of the female during copulation, and the apical tip of the hemipenis of *A. carolinensis* is situated between the two oviducts of the female. The epithelium of the cloaca between the oviducts is covered with secretory cells and glands in other lizards, though the physiological role during copulation of these structures has not been investigated (Sánchez-Martínez, Ramirez-Pinilla, & Miranda-

Esquivel, 2007). If the wider apical horns in the *U. stansburiana* usurpers have an adaptive function, functions could include providing a more efficient path for the sperm into the oviducts, or perhaps stimulation of the female. Usurpers have high testosterone levels and benefit from greater endurance and control over female home-ranges than the other morphs, but at the cost of lower survival rates (Sinervo et al., 2000a). Therefore, it is possible that the apical horn could provide a fitness advantage for usurper morphs, or may be tied to other behavioral differences across morphs, such as copulation duration. Larger hemipenes have been correlated with more frequent copulation rates in *Anolis* lizards (Johnson et al. 2014) and longer and more complex longer hemipenes are associated with greater copulation duration in gartersnakes (King et al. 2009). Extensive observations on copulation location in *Uta* in nature (Sinervo, *pers. obs.*) indicate that both territorial morphs copulate on rocks in the open, but that sneaker males copulate under rock edges and in grassy environments. Morph-specific mating behavior could drive differences in relative hemipenis length and ornamentation (King et al. 2009, Johnson et al. 2014). Fitness studies using surgical manipulations of the horn, mating behavior studies, more detailed measurements at key areas of contact, and micro-CT images of *U. stansburiana* in copula could provide valuable information and direction for future study.

In our study, the hemipenis of *U. stansburiana* scaled isometrically, while the tibia showed a slightly significant negative allometric slope. The scaling relationship of genitalia with body size has been examined across and within taxa in order to determine the driving forces behind genital diversity and highlight the overall scaling patterns within groups. While insects and spiders have been shown to generally have negative

allometry, scaling patterns vary across other groups (Eberhardt, 2009b; Voje, 2016; Hosken & Stockley, 2004). Inconsistent scaling relationships across taxa in vertebrates may be due to a number of factors, such as ecology and how males use genitalia (i.e., where in the habitat the mating occurs could affect function, and whether the male thrusts repeatedly or insertion occurs once) (Eberhard, 2009b). Klaczko & Stuart (2015) showed that the slopes for both genitalia and limbs in one *Anolis* subspecies group were less than one, while in another subspecies both traits scaled isometrically with body size. Klaczko & Stuart (2015) suggest that genitalia are under selective pressure in the subspecies they studied, potentially leading to speciation. King et al. (2009) propose that if genitalia scale with negative allometry, small males may benefit from larger relative hemipenis lengths with increased copulation duration, as hemipenis length and copulation duration correlated in their study. Dill et al. (2013) suggest that allometric differences in limb lengths within *Anolis* species reflect local adaptation required for locomotion. Whereas ecomorphological data on lizards is abundant, data on genital scaling relationships in squamates is sparse. Clearly, more studies are needed to understand the selection pressures, particularly for genitalia, across species and social systems.

The yellow sneaker morphs, who morphologically and behaviorally mimic females (Sinervo et al., 2000b), were the smallest morph in our study. Not only did sneakers have significantly smaller relative body masses than the other two morphs, they also had shorter relative tibia lengths than the usurper males. Our findings support those of earlier studies showing distinct behavioral, morphological, and physiological differences across *U. stansburiana* morphs (Sinervo & Lively, 1996; Sinervo et al., 2000a; Svensson, Sinervo, & Comendant, 2001; Mills et al., 2008; LaDage, Riggs,

Sinervo, & Pravosudov, 2009). Smaller body masses and shorter tibia lengths could be associated with the territory holding behavior differences across the morphs, particularly the differences between the sneakers and the two territorial morphs. Mills et al. (2008) found that usurpers and mate-guarders have faster sprint speeds and greater endurance than sneaker males. The authors suggest these performance traits in the two territorial morphs are needed to maintain territories and gain access to females. This complex of differences in body size, performance, mating behavior, physiology, life expectancy, and genitalia across morphs may be determined by alternative investment strategies (Alonzo & Warner, 2000; Neff et al., 2003)

In this paper we provide the first morphological description of the male copulatory organ of *Uta stansburiana*, across three alternative mating strategy morphs. We found differences in relative hemipenis size and ornamentation across morphs. To our knowledge, this is the first documentation of morph-specific genitalia in a terrestrial vertebrate. The fact that we were able to detect differences in hemipenes not only within a single species, but within a single population of that species, suggests that sexual selection can have strong role in rapidly altering hemipenis morphology. However, as our study tested small sample sizes within only one population, much more data is needed to address whether our findings represent true patterns in terrestrial polymorphic populations or are an anomaly resulting from our methods and population.

Figure 4.1: One hemipenis from each morph (bb:mate-guarding, oo:usurper, yy:sneaker) shown in three views. From the left: apical, with the horn (h); sulcal, with the sulcus spermaticus running up the midline (s), and lateral, with the trunk (t), and apex (a).

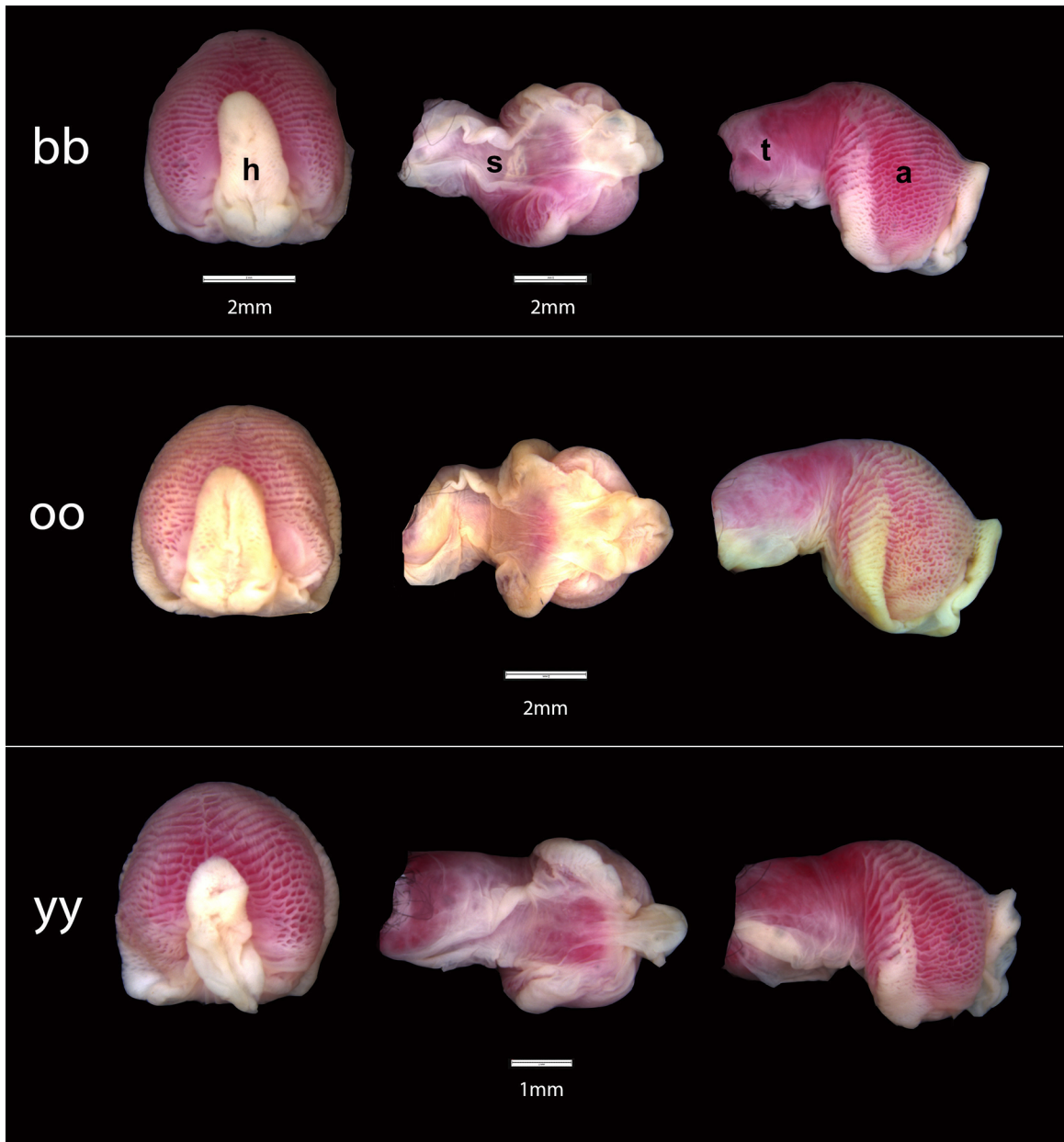


Table 4.1: Sexual and non-sexual trait comparisons across the three morphs. ICC coefficients (repeatability of measurements), ANCOVA results for differences in traits across morphs and interaction between morph and body size (SVL), and post-hoc comparisons between morphs. Significant results are shown in bold with asterisks.

	ICC Coefficient	ANCOVA $F(2,17), P$	Tukey HSD, P		
			oo-bb	yy-bb	yy-oo
Body Mass Morph x SVL	--	4.57, 0.026* 0.03, 0.976	1.00	0.042*	0.043*
Tibia Length Morph x SVL	0.974	5.63, 0.013* 1.55, 0.242	0.420	0.122	0.010*
Sulcal Base Width Morph x SVL	0.996	1.17, 0.335 1.70, 0.213	--	--	--
Sulcal Apical Width Morph x SVL	0.997	2.89, 0.083 0.16, 0.857	--	--	--
Hemipenis Length Morph x SVL	0.999	5.34, 0.016* 0.42, 0.663	1.00	0.027*	0.028*
Lateral Apical Length Morph x SVL	0.999	0.74, 0.492 2.61, 0.103	--	--	--
Lateral Base Width Morph x SVL	0.997	2.36, 0.124 2.43, 0.118	--	--	--
Horn Length Morph x SVL	0.998	2.02, 0.163 1.27, 0.305	--	--	--
Horn Base Width Morph x SVL	0.997	4.27, 0.032* 0.47, 0.635	0.467	0.216	0.025*
Horn Tip Width Morph x SVL	0.996	6.21, 0.009** 0.67, 0.523	0.075	0.494	0.008**
Apical Area Morph x SVL	0.999, 0.990	0.24, 0.790 0.31, 0.740	--	--	--
Lateral Aspect Ratio Morph x SVL	--	2.34, 0.126 0.21, 0.809	--	--	--
Sulcal Aspect Ratio Morph x SVL	--	0.29, 0.750 2.07, 0.157	--	--	--

Figure 4.2: Static allometry of the tibia and hemipenis of all males in the study. While the tibia (A) scaled significantly lower than one in the males in our study, the hemipenis (B) did not scale significantly different from one. The morphs are color and shape coded as orange circle: (oo) usurper, blue square: (bb) mate-guarding, and yellow triangle: (yy) sneaker.

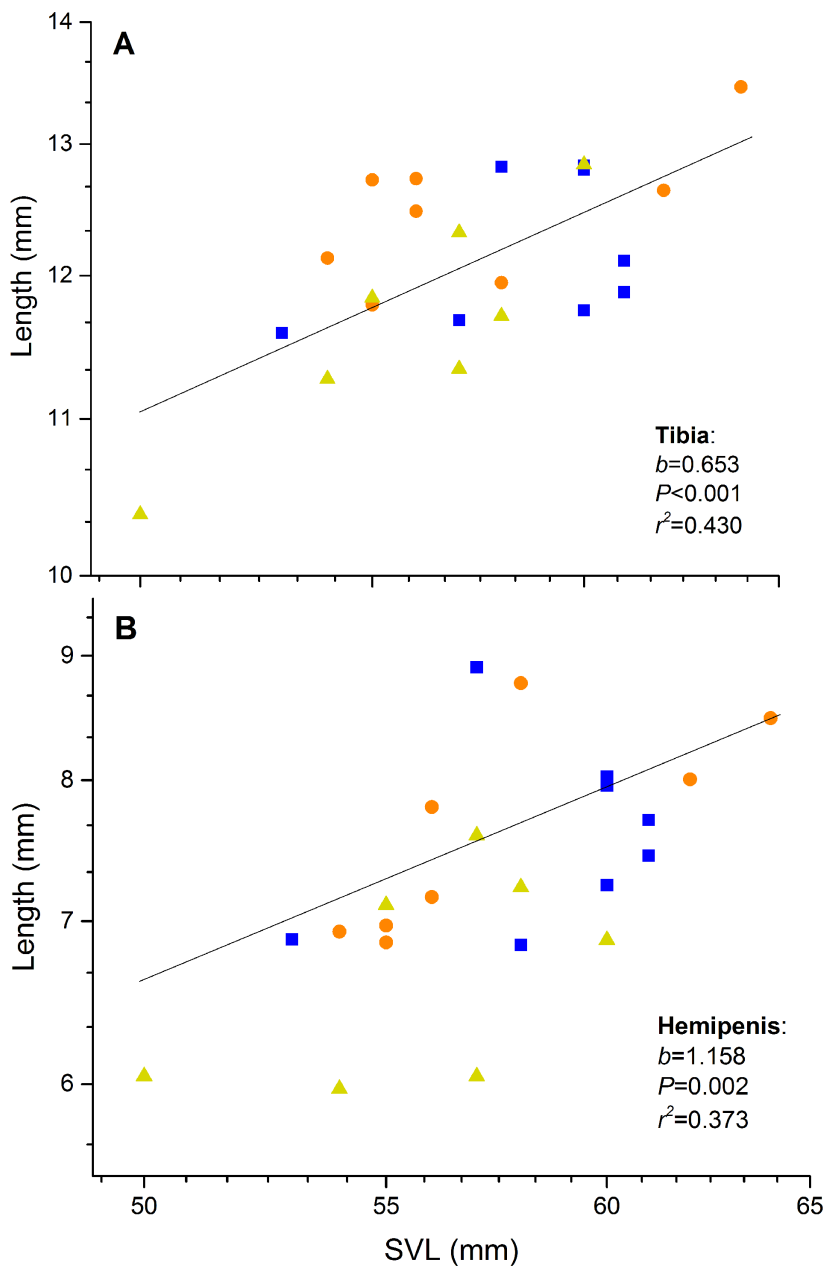


Figure 4.3: Relationship between the first two principal components of the harmonics from the elliptical Fourier analysis of the hemipenis lateral outlines. PC1 explained 73% of the variation in shape, with hemipenes becoming less curved with increasing values of PC1. PC2 explained 12% of the variation, with hemipenes becoming squatter and more bulbous with increasing values of PC2. There was no significant difference in lateral shape across morphs ($P=0.89$).

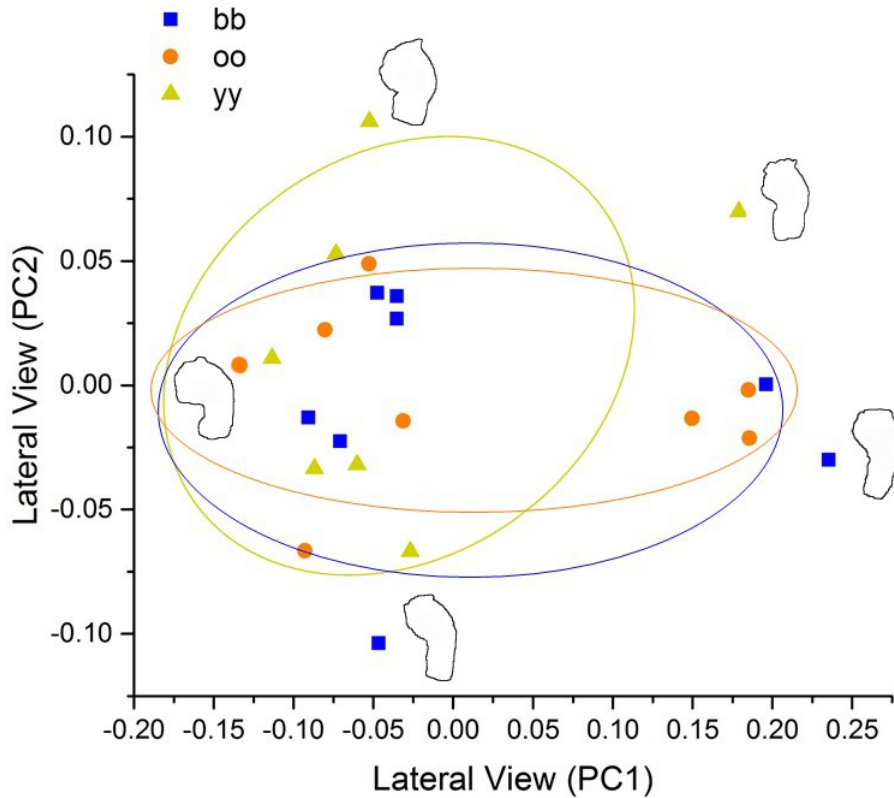


Figure 4.4: Relationship between the first two principal components of the harmonics from the elliptical Fourier analysis of the hemipenis sulcal outlines. PC1 explained 53% of the variation in shape, with hemipenes becoming slimmer with increasing values of PC1. PC2 explained 18% of the variation, with hemipenes becoming shorter and squatter with increasing values of PC2. There was no significant difference in sulcal shape across morphs ($P=0.64$).

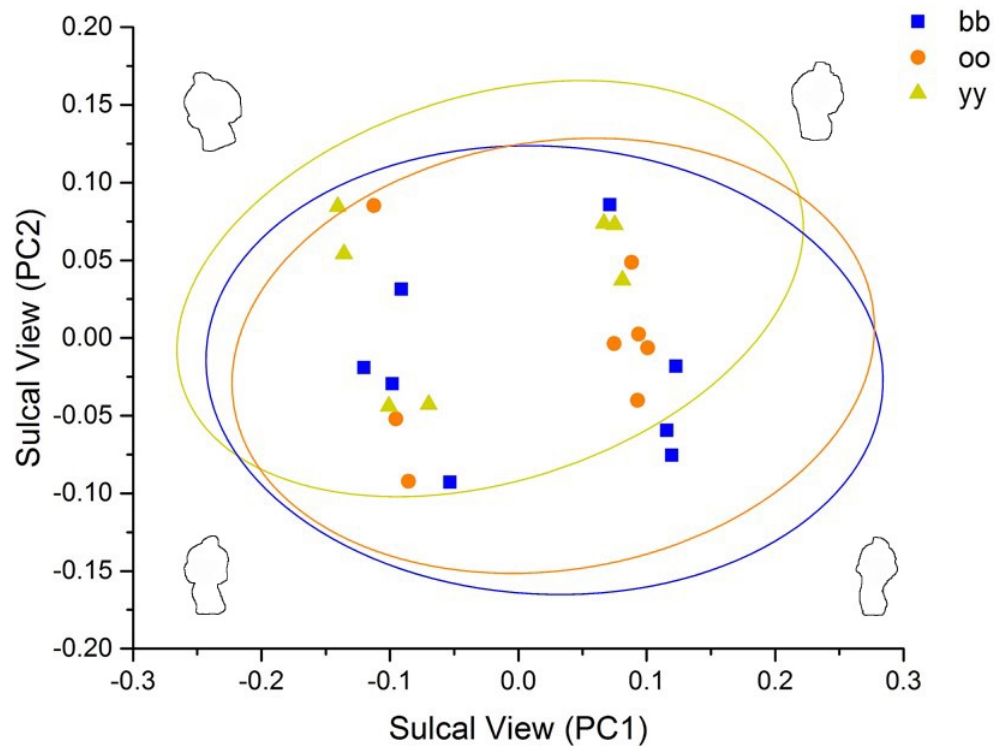
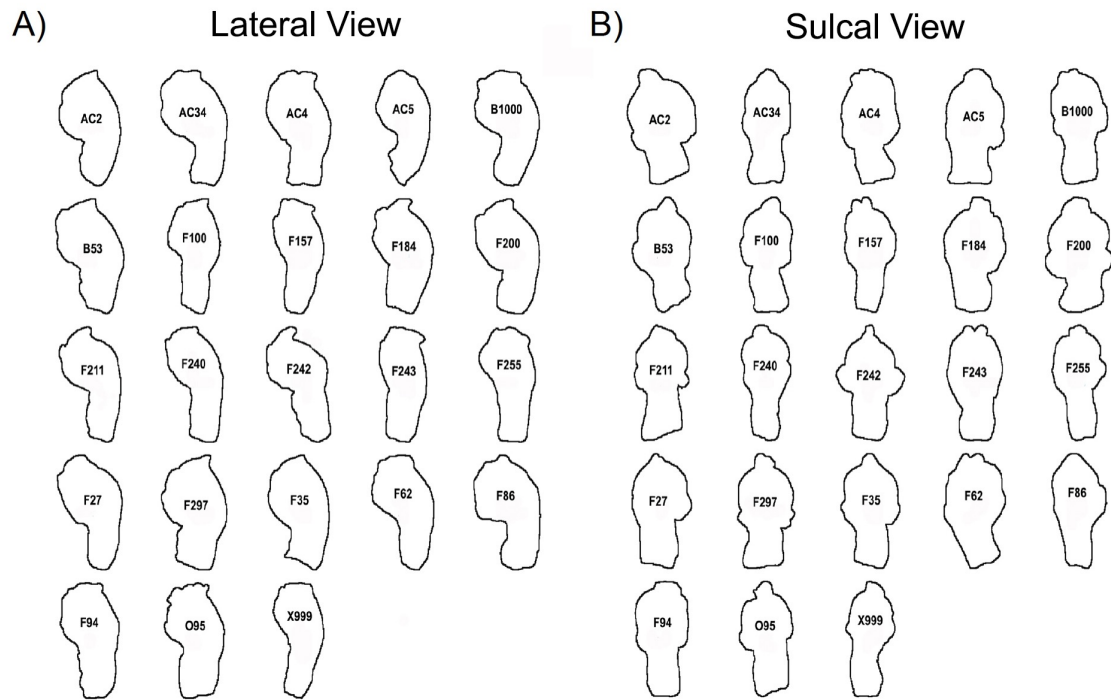


Figure 4.S1: Outlines of hemipenes of 23 individuals generated by Momocs from digital images. These outlines were used for elliptical Fourier analysis of A) lateral shape, and B) sulcal shape. Sample IDs are given within the outlines.



BIBLIOGRAPHY

- Alavi, S. M. H., Psenicka, M., Policar, T., Rodina, M., Hamackova, J., Kozak, P., & Linhart, O. (2009). Sperm quality in male *Barbus barbus* L. fed different diets during the spawning season. *Fish Physiology and Biochemistry*, 35, 683–693.
- Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton, NJ: Princeton University Press.
- Alexander, R.M. (1991). Elastic mechanisms in primate locomotion. *Z. Morphol. Anthro.*, 78, 315-320.
- Alonzo, S. H., & Warner, R. R. (2000). Allocation to Mate Guarding or Increased Sperm Production in a Mediterranean Wrasse. *The American Naturalist*, 156, 266–275.
- Altuna, C., & Lessa, E. (1985). Penial Morphology in Uruguayan Species of *Ctenomys* (rodentia, Octodontidae). *Journal of Mammalogy*, 66, 483–488.
- Amo, L., Lopez, P., & Martin, J. (2007). Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biological Conservation*, 135, 77–85.
- Arnold, S. (1983). Morphology, Performance and Fitness. *American Zoologist*, 23, 347–361.
- Arnqvist, G. (1998). Comparative evidence for the evolution of genitalia by sexual selection. *Nature*, 393, 784–786.
- Arnqvist, G., & Rowe, L. (2002). Correlated evolution of male and female morphologies in water striders. *Evolution*, 56, 936–947.
- Arteaga-Silva, M., Viguera-Villasenor, R. M., Retana-Marquez, S., Hernandez-Gonzalez, M., Chihuahua-Serrano, C., Bonilla-Jaime, H., Contreras, J. L., & Morali, G. (2008). Testosterone, androstenedione, and 5 alpha-dihydrotestosterone on male sexual behavior and penile spines in the hamster. *Physiology & Behavior*, 94, 412–421.
- August, P. V. (1983). The Role of Habitat Complexity and Heterogeneity in Structuring Tropical Mammal Communities. *Ecology*, 64, 1495–1507.
- Badyaev, A. V., Young, R. L., Oh, K. P., & Addison, C. (2008). Evolution on a local scale: Developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution*, 62, 1951–1964.
- Bakker, T. C. M., Hollmann, M., Mehlis, M., & Zbinden, M. (2014). Functional variation of sperm morphology in sticklebacks. *Behavioral Ecology and Sociobiology*, 68, 617–627.
- Battles, A. C., Whittle, T. K., Stehle, C. M., & Johnson, M. A. (2013). Effects of Human Land Use on Prey Availability and Body Condition in the Green Anole Lizard, *Anolis carolinensis*. *Herpetological Conservation and Biology*, 8, 16–26.
- Beck, L. A., & Wade, J. (2008). Steroid receptor expression in the developing copulatory system of the green anole lizard (*Anolis carolinensis*). *General and Comparative Endocrinology*, 157, 70–74.
- Bels, V. L., Theys, J., Bennett, M. R. and Legrand, L. (1992). Biomechanical analysis of jumping in *Anolis carolinensis* (Reptilia: Iguanidae). *Copeia* 2, 492-504.

- Bennett, N.C., Faulkes, C.G., & Molteno, A.J. (2000). Reproduction in subterranean rodents. In G.N. Cameron, E.A. Lacey, & J. Patton (Eds.), *Life underground, the biology of subterranean rodents* (pp. 145–177). Chicago, IL: University of Chicago Press.
- Bertin, A., & Fairbairn, D. J. (2007). The form of sexual selection on male genitalia cannot be inferred from within-population variance and allometry - A case study in *Aquarius remigis*. *Evolution*, 61, 825–837.
- Biewener, A. (2003). *Animal Locomotion*. Oxford, UK: Oxford University Press.
- Blengini, C. S., Naretto, S., Cardozo, G., Giojalas, L. C., & Chiaraviglio, M. (2016). Relationship between pre- and post-copulatory traits in *Salvator rufescens* (Squamata: Teiidae). *Biological Journal of the Linnean Society*, 119, 932–942.
- Bloch, N., & Irschick, D. J. (2006). An analysis of inter-population divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). *Ethology*, 112, 370–378.
- Böhme, W., & Ziegler, T. (2009). A review of iguanian and anguimorph lizard genitalia (Squamata: Chamaeleonidae; Varanoidea, Shinisauridae, Xenosauridae, Anguinae) and their phylogenetic significance: comparisons with molecular data sets. *Journal of Zoological Systematics and Evolutionary Research*, 47, 189–202.
- Bonser, R. H. C. (1999). Branching out in locomotion: The mechanics of perch use in birds and primates. *Journal of Experimental Biology* 202, 1459-1463.
- Bonhomme, V., Picq, S., Gaucherel, C., & Claude, J. (2014). Momocs: Outline Analysis Using R. *Journal of Statistical Software*, 56, 1–24.
- Boughman, J. W. (2001). Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*, 411, 944–948.
- Brandt, Y. (2003). Lizard threat display handicaps endurance. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 1061–1068.
- Brennan, P. L. R., Clark, C. J., & Prum, R. O. (2010). Explosive eversion and functional morphology of the duck penis supports sexual conflict in waterfowl genitalia. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1309–1314.
- Butler, M. A., & Losos, J. B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecological Monographs*, 72, 541–559.
- Butler, M. A., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* Lizards. *Evolution*, 54, 259–272.
- Calhim, S., Double, M. C., Margraf, N., Birkhead, T. R., & Cockburn, A. (2011). Maintenance of Sperm Variation in a Highly Promiscuous Wild Bird. *PLOS ONE*, 6, e28809.
- Calsbeek, R. and Irschick, D. J. (2007). The quick and the dead: Correlational selection on morphology, performance, and habitat use in island lizards. *Evolution* 61, 2493-2503.
- Channon, A. J., Gunther, M. M., Crompton, R. H., D'Aout, K., Preuschoft, H. and Vereecke E. E. (2011). The effect of substrate compliance on the biomechanics of gibbon leaps. *Journal of Experimental Biology*, 214, 687-696.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brososfske, K. D., Mroz, G. D., Brookshire, B.L., & Franklin, J. F. (1999). Microclimate in forest ecosystem and

- landscape ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, 49, 288–297.
- Conner, J., & Crews, D. (1980). Sperm Transfer and Storage in the Lizard, *Anolis carolinensis*. *Journal of Morphology*, 163, 331–348.
- Cordoba-Aguilar, A. (1999). Male copulatory sensory stimulation induces female ejection of rival sperm in a damselfly. *Proceedings of the Royal Society B-Biological Sciences*, 266, 779–784.
- Corl, A., Davis, A. R., Kuchta, S. R., & Sinervo, B. (2010). Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 4254–4259.
- Crean, A. J., & Marshall, D. J. (2008). Gamete plasticity in a broadcast spawning marine invertebrate. *Proceedings of the National Academy of Sciences*, 105, 13508–13513.
- Crompton, R. H., Sellers, W. I. & Gunther, M. M. (1993). Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. *Proc. Biol. Sci.* 254, 41-45.
- Dagosto, M. (1994). Testing Positional Behavior of Malagasy Lemurs - a Randomization Approach. *American Journal of Physical Anthropology*, 94, 189–202.
- Dagosto, M. & Yamashita, N. (1998). Effect of habitat structure on positional behavior and support use in three species of lemur. *Primates*, 39, 459–472.
- Davidowitz, G., & Rosenzweig, M. L. (1998). The latitudinal gradient of species diversity among North American grasshoppers (Acrididae) within a single habitat: a test of the spatial heterogeneity hypothesis. *Journal of Biogeography*, 25, 553–560.
- Demes, B., Jungers, W. L., Gross, T. S. & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *Am. J. Phys. Anthropol.*, 96, 419-429.
- Denno, R. F., Finke, D. L., & Langellotto, G. A. (2005). Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In: Barbosa P, Castellanos I, editors. *Ecology of predator-prey interactions*. Oxford: Oxford University Press pp. 211–239.
- Dill, A. K., Sanger, T. J., Battles, A. C., & Johnson, M. A. (2013). Sexual dimorphisms in habitat-specific morphology and behavior in the green anole lizard. *Journal of Zoology*, 290, 135–142.
- Dominey, W. J. (1984). Alternative Mating Tactics and Evolutionarily Stable Strategies. *American Zoologist*, 24, 385–396.
- Doums, C., Viard, F., & Jarne, P. (1998). The evolution of phally polymorphism. *Biological Journal of the Linnean Society*, 64, 273–296.
- Dowling, H. G. & J. M. Savage. (1960). A guide to snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica*, 45,17–28.
- Dupoué, A., Rutschmann, A., Le Galliard, J. F., Miles, D. B., Clobert, J., DeNardo, D. F., Bruschi, G.A., & Meylan, S. (2017). Water availability and environmental temperature correlate with geographic variation in water balance in common lizards. *Oecologia*, 185, 561–571.

- Eberhard, W. (1990). Animal Genitalia and Female Choice. *American Scientist*, 78, 134–141.
- Eberhard, W. G. (2009). Static Allometry and Animal Genitalia. *Evolution*, 63, 48–66.
- Eberhard, W. G. (2010). Evolution of genitalia: theories, evidence, and new directions. *Genetica*, 138, 5–18.
- Eberhard, W. G., Huber, B. A., S., R. L. R., Briceño, R. D., Salas, I., & Rodriguez, V. (1998). One Size Fits All? Relationships Between the Size and Degree of Variation in Genitalia and Other Body Parts in Twenty Species of Insects and Spiders. *Evolution*, 52, 415–431.
- Eberhard, W. G., Rodriguez, R. L., Huber, B. A., Speck, B., Miller, H., Buzatto, B. A., & Machado, G. (2018). Sexual Selection and Static Allometry: The Importance of Function. *Quarterly Review of Biology*, 93, 207–250.
- Edwards, J. R., & Lailvaux, S. P. (2012). Display Behavior and Habitat Use in Single and Mixed Populations of *Anolis carolinensis* and *Anolis sagrei* Lizards. *Ethology*, 118, 494–502.
- Emlen, D. J. (1997). Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology*, 41, 335–341.
- Emlen, D. J. (2001). Costs and the diversification of exaggerated animal structures. *Science*, 291, 1534–1536.
- Emlen, S., & Oring, L. (1977). Ecology, Sexual Selection, and Evolution of Mating Systems. *Science*, 197, 215–223.
- Ellerby, D.J. & Gerry, S. P. (2011). Sympatric Divergence and Performance Trade-Offs of Bluegill Ecomorphs. *Evolutionary Biology*, 38, 422-433.
- Falk, B. G., Snow, R. W., & Reed, R. N. (2017). A validation of 11 body-condition indices in a giant snake species that exhibits positive allometry. *PLOS ONE*, 12, e0180791.
- Fitzpatrick, J. L., Kempster, R. M., Daly-Engel, T. S., Collin, S. P., & Evans, J. P. (2012). Assessing the potential for post-copulatory sexual selection in elasmobranchs. *Journal of Fish Biology*, 80, 1141–1158.
- Flaherty, E. A. Ben-David, M. & Smith, W. P. (2010). Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding. *Journal of Comparative Physiology B - Biochemical, Systemic and Environmental Physiology*, 180, 1067-1078.
- Fleagle, J.G. & Mittermeier, R.A. (1980). Locomotor behavior, body size, and comparative ecology of 7 Surinam monkeys. *American Journal of Physical Anthropology*, 52, 301-314.
- Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, 6, 379–416.
- Friesen, C. R., Uhrig, E. J., Mason, R. T., & Brennan, P. L. R. (2016). Female behaviour and the interaction of male and female genital traits mediate sperm transfer during mating. *Journal of Evolutionary Biology*, 29, 952–964.
- Friesen, C. R., Uhrig, E. J., Squire, M. K., Mason, R. T., & Brennan, P. L. R. (2014). Sexual conflict over mating in red-sided garter snakes (*Thamnophis sirtalis*) as indicated by experimental manipulation of genitalia. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20132694.

- Fulton, C. J., Bellwood, D. R. & Wainwright, P. C. (2001). The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar. Biol.*, 139, 25-33.
- Gabaldón, A. M., Nelson, F. E. & Roberts, T. J. (2004). Mechanical function of two ankle extensors in wild turkeys: shifts from energy production to energy absorption during incline versus decline running. *J. Exp. Biol.*, 207, 2277-2288.
- Gage, M. J. G., Stockley, P., & Parker, G. A. (1995). Effects of Alternative Male Mating Strategies on Characteristics of Sperm Production in the Atlantic Salmon (*Salmo salar*): Theoretical and Empirical Investigations. *Philosophical Transactions: Biological Sciences*, 350, 391–399.
- Gallego-Carmona, C. A., Castro-Arango, J. A., & Bernal-Bautista, M. H. (2016). Effect of Habitat Disturbance on the Body Condition Index of the Colombian Endemic Lizard *Anolis antonii* (Squamata: Dactyloidae). *South American Journal of Herpetology*, 11, 183–187.
- Gilman, C.A., Bartlett, M.D., Gillis, G.B. & Irschick, D. J. (2012). Total recoil: Perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*). *Journal of Experimental Biology*, 215, 220-226.
- Gilman, C.A., Corl, A., Sinervo, B., & Irschick, D.J. (*in press*). Genital morphology associated with mating strategy in the polymorphic lizard, *Uta stansburiana*. *Journal of Morphology*.
- Gilman, C. A., & Irschick, D. J. (2013). Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. *Functional Ecology*, 27, 374–381.
- Gillis, G. B., Bonvini, L. & Irschick, D. J. (2009). Losing stability: tail loss and jumping in the 380 arboreal lizard *Anolis carolinensis*. *J. Exp. Biol.*, 212, 604-609.
- Garland, T., Jr. & Losos, J.B. (1994) Ecological morphology of locomotor performance in squamate reptiles. *Ecological morphology: Integrative organismal biology* (eds P. Wainwright & S.M. Reilly), pp. 240-302. University of Chicago Press, Chicago.
- Gomendio, M., Malo, A. F., Garde, J., & Roldan, E. R. S. (2007). Sperm traits and male fertility in natural populations. *Reproduction*, 134, 19–29.
- González-Megías, A., Gómez, J. M., & Sánchez-Piñero, F. (2007). Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography*, 30, 31–41.
- Greenstone, M. (1984). Determinants of Web Spider Species-Diversity - Vegetation Structural Diversity Vs Prey Availability. *Oecologia*, 62, 299–304.
- Greven, H. (2005). Structural and behavioural traits associated with sperm transfer in Poeciliinae. In M. C. Uribe & H. J. Grier (Eds.), *Viviparous fishes, Chapter: Structural and behavioural traits associated with sperm transfer in Poeciliinae* (pp. 147–165). Homestead, FL: New Life Publications.
- Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution*, 11, 92–98.
- Halaj, J., Ross, D. W., & Moldenke, A. R. (2000). Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, 90, 139–152.
- Halliday, D., Resnick, R. and Walker, J. (2005). *Fundamentals of Physics* 7th ed. Hoboken, NJ: John Wiley & Sons, Inc.

- Hernandez-Jimenez, A., & Rios-Cardenas, O. (2017). Condition-dependent female preference for male genitalia length is based on male reproductive tactics. *Proceedings of the Royal Society B-Biological Sciences*, 284, 20172223.
- Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B. (1985). *Functional Vertebrate Morphology*. Cambridge, MA: Belknap Press of Harvard University Press.
- Hill, R. W., Wyse, G. A. & Anderson, M. (2008). *Animal Physiology*. Sunderland, MA: Sinauer associates.
- Hollander, J., Adams, D. C., & Johannesson, K. (2006). Evolution of adaptation through allometric shifts in a marine snail. *Evolution*, 60, 2490–2497.
- Holmes, M. M., & Wade, J. (2005). Sexual differentiation of the copulatory neuromuscular system in green anoles (*Anolis carolinensis*): Normal ontogeny and manipulation of steroid hormones. *The Journal of Comparative Neurology*, 489, 480–490.
- Hosken, D. J., & Stockley, P. (2004). Sexual selection and genital evolution. *Trends in Ecology & Evolution*, 19, 87–93.
- Huey, R. (1991). Physiological Consequences of Habitat Selection. *American Naturalist*, 137, S91–S115.
- Hugel, V., Hackert, R. & Abourachid, A. (2011). Kinematic modeling of bird locomotion from experimental data. *IEEE Trans. Rob.*, 27, 185-200.
- Immler, S., Pryke, S. R., Birkhead, T. R., & Griffith, S. C. (2010). Pronounced Within-Individual Plasticity in Sperm Morphometry Across Social Environments. *Evolution*, 64, 1634–1643.
- Irschick, D. J. & Garland, T. (2001). Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.*, 32, 367-396.
- Irschick, D. J. & Losos, J. B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, 52, 219-226.
- Irschick, D. J. & Losos, J. B. (1999). Do lizards avoid habitats in which their performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Amer. Nat.*, 154, 293-305.
- Irschick, D.J., Meyers, J. J., Husak, J. F. & Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.*, 10, 177-196.
- Irschick, D.J., Vanhooydonck, B., Herrel, A. & Meyers, J. (2005a). Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol. J. Linnean Soc.*, 85, 211-221.
- Irschick, D. J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B., Meyers, J. & Herrel, A. (2005b). A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol. J. Linnean Soc.*, 85, 223-234.
- Iwata, Y., Shaw, P., Fujiwara, E., Shiba, K., Kakiuchi, Y., & Hirohashi, N. (2011). Why small males have big sperm: dimorphic squid sperm linked to alternative mating behaviours. *Bmc Evolutionary Biology*, 11, 236.

- Jenssen, T. A., Congdon, J. D., Fischer, R. U., Estes, R., Kling, D., & Edmands, S. (1995). Morphological Characteristics of the Lizard *Anolis carolinensis* from South Carolina. *Herpetologica*, 51, 401–411.
- Johansen, J. L., Fulton, C. J. & Bellwood, D. R. (2007). Avoiding the flow: refuges expand the swimming potential of coral reef fishes. *Coral Reefs*, 26, 577–583.
- Johnson, M. A., Cohen, R. E., Vandecar, J. R., & Wade, J. (2011). Relationships among reproductive morphology, behavior, and testosterone in a natural population of green anole lizards. *Physiology & Behavior*, 104, 437–445.
- Johnson, M. A., Lopez, M. V., Whittle, T. K., Kircher, B. K., Dill, A. K., Varghese, D., & Wade, J. (2014). The evolution of copulation frequency and the mechanisms of reproduction in male *Anolis* lizards. *Current Zoology*, 60, 768–777.
- Jukema, J., & Piersma, T. (2006). Permanent female mimics in a lekking shorebird. *Biology Letters*, 2, 161–164.
- Kahrl, A. F., & Cox, R. M. (2015). Diet affects ejaculate traits in a lizard with condition-dependent fertilization success. *Behavioral Ecology*, 26, 1502–1511.
- Kahrl, A. F., & Cox, R. M. (2017). Consistent Differences in Sperm Morphology and Testis Size between Native and Introduced Populations of Three *Anolis* Lizard Species. *Journal of Herpetology*, 51, 532–537.
- Kahrl, A. F., Cox, C. L., & Cox, R. M. (2016). Correlated evolution between targets of pre- and postcopulatory sexual selection across squamate reptiles. *Ecology and Evolution*, 6, 6452–6459.
- Kamath, A., & Losos, J. (2017). The erratic and contingent progression of research on territoriality: a case study. *Behavioral Ecology and Sociobiology*, 71, UNSP 89.
- Kamath, A., Stuart, Y. E., & Campbell, T. S. (2013). Behavioral Partitioning by the Native Lizard *Anolis carolinensis* in the Presence and Absence of the Invasive *Anolis sagrei* in Florida. *Breviora*, 1–10.
- Katandukila, J. V., & Bennett, N. C. (2016). Pattern of ovulation in the East African root rat (*Tachyoryctes splendens*) from Tanzania: induced or spontaneous ovulator? *Canadian Journal of Zoology*, 94, 345–351.
- Kattan, G. H., & Lillywhite, H. B. (1989). Humidity Acclimation and Skin Permeability in the Lizard *Anolis carolinensis*. *Physiological Zoology*, 62, 593–606.
- Kelly, D. A. (2016). Intromittent Organ Morphology and Biomechanics: Defining the Physical Challenges of Copulation. *Integrative and Comparative Biology*, 56, 705–714.
- Kerver, H. N., & Wade, J. (2013). Seasonal and sexual dimorphisms in expression of androgen receptor and its coactivators in brain and peripheral copulatory tissues of the green anole. *General and Comparative Endocrinology*, 193, 56–67.
- Kilmer, J. T., & Rodríguez, R. L. (2017). Ordinary least squares regression is indicated for studies of allometry. *Journal of Evolutionary Biology*, 30, 4–12.
- King, D.A. (1998). Relationship between crown architecture and branch orientation in rain forest trees. *Annals of Botany*, 82, 1–7.
- Kie, J. G., & Bowyer, R. T. (1999). Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy*, 80, 1004–1020.

- King, R. B., Jadin, R. C., Grue, M., & Walley, H. D. (2009). Behavioural correlates with hemipenis morphology in New World natricine snakes. *Biological Journal of the Linnean Society*, 98, 110–120.
- Klaczko, J., Gilman, C. A., & Irschick, D. J. (2017). Hemipenis shape and hindlimb size are highly correlated in *Anolis* lizards. *Biological Journal of the Linnean Society*, 122, 627–634.
- Klaczko, J., & Stuart, Y. (2015). Hemipenial Allometry in *Anolis grahami*. *Journal of Herpetology*, 49, 462–467.
- Klaver, C., & Böhme, W. (1986). Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. *Bonner zoologische Monographien*, 22, 1-64.
- Köhler, G., & Sunyer, J. (2008). Two new species of anoles formerly referred to as *Anolis limifrons* (Squamata : Polychrotidae). *Herpetologica*, 64, 92–108.
- Köhler, G., & Vesely, M. (2010). A Revision of the *Anolis sericeus* Complex with the Resurrection of *A. wellbornae* and the Description of a New Species (Squamata: Polychrotidae). *Herpetologica*, 66, 207–228.
- Kohlsdorf, T., Jr, T. G., & Navas, C. A. (2001). Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology*, 248, 151–164.
- Kokko, H., & Rankin, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 361, 319–334.
- Kolbe, J. J., & Losos, J. B. (2005). Hind-Limb Length Plasticity in *Anolis carolinensis*. *Journal of Herpetology*, 39, 674–678.
- Korff, W. L. & McHenry, M. J. (2011). Environmental differences in substrate mechanics do not affect sprinting performance in sand lizards (*Uma scoparia* and *Callisaurus draconoides*). *J. Exp. Biol.*, 214, 122-130.
- Krajewski, J.P., Floeter, S.R., Jones, G.P. & Leite, F.P.P. (2011). Patterns of variation in behaviour within and among reef fish species on an isolated tropical island: influence of exposure and substratum. *Journal of the Marine Biological Association of the U.K.*, 91, 1359–1368.
- Kuo, C. Y., Gillis, G. B. & Irschick, D. J. (2011). Loading effects on jump performance in green anole lizards *Anolis carolinensis*. *J. Exp. Biol.*, 214, 2073-2079.
- LaDage, L. D., Riggs, B. J., Sinervo, B., & Pravosudov, V. V. (2009). Dorsal cortex volume in male side-blotched lizards, *Uta stansburiana*, is associated with different space use strategies. *Animal Behaviour*, 78, 91–96.
- Lailvaux, S. P., Gilbert, R. L., & Edwards, J. R. (2012). A performance-based cost to honest signalling in male green anole lizards (*Anolis carolinensis*). *Proceedings of the Royal Society B: Biological Sciences*, 279, 2841–2848.
- Lailvaux, S. P. & Irschick, D. J. (2007). Effects of temperature and sex on jump performance and biomechanics in the lizard *Anolis carolinensis*. *Funct. Ecol.*, 21, 534-543.
- Larson, S. G. & Demes, B. (2011). Weight Support Distribution During Quadrupedal Walking in *Ateles* and *Cebus*. *Am. J. Phys. Anthropol.*, 144, 633-642.
- Losos, J. B. (1990). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* 60, 369-388.

- Losos, J.B. (2009). *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley: University of California Press.
- Losos, J. B. & Irschick, D. J. (1996). The effect of perch diameter on escape behaviour of *Anolis* lizards: Laboratory predictions and field tests. *Anim. Behav.*, 51, 593–602.
- Losos, J. B. & Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.*, 145, 23–30.
- Lovern, M. B., Holmes, M. M., & Wade, J. (2004). The green anole (*Anolis carolinensis*): A reptilian model for laboratory studies of reproductive morphology and behavior. *Illar Journal*, 45, 54–64.
- Lüpold, S., Tomkins, J. L., Simmons, L. W., & Fitzpatrick, J. L. (2014). Female monopolization mediates the relationship between pre- and postcopulatory sexual traits. *Nature Communications*, 5, 3184.
- Lüpold, S., Westneat, D. F., & Birkhead, T. R. (2011). Geographical variation in sperm morphology in the red-winged blackbird (*Agelaius phoeniceus*). *Evolutionary Ecology*, 25, 373–390.
- Macrini, T.E. & Irschick, D.J. (1998). An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biological Journal of the Linnean Society*, 63, 579–591.
- Martin, J., & Lopez, P. (1999). An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos*, 84, 499–505.
- Martin, J., & Lopez, P. (2000). Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. *Canadian Journal of Zoology*, 78, 265–270.
- Marentette, J. R., Fitzpatrick, J. L., Berger, R. G., & Balshine, S. (2009). Multiple male reproductive morphs in the invasive round goby (*Apollonia melanostoma*). *Journal of Great Lakes Research*, 35, 302–308.
- Mattingly, W. B. & Jayne, B. C. (2004). Resource use in arboreal habitats: Structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, 85, 1111–1124.
- McCoy, K. J., T. A. Baird, & S. F. Fox. 2003. Sexual selection, social behaviour, and the environmental potential for polygyny; pp. 149–171. In: S. F. Fox, J. K. McCoy, and T. A. Baird (Eds.), *Lizard Social Behavior*. The Johns Hopkins University Press, Baltimore.
- McElroy, E. J., Meyers, J. J., Reilly, S. M. & Irschick, D. J. (2007). Dissecting the effects of behaviour and habitat on the locomotion of a lizard (*Urosaurus ornatus*). *Animal Behaviour*, 73, 359–365.
- McMillan, D. M., & Irschick, D. J. (2010). Experimental Test of Predation and Competition Pressures on the Green Anole (*Anolis carolinensis*) in Varying Structural Habitats. *Journal of Herpetology*, 44, 272–278.
- Merrells, K.J., Blewett, H., Jamieson, J.A., Taylor, C.G., & Suh, M. (2009). Relationship between abnormal sperm morphology induced by dietary zinc deficiency and lipid composition in testes of growing rats. *Brit J Nut.*, 102, 226–232.
- Miles, D. B. (2004). The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evolutionary Ecology Research*, 6, 63–75.
- Miller, C. W. (2013). Sexual selection: Male–male competition. In J. Losos (Ed.), *The Princeton guide to evolution* (pp. 641–646). Princeton, NJ: Princeton Univ. Press.

- Mills, S. C., Hazard, L., Lancaster, L., Mappes, T., Miles, D., Oksanen, T. A., & Sinervo, B. (2008). Gonadotropin hormone modulation of testosterone, immune function, performance, and Behavioral trade-offs among male morphs of the lizard *Uta stansburiana*. *American Naturalist*, 171, 339–357.
- Moczek, A. P., & Emlen, D. J. (2000). Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? *Animal Behaviour*, 59, 459–466.
- Moore, I. T., Lerner, J. P., Lerner, D. T., & Mason, R. T. (2000). Relationships between annual cycles of testosterone, corticosterone, and body condition in male red-spotted garter snakes, *Thamnophis sirtalis concinnus*. *Physiological and Biochemical Zoology*, 73, 307–312.
- Moritz, C. T. & Farley, C. T. (2003). Human hopping on damped surfaces: strategies for adjusting leg mechanics. *Proc. R. Soc. Lond. [Biol.]*, 270, 1741-1746.
- Morrow, E. H., & Gage, M. J. G. (2001). Consistent significant variation between individual males in spermatozoal morphometry. *Journal of Zoology*, 254, 147–153.
- Mound, L. A., Crespi, B. J., & Tucker, A. (1998). Polymorphism and kleptoparasitism in thrips (Thysanoptera: Phlaeothripidae) from woody galls on Casuarina trees. *Australian Journal of Entomology*, 37, 8–16.
- Mutanen, M., & Kaitala, A. (2006). Genital variation in a dimorphic moth *Selenia tetralunaria* (Lepidoptera, Geometridae). *Biological Journal of the Linnean Society*, 87, 297–307.
- Naretto, S., Blengini, C. S., Cardozo, G., & Chiaraviglio, M. (2016). Pre- and Postcopulatory Traits of Salvator Male Lizards in Allopatry and Sympatry. *Scientifica*, UNSP 8176267.
- Neff, B. D., Fu, P., & Gross, M. R. (2003). Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology*, 14, 634–641.
- Nunez, S. C., Jenssen, T. A., & Ersland, K. (1997). Female activity profile of a polygynous lizard (*Anolis carolinensis*): Evidence of intersexual asymmetry. *Behaviour*, 134, 205–223.
- Oliveira, R. F., Canario, A. V. M., & Grober, M. S. (2001a). Male Sexual Polymorphism, Alternative Reproductive Tactics, and Androgens in Combtooth Blennies (Pisces: Blenniidae). *Hormones and Behavior*, 40, 266–275.
- Oliveira, R. F., Carneiro, L. A., Gonçalves, D. M., Canario, A. V. M., & Grober, M. S. (2001b). 11-ketotestosterone inhibits the alternative mating tactic in sneaker males of the peacock blenny, *Salaria pavo*. *Brain Behavior and Evolution*, 58, 28–37.
- Oliveira, R. F., Ros, A. F. H., & Gonçalves, D. M. (2005). Intra-sexual variation in male reproduction in teleost fish: a comparative approach. *Hormones and Behavior*, 48, 430–439.
- Oliveira, R. F., Taborsky, M., & Brockmann, H. J. (2008). *Alternative reproductive tactics: an integrative approach*. Cambridge, UK; New York: Cambridge University Press.

- Olsson, M., Schwartz, T., Uller, T., & Healey, M. (2009). Effects of sperm storage and male colour on probability of paternity in a polychromatic lizard. *Animal Behaviour*, 77, 419–424.
- Orr, T. J., & Brennan, P. L. R. (2016). All Features Great and Small—the Potential Roles of the Baculum and Penile Spines in Mammals. *Integrative and Comparative Biology*, 56, 635–643.
- Passek, K. M. (2002). Extra-pair paternity within the female-defense polygyny of the lizard, *Anolis carolinensis*: Evidence of alternative mating strategies. Dissertation, Virginia Polytechnic Institute, 537 Blacksburg, USA.
- Peattie, A.M. (2009) Functional demands of dynamic biological adhesion: an integrative approach. *Journal of Comparative Physiology B – Biochemical, Systemic and Environmental Physiology*, 179, 231-239.
- Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, 118, 1883–1891.
- Peig, J., & Green, A. J. (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology*, 24, 1323–1332.
- Perez-Tris, J., Diaz, J. A., & Telleria, J. L. (2004). Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? *Animal Behaviour*, 67, 511–521.
- Petren, K., & Case, T. J. (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Academy of Sciences*, 95, 11739–11744.
- Pomiankowski, A., & Moller, A. (1995). A Resolution of the Lek Paradox. *Proceedings of the Royal Society B-Biological Sciences*, 260, 21–29.
- Pounds, J. (1988). Ecomorphology, Locomotion, and Microhabitat Structure - Patterns in a Tropical Mainland *Anolis* Community. *Ecological Monographs*, 58, 299–320.
- R Core Team. (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rasband, W.S. (1997-2012). ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA.
- Reynolds, C., & Byrne, M. J. (2013). Alternate Reproductive Tactics in an African Dung Beetle, *Circellium bacchus* (Scarabeidae). *Journal of Insect Behavior*, 26, 440–452.
- Ricciardella, L. F., Bliley, J. M., Feth, C. C. and Woodley, S. K. (2010). Acute stressors increase plasma corticosterone and decrease locomotor activity in a terrestrial salamander (*Desmognathus ochrophaeus*). *Physiol. Behav.*, 101, 81-86.
- Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, 43, 223-225.
- Rivera, A. C., Andres, J. A., Cordoba-Aguilar, A., & Utzeri, C. (2004). Postmating sexual selection: Allopatric evolution of sperm competition mechanisms and genital morphology in calopterygid damselflies (Insecta : Odonata). *Evolution*, 58, 349–359.
- Rodriguez-Prieto, I., Martin, J., & Fernandez-Juricic, E. (2010). Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology*, 64, 1937–1945.

- Romero-Alcaraz, E., & Avila, J. M. (2000). Landscape heterogeneity in relation to variations in epigaeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. *Biodiversity and Conservation*, 9, 985–1005.
- Rotenberry, J., & Wiens, J. (1980). Habitat Structure, Patchiness, and Avian Communities in North-American Steppe Vegetation - a Multivariate-Analysis. *Ecology*, 61, 1228–1250.
- Rowe, L., & Arnqvist, G. (2012). Sexual Selection and the Evolution of Genital Shape and Complexity in Water Striders. *Evolution*, 66, 40–54.
- Rowe, L., Arnqvist, G., Sih, A., & Krupa, J. (1994). Sexual Conflict and the Evolutionary Ecology of Mating Patterns - Water Striders as a Model System. *Trends in Ecology & Evolution*, 9, 289–293.
- Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B*, 263, 1415–1421.
- Sachs, B., Glater, G., & Ohanlon, J. (1984). Morphology of the Erect Glans Penis in Rats Under Various Gonadal Hormone Conditions. *Anatomical Record*, 210, 45–52.
- Sanchez-Martinez, P. M., Ramirez-Pinilla, M. P., & Miranda-Esquivel, D. R. (2007). Comparative histology of the vaginal-cloacal region in Squamata and its phylogenetic implications. *Acta Zoologica*, 88, 289–307.
- Savage, J. M. (1997). On terminology for the description of the hemipenes of squamate reptiles. *Herpetological Journal*, 7, 23-25.
- Schrag, S. J., & Read, A. F. (1996). Loss of male outcrossing ability in simultaneous hermaphrodites: Phylogenetic analyses of pulmonate snails. *Journal of Zoology*, 238, 287–299.
- Schoenfuss, H. L., Roos, J. D., Rivera, A. R. V. & Blob, R. W. (2010). Motor patterns of distal hind limb muscles in walking turtles: implications for models of limb bone loading. *J. Morphol.* 271, 1527-1536.
- Setchell, J. M., & Dixson, A. F. (2001). Arrested development of secondary sexual adornments in subordinate adult male mandrills (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 115, 245–252.
- Shepard, D. B. (2007). Habitat but not body shape affects predator attack frequency on lizard models in the Brazilian Cerrado. *Herpetologica*, 63, 193–202.
- Shine, R. (1991). Intersexual Dietary Divergence and the Evolution of Sexual Dimorphism in Snakes. *American Naturalist*, 138, 103–122.
- Shuster, S. M. (1989). Male Alternative Reproductive Strategies in a Marine Isopod Crustacean (*Paracerceis sculpta*): The Use of Genetic Markers to Measure Differences in Fertilization Success Among α -, β -, and γ -Males. *Evolution*, 43, 1683–1698.
- Simmons, L. W. (2014). Sexual selection and genital evolution. *Austral Entomology*, 53, 1–17.
- Simmons, L. W., & Garcia-Gonzalez, F. (2011). Experimental coevolution of male and female genital morphology. *Nature Communications*, 2, 374.
- Simmons, L. W., Tomkins, J. L., & Hunt, J. (1999). Sperm competition games played by dimorphic male beetles. *Proceedings of the Royal Society B-Biological Sciences*, 266, 145–150.
- Sinervo, B. (2001). Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica*, 112, 417–434.

- Sinervo, B., Bleay, C. & Adamopoulou, C. (2001). Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution*, 55, 2040–2052.
- Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L., Lancaster, L., McAdam, A. G., Alonzo, S., Corrigan, G., & Hochberg, M. E. (2006). Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 7372–7377.
- Sinervo, B., & Clobert, J. (2003). Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science*, 300, 1949–1951.
- Sinervo, B., & Lively, C. M. (1996). The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, 380, 240–243.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M.L., Meza-Lazaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibarguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., & Sites J.W. Jr. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899.
- Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M., & DeNardo, D. F. (2000a). Testosterone, endurance, and darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior*, 38, 222–233.
- Sinervo, B., Svensson, E., & Comendant, T. 2000b. Density cycles and offspring quantity and quality game driven by natural selection. *Nature*, 406, 985–988.
- Smith, C. C., & Ryan, M. J. (2010). Evolution of sperm quality but not quantity in the internally fertilized fish *Xiphophorus nigrensis*. *Journal of Evolutionary Biology*, 23, 1759–1771.
- Spezzano, L. C. and Jayne, B. C. (2004). The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). *J. Exp. Biol.* 207, 2115-2131.
- Sponberg, S. & Full, R. J. (2008). Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain. *J. Exp. Biol.* 211, 433-446.
- Stehle, C. M., Battles, A. C., Sparks, M. N., & Johnson, M. A. (2017). Prey availability affects territory size, but not territorial display behavior, in green anole lizards. *Acta Oecologica*, 84, 41–47.
- Svensson, E., Sinervo, B., & Comendant, T. (2001). Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 12561-12565.
- Taborsky, M. (2008). Alternative reproductive tactics in fish. In R.F. Oliveira, M. Taborsky, & H. J. Brockman (Eds.), *Alternative Reproductive Tactics* (pp. 251–299). Cambridge: Cambridge University Press.
- Tanabe, S. I., Toda, M. J., & Vinokurova, A. V. (2001). Tree shape, forest structure and diversity of drosophilid community: Comparison between boreal and temperate birch forests. *Ecological Research*, 16, 369–385.

- Thorpe, S.K.S., Holder R. & Crompton, R.H. (2009) Orangutans employ unique strategies to control branch flexibility. *Proceedings of the National Academy of Sciences*, 106, 12646–12651.
- Toro, E., Herrel, A. & Irschick D. (2004). The evolution of jumping performance in Caribbean *Anolis* lizards: solutions to biomechanical trade-offs. *Amer. Nat.* 163, 844-857.
- Toro, E., Herrel, A., Vanhooydonck, B. & Irschick, D. J. (2003). A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. *J. Exp. Biol.* 206, 2641-2652.
- Turchin, P. (1998). *Quantitative Analysis of Movement: measuring and modeling population redistribution in plants and animals*. Sunderland, MA: Sinauer Associates.
- Uglem, I., Galloway, T., Rosenqvist, G., & Folstad, I. (2001). Male dimorphism, sperm traits and immunology in the corkwing wrasse *Symphodus melops*. *Behavioral Ecology and Sociobiology*, 50, 511–518.
- Uller, T., & Olsson, M. (2008). Multiple paternity in reptiles: patterns and processes. *Molecular Ecology*, 17, 2566–2580.
- van Casteren, A. and Codd, J. R. (2010). Foot morphology and substrate adhesion in the Madagascan hissing cockroach, *Gromphadorhina portentosa*. *J. Insect Sci.* 10, 40.
- Vanhooydonck, B., Herrel, A., Van Damme, R., Meyers, J. & Irschick, D. (2005). The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population. *Behav. Ecol. Sociobiol.*, 59, 157-165.
- Vanhooydonck, B., Herrel, A. and Irschick, D. J. (2006). Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. *J. Exp. Biol.*, 209, 4515-4523.
- Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth Edition. Springer, New York. ISBN 0-387-95457-0
- Voje, K. L. (2016). Scaling of Morphological Characters across Trait Type, Sex, and Environment: A Meta-analysis of Static Allometries. *American Naturalist*, 187, 89–98.
- Voje, K. L., & Hansen, T. F. (2013). Evolution of Static Allometries: Adaptive Change in Allometric Slopes of Eye Span in Stalk-Eyed Flies. *Evolution*, 67, 453–467.
- Voje, K. L., Hansen, T. F., Egset, C. K., Bolstad, G. H., & Pelabon, C. (2014). Allometric Constraints and the Evolution of Allometry. *Evolution*, 68, 866–885.
- Walker, S.E. (2005). Leaping behavior of *Pithecia pithecia* and *Chiropotes satanas* in eastern Venezuela. *American Journal of Primatology*, 66, 369-387.
- Warren, R.D. & Crompton, R.H. (1997). Locomotor ecology of *Leptilemur edwardsi* and *Avahi occidentalis*. *American Journal of Physical Anthropology*, 104, 471-486.
- Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3-an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3, 257–259.
- Warton, D. I., Wright, I. J., Falster, D. S., & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biological Reviews*, 81, 259–291.

- Webb, P. W. & Cotel, A. J. (2010). Turbulence: Does vorticity affect the structure and shape of body and fin propulsors? *Int. Comp. Biol.*, 50, 1155-1166.
- Widemo, F. (1998). Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Animal Behaviour*, 56, 329–336.
- Wiens, J. A., & Rotenberry, J. T. (1981). Habitat Associations and Community Structure of Birds in Shrubsteppe Environments. *Ecological Monographs*, 51, 21–41.
- Williams, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evol. Biol.*, 6, 47-89.
- Williams, E. E. (1983). Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In *Lizard ecology: studies of a model organism* (eds. R. B. Huey, E. R. Pianka, and T. W. Schoener). Cambridge, MA: Harvard Univ. Press.
- Winchell, K. M., Maayan, I., Fredette, J. R., & Revell, L. J. (2018). Linking locomotor performance to morphological shifts in urban lizards. *Proc. R. Soc. B*, 285, 20180229.
- Wolak, M.E., Fairbairn, D.J., & Paulsen, Y.R. (2012) Guidelines for Estimating Repeatability. *Methods in Ecology and Evolution*, 3, 129-137.
- Yang, E. J., & Wilczynski, W. (2002). Relationships between hormones and aggressive behavior in green anole lizards: An analysis using structural equation modeling. *Hormones and Behavior*, 42, 192–205.
- Youlatos, D. and Samaras, A. (2011). Arboreal locomotor and postural behaviour of European red squirrels (*Sciurus vulgaris* L.) in northern Greece. *J. Ethol.* 29, 235-242.
- Zaher, H., & Prudente L.C. (2003). Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and Techniques of Hemipenial Preparation in Snakes: A Response to Dowling. *Herpetological Review*, 34, 302–306.
- Zamudio, K. R., & Sinervo, E. (2000). Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 14427–14432.
- Zarrow, M., & Clark, J. (1968). Ovulation Following Vaginal Stimulation in a Spontaneous Ovulator and Its Implications. *Journal of Endocrinology*, 40, 343-352.
- Zhong, G. S., Sharma, K. & Harris-Warrick, R. M. (2011). Frequency-dependent recruitment of V2a interneurons during fictive locomotion in the mouse spinal cord. *Nature Comm.*, 2, 274.