UNIVERSITY OF CALIFORNIA

Los Angeles

The evolution and ecology of interspecific territoriality: Studies of *Anolis* lizards and North American wood-warblers

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Neil John Eric Losin

2012

ABSTRACT OF THE DISSERTATION

The evolution and ecology of interspecific territoriality:

Studies of *Anolis* lizards and North American wood-warblers

by

Neil John Eric Losin

Doctor of Philosophy in Biology

University of California, Los Angeles, 2012

Professor Gregory F. Grether, Chair

Competition among species, whether mediated through shared resources or direct behavioral interactions, has significant evolutionary effects. Ecological and agonistic character displacement (ECD and ACD) are processes by which competition drives evolutionary shifts in resource use and interspecific aggression, respectively. Recent contact zones provide opportunities to study these processes. In Chapters 1-3, we used the invasion of Florida by two lizards, *Anolis sagrei* and *A. cristatellus,* to investigate the role of interspecific competition in their evolution. First, we asked whether ECD has occurred in these species. We measured morphology and bite force in sympatric and allopatric populations, and found that *A. cristatellus* had a more robust head and greater bite force in sympatry. This shift results in phenotypic divergence, consistent with ECD. Next, we asked whether interspecific fights have driven shifts in aggressive behavior through ACD. We found that male *A. sagrei* were less aggressive toward heterospecifics in sympatry

than in allopatry, while male *A. cristatellus* were behaviorally dominant. *A. sagrei*'s reduced heterospecific aggression in sympatry may represent an adaptation to avoid fights with *A. cristatellus*. Finally, the effects of competition depend on its intensity, so we used a species-removal experiment to ask whether *A. sagrei* and *A. cristatellus* were competing in South Miami. While the two species' habitat use differed significantly, the removals did not influence their habitat use, movements, or body condition. In summary, the morphology and behavior of *A. sagrei* and *A. cristatellus* suggest that competition may have influenced their evolution, but we found little evidence of contemporary competition between them. In Chapter 4, we present a comparative analysis of the ecological and evolutionary factors underlying interspecific territoriality (IT) in North American warblers (Parulidae). We searched the literature for records of IT and compared species that exhibited IT with species that did not. Over half of North American parulids showed IT. Species exhibiting IT were more similar to one another in morphology, feeding guild, and habitat than expected by chance, but phylogenetic relatedness was a better predictor of IT than any of these factors, highlighting the role that evolutionary history plays in current ecological interactions.

The dissertation of Neil John Eric Losin is approved.

Priyanga A. Amarasekare

Thomas Welch Gillespie

Thomas Bates Smith

Gregory F. Grether, Committee Chair

University of California, Los Angeles

2012

Table of Contents

Abstract of the Dissertation ii

Acknowledgments vii

Biographical Sketch ix

Chapter 1: Evidence for ecological character displacement in a recent contact zone: Invasive *Anolis* lizards in South Florida 1

Chapter 2: Competitive asymmetry and asymmetrical agonistic character displacement in two invasive *Anolis* lizards in South Florida 25

Chapter 3: Invasive vs. invasive: Do two invasive Caribbean lizards compete in a shared habitat in South Florida? 49

Chapter 4: Ecological and evolutionary correlates of interspecific territoriality: A comparative study of wood-warblers (Aves: Parulidae) 79

Appendix 1 96

Literature cited 98

Figures:

Figure 1.1 11

Figure 1.2 12

Figure 1.3 13

Figure 1.4 15

Figure 2.1 38

Figure 2.2 40

Figure 2.3 41

Figure 3.1 63

Figure 3.2 65

Figure 3.3 71

Figure 4.1 90

Tables:

Table 1.1 10

Table 1.2 12

Table 1.3 13

Table 1.4 14

Table 2.1 38

Table 3.1 62

Table 3.2 70

Table 4.1 89

Acknowledgments

General acknowledgments: Priyanga Amarasekare, Tom Gillespie, Tom Smith, Greg Grether, Chris Anderson, J. P. Drury, Kathryn Peiman, Adrea Gonzalez-Karlsson, and Rachel Chock provided valuable comments on earlier versions of each dissertation chapter. James Liu, Miles Meyer, Lauren Telban, Matt Martino, Karen Villa, Liz Losin, and Nate Dappen provided field assistance for the work described in Chapters 1-3. Josh Wiley and the UCLA ATS Statistical Consulting office helped design and implement statistical analyses used in Chapters 1-3.

Collaborators: Chapter 3 will be submitted to journals with two co-authors, Matt Martino and Karen Villa. Both provided invaluable support in the field and contributed significantly to data processing and analysis, while I wrote the manuscript. Chapter 4 will be submitted to journals with three go-authors, Greg Grether, Kathryn Peiman, and Chaya Storch. All four of us met regularly and contributed to the initial design and subsequent refinement of the study. Storch led the literature search that generated the data on which our analyses are based and wrote part of the methods section; I performed the statistical analyses and wrote the remainder of the manuscript.

Funding: I have been supported by several fellowships during my tenure at UCLA, including the UCLA Graduate Division's Pauley Fellowship (2006-2008), UCLA Dept. of EEB's Lida Scott Brown Fellowship for Avian Studies (2006-2011), an NSF Graduate Research Fellowship (2008-2011), and a UCLA Graduate Division Dissertation Year Fellowship (2011-2012). The research described in Chapters 1-3 was supported by a UCLA Dept. of EEB Lida Scott Brown Research Award (2009), an American Philosophical Society Lewis and Clark Grant (2009), a National

Geographic Young Explorers Grant (2009), a Sigma Xi Grant-In-Aid of Research (2010), and two UCLA Dept. of EEB Research Awards (2011, 2010). Chaya Storch (a collaborator on the work described in Chapter 4) was supported by a UCLA Undergraduate Research Fellows Program grant in 2011.

Special thanks: I would like to thank my advisor, Greg Grether, for all of his guidance over the last six years. He gave me plenty of freedom to explore my research interests, but was always available when I needed his advice or assistance. The intellectual acuity and experimental rigor with which he pursues his research was the model to which I aspired in my own work. I could not have asked for a better scientific mentor.

Finally, I would like to thank my wonderful wife, Liz Reynolds Losin, for her unwavering love and support; not only did she tolerate my absence while I was in the field, but she gave me smart advice and a sympathetic ear through all the twists and turns of my dissertation – all while earning her Ph.D. in neuroscience, conducting innovative research, and amassing a publication record that would make any newly minted Ph.D. jealous!

Biographical Sketch: Neil Losin

Professional contact information:
E-mail: neil.losin@gmail.com
Twitter: @neillosin

On the web:
Photography: www.neillosin.com
Video: www.daysedgeproductions.com

Undergraduate education
University of Virginia: B.S. with Distinction (Biology); May 2004

Graduate education
University of California, Los Angeles, Ph.D. (Biology); June 2012
Dissertation advisor / Committee Chair: Gregory F. Grether

Peer-reviewed publications

Stuart, Y. E., N. Dappen, **N. Losin**. Now you see me: Conspicuousness and predation rates in a highly variable aposematic frog. Submitted to *Behavioral Ecology and Sociobiology*.

Kolbe, J. J., P. S. VanMiddlesworth, **N. Losin**, N. Dappen, J. B. Losos. *In press.* Climatic niche shift predicts thermal trait response in one but not both introductions of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, USA. *Ecology and Evolution*.

Grether, G. F., **N. Losin**, C. N. Anderson, K. Okamoto. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews* 84:617-635.

Krakauer, A. H., M. Tyrrell, K. Lehmann, **N. Losin**, F. Goller, G. L. Patricelli. 2009. Vocal and anatomical evidence for two-voiced sound production in the greater sage-grouse *Centrocercus urophasianus*. *Journal of Experimental Biology* 212:3719-3727.

Narins, P. M., **N. Losin**, C. E. O'Connell-Rodwell. 2009. Seismic and Vibrational Signals in Animals. Pages 545-549 in *Encyclopedia of Neuroscience*. Ed. Larry Squire. Elsevier.

Losin, N., C. H. Floyd, T. E. Schweitzer, S. J. Keller. 2006. Relationship between aspen heartwood rot and the location of cavity excavation by a primary cavity-nester, the Red-naped Sapsucker. *Condor* 108:706-710.

T. M. Blackburn, K. E. Jones, P. Cassey **N. Losin**. 2004. The influence of spatial resolution on macroecological patterns of range size variation: a case study using parrots (Psittaciformes) of the world. *Journal of Biogeography* 31:285-293.

Fellowships and grants

UCLA Dept. of EEB Research Award (2011, 2010); Sigma Xi Grant-In-Aid of Research (2010); National Geographic Young Explorers Grant (2009); American Philosophical Society Lewis and Clark Grant (2009); Santa Monica Bay Audubon Society Grant (2011, 2009); UCLA Dept. of EEB Lida Scott Brown Research Award (2009, 2008, 2007); AMNH Frank Chapman Grant (2009); AMNH Collection Study Grant (2008); AAAS Pacific Division Alan E. Leviton Student Research Award (2008); LA Audubon Society Ralph Schreiber Ornithology Research Award (2008); Explorers Club: Exploration Fund (2007); American Ornithologists' Union: Research Award (2007); NSF Graduate Research Fellowship (2008-2011); UCLA Dept. of EEB: Lida

Scott Brown Fellowship for Avian Studies (2006-2011); UCLA Graduate Division: Pauley Fellowship (2006-2008)

Popular publications

N. Losin. 2011. "There Goes the Neighborhood: Understanding territoriality in bird communities." *Living Bird*, Spring 2011 (with 4 photographs by the author)

N. Losin. 2011. "Underground Owl." *Birders World*, February 2011. (with 3 photographs by the author, including front cover)

N. Losin. 2010. "Hotspots Near You: Franklin Canyon." *Birders World*, June 2010 (with 2 photographs by the author).

N. Losin. 2009. "Hotspots Near You: Malibu Lagoon." *Birders World* April 2009 (with 1 photograph by the author)

N. Losin. 2007. "King of the Western Sage: The Life and Plight of North America's Largest Grouse." *Living Bird* 26(3):10-19. (with 8 photographs by the author)

Teaching, outreach, and service

- October 2011: Presented on my research on invasive lizards at an *NG Live!* "Young Explorers Salon" at National Geographic Society headquarters in Washington, D.C.
- October 2011: Delivered an invited guest lecture ("The Science of Bird Song") to an undergraduate class for music majors in UCLA's Herb Alpert School of Music.
- August 2010, 2011: Co-organized and taught full-day workshops at Ecological Society of America (ESA) meetings: "Photography for Ecologists." Developed a PDF guide to digital photography for working field biologists; led classroom discussions and field exercises.
- November 2010: Delivered an invited guest lecture ("The Science of Bird Song") at the monthly meeting of the Santa Monica Bay Audubon Society.
- May 2009: Received UCLA Dept. of Ecology and Evolutionary Biology A. M. Schechtman Award for Distinguished Teaching
- Winter 2009: Teaching assistant for *EEB 132: Field Behavioral Ecology*. First 3 weeks: taught 2 180-minute discussion sections per week (topics: field biology methods, statistics, experimental design). Second 3 weeks: at Makerere University Biological Station in Kibale National Park, Uganda, mentored students conducting independent research. Final 3 weeks: advised students as they analyzed data and prepared a final research paper and presentation.
- November 2007: Delivered an invited guest lecture ("The Science of Bird Song") at a concert celebrating the music of Olivier Messiaen. Hosted by UCLA Herb Alpert School of Music.
- Fall quarter 2007, Winter quarter 2010, Winter quarter 2011: TA for *EEB 100: Introduction to Ecology and Behavior*. Taught 2-6 110-minute or 50-minute discussion sections per week (20-24 students each); prepared short lectures and led discussions and lab exercises.
- Spring 2003 to present: Gave 13 invited lectures to high school groups (biology classes and extra-curricular organizations). Topics have included: my own research (various projects), birdsong, experimental design, and how to become involved in research as a student.

Chapter 1: Evidence for ecological character displacement in a recent contact zone: Invasive *Anolis* lizards in South Florida

Abstract: Interspecific competition is a major driver of adaptive evolution, and often favors ecological divergence between species through ecological character displacement (ECD). Recent contact zones can provide opportunities to study this process in action. In this study, I used the invasion of South Florida by two lizards, *Anolis sagrei* and *A. cristatellus,* to test whether ECD is driving morphological divergence between them. I measured several morphological traits and a functional trait, bite force, in sympatric and allopatric populations of each species, and tested whether the two species were more divergent in these traits in sympatry than allopatry. I found that while *A. sagrei* did not differ between sympatric and allopatric populations, *A. cristatellus* had a more robust head and greater bite force in sympatry than in allopatry. These shifts result in greater phenotypic differences between species in sympatry than allopatry, consistent with ECD driving natural selection. In addition to these shifts in head shape, *A. cristatellus* had greater body condition and relatively shorter legs in sympatric than allopatric populations; neither result was predicted by ACD, but possible alternative explanations are discussed. Biological invasions are natural experiments in ecology and evolution, and studying evolutionary shifts that occur following invasions can provide considerable insight into the role that interspecific interactions play in evolution and community ecology, both in natural and invaded systems.

Introduction: Competitive interactions between species can drive phenotypic evolution in a variety of traits (Grether et al. 2009, Pfennig and Pfennig 2009). Both exploitative competition and behavioral interference can result in adaptive phenotypic shifts that facilitate species coexistence (Brown and Wilson 1956, Grether et al. 2009). Biological invasions often create novel contact zones between potential competitors, and provide opportunities to observe these evolutionary processes in action. In this study, we used the contemporary invasion of two Caribbean anoles (Polychrotidae: *Anolis*) in South Florida as a case study to investigate phenotypic shifts that occur following contact between two potential competitors.

One well-studied mechanism promoting divergent phenotypic evolution between sympatric competitors is ecological character displacement (ECD). ECD is a process by which exploitative competition between species generates selection favoring divergence in traits that influence resource use, such as habitat preferences and dietary adaptations (Brown and Wilson 1956, Schluter 2000). Through ECD, individuals with phenotypes divergent from the rival species experience greater fitness than those with non-divergent phenotypes, and divergence between sympatric species is expected under most ecological conditions (Grant 1972). ECD is thought to have played an important role in the diversification of many lineages, and there is strong empirical evidence for ECD in diverse taxa (Schluter 2000).

Some of the best-studied examples of interspecific competition – and its effects on the evolution of ecologically relevant traits – come from lizards in the genus *Anolis*, commonly known as anoles (Losos 2009). Competition has been implicated in driving the spectacular replicated adaptive radiations of anoles in the Greater Antilles (Williams 1972, Beuttell and Losos 1999). Anoles in the Greater Antilles can be categorized into several discrete *ecomorphs* based on their body size, shape, and habitat preferences (Williams 1972), and these ecomorphs

have arisen independently on each island of the Greater Antilles (Losos et al. 1998). Species belonging to the same ecomorph seldom occupy the same geographic range, but when they do, they typically differ substantially in other ecological attributes or body size, both of which likely reduce the competition between these coexisting species (Losos 2009).

In anoles and other lizards, several morphological traits have been shown to have strong ecological and functional consequences within and among species (Losos 1990a, 1994). The morphology of the head, for example, influences the type of prey that can be captured, subdued, and consumed; within and across species, lizards with wider and deeper heads tend to have greater bite force (Anderson et al. 2008). Anoles also bite one another during territorial contests, and bite force – which is strongly influenced by head morphology within and among species – is a significant determinant of contest outcomes (Lailvaux et al. 2004, but see Lailvaux and Irschick 2007). Limb length is also under selection based on the physical environment, and may undergo rapid evolution (Losos et al. 1997, Losos et al. 2001, Losos et al. 2004, Losos et al. 2006, Marnocha et al. 2011). Long hindlimbs generally facilitate locomotion on large-diameter perches (Losos and Sinervo 1989), and the limbs of different anole ecomorphs vary in concert with their preferred perching substrates (Beuttell and Losos 1999, Calsbeek et al. 2007). Hindlimb length also has an environmental component; limb development may be influenced by the size of perches available to a growing anole (Losos et al. 2000, Kolbe and Losos 2005).

While the influence of competition on diversification (including ECD and related processes) is often inferred from geographic patterns of variation (e.g. phenotypic differences between sympatric and allopatric populations of a species) or community structure (Dayan and Simberloff 2005), species that have recently come into contact provide opportunities to study ECD in action. While novel species interactions can occur during natural range expansions, in

human-dominated environments, biological invasions increasingly create new contact zones between species (Carroll 2011, Jones and Gomulkiewicz 2012, Perkins 2012). Anthropogenic introductions of exotic species may bring closely related or ecologically similar species into contact, creating the conditions for interspecific competition, both through exploitation and interference (Vellend et al. 2007). Invasive species, therefore, may provide opportunities to study the evolutionary consequences of species interactions (Mack et al. 2000).

A different suite of competitors is not the only potential ecological difference between a species' native and introduced ranges (Prentis et al. 2008). Non-native species may encounter different prey, predators, parasites, and pathogens than they have experienced in their native range, and this new biotic community can exert selection on both exotic and native species (Strauss et al. 2006). Non-native species may also experience different abiotic conditions in their introduced ranges than those encountered in their native range (Jones and Gomulkiewicz 2012). Differences in the physical environment between native and non-native populations may include habitat structure and climatic factors (Losos et al. 2001, Broennimann et al. 2007, Gallagher et al. 2010, Angetter et al. 2011). While such factors may limit the establishment and spread of exotic species, they may also drive rapid evolution in morphology, behavior, and environmental tolerances (Losos et al. 1997, Kolbe et al. *in press*). A species' ability to adapt to novel environmental conditions may influence its success as an invasive (Hastings et al. 2004). Whether biotic or abiotic, environmental differences between a species' native and introduced ranges may impose novel selective pressures on species occurring in new environments, which in turn may drive adaptive evolution (Suarez and Tsutsui 2008, Whitney and Gabler 2008).

In this study, I used the contemporary invasion of peninsular Florida by two anoles, *Anolis sagrei* (a native of Cuba) and *A. cristatellus* (a native of Puerto Rico) to investigate the

influence of a sympatric competitor on ecological traits. These two species have co-occurred in Miami since the 1970s, belong to the same ecomorph, and are found syntopically at many sites in the Miami area. I quantified morphological variation among sympatric and allopatric populations of both species and tested the hypothesis that interspecific competition in sympatry has driven divergent phenotypic shifts consistent with ECD. I documented geographic variation in morphological traits (hindlimb length, head morphology), as well as a functional correlate of head morphology, bite force. I predicted that each species' hindlimb length would diverge in sympatry, consistent with documented habitat differences between species (Salzburg 1984). I further predicted that ECD would result in exaggerated species differences in head morphology and concomitant shifts in bite force at sympatric sites compared to allopatric sites.

Methods:

Study system: I investigated the morphology of *Anolis sagrei*, a native of Cuba, and *A. cristatellus*, a native of Puerto Rico, at sites where the two species were sympatric and sites where only one species occurred. This study was part of a larger project focusing on interspecific competition and territoriality in these species, so my sampling efforts were focused on males (the more territorial sex in both species). *A. sagrei* has undergone several independent invasions into Florida, beginning in the late 19th century, and is now ubiquitous in south Florida (Kolbe et al. 2004, Krysko et al. 2011, Meshaka 2011). *A. cristatellus* is a more recent arrival, first recorded in South Florida in the 1970s (Schwartz and Thomas 1975, Brach 1977, Wilson and Porras 1983, Bartlett and Bartlett 1999, Krysko et al. 2011). At present, *A. cristatellus* has not spread outside the Miami area, but it can be quite abundant locally. Populations of *A. cristatellus* in mainland South Miami (hereafter *Invasion 1*) and on Key Biscayne (*Invasion 2*) apparently constitute two

independent invasions from separate Puerto Rican source populations (Kolbe et al. 2007). *A. sagrei* and *A. cristatellus* are not the only invasive anoles in South Florida, but they are unique among the invasive species in being sympatric in their invasive range and belonging to the same ecomorph; both species are "trunk-ground" anoles (Losos 2009).

Study sites: For *A. sagrei*, both sympatric and allopatric sites can be found in South Miami, while for *A. cristatellus*, there are no known allopatric sites in the invasive range of South Florida; the more widespread *A. sagrei* occurs at all sites where *A. cristatellus* is observed. Therefore, to obtain measurements of allopatric *A. cristatellus*, I visited sites in two areas of Puerto Rico representing the two putative source populations of Florida's *A. cristatellus* invasions (Kolbe et al. 2007). All sites in Florida and Puerto Rico were in public parks and other public lands, and appropriate permits were obtained. Florida sites were selected based on prior surveys conducted by J. J. Kolbe (*pers. comm.*); further, I re-surveyed each site to assess both species' presence before assigning it to either the "sympatric" or "allopatric" population type.

Morphological measurements: I captured male anoles from April-June 2010 and April-August 2011. Anoles were captured by hand or using a polyester noose at the end of a graphite fishing rod. I measured each male's mass using an electronic balance accurate to 0.1g (Ohaus Scout Pro). I measured snout-vent length (hereafter SVL) and tail length to the nearest 0.5 mm by gently flattening the male's ventral side against a transparent ruler. I recorded whether or not the tail was intact, as anoles may lose their tails while avoiding predators (e.g. Bateman and Fleming 2011). Hindspan, the distance between the left and right femoral-tibial joints when the legs are perpendicular to the body, was used as a proxy for hindlimb length (Marnocha et al. 2011).

Head measurements were taken with an electronic caliper (Fowler Euro-Cal III) accurate to 0.01mm. The neck musculature of male anoles made acquiring an accurate, highly repeatable measure of whole-skull length impractical. Therefore, head length was measured as the distance from the tip of the snout to the posterior edge of a 2x2 pattern of four roughly square scales just behind the parietal eye. Head width and depth were both measured just behind the eye. I made all morphological measurements to ensure consistency across study sites and species.

Bite force: I used a custom-made apparatus for measuring bite force in small animals. The apparatus consisted of a piezoelectric force transducer (Kistler 9203) tethered to a charge amplifier (Kistler 5995A). Custom-fabricated steel bite plates formed a lever, such that when a compressional force was applied to the bite plates on one side of the fulcrum, a tensile force was measured by the force transducer on the other. A micrometer head ensured consistent spacing of the bite plates, which helped to maintain a similar gape angle among subjects. Prior to analysis, raw measurements obtained from this apparatus were adjusted to yield true bite force measures, in Newtons, based on the mechanical advantage of the steel lever arm / bite plate apparatus.

Several factors may influence observed bite force, including motivation, gape angle and jaw position, and body temperature (reviewed in Anderson et al. 2008). Male *A. sagrei* and *A. cristatellus* are enthusiastic biters and rarely refuse an opportunity to bite whatever is in reach, including the apparatus described above. Nevertheless, I made three bite force measurements with each male, with 30 minutes of rest between trials, and each male's maximum measured bite force was used in subsequent analyses, similar to previous studies of bite force in *Anolis* lizards (e.g. Lailvaux and Irschick 2007). Gape angle and jaw position are also important determinants of bite force measurements, so I was careful to position each male so that its jaws made contact

with the bite plates midway between the anterior corner of the eye and the tip of the snout. In ectotherms, body temperature can influence bite force, so all anoles were measured after being held indoors at temperatures of 30-31°C for > 1 hr, and this ambient temperature was maintained throughout the measurement period.

Analysis: Morphological variation in sympatric and allopatric *A. sagrei* and *A. cristatellus* were analyzed using univariate mixed-effects ANOVA implemented in R package *nlme* (Pinheiro et al. 2012), with planned comparisons among groups using R function "glht" from package *multcomp* (Hothorn et al. 2008). Population Type (sympatric / allopatric) was a fixed effect, and Site was a random effect nested within Population Type. When appropriate, I included SVL as a covariate to control for the effects of body size. Because sampling dates differed somewhat among sites, among-site variation in absolute body size could potentially be influenced by seasonal growth patterns. Therefore, my primary interest was whether populations differed in body and head proportions, rather than absolute body size.

To investigate variation in *A. cristatellus* head shape in greater detail, I used principal component analysis (PCA) to explore the relationships between head length, width, and depth. I expected that the first principal component would show a positive relationship between all three head measurements, and could serve as a useful proxy for overall head size, while the remaining components would explain the remaining variation in head shape; these shape components would be used in subsequent analyses of head morphology and bite force (see Results).

I used univariate mixed-effects ANOVA to compare bite force among populations of *A. cristatellus*. Preliminary analysis of bite force data revealed a complex relationship with head morphology and body condition, both of which were also related to population type (sympatric /

allopatric). Therefore, I took a path analysis approach using the R package *OpenMx* (Boker et al. 2011, 2012) to investigate the relationship between population type, body condition, head morphology and bite force. Specifically, I asked whether inter-population differences in body condition and head shape explained variation in bite force within and among populations, and whether these effects were consistent among populations.

Results:

Morphology: I captured and measured 637 male *A. cristatellus* in 2010-2011, both in their introduced range in Miami (where they are sympatric with *A. sagrei*) and their native range in Puerto Rico. I measured 186 males at 5 allopatric sites, and 451 males at 8 sympatric sites (Table 1.1). South Miami and Key Biscayne invasive populations of *A. cristatellus* were sampled, as well as Puerto Rican populations near the putative sources of each invasion (Kolbe et al. 2007).

To test for sympatric / allopatric morphological differences in *A. cristatellus*, I used ANOVA and ANCOVA to evaluate differences between sympatric and allopatric populations, with Site as a nested random effect. Because there were two independent introductions of *A. cristatellus* into the Miami area, I included Invasion as a factor in each model, and dropped it from the model if its interaction with Population Type (i.e., sympatric / allopatric) was non-significant. Sympatric and allopatric male *A. cristatellus* did not differ in body mass ($F_{1,10}$ = 0.00, p = 0.96) or SVL ($F_{1,10}$ = 3.27, p = 0.10). I then calculated a regression of mass-related covariates (SVL^3 and tail length) on body mass and used the residuals from this model as an index of body condition. Using this measure, sympatric males were in better condition than allopatric males ($F_{1,10}$ = 15.971, p = 0.0025; Fig. 1.1a). As with the *A. sagrei* analyses above, I next controlled for SVL to test whether populations differed in hindlimb length, head size, and

Table 1.1: Sample size of anoles measured in 2010-2011 sampling efforts. All individual represented are males. Number of males measured is shown, with number of sites in parentheses.

	A. sagrei	*A. cristatellus*	
		Invasion 1	**Invasion 2**
Sympatric	334 (6)	346 (5)	105 (2)
Allopatric	176 (5)	95 (3)	91 (2)

head shape. Male *A. cristatellus* had relatively shorter hindlimbs in sympatry than in allopatry ($F_{1,5} = 7.78$, $p = 0.039$; Fig. 1.1b; d.f. differs between this and other analyses because leg length was measured only in 2011). Head morphology also differed between sympatric and allopatric populations. After controlling for body size, sympatric and allopatric male *A. cristatellus* did not differ in head length ($F_{1,10} = 3.74$, $p = 0.08$; Fig. 1.1c), but differed significantly in head width and depth. Sympatric males had relatively wider ($F_{1,10} = 28.68$, $p < 0.001$; Fig. 1.1d) and deeper heads ($F_{1,10} = 13.22$, $p = 0.0046$; Fig. 1.1e) than allopatric males. All sympatric/allopatric differences were indistinguishable between the two invasions (all interaction $p > 0.1$).

To investigate the shifts in *A. cristatellus* head morphology further, I used PCA to identify the primary axes of variation in head dimensions. Not surprisingly, the first principal component explained most of the variation in head measurements; all three head measurements loaded negatively on this component, which can be interpreted as a head size axis (Table 1.2). The second principal component (hereafter *head shape*) had a positive loading for head length, but negative loadings for head width and depth (Table 1.2). Given the observed shifts in head width and depth (Fig. 1.1), I predicted that head shape score would differ between sympatric and allopatric *A. cristatellus*. As expected, sympatric males had lower head shape scores ($F_{1,10} = 35.01$, $p < 0.001$, Fig. 1.2a), indicating that they had relatively shorter, broader, and deeper heads than allopatric males. This sympatric shift in head shape score was indistinguishable between invasions (Invasion * Population Type interaction $F_{1,9} = 0.03$, $p = 0.86$; Invasion main effect and

interaction dropped from subsequent analyses). Given that my head measurements were external measurements made with calipers, and sympatric male *A. cristatellus* were relatively heavier than allopatric males, I controlled for body condition to test whether the differences in measured head shape could be explained by enhanced body condition in sympatry. Body condition had a significant negative effect on PC2, but even after controlling for body condition, PC2 was still lower in sympatric than allopatric males ($F_{1,10} = 22.31$, $p < 0.001$; Table 1.3), and this shift was statistically indistinguishable between invasions.

From 2010-2011, I captured and measured 520 male *A. sagrei* in the greater Miami area: 176 males at 5 allopatric sites (outside the introduced range of *A. cristatellus*), and 334 males at six sympatric sites (Table 1.1). One South Miami site was not easily classified as sympatric or allopatric; no *A. cristatellus* were observed there, either by the author or by others (J. Kolbe *pers. comm*.), but the site was surrounded by sites at which *A. cristatellus* was found regularly. This site ($n = 10$ *A. sagrei*) was excluded from subsequent analyses.

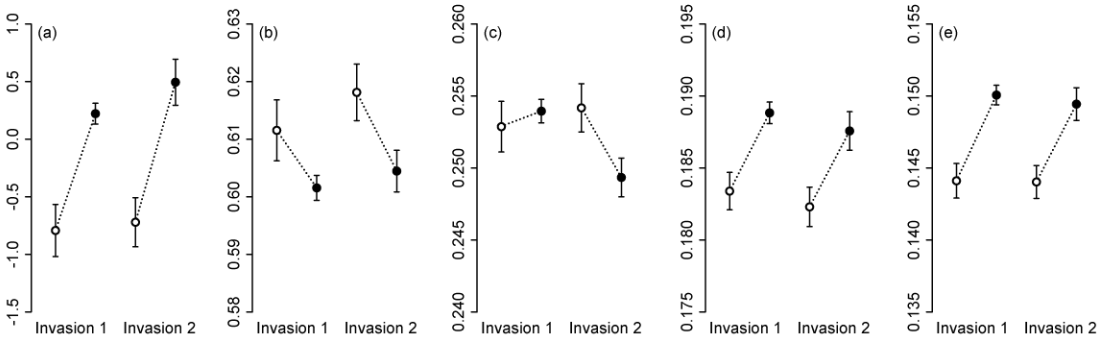


Figure 1.1: Sympatric shifts in morphology of male *A. cristatellus*. (a) Body condition (residuals of a regression of body mass on SVL^3 and tail length); (b) Relative hindlimb length, expressed as hindspan divided by SVL; (c) Relative head length; (d) Relative head width; (e) Relative head depth. (c)-(e) are expressed as head measurements divided by SVL. *Invasion 1* includes sites in northeastern Puerto Rico (allopatric) and South Miami (sympatric). *Invasion 2* includes sites in the San Juan area (allopatric) and Key Biscayne (sympatric). Unfilled circles represent allopatric population means, while filled circles represent sympatric means. Means and 95% confidence intervals are shown in each plot. Significant differences occur between sympatric and allopatric populations in (a), (b), (d), and (e). Population type * Invasion interactions are non-significant for all morphological variables shown.

Table 1.2: Principal component analysis on head morphology of *A. cristatellus* males. PC1 has negative loadings for all three head measurements and can be interpreted as a size axis of variation. PC2 ("head shape") explains most of the remaining variation in head morphology and can be interpreted as an axis of head robustness: lower PC2 scores represent shorter, broader, and deeper heads.

Factor loadings:	**PC1**	**PC2**	**PC3**
Head length	-0.708	0.706	
Head width	-0.553	-0.570	-0.608
Head depth	-0.440	-0.420	0.794
Component importance:			
Standard deviation	1.6736	0.3933	0.2866
Proportion of variance explained	0.9220	0.0509	0.0270

Sympatric and allopatric male *A. sagrei* did not differ in body mass ($F_{1,9} = 1.10$, $p = 0.32$) or SVL ($F_{1,9} = 0.93$, $p = 0.36$), nor did they differ in body mass after controlling for mass-related covariates, SVL^3 and tail length ($F_{1,9} = 0.04$, $p = 0.85$). Next, I tested for differences in hindlimb length and head morphology between populations, controlling for body size by including SVL as a covariate. Sympatric and allopatric male *A. sagrei* did not differ in hindlimb length ($F_{1,5} = 2.86$, $p = 0.15$), head length ($F_{1,9} = 2.37$, $p = 0.16$), head width ($F_{1,9} = 0.38$, $p = 0.55$), or head depth ($F_{1,9} = 3.00$, $p = 0.12$). Because head dimensions were inter-correlated, I used PCA to identify the principal axes of variation in head morphology. None of the three principal components differed significantly between sympatric and allopatric populations (all $p > 0.3$).

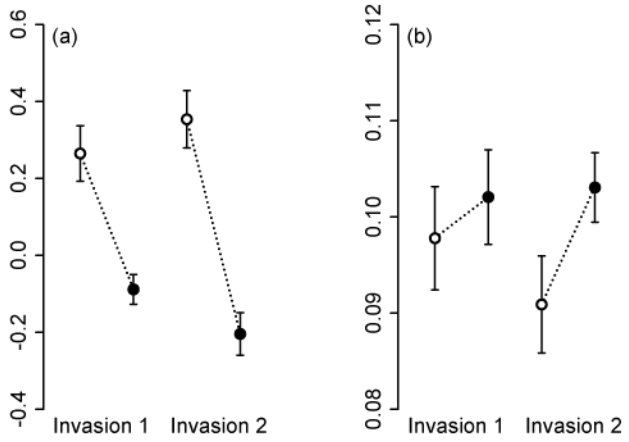


Figure 2: Sympatric shifts in head shape score (PC2) and maximum bite force in male *A. cristatellus*. (a) Sympatric *A. cristatellus* have a lower head shape score, representing a shift toward shorter, broader, and deeper heads. The Population type * Invasion interaction is non-significant. (b) Sympatric male *A. cristatellus* bite harder than allopatric males, after controlling for SVL; maximum bite force (N) divided by SVL (mm) is shown. Unfilled circles represent allopatric population means, while filled circles represent sympatric means. Means and 95% confidence intervals are shown in each plot.

Table 1.3: Mixed-effects ANCOVA testing the effects of body size, body condition, and population type (sympatric vs. allopatric) on *A. cristatellus* head shape score (head morphology PC2). Interaction effects were non-significant and were not included in the model presented here.

	Numerator DF	Denominator DF	F-ratio	*p*-value
Snout-vent length	1	595	1.3363	0.2481
Body condition	1	595	51.4194	< 0.0001
Population type	1	10	23.4488	0.0007

Finally, I compared head shape scores between *A. cristatellus* and *A. sagrei* in sympatry and allopatry. I used the principal component loadings from the *A. cristatellus* analysis above to calculate principal component scores for all *A. sagrei* males. Sympatric and allopatric *A. sagrei* did not differ in this head shape score, nor did allopatric *A. cristatellus* differ from *A. sagrei* (Tukey's test, all adjusted $p > 0.9$). Sympatric *A. cristatellus*, however, had lower head shape scores than sympatric or allopatric *A. sagrei* and allopatric *A. cristatellus*, representing a divergent shift in head shape (Tukey's test, all $p < 0.001$; Fig. 1.3).

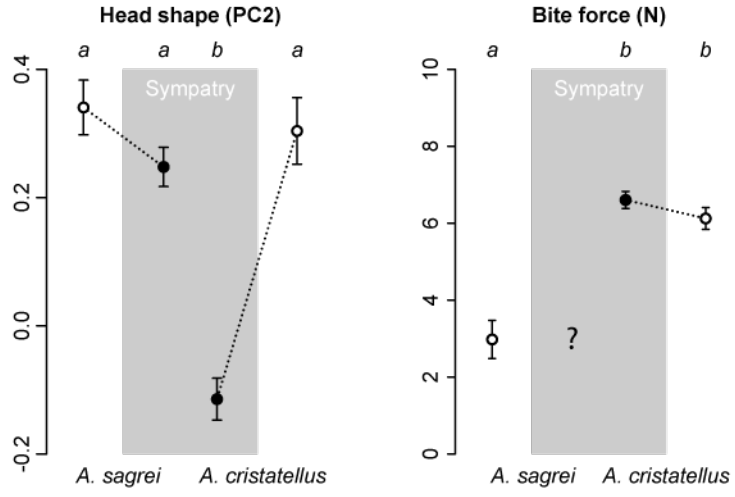


Figure 1.3: Comparison of sympatric and allopatric populations of *A. sagrei* and *A. cristatellus*. *Left*: While there are no significant differences in head shape score between sympatric and allopatric *A. sagrei*, sympatric *A. cristatellus* has diverged significantly from *A. sagrei* and allopatric *A. cristatellus*. *Right*: Sympatric and allopatric *A. cristatellus* have greater bite force than allopatric *A. sagrei*. Bite force was not measured in sympatric *A. sagrei*, but I would not predict a difference in bite force because sympatric and allopatric *A. sagrei* did not differ in head shape. Unfilled circles represent allopatric population means, while filled circles represent sympatric means. Means and 95% confidence intervals are shown in each plot.

Table 1.4: ANOVA table showing the effects of body size, head size, body condition, and head shape score on *A. cristatellus* maximum bite force. Model terms are shown in the order they were added to the model. Even when head shape is the last term entered in the model, it still explains significant variation in bite force.

	Numerator DF	Denominator DF	F-ratio	*p*-value
Snout-vent length	1	155	256.520	< 0.0001
Head size (PC1)	1	155	74.053	< 0.0001
Body condition	1	155	53.504	< 0.0001
Head shape (PC2)	1	155	15.347	0.0001

Bite force: Given the head shape differences observed between sympatric and allopatric *A. cristatellus*, I tested whether these population differences were related to in changes in bite force. I measured the bite force of 160 male *A. cristatellus*, 80 males from each invasion, divided evenly between sympatric and allopatric sites. As predicted, head shape score had a negative effect on maximum bite force (i.e., individuals with more robust heads had greater bite force), even after controlling for the effects of SVL, PC1 (a proxy for overall head size), and body condition (Table 1.4). Given the population differences in head shape score, it is not surprising that sympatric males had significantly greater bite force than allopatric populations after controlling for SVL ($F_{1,4} = 9.74$, $p = 0.036$). Models that included Population Type (sympatric vs. allopatric) along with body condition, head shape, or both were not stable; these predictors suffered from multicollinearity issues. Since body condition and head shape are strongly correlated, and both attributes differed between sympatric and allopatric *A. cristatellus*, a statistical approach that could incorporate these related factors was warranted.

I used a path analysis approach to evaluate the contribution of each variable to population differences in bite force (Fig. 1.4). Population Type significantly predicted both body condition ($z = 8.23$, $p < 0.001$) and head shape score ($z = -4.26$, $p < 0.001$); sympatric males had greater body condition and lower head shape scores. Body condition and head shape score predicted variation in maximum bite force (body condition: $z = 3.12$, $p = 0.002$; PC2: $z = -4.28$, $p < 0.001$), and body condition also predicted variation in head shape score ($z = -4.99$, $p < 0.001$).

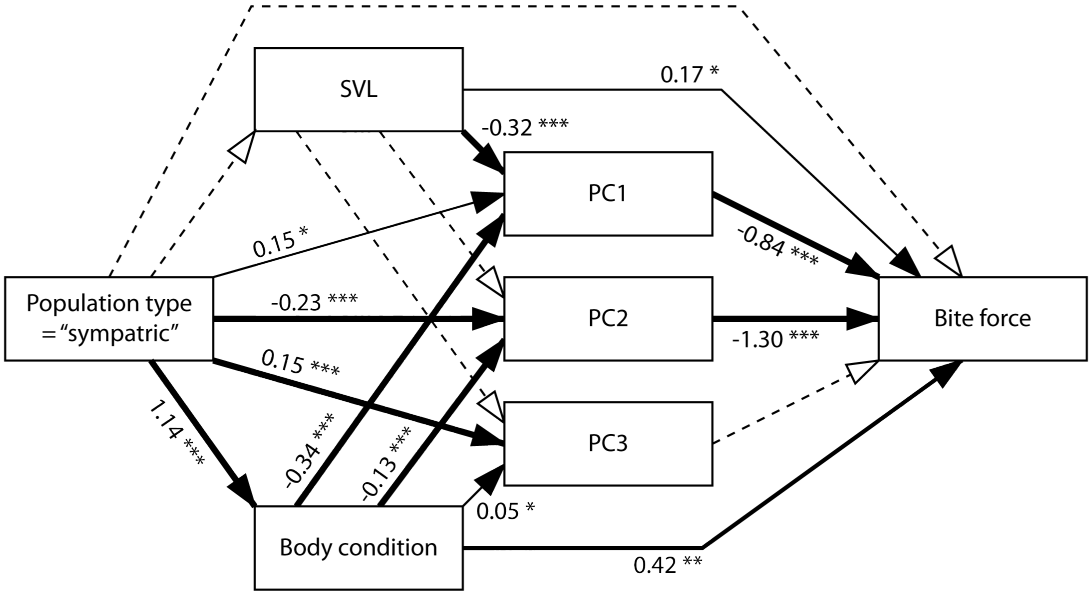


Figure 1.4: Path diagram explaining variation in maximum bite force between sympatric and allopatric populations of *A. cristatellus*. Sympatric and allopatric populations differed in both body condition and head shape score (PC2), and path analysis shows that Population Type had effects on maximum bite force that are mediated by head shape score, body condition, and an indirect effect of body condition through head shape score. Path coefficients did not differ significantly between sub-models fit separately for sympatric and allopatric *A. cristatellus*, suggesting that variation in PC2 and body condition is responsible for driving differences in bite force across populations. Paths with non-significant regression coefficients are shown as dashed lines with unfilled arrows, and significant paths are shows as solid lines with filled arrows. Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

To investigate whether sympatric / allopatric differences in morphology (e.g. body condition and head shape) could explain population differences in bite force, I fit two separate path models to sympatric and allopatric datasets. Initially, I allowed all path coefficients to be estimated freely. Then, for each path in the model, I fit an alternative pair of models in which the coefficient of the path of interest was constrained to be equal between sympatric and allopatric models. Each of these constrained model pairs was then compared to the unconstrained models using a likelihood-ratio test. No path coefficients differed significantly between sympatry and

allopatry (before Bonferroni correction, all $p > 0.05$), suggesting that variation in head shape and body condition drives population differences in maximum bite force.

Finally, I measured bite force in a small sample of allopatric *A. sagrei* ($n = 20$). I was not able to measure bite force in sympatric *A. sagrei*, but sympatric and allopatric *A. sagrei* did not differ in head morphology, so I would not have predicted any differences in bite force among populations. Both sympatric and allopatric *A. cristatellus* had significantly greater bite force than *A. sagrei* (Tukey's test, both $p < 0.001$; Fig. 1.3).

Discussion: I tested for evidence of character displacement in *Anolis sagrei* and *A. cristatellus* from sympatric and allopatric populations in South Florida and Puerto Rico. Sympatric and allopatric *A. sagrei* did not differ in morphology, but sympatric (South Florida) and allopatric (Puerto Rico) *A. cristatellus* differed significantly in body condition, hindlimb length, and head shape. Sympatric male *A. cristatellus* had greater body condition, shorter legs, and more robust heads than allopatric males. These differences were consistent across two separate invasions of South Florida, each originating from a different Puerto Rican source population. Based on population differences in head shape, I predicted that male *A. cristatellus* would have greater bite force in sympatry than in allopatry; an analysis of bite force confirmed this prediction.

Sympatric *A. cristatellus* were in better overall condition than allopatric males. Sympatric populations are also invasive, and invasive populations may be expected to be in better condition if they encounter reduced predation, fewer competitors, or an absence of pathogens and parasites in their invasive range (Liu and Stiling 2006). Can this release from natural enemies explain the enhanced body condition of sympatric *A. cristatellus*? With only one native anole species (the trunk-crown anole *A. carolinensis*), Florida has few predators that specialize on anoles. Many

generalist predators, however, prey on invasive trunk-ground anoles in South Florida (Meshaka 2011). It is not known whether the overall risk of predation differs between the sympatric and allopatric range. There is no difference between sympatric and allopatric sites, however, in the rate of tail loss ($\chi^2 = 1.32$, d.f. = 1, $p = 0.25$), which may reflect predation intensity (Bateman and Fleming 2011). Therefore, reduced predation seems an unlikely explanation for the greater body condition observed in sympatric *A. cristatellus*. Could a reduction in competition explain the increased body condition observed in sympatry? While *A. carolinensis* is the only native anole in Florida, *A. sagrei* is a trunk-ground ecomorph that was established and abundant in the Miami area well before the arrival of *A. cristatellus* (Krysko et al. 2011). In contrast, *A. cristatellus* was the only trunk-ground anole I observed at allopatric sites. Therefore, with an abundant potential rival in Florida, it seems unlikely that competitor release could cause the sympatric increase in *A. cristatellus* body condition that I observed. The incidence of parasites and pathogens could differ between sites; I have no systematic data, however, on the incidence of anole pathogens and parasites in *A. cristatellus* in Miami and Florida. Nevertheless, some anecdotal evidence suggests that parasites may be more frequent in Puerto Rico. While being handled and measured, anoles frequently defecate, and I noted a handful of times in Puerto Rico when helminth parasites were visible in the feces of *A. cristatellus* (unfortunately I could not collect any parasite samples for identification). Despite handling hundreds of anoles in South Florida, I have not observed such parasites while handling *A. cristatellus* anywhere in its invasive range. Little is known about the parasites of *A. cristatellus* (Dyer et al. 2001), and a more systematic assessment of parasite prevalence in the native and invasive range of *A. cristatellus* would be valuable to test whether the parasite-release hypothesis can explain the enhanced body condition of *A. cristatellus* in Florida. Finally, another factor that may influence body condition is prey availability; perhaps

there is simply more prey available for anoles in Florida than in Puerto Rico. Prey availability has been shown to limit the growth and condition of *A. cristatellus* in Puerto Rico (Licht 1974), so increased food availability in Florida might allow increased growth rates or enhanced body condition. A direct test of this hypothesis would require measuring the abundance of possible anole prey at Puerto Rican and Florida study sites.

I observed a shift toward shorter hindlimbs, relative to body size, in sympatric versus allopatric *A. cristatellus*. In *Anolis* lizards, hindlimb length has well-documented functional consequences. Species with longer limbs move faster on large-diameter perches (Losos 1990b, Spezzano and Jayne 2004, Vanhooydonck et al. 2006), and changes in habitat (or in habitat use) have been shown to drive rapid evolution in limb length (Losos et al. 1997, Losos et al. 2006). Limb length is also phenotypically plastic in some anoles; individuals reared on small perches develop shorter legs, while those provided large perches develop longer legs (Losos et al. 2000, Kolbe and Losos 2005). Additionally, leg length is related to jumping performance in *Anolis*, with longer-legged lizards achieving greater acceleration and jumping distance than shorter-legged lizards (Losos 1990b, Toro et al. 2003, Toro et al. 2004). In sympatric populations in South Miami, Salzburg (1984) showed that male *A. cristatellus* were found on larger-diameter perches than male *A. sagrei*. In general, *A. sagrei* is observed in more marginal habitat than *A. cristatellus* (*pers. obs.*) and it has shorter legs, relative to its body length. Assuming these habitat differences existed at the time of secondary contact in Florida, I had predicted that male *A. cristatellus* would evolve even longer legs in sympatry, accentuating existing differences in microhabitat use and morphology (consistent with ecological character displacement). Instead, contrary to this prediction, *A. cristatellus* had relatively shorter legs in sympatry than in allopatry. The reasons for this shift are not clear. Male *A. cristatellus* in this study were generally

sampled from sites with significant human impact (e.g. landscaped areas and heavily disturbed second growth), both in sympatry and allopatry. Nevertheless, it is possible that regional variation in the size of available perches could drive the observed difference in hindlimb length among populations, either through selection or plasticity. Systematic measurements of the perches available at sympatric and allopatric sites would permit a test of this hypothesis. A second alternative is that shorter limbs are an adaptation to the colder temperatures that occur in Florida than in Puerto Rico. Allen's Rule (Allen 1877) posits that organisms have shorter extremities at higher latitudes; while originally conceived to explain geographic variation in body proportions of endotherms, it has occasionally been applied to ectotherms as well (e.g. Yuan-Ting et al. 2006). Consistent with this idea, the tails of male *A. cristatellus* are also relatively shorter in Florida than in Puerto Rico ($F_{1,8} = 88.41$, $p < 0.001$). Indeed, *A. cristatellus* shows greater low-temperature thermal acclimatization ability in South Miami than in its native range (Kolbe et al. *in press*); the same is not true, however, for invasive populations on Key Biscayne, which has a similar climate to South Miami and shows a comparable reduction in hindlimb length. Clearly, more data on the relationship between morphology and cold-temperature physiology is needed to evaluate this hypothesis.

Male *A. cristatellus* have diverged significantly in head shape in sympatry, resulting in greater phenotypic differences between sympatric populations of the two species than between allopatric populations. This sympatric shift is partly explained by population differences in body condition; the measurements of head dimensions in this study necessarily include muscle and other soft tissue between the skull and skin. Even when using analyses that controlled for body condition, however, I found that sympatric and allopatric populations differed in head shape,

with sympatric populations having more robust heads. This shift resulted in exaggerated phenotypic differences between the two species in sympatry, consistent with ECD.

Head shape strongly affects bite force in *Anolis* and other lizards; shorter, wider, and deeper heads are generally correlated with to stronger bite force (e.g. Herrel et al. 2006, Herrel et al. 2007, Huyghe et al. 2008). Based on the sympatric shift I observed in head shape, I predicted that sympatric male *A. cristatellus* would bite harder than allopatric males. The data supported this prediction, and population differences in bite force could be attributed to the effects of head morphology and greater body condition in sympatry. Bite force has obvious implications for prey handling (e.g. Metzger and Herrel 2005, Herrel et al. 2006), and it remains to be tested whether the available prey for anoles differ in size or hardness between sympatric (Florida) and allopatric (Puerto Rico) sites. While similar habitats are present in both areas, a systematic survey of the prey community and comparative diet analysis of *A. cristatellus* in both areas is required to test the influence of diet on selection for increased bite force. For territorial anoles (including *A. sagrei* and *A. cristatellus*), bite force may also significantly predict the outcomes of intraspecific fights; males with greater bite force generally defeat males with weaker bite force in staged territorial contests (Lailvaux et al. 2004, Lailvaux and Irschick 2007).

The sympatric shift I observed in the head shape of *A. cristatellus* is consistent with the hypothesis that competition with *A. sagrei* is driving the evolution of *A. cristatellus* head shape. Three alternative explanations remain, however. First, since the sympatric shift seems to result in greater bite force, alpha-selection is a plausible explanation. Alpha-selection is defined as selection for increased interference competitive ability in sympatry (Gill 1974). If two species compete through interference mechanisms such as territoriality, alpha-selection may favor adaptations that confer greater success in interspecific interference competition (e.g. Hairston

1983). To evaluate alpha-selection as a possible driver of phenotypic evolution in the anoles, it would be necessary to test whether increased bite force gave sympatric male *A. cristatellus* a unique advantage in interspecific contests – an advantage not gained in intraspecific contests. For example, perhaps a greater bite force would allow sympatric males to resolve contests with neighboring *A. sagrei* more quickly, or provide a counter to a specific *A. sagrei* attack strategy. A related possibility (which would not constitute alpha-selection *per se*) is that the overall density of potential interference competitors is greater in sympatry than it is in allopatry, putting a greater premium on traits that influence fighting ability.

The other two alternatives to ECD arise from the fact that there are no known sites in Florida where *A. cristatellus* occurs in the absence of *A. sagrei*. Therefore, "sympatry" and "allopatry" are synonymous with "introduced range" and "native range" in the former species. Rather than interspecific competition, sympatric shifts in head shape could be driven instead by environmental differences between the native and invasive range of *A. cristatellus* – differences unrelated to the presence of *A. sagrei*. Variation in the distribution of prey size, for example, might explain the robust head morphology and increased bite force of sympatric *A. cristatellus*. Experiments that measured the handling times of different prey, coupled with a systematic assessment of the prey size distribution at sympatric and allopatric sites, could be used to test this hypothesis. *A. sagrei*, however, with its weaker bite and more gracile head, has flourished in the same habitats as *A. cristatellus*. So has the native *A. carolinensis*, which has an even more slightly built head and, presumably, a still weaker bite. Since these more slender-headed competitors persist and thrive in Florida, differences in the prey community alone do not constitute a satisfying explanation for the sympatric shift in *A. cristatellus* head shape.

The final alternative is that interspecific competition *has* played a role in the evolution of head shape in *A. cristatellus*, but not competition with *A. sagrei.* The presence or absence of *A. sagrei* is not the only difference in the anole assemblage of sympatric and allopatric *A. cristatellus* sites. Could the sympatric shift in *A. cristatellus* head shape be attributed to competition with another species in Florida, or to release from competition with a co-occurring species in the native range? After all, *A. cristatellus* can be found alongside several other anole species in Puerto Rico, and the sites in Florida where *A. cristatellus* has become established are also home to other invasive species, such as *A. distichus* and *A. equestris*. The intensity of competition between species, however, is predicted to be greatest between species that compete for the same resources (Pacala and Roughgarden 1982, 1985, Rummel and Roughgarden 1985). Among anoles, species that belong to the same ecomorph are the most likely competitors. While *A. cristatellus* is sympatric in parts of its native range with other trunk-ground anoles [e.g. *A. gundlachi* (Hess and Losos 1991) and *A. cooki* (Jenssen et al. 1984, Hertz 1992)], it was the only trunk-ground ecomorph detected at the sampling sites I visited in Puerto Rico for this study. In Florida, *A. sagrei* is the only trunk-ground ecomorph present at the sites where *A. cristatellus* is established. Therefore, competition with *A. sagrei* seems the most plausible explanation for the sympatric shift observed in head shape. Nevertheless, competition experiments in field enclosures could provide considerable insight into the intensity of competition between *A. cristatellus* and its potential competitors, both in Florida and Puerto Rico.

This study revealed sympatric shifts in the morphology of *A. cristatellus*, but not *A. sagrei*. If ECD is responsible for these shifts, why are its effects asymmetric? ECD occurs when species have similar resource requirements and, in the absence of competitors, would be using the same resources (Brown and Wilson 1956). Early models of ECD did not explicitly model the

dynamics of the resource base (e.g. Slatkin 1980), but subsequent theoretical work (e.g. Abrams 1986, 1987, Abrams et al. 2008) has shown that properties of the underlying resource over which competition is occurring can influence the outcome of character displacement. Divergence may not be possible, for example, if the current phenotype of one species is best suited to prey at one end of the prey size distribution. Also relevant is the relative abundance of each species (Stevens and Willig 2000). At present, *A. cristatellus* occurs at similar densities to *A. sagrei* at most study sites. Upon the initial invasion of Florida by *A. cristatellus*, however, *A. sagrei* was already established and abundant, so *A. cristatellus* would have been substantially outnumbered. This will also be the case at the leading edge of its expanding range in Miami. When one species is much more abundant than the other, selection for divergence (e.g. in ECD, reproductive character displacement, etc.) will be stronger on the less abundant species (e.g. Cooley 2007). In this case, if *A. sagrei* and *A. cristatellus* compete for common resources, *A. cristatellus* may have experienced more intense selection favoring divergence in resource-use traits than *A. sagrei*, which could explain the asymmetry in character displacement observed in this study.

The results of this study suggest a number of questions for future work. First, more data is needed to test whether sympatric shifts in morphology – particularly the observed shift in leg length, which is known to be phenotypically plastic – are genetically based or the result of environmental influences during development. Second, while bite force has well-documented behavioral and ecological consequences (Anderson et al. 2008), a more detailed study of the functional morphology of *A. cristatellus* would be a significant step toward understanding the biomechanical basis of bite force shifts, and the possible fitness benefits of having a robust head in sympatry. Finally, experiments that evaluate the relative fighting ability of *A. sagrei* and *A. cristatellus* in sympatry and allopatry could be used to test whether the sympatric shift in bite

force has functional consequences in the context of interspecific territorial contests, and therefore shed light on the potential for alpha-selection in these species.

Although alternative hypotheses cannot be fully discounted, the present study shows that sympatric *A. cristatellus* have undergone morphological shifts relative to allopatric populations. Among these is a divergent shift in head morphology with respect to the congeneric competitor *A. sagrei*, consistent with ecological character displacement. The present study suggests several profitable avenues for further inquiry, and highlights the difficulty of distinguishing between alternative hypotheses to explain morphological shifts between populations. The geographic pattern of variation observed in this study suggests that competition with a congener plays a role in driving phenotypic change. More broadly, invasive species can provide useful test cases for investigating how interspecific competition affects evolution. In studies of evolution in invasive species, the evolutionary consequences of exploitative and interference competition with heterospecifics, both native and non-native, should not be ignored.

Chapter 2: Competitive asymmetry and asymmetrical agonistic character displacement in two invasive *Anolis* lizards in South Florida

Abstract: Interspecific interference competition is an under-studied but potentially important driver of phenotypic evolution in traits that mediate aggressive interactions between species. Agonistic character displacement (ACD) is the process by which interference competition between species drives evolutionary shifts in agonistic signals or competitor recognition. In this study, I used live, tethered territorial intruders to test whether two recently sympatric species, *Anolis sagrei* and *A. cristatellus*, show differential responses to conspecific and heterospecific territorial intruders in sympatry and allopatry. I also assessed the behavioral dominance of the two species in a controlled laboratory environment. I found that while *A. cristatellus*, the larger species, showed similar, moderate levels of aggression toward *A. sagrei* in sympatry and allopatry, *A. sagrei* were significantly less aggressive toward heterospecific rivals in sympatry than in allopatry. In the lab, I found that *A. cristatellus* tended to be behaviorally dominant over *A. sagrei*, consistent with its larger body size and greater bite force. I propose that the reduced heterospecific aggression observed in sympatric *A. sagrei* represents an adaptive response to the presence of *A. cristatellus* – since a small male *A. sagrei* is not likely to win in a fight with a large heterospecific rival, *A. sagrei* males may avoid aggressive confrontations with the latter species. Further work is needed to determine whether these shifts in behavior are genetically based or represent developmentally plastic responses to the presence of heterospecifics.

Introduction: When two species compete through behavioral interference, their interactions may drive phenotypic evolution in traits that mediate interference competition. This process is called *agonistic character displacement* (hereafter ACD; Grether et al. 2009). Historically, ACD has not received as much theoretical or empirical attention as ecological character displacement, a process driven by exploitative competition (ECD; Brown and Wilson 1956, Schluter 2000), or reproductive character displacement, a process driven by reproductive interference (RCD; Brown and Wilson 1956, Gröning and Hochkirch 2008, Pfennig and Pfennig 2009). While ACD and related processes have been considered forms of ECD by some authors (e.g. Vallin et al. 2011), the evolutionary dynamics of ACD are distinct from those of either ECD or RCD, and ACD yields unique predictions about the evolutionary outcomes of interspecific competitive interactions (Grether et al. 2009).

Interspecific interference competition, such as interspecific territoriality, has potential fitness costs (e.g. injury or death, time wasted fighting with heterospecifics) and benefits (e.g. exclusive use of feeding areas, access to resources) (Grether et al. 2009, Peiman and Robinson 2010). The magnitudes of these costs and benefits affect whether interspecific territoriality is adaptive. If interspecific territoriality is adaptive, ACD predicts that selection will favor traits that facilitate territorial interactions between species (Cody 1969). If not, ACD predicts that selection will favor traits that reduce territorial interactions between species (Lorenz 1962). Though originally formulated as verbal arguments, these predictions have been formalized through an individual-based model of ACD (Grether et al. 2009). In the model, interspecific niche overlap is equal to the fitness cost of sharing a territory with a heterospecific, expressed as a proportion of the cost of sharing a territory with a conspecific. Consistent with the predictions made from earlier verbal models, increasing the extent of niche overlap between two species

shifts the predicted evolutionary outcome of ACD from agonistic signal divergence (at low levels of niche overlap) to convergence (at high niche overlap) (Grether et al. 2009).

For one individual to recognize another as a competitor, it must evaluate phenotypic cues of the potential rival and respond in an appropriate way (Grether 2011). From the perspective of any individual, a *competitor* may be defined as another individual that shares common resources, and whose access to those resources can be limited through behavioral interference. Under this definition, both conspecifics and heterospecifics may be competitors. Individuals that fail to respond to heterospecific competitors as such may suffer fitness costs from the depletion of shared resources, just as they would if they failed to treat conspecifics as competitors (e.g. Rohwer 1973, Peiman and Robinson 2007). Likewise, individuals that treat heterospecific non-competitors as competitors may suffer fitness costs from unnecessary fights, as well as wasted time that could be spent more profitably on other activities (e.g. Alatalo et al. 1994, Anderson and Grether 2010b). Therefore, selection should favor traits that improve the accuracy of discrimination between competitors and non-competitors.

Shifts in the recognition of competitors may be accomplished through changes in the phenotypic cues used for recognition (often, but not always, the signals used in interference competition), the cognitive mechanisms of recognition, or both (Grether et al. 2009, Grether 2011). Such evolutionary shifts are best observed in pairs of species with partially overlapping geographic ranges. When heterospecifics are competitors, ACD predicts sympatric convergence in recognition cues and increased heterospecific recognition in sympatry. If heterospecifics are non-competitors, ACD instead predicts sympatric divergence in recognition cues and reduced heterospecific recognition in sympatry. Empirical evidence for both processes can be found in the literature (reviewed in Grether et al. 2009). For example, brook sticklebacks in Ontario are

found in sympatry and allopatry with ninespine sticklebacks, and appear to compete for common resources (Gray and Robinson 2002, Gray et al. 2005). Sympatric brooks are more aggressive toward ninespines than are allopatric brooks, and these population differences persist when the offspring of wild populations are raised in a common laboratory environment, suggesting that this shift in behavior has a genetic basis (Peiman and Robinson 2007). In Mexico, heterospecific *Hetaerina* damselflies defend mating territories on the same streams, but do not compete for the same mates. Anderson and Grether (2010b, a) found that males from sympatric populations are less aggressive toward heterospecific territorial intruders than males from allopatric populations, and that each species' wing coloration diverged from the other in populations where heterospecifics were numerically dominant.

As a theoretical framework, ACD has the potential to explain geographic variation in agonistic signals and aggression toward heterospecifics. Thus far, there has been no theoretical consideration of the role of species' behavioral dominance in ACD (Grether et al. 2009), but the costs and benefits of interspecific interference competition likely differ between species that are unequal in fighting ability – the costs of fighting may differ between species, and the expected payoff of interspecific fights will differ between behaviorally dominant and subordinate species. Asymmetries in interspecific aggression and dominance may be related to body size (e.g. Rice 1978, Rychlik and Zwolak 2006), but behavioral dominance may also be influenced by species characteristics other than body size (e.g. Pearson and Rohwer 2000, Langkilde and Shine 2007). I hypothesize that in general, subordinate species incur greater costs of fighting than dominant species, and that the expected payoff of an interspecific fight is lower for a subordinate species (due to its lower chance of victory). Therefore, the benefits of interspecific territoriality are fewer

for a behaviorally subordinate species than for a behaviorally dominant species, and ACD should result in divergent recognition cues and reduced interspecific aggression in subordinate species.

Territoriality is one pervasive form of interference competition, and many animals use territoriality to ensure exclusive access to space used for mating, feeding, and other activities. Lizards in the genus *Anolis* (hereafter anoles) defend all-purpose territories and are a model taxon for studying the economics of territory defense (e.g. Stamps 1977), the formation of territories (e.g. Stamps and Krishnan 1994a, b, 1995, 1998), the influence of habitat on territoriality and territorial displays (Leal and Fleishman 2002, 2004, Johnson et al. 2010, Ord 2011), and the recognition of territorial competitors (Losos 1985, Ord and Martins 2006, Ord and Stamps 2009). During territory defense, anoles use a combination of push-ups, head-bobs, and dewlap displays (which involve a colorful throat-fan) to advertise their territory ownership and signal aggressively to rival males (Ord and Martins 2006). Losos (1985) manipulated the color of the dewlap in two sympatric anoles and found that anoles use dewlap color as a competitor recognition cue. Evidence suggests that the pattern of head-bob displays also conveys species identity information; species living in more speciose anole assemblages tend to have more complex head-bob displays (Ord and Martins 2006).

In the Greater Antilles, many anoles can be categorized into discrete *ecomorphs*, each defined by a suite of morphological, behavioral, and habitat traits. Anoles in the same ecomorph are expected to compete for common habitats and resources; therefore, when two species of the same ecomorph are sympatric, they typically differ significantly in size, thermal ecology, or another important ecological trait, facilitating their coexistence (Losos 2009). Territoriality in anoles may occur between heterospecifics as well as conspecifics, and species belonging to the same ecomorph are natural candidates for interspecific territoriality. Indeed, intense interspecific

interactions – approaching the intensity of intraspecific aggression – have been observed in Puerto Rico between sympatric *Anolis cristatellus* and *A. gundlachi* (Hess and Losos 1991), and between *A. cristatellus* and *A. cooki* (Jenssen et al. 1984). Both of these cases involve pairs of anole species that belong to the same ecomorph (Williams 1972). Hess and Losos (1991) compared the behavior of sympatric and allopatric *A. cristatellus* to test whether selection favored reduced or heightened aggression toward a heterospecific rival, *A. gundlachi*, in sympatry. They found no difference in heterospecific aggression between the populations, suggesting that there was no strong selection for increased or reduced heterospecific aggression in sympatry. Tokarz and Beck (1987) tested whether two sympatric anole species belonging to different ecomorphs, a trunk-crown species (*A. carolinensis*, a native of the southeastern United States) and a trunk-ground species (*A. sagrei*, an invasive species in Florida, native to Cuba) responded to each other as territorial competitors. In this case, neither species responded intensely to intruders that belonged to a different ecomorph.

In southern Florida, two trunk-ground anoles, the Cuban species *A. sagrei* and the Puerto Rican species *A. cristatellus*, are both invasive and have become established sympatrically in the Miami area. *A. sagrei* has been introduced into Florida several times beginning in the late 19th century, and is now ubiquitous in Southern Florida (Kolbe et al. 2004, Krysko et al. 2011, Meshaka 2011). *A. cristatellus* is a more recent arrival, having been first recorded in South Florida in the 1970s (Brach 1977, Kolbe et al. 2007, Krysko et al. 2011). Salzburg (1984) showed that removing *A. cristatellus* from sympatric sites in South Miami caused shifts in habitat use of *A. sagrei*, but it is not clear whether these shifts were caused by relaxed interference competition from *A. cristatellus* or were mediated through exploitative competition or some other process. Moreover, it is not known whether *A. sagrei* similarly affects the habitat

use of *A. cristatellus*. At some locations formerly occupied by *A. sagrei*, *A. cristatellus* has almost completely replaced *A. sagrei* (Meshaka 2011). A preliminary study I conducted in South Miami in 2009 suggested that males of both species respond aggressively to staged territorial intrusions by both con- and heterospecific males, though territorial residents tended to be less aggressive toward heterospecific than conspecific intruders (N. Losin, *unpubl. data*).

In this study, I tested the hypothesis that aggressive interactions between male *A. sagrei* and *A. cristatellus* in their recent contact zone in South Florida have driven adaptive shifts in heterospecific aggression through ACD. I conducted a laboratory-based test in experimental arenas to evaluate the relative fighting ability of each species. I predicted that *A. cristatellus*, the larger species, would be behaviorally dominant in interspecific contests. I then simulated natural territorial intrusions by presenting wild males with tethered male intruders of each species, and assessed the resident males' responses to each intruder. I made the following predictions: 1) Because *A. sagrei* is generally smaller than *A. cristatellus*, it would not benefit from aggression toward male *A. cristatellus*; therefore, *A. sagrei* males would show reduced aggression toward *A. cristatellus* intruders in sympatry, or uniformly low heterospecific aggression in sympatric and allopatric sites. 2) *A. cristatellus*, the larger species, would benefit from aggression directed at *A. sagrei*, so *A. cristatellus* males would show heightened heterospecific aggression in sympatric populations, or uniformly high heterospecific aggression across sites.

Methods:

Study sites: In the Miami area, *Anolis sagrei* is widespread, while *A. cristatellus* has a restricted, discontinuous range in South Miami and on nearby Key Biscayne. The South Miami and Key Biscayne populations appear to have resulted from independent introductions, originating from

different areas of Puerto Rico (Kolbe et al. 2007). There are no allopatric sites for *A. cristatellus* in Florida; *A. sagrei* occurs – at least at low abundances – everywhere *A. cristatellus* is found. For field experiments with *A. sagrei*, I selected three sympatric and three allopatric sites, all in South Miami. I used existing survey data (J. J. Kolbe, *pers. comm*.) and *in situ* observations to classify these sites as sympatric or allopatric based on the presence or absence of *A. cristatellus*. For *A. cristatellus*, I selected two sympatric sites in Florida, one in South Miami and one on Key Biscayne, and two allopatric sites in Puerto Rico. One Puerto Rican site was in the San Juan area (the putative source of the Key Biscayne population) and the other was in northeastern Puerto Rico near Fajardo (the putative source of the South Miami population) (Kolbe et al. 2007).

Resident males: At each site, I spent one day capturing, marking, and re-releasing resident males. Male anoles were captured by hand or with a polyester noose at the end of a fishing rod. After capture, each male was weighed, measured, and given a unique alphanumeric marking on its flanks with a non-toxic, fine-tip white paint marker (Pentel, Inc.). These markings could be read easily through binoculars, and they persisted until a lizard shed its skin. Since the study species shed their skin approximately every two weeks (*pers. obs.*), most males remained marked for at least 2-4 days after marking, the period during which tethered-intruder trials took place. After marking, each resident was re-released at its capture site.

Intruder males: On the same day that resident males were marked (see above), I captured intruder males of both species. For sympatric sites, intruders of both species were captured at nearby locations; for allopatric sites, conspecific males were captured nearby and heterospecific males were captured from the closest possible sympatric sites. In all cases, I avoided capturing

intruders within ~100m of the areas where I marked residents, because there is some evidence for individual neighbor recognition in *Anolis* (Paterson and McMann 2004). Each intruder male was weighed, measured, and marked using the procedures described in the previous section. Intruders were held individually in 1-quart plastic food containers with holes in the lid for air exchange. Each container had a slightly moistened paper towel, which provided shelter and maintained humid conditions in the container. Intruder males were held for 2-3 days, during which they served as a tethered intruder no more than 1 time per day. Each afternoon, I sprayed each container with water to allow the intruders to drink and to re-moisten the paper towel. If poor weather conditions required intruders to be held for more than 2 days, I added 2-3 small crickets or mealworms to the container on the second day. The *A. sagrei* males used as intruders in trials with *A. cristatellus* residents in Puerto Rico were collected at sympatric sites in South Miami. These males were held for up to 7 days while behavioral trials were conducted in Puerto Rico (with water and food provided as described above), but no individual was used as an intruder more than 2 times during this period.

Behavioral trials: At each site, after marking resident males I spent 2-3 days re-sighting resident males and performing behavioral trials with tethered intruders. When a male was re-sighted, it was deemed "on territory" if it was on the same perch on which it was initially captured, or if it was on a perch within 3m of the initial capture site *and* in the characteristic downward-facing, head-up "survey" posture that male trunk-ground anoles assume when they are at rest and alert, waiting for potential prey (Losos 2009). When I re-sighted a marked resident male on its territory, I attempted a behavioral trial with that resident. If it was a male's first behavioral trial, I selected the intruder male at random from the available intruders; if a male had already

undergone a behavior trial with one intruder species on the previous day, I selected an intruder of the other species at random.

I tethered intruders in a similar way to other studies on territorial behavior in *Anolis* lizards (e.g. Hess and Losos 1991, Calsbeek and Marnocha 2006); I fitted the intruder with an embroidery-thread harness around the waist, which did not inhibit its locomotion or aggressive displays. The harness was on a 0.75m tether attached to the end of a 3m fishing pole, which allowed me to place the intruder within the resident's territory without disturbing the resident. I carefully sat within 3m of the resident male, making sure not to startle it with my approach. The intruder remained inside a cotton bag, out of the resident's view. Once I was in place, I began a 5-minute pre-trial observation period, the purpose of which was to allow the resident to become acclimated to my presence. At the end of this period, I retrieved the intruder from its cotton bag and used the fishing pole to introduce the intruder into the resident's territory. Whenever possible, I placed the intruder on a conspicuous perch 1-1.5m from the resident. When the intruder was in place and in clear view of the resident, I began the trial.

Each trial lasted 8 minutes; a preliminary experiment (NL, *unpubl. data*) indicated that the most aggressive behaviors occurred in the first 5 minutes after introducing an intruder into a male's territory, so 8 minutes captured most aggressive responses from resident males. During the 8-minute trial, I dictated the resident's agonistic behaviors, including approaches toward the intruder, push-ups, head-bobs, dewlap displays, lunges, bites, jaw-locking, and other, less frequent behaviors. At the end of the 8-minute trial, I retrieved the intruder and replaced it in its plastic container. Occasionally, a trial would be interrupted before 8 minutes had elapsed (e.g. if the resident disappeared, or if resident and intruder were both startled by a passing hawk). Data from these trials were not discarded, but the trial length was taken into account in the subsequent

analyses (see below). Residents were not subjected to multiple behavioral trials in the same day; after one successful behavioral trial with each resident, I attempted to re-sight the same resident on subsequent days to conduct a behavioral trial with an intruder of the other species.

Assessing dominance: Assessing dominance in tethered-intruder experiments is not possible, because there is an inherent asymmetry in these interactions – the intruder has been removed from its own territory, handled, and fitted with a harness, while the resident is unrestrained and defending its own territory. Therefore, I conducted a lab experiment to assess the behavioral dominance of *A. sagrei* and *A. cristatellus* in interspecific contests.

I collected 20 male *A. cristatellus* from two sites in Puerto Rico, and 20 male *A. sagrei* from two allopatric sites in South Miami. I use allopatric males of each species to eliminate the effects of prior experience with heterospecifics on their aggression and behavioral dominance. The situation in which males of two species, each having no experience with the other species, are competing over shared space is the best analogue of secondary contact between formerly allopatric species. I brought all anoles into the lab at UCLA, being careful to keep each species visually isolated from the other during transport and housing in the lab. Anoles were housed individually in the lab to prevent aggressive interactions among males, and were maintained in the lab for several weeks before behavioral experiments began. I assigned each male to one heterospecific rival; pairs were matched as closely as possible by standardized size (i.e. large *A. cristatellus* were paired with large *A. sagrei*). Each pair was introduced into a large, screen-sided arena enclosure, 1.5m long x 1m tall x 0.5m deep. Initially, rivals were placed on either side of two opaque barriers that restricted their access to the center section of the arena (cf. Perry et al. 2004). Males were allowed to acclimate to the arena for at least 1 week before the barriers were

removed. After this acclimation period, I removed the opaque barriers and allowed both males access to the center section of the arena, which included a T-shaped perch under a 38w incandescent heat lamp. For the first 1h following barrier removal, I recorded all aggressive behaviors exhibited by each individual. For the next 4 days, I recorded each male's location in the arena hourly from 1300-1600h (a total of 16 observations on each male over a 4-day period).

In addition to these paired arena trials, males of each species were introduced into the arena enclosures individually, so their behavior could be assessed in the absence of any rivals. Males were introduced to arenas (this time with no barriers in place) and allowed to acclimate to their new enclosures for approximately 48 hours. Then, for 4 consecutive days, as in the paired trials, I recorded each male's location in the arena hourly from 1300-1600h, resulting in a similar series of observations as those collected during the paired arena trials.

Analysis: In both the tethered-intruder and arena experiments, the outcome variables were counts (e.g. number of aggressive displays, or number of observations during which an individual used the basking perch) and latencies (e.g. the latency to first attack). Count data were analyzed using negative binomial regression models as implemented in the R package *glmmADMB*, which uses the open-source AD Model Builder optimizer to fit nonlinear models (Fournier et al. 2012, Skaug et al. 2012). Differences in trial length – a result of trials that were cut short for various reasons – were incorporated by including trial length as an offset parameter in the model. Parameter estimates and standard errors were extracted from these models and used to calculate t-statistics, which were evaluated using degrees of freedom calculated using a standard between-groups / within-groups method for mixed-effects ANOVA. Latency data were in some cases right-censored (e.g. if a behavior did not occur during the trial) and did not fit the distributional

assumptions of standard regression. Therefore, I analyzed the latency variables using a mixed-effects Cox regression approach, as implemented in the R package *coxme* (Therneau 2011).

Results:

Responses of wild males to conspecific and heterospecific territorial intruders: I presented conspecific and heterospecific male intruders to resident males of both species (resident *A. sagrei*: n = 19 allopatric, n = 20 sympatric; resident *A. cristatellus*: n = 19 allopatric, n = 26 sympatric). For each species, I tested whether resident males responded differently to conspecific versus heterospecific intruders, and whether sympatric and allopatric residents differed in their responses to each intruder species. The intensity of territorial responses was quantified in two ways: total signals (the sum of pushups, head-bobs, and dewlap displays given by the resident during a trial) and total fights (the sum of lunges, bites, and bouts of jaw-locking initiated by the resident during a trial). Including "site" as a random effect did not significantly improve the fit of these models, and is not included in the models presented below.

For male *A. sagrei*, there was no effect of intruder species on signaling behavior, but there was a significant interaction between intruder species and population type (i.e. sympatric vs. allopatric; Table 2.1, Fig. 2.1a). Analyzing sympatric and allopatric data separately shows that while allopatric *A. sagrei* did not distinguish between intruder species in their signaling behavior (t = -1.41, df = 18, p = 0.18), sympatric males performed fewer displays toward heterospecific intruders than toward conspecific ones (t = -3.03, df = 19, p = 0.007). A qualitatively similar pattern was observed in the data on fighting behavior, but in the latter case, the interaction between intruder species and population type was not significant (t = -1.08, df = 37, p = 0.29; Fig. 2.1b).

Table 2.1: Results of a negative binomial regression, showing a sympatric shift in *A. sagrei* aggressive signaling behavior toward *A. cristatellus* intruders. Male *A. sagrei* show increased discrimination (i.e. reduced aggressiveness toward heterospecific *A. cristatellus* intruders) in sympatry vs. allopatry.

Model term	Estimate	Std. error	*t* value	D.F.	*p* value
Intercept	4.74000	0.11825	40.08	37	< 0.001
Heterospecific (vs. Conspecific)	-0.12299	0.15200	-0.81	37	0.424
Sympatric (vs. Allopatric)	-0.00448	0.16551	-0.03	37	0.978
*Interaction (Heterospecific * Sympatric)*	-0.45778	0.21370	-2.14	37	0.039

Next, I tested whether resident *A. sagrei* differed in their latency to respond to each species of intruder, and whether these latencies differed between sympatric and allopatric residents. I analyzed resident males' latency to signal, latency to approach the intruder, and latency to fight. I found that the latency of male *A. sagrei* to signal to, approach, or fight a rival did not depend on the intruder's species (all $p > 0.1$). Allopatric males, however, were quicker to signal toward intruders, regardless of species, than sympatric males ($z = -2.32$, $p = 0.02$). A qualitatively similar pattern was observed in the latency to approach and to fight, but neither effect was significant (both $p > 0.1$; Fig. 2.2a).

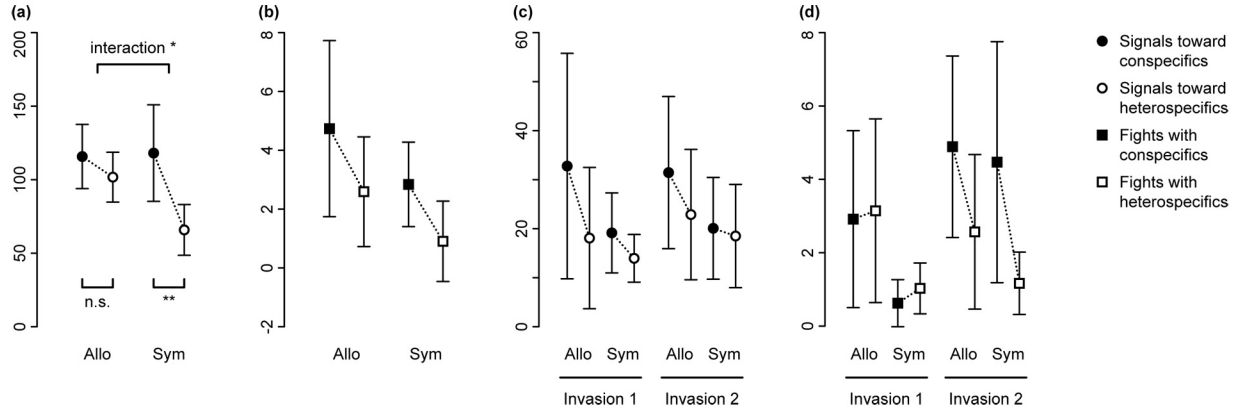


Figure 2.1: Behavior of *A. sagrei* and *A. cristatellus* residents toward conspecific and heterospecific territorial intruders during staged intruder presentations. (a) Number of *A. sagrei* signaling behaviors (pushups, head-bobs, and dewlap displays). (b) Number of *A. sagrei* fighting behaviors (lunges, bites, and jaw-locking). (c) Number of *A. cristatellus* signaling behaviors. (d) Number of *A. cristatellus* fighting behaviors. In panels (a)-(d), filled symbols represent responses to conspecific intruders, while unfilled symbols represent responses to heterospecific intruders. Circles represent means of signaling behaviors, and squares represent mean fighting behaviors. Error bars represent 95% confidence intervals of the mean. In panels (c) and (d), "Invasion 1" includes allopatric males in Fajardo, PR and sympatric males in South Miami, FL. "Invasion 2" includes allopatric males in San Juan, PR and sympatric males on Key Biscayne, FL. Key to significance symbols: * $p < 0.05$.

For male *A. cristatellus*, the results were quite different. Because *A. cristatellus* males were tested in allopatric and sympatric populations that represented two independent secondary contact events (i.e., two separate invasions of *A. cristatellus* into Florida), I included "invasion" as a fixed effect in these models. Resident males showed a marginally non-significant tendency to signal more intensely toward conspecific than heterospecific intruders (t = -1.98, df = 42, p = 0.054; Fig. 2.1c), but sympatric and allopatric males did not differ in their relative responses to each intruder species (t = -0.92, df = 41, p = 0.36). The two invasions did not differ in signaling intensity, and there were no significant interactions involving invasion (all $p > 0.1$). Sympatric males initiated fights at lower rates than allopatric males (t = -2.70, df = 41, p = 0.01; Fig. 2.1d), but the rate of fighting was not affected by the species of the intruder (t = 0.61, df = 42, p = 0.54). Interestingly, there was a significant interaction between invasion and intruder species (t = -2.22, df = 42, p = 0.032; Fig. 2.1d); in terms of their fighting behavior, males in the San Juan / Key Biscayne invasion discriminated more between conspecific and heterospecific intruders than did males in the Fajardo / South Miami invasion (when analyzed separately, however, in neither invasion did intruder species have a significant effect on resident fighting behavior).

Resident *A. cristatellus* did not differ in their latency to signal or approach an intruder based on the intruder's species or their own population of origin (all $p > 0.1$; Fig. 2.2b). For latency to fight, however, I found that males in the San Juan / Key Biscayne invasion were quicker to fight than males in the Fajardo / South Miami invasion (z = 2.59, p = 0.001). There was also a marginally significant trend for males in the San Juan / Key Biscayne invasion to discriminate against heterospecifics (i.e., greater latency to fight with heterospecifics than with conspecifics) to a greater extent than males in the Fajardo / South Miami invasion (z = -1.79, p = 0.074), consistent with the intensity of fighting behaviors observed in *A. cristatellus* (see above).

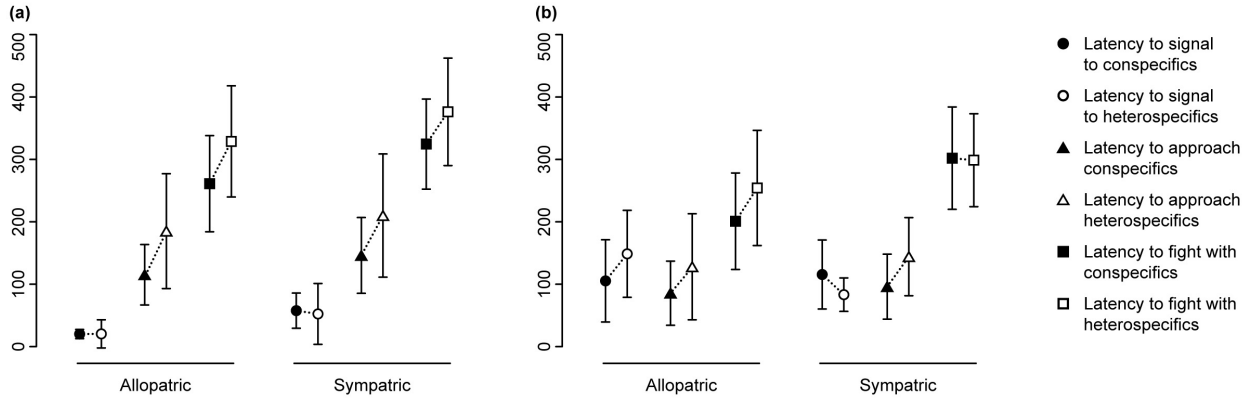


Figure 2.2: Behavioral latency of *A. sagrei* and *A. cristatellus* residents during staged intruder presentations. (a) *A. sagrei* behavioral latency (s). (b) *A. cristatellus* behavioral latency (s). Filled symbols represent mean responses to conspecific intruders, while unfilled symbols represent mean responses to heterospecific intruders. Error bars show 95% confidence intervals of the mean. Key to symbols: circles represent latency to perform signaling behaviors (pushups, head-bobs, and dewlap displays), triangles represent latency to approach the intruder, and squares represent latency to perform fighting behaviors (lunges, bites, and jaw-locking).

Behavioral dominance in staged contests: I recorded each male's behavioral response to its heterospecific rival during the first hour of interaction. Male *A. sagrei* signaled more intensely than their *A. cristatellus* rivals ($t = 3.97$, df = 12, $p = 0.002$), but neither species was more likely than the other to engage in fighting behavior ($t = -1.02$, df = 12, $p = 0.33$; Fig. 2.3a). In terms of behavioral latency, neither species was quicker to signal ($z = 1.30$, $p = 0.19$) or fight ($z = -1.05$, p = 0.29), but male *A. cristatellus* were quicker to approach heterospecific rivals than male *A. sagrei* ($z = -2.76$, $p = 0.006$; Fig. 2.3b).

These data on aggression, however, do not directly address the question of behavioral dominance. We allowed each pair of males to interact for 4 days after their initial meeting, and monitored their use of space in the enclosure. In a sample of males that were introduced into the arena enclosures without a rival male present, the central basking perch was occupied far more often than expected by chance; while the perch constituted less than 1% of the available perching

surface in the enclosure, anoles spent, on average, nearly three-quarters of their time on the perch (mean = 72.9%, sd = 26.6%). The two species did not differ in the amount of time spent on the preferred perch when they were in the cage alone (t = -0.06, df = 23, p = 0.96). When paired, however, male *A. cristatellus* tended to spend more time on the preferred perch than their *A. sagrei* rivals (t = -2.13, df = 12, p = 0.054; Fig. 3.3c). This tendency did not meet the strict threshold for statistical significance (α = 0.05), but given this experiment's relatively small sample size (n = 13 heterospecific pairs), the data suggest that *A. cristatellus* may be behaviorally dominant in interspecific contests.

Discussion: I investigated the territorial behavior of two anole species, *Anolis sagrei* and *A. cristatellus*, at sympatric and allopatric sites. I found that male *A. sagrei* performed fewer aggressive signaling behaviors toward heterospecific than conspecific intruders in sympatry, but not in allopatry. Allopatric *A. sagrei* also signaled to intruders more quickly than sympatric *A.*

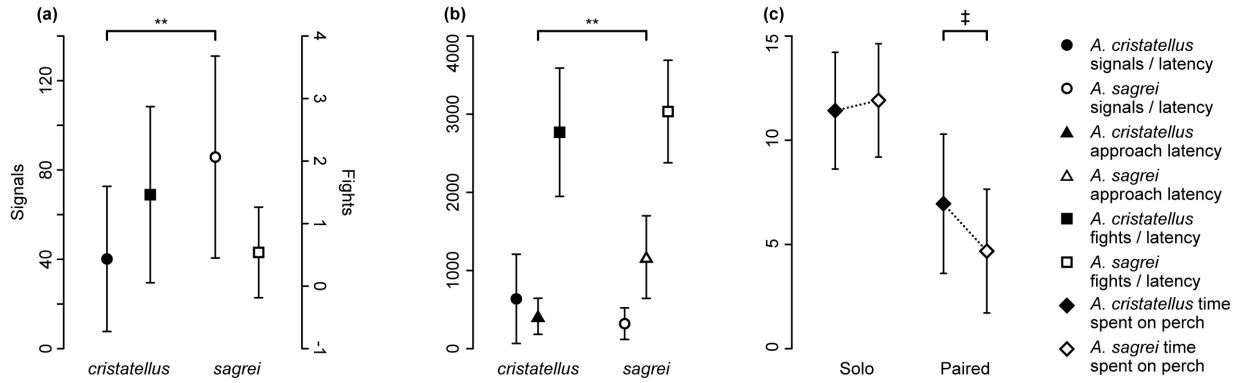


Figure 2.3: Behavior of male *A. sagrei* and *A. cristatellus* during staged contests in experimental arenas. (a) Signaling (pushups, head-bobs, and dewlap displays) and fighting behaviors (lunges, bites, and jaw-locking) of both species. Circles represent signaling means, while squares represent fighting means. Signaling data uses the y-axis on the left side of the figure; fighting data uses the y-axis on the right. (b) Behavioral latency of each species. Signaling latency is represented by circles; approach latency by triangles; and fighting latency by squares. (c) Mean number of observations during which individuals were perched on the contested central basking perch, both during solo and paired trials. Error bars represent 95% confidence intervals of the mean. *A. cristatellus* means are represented by filled symbols, and *A. sagrei* means by unfilled symbols. Key to significance symbols: ‡ $p < 0.1$, ** $p < 0.01$.

sagrei. In contrast, resident male *A. cristatellus* tended to signal less intensely to heterospecific than conspecific intruders, regardless of their own population of origin. Allopatric *A. cristatellus* engaged in more fighting behavior with intruders, regardless of their species, than sympatric *A. cristatellus*. In staged interspecific contests in the laboratory, male *A. sagrei* signaled more intensely than male *A. cristatellus*, but *A. cristatellus* tended to be behaviorally dominant, occupying a preferred basking perch more often than *A. sagrei* rivals.

Animals that compete through aggressive interference are expected to behave more aggressively toward conspecific than toward heterospecific rivals (Grether et al. 2009, Peiman and Robinson 2010). Conspecifics share similar resource requirements and may be competitiors for mates, so the potential benefits of conspecifics aggression are likely to be greater than those of heterospecific aggression. In studies that have examined aggression toward heterospecifics and conspecifics, however, results have been mixed (Ord and Stamps 2009, Peiman and Robinson 2010, Ord et al. 2011). Cases in which species behave aggressively toward heterospecific territorial rivals have been interpreted either as adaptive interspecific territoriality (Orians and Willson 1964, Cody 1969) or as maladaptive misdirected aggression (Murray 1971, 1976), and the literature contains cases that appear to support each interpretation.

Comparing the responses of sympatric and allopatric populations toward con- and heterospecific rivals can yield novel insight about the adaptiveness and, in turn, the evolution of interspecific territoriality (Grether et al. 2009). As mentioned above, there was no overall effect of intruder species on territorial aggression in male *A. sagrei*; sympatric and allopatric males, however, differed significantly in their relative responses to con- and heterospecific intruders. Sympatric males showed reduced aggressive signaling toward *A. cristatellus* intruders, while allopatric males did not. Sympatric males were also slower to signal than allopatric males,

regardless of the intruder's species. Sympatric male *A. sagrei* may not benefit from behaving aggressively toward male *A. cristatellus*; this could occur either if a) the costs of fighting with *A. cristatellus* (which are larger than *A. sagrei*, on average) are too high, or b) the two species do not overlap enough in their resource requirements to warrant interspecific territorial behavior. In either case, reduced heterospecific aggression in sympatric *A. sagrei* could be interpreted as an adaptive shift in behavior driven by the presence of *A. cristatellus*. If discriminating between two rival species benefits sympatric *A. sagrei*, this could also explain the greater latency to signal in sympatric males. Identifying a rival likely takes time; if so, allopatric males, which are not under selection to discriminate between rival species, should not waste time assessing opponents before initiating an aggressive response, because all of their rivals are likely to be conspecifics.

In contrast to the results with *A. sagrei* residents, I found no effect of sympatry on the relative responses of resident *A. cristatellus* to con- and heterospecific intruders. Instead, male *A. cristatellus*, whether in sympatry or allopatry, showed a non-significant tendency to perform more signals toward con- than heterospecific intruders. This finding suggests that the reason for the diminished heterospecific aggression in sympatric *A. sagrei* is not insufficient niche overlap between species; if that were the case, I would have expected a similar sympatric reduction in heterospecific aggression in *A. cristatellus*. Instead, since the two species belong to the same ecomorph and share similar diet and habitat, I predicted that as a result of this likely niche overlap, aggression of *A. cristatellus* toward *A. sagrei* would be similar between sympatric and allopatric *A. cristatellus* populations, or perhaps even greater in sympatry because *A. cristatellus* is behaviorally dominant. The data are consistent with this interpretation, but do not provide unambiguous evidence for an adaptive role of interspecific aggression in *A. cristatellus*. An alternative interpretation of these results is that selection does favor increased (or diminished)

responses to heterospecific competitors in sympatry, but there has not been sufficient time to evolve an appropriate response.

Male *A. cristatellus* in Invasion 1 discriminated between species more than males in Invasion 2, in terms of their fighting behavior. The reason for this behavioral difference between invasions is not clear, but dewlap color may play a role in species recognition (Williams and Rand 1977, Losos 1985). The dewlap of *A. sagrei* is a rich scarlet color, while the dewlap of *A. cristatellus* is yellow in the center and orange at the margin. Male *A. cristatellus* in Invasion 1 (Fajardo and South Miami) have richer, more chromatic dewlaps than the Invasion 2 (San Juan and Key Biscayne) males (N. Losin, *unpubl. data*), which might cause greater confusion between the dewlap color of *A. sagrei* and conspecifics at these sites. Regardless of site, however, species differences in dewlap color are much greater than intraspecific variation among populations.

Why would a sympatric shift in heterospecific aggression occur in one species, but not the other? I predicted that selection would favor reduced interspecific aggression in the smaller species, because that species would likely be behaviorally subordinate to the larger species. The data on the territorial responses of *A. sagrei* are consistent with this prediction, but are *A. sagrei* behaviorally subordinate to *A. cristatellus*? In a laboratory experiment, I found that although the evidence of aggressive asymmetries between the two species was mixed – *A. sagrei* signaled more intensely than *A. cristatellus*, but *A. cristatellus* was quicker to approach a heterospecific rival – *A. cristatellus* tended to monopolize a basking perch that was preferred by both species. This finding suggests a competitive asymmetry between the species. Several lines of evidence support the notion that *A. cristatellus* is the behaviorally dominant species. Male *A. cristatellus* are larger, have larger heads, and bite harder than male *A. sagrei* (N. Losin, *unpubl. data*). Body size influences the outcomes of intraspecific interactions in *Anolis* (Tokarz 1985). Bite force is

also an important determinant of intraspecific fighting ability in anoles (Lailvaux and Irschick 2007). Authors who have observed both species in sympatry in Miami note that *A. cristatellus* has displaced *A. sagrei* from many areas where *A. sagrei* formerly thrived (while the reverse scenario has not been observed), again suggesting that *A. cristatellus* may be competitively dominant over *A. sagrei* (Meshaka 2011). Finally, in a species-removal experiment in South Miami, Salzburg (1984) found that removing *A. cristatellus* from experimental plots caused shifts in *A. sagrei* habitat use consistent with behavioral exclusion of *A. sagrei* from preferred microhabitats (note, however, that Salzburg's data should be interpreted with some caution; see discussion of Salzburg's methods in Ch. 3). On the whole, the evidence points to a competitive asymmetry between the two species, with *A. cristatellus* being dominant in interspecific contests. This is consistent with my predictions, data from a laboratory experiment, and data on sympatric behavioral shifts in *A. sagrei*. I used allopatric males in the laboratory experiment, because my goal was to simulate the encounters between naïve males that would have occurred during the initial contact between these two species in Florida. It would be valuable, however, to compare these results with similar data from sympatric individuals; such an approach would be useful to detect sympatric shifts in competitive ability in each species (i.e. alpha-selection; Gill 1974). Shifts in heterospecific aggression, such as those documented in this study, are often attributed to alpha-selection (e.g. Peiman and Robinson 2007, Deitloff et al. 2009), but aggression does not necessarily entail increased competitive ability or social dominance (Francis 1988).

The findings in this study should be interpreted with some caution, as I was only able to collect data in one secondary contact zone for *A. sagrei*. Therefore, behavioral shifts between sympatric and allopatric populations could be due to factors other than the presence or absence of *A. cristatellus*. The overall abundance of *A. sagrei*, the available habitats, and the assemblage

of *Anolis* species were comparable between the sympatric and allopatric sites (N. Losin, *unpubl. data*), so these factors are unlikely to contribute to the behavioral differences observed. To rule out the possibility of unmeasured differences between sympatric and allopatric populations driving behavioral shifts, however, it would be valuable to expand the experiment to *A. sagrei* living in other contact zones between the two species. With *A. cristatellus*, I was able to test males at allopatric (Puerto Rican native) and sympatric (Florida invasive) sites in two separate invasions of Florida. While there were some behavioral differences between invasions, there were no significant statistical interactions between invasion and population type (i.e. sympatric vs. allopatric). Therefore, while sympatric and allopatric populations sometimes differed in behavior, these differences were consistent between the two invasions of the Miami area by *A. cristatellus*. Given the history of the invasion of Florida by *A. cristatellus,* there are only two independent secondary contact events. A robust test of the effect of sympatry on heterospecific aggression (or any other trait) would ideally include many independent instances of secondary contact (Schluter 2000, Grether et al. 2009), but this condition cannot always be met in nature.

Does the sympatric shift in aggressive behavior observed in *A. sagrei* represent an evolutionary adaptation, or behavioral plasticity? *A. sagrei* and *A. cristatellus* have been in secondary contact for approximately 40 years in each contact zone (Krysko et al. 2011, Meshaka 2011). Rapid morphological evolution in *Anolis* is well documented (e.g. Losos et al. 1997, Losos et al. 2006) and there is no *a priori* reason that a behavioral trait such as a response to heterospecific intruders might not evolve just as quickly. However, anoles also have considerable flexibility in their aggressive behavior; there is even evidence for individual neighbor recognition (Qualls and Jaeger 1991, Paterson and McMann 2004). Furthermore, while there are barriers to dispersal (including a major highway) between the sympatric and allopatric *A. sagrei* populations

used in this study, none of the sites is more than 8km from any other site, reducing the opportunity for substantial genetic divergence between them. Further work, including learning experiments and common-garden or cross-fostering experiments, will be required to elucidate the genetic and developmental basis of population differences in behavior.

Few studies have attempted both to quantify geographic variation in aggressive behavior between species and to characterize their relative behavioral dominance. The effects of resource overlap between species on the adaptiveness of interspecific aggression have been discussed for some years (e.g. Lorenz 1962, Cody 1969) and have also been considered in an individual-based modeling framework (Grether et al. 2009). The effects of behavioral dominance on the evolution of interspecific territoriality, however, have not received as much attention. Aggression is not a useful proxy for dominance in all cases (Francis 1988, but see Simon 2011). Various authors have suggested that a competitively dominant species will benefit from engaging in interspecific aggressive behavior, while a subordinate species will not (Case and Gilpin 1974, Rice 1978, Dickman 1991). Mikami and Kawata (2004) model the conditions under which interspecific territoriality should be adaptive, and conclude that territorial residents should exclude rivals with a high "exclusion efficiency," a model term into which fighting ability is subsumed. Intraspecific models of territoriality and empirical data, however, show that aggression can sometimes be the optimal strategy, even for males who are unlikely to win contests (Just and Morris 2003, Jenssen et al. 2005, Morrell et al. 2005, Just et al. 2007). Based on a simple verbal model, I predicted that a smaller, behaviorally subordinate species would not benefit from engaging in interspecific aggression, while a larger, dominant species would; the data I gathered on aggressive behavior in sympatric and allopatric populations were consistent with this prediction. There is currently no quantitative theory on the evolution of interspecific aggression that explicitly takes into account

the costs of fighting, the accuracy of rival assessment, and other related factors. Such theory will allow researchers to develop robust empirical predictions in future studies on the adaptiveness of interspecific aggression between species that differ in their fighting ability.

In this study, I examined the territorial behavior of two species, *Anolis sagrei* and *A. cristatellus*, that have come into recent secondary contact in South Florida, where both species are invasive. My results suggest that *A. sagrei* is behaviorally subordinate to *A. cristatellus*, and in sympatry has reduced its aggressiveness toward the larger, more dominant *A. cristatellus*. I did not observe any concomitant shift in the behavior of *A. cristatellus*. These findings are consistent with the hypothesis that even if two species share common resources, interspecific territoriality may not be adaptive for a smaller, behaviorally subordinate species. Further work is required to determine the genetic and developmental basis for the population differences in behavior. It is not yet known whether the behavioral shifts observed in this study have facilitated species coexistence during the ongoing spread of the recently established invasive *A. cristatellus* into areas previously dominated by *A. sagrei*. Invasive species provide useful model systems for examining the effects of species interactions on the evolution of a variety of traits, including behavioral traits such as interspecific aggression. The results presented here underscore a need for further empirical and theoretical inquiry into the role of behavioral dominance in the evolution of interspecific aggressive interactions.

Chapter 3: Invasive vs. invasive: Do two invasive Caribbean lizards compete in a shared habitat in South Florida?

Abstract: When ecologically similar species occur sympatrically, they often compete through exploitative or interference mechanisms. Competition may drive phenotypic evolution in these species through ecological or agonistic character displacement. In South Florida, two species of invasive *Anolis* lizards have recently come into contact, and geographic variation in each species suggests that interactions between the two species may have driven shifts in their morphology and behavior. The intensity of competition between these species, however, has not yet been measured. In this study, we used a large-scale removal experiment to test the hypothesis that *Anolis sagrei* and *A. cristatellus* are competing through exploitative and interference mechanisms in a shared habitat in South Miami. Although the two species belong to the same ecomorph, we found that their microhabitats differed significantly at a sympatric site. We failed to observe any significant effects of the species-removal treatment on anole habitat use, movements, or body condition. Our data on arthropod abundance throughout the experiment suggest that removing *A. cristatellus* may have increased prey availability, but this effect was weak and did not seem to affect the behavior or body condition of the non-removed anoles. While we did not find strong evidence of competition in this experiment, we caution that the intensity of competition may vary seasonally, and that the level of interspecific competition observed in 2011, nearly 40 years after the two species' initial contact in South Florida following the arrival of *A. cristatellus*, may not reflect the historical intensity of competition between the species.

Introduction: Ecological and behavioral interactions between closely related species may drive their evolution. Competition between species may favor adaptations that facilitate coexistence and prevent competitive exclusion (Brown and Wilson 1956). Interspecific competition occurs in two forms: exploitation – indirect competition mediated through a shared, limiting resource – or interference – competition through direct behavioral interactions. In this study, we used species-removal field experiments to assess the intensity of exploitative and interference competition in two congeneric invasive lizards (*Anolis sagrei* and *A. cristatellus*) in South Florida. Previous work (See Ch. 1 and Ch. 2) suggests that interspecific interactions may drive sympatric shifts in these species' morphology and aggressive behavior. The nature (i.e., exploitative or interference) and intensity of competition between the two species, however, is not yet known.

When closely related species occur sympatrically, selection often favors divergence in traits related to resource acquisition, such as bill size in birds (Schluter et al. 1985) or habitat preferences in sticklebacks (Schluter and McPhail 1992). Such sympatric divergence is often cited as evidence for *ecological character displacement* (ECD), an evolutionary process in which individuals with phenotypes most different from those of their competitors enjoy a selective advantage, often resulting in sympatric populations of two species that are more divergent than allopatric populations of the same species (Brown and Wilson 1956, Schluter 2000, Pfennig and Pfennig 2009). When interspecific competition is mediated by behavioral interference, however, selection may drive adaptive shifts in traits related to the expression of interspecific interference behaviors, such as aggression or agonistic signals (Grether et al. 2009, Peiman and Robinson 2010). The latter process has been termed *agonistic character displacement* (ACD), and its evolutionary outcome depends largely on whether interspecific interference is adaptive (Grether et al. 2009). Maintaining exclusive access to a resource through inter- or intraspecific behavioral

interference requires both time and energy. Therefore, interspecific interference competition will only be maintained when the benefits of exclusive access to that resource exceed the costs (e.g. (Cody 1969, Peiman and Robinson 2007). If a rival species does not use the resource in question, the resource is not defensible, or it is not in limited supply, interference competition will not be favored by selection (e.g. Lorenz 1962, Anderson and Grether 2010b, a). In an individual-based model of ACD in territorial behavior, Grether and colleagues (2009) found that interspecific resource overlap predicted the outcome of ACD; at low levels of overlap, selection favored traits that reduced interspecific territoriality, while at high levels of overlap, selection favored traits that increased interspecific territoriality.

Anoles (Polychrotidae: *Anolis*) have become a model system for examining the role of interspecific competition in diversification (Losos 1994, 2009). The independent origin of anole *ecomorphs* on different islands of the Greater Antilles has become a textbook example of a replicated adaptive radiation (Williams 1972, Losos et al. 1998). Anole ecomorphs are defined by a suite of morphological, ecological, and behavioral traits, and they are named (e.g. "trunk-ground") for the microhabitat that they tend to occupy. When anoles of the same ecomorph have overlapping ranges, they typically differ in body size or thermal microhabitat – species of the same ecomorph do not co-occur broadly without some ecological differences (Losos 2009). Species with similar resource requirements compete more intensely than those with divergent resource requirements (Pacala and Roughgarden 1982, 1985).

In an anole assemblage created by humans via accidental species introductions, however, the community composition is more likely a result of historical contingency than of ecological opportunity. Newly sympatric species may not have had sufficient time to evolve traits that allow niche partitioning or appropriate competitor recognition (Orians and Willson 1964, Murray

1976). Therefore, such a community is an ideal stage for examining the role that competition plays in shaping the evolution of resource use and behavioral interference. South Florida has only one native anole (*Anolis carolinensis*), but several others were introduced in the 20th century (Krysko et al. 2011, Meshaka 2011). In the Miami area, two invasive species, the Cuban *A. sagrei* and the Puerto Rican *A. cristatellus*, belong to the *trunk-ground* ecomorph, and available evidence suggests that they are more similar in habitat use and diet than are other anole species in South Florida (T. Campbell, *pers. comm.*). Sympatric and allopatric populations of these two species differ in morphology and behavior (see Ch. 1, Ch. 2), but the intensity of competition between them is unknown.

Assessing the intensity of interspecific competition typically entails manipulating the density of each species through field enclosure experiments (e.g. Pacala and Roughgarden 1982, 1985, Petren and Case 1996, Byers 2000) or reciprocal species-removal field experiments (reviewed in Schoener 1983, e.g. Hairston et al. 1987, Leal et al. 1998, Török and Tóth 1999, Harris and Macdonald 2007). Species-removal experiments enable us to measure ecological variables, such as growth and reproduction, as well as behavioral variables, such as home range size and microhabitat use, in the presence and absence of a potential rival. Removal experiments also allow us to ask whether the presence of a rival species affects the availability of food resources for the non-removed species (e.g. Pacala and Roughgarden 1984, Dial and Roughgarden 1995). Such field experiments, when applied to anoles, have provided considerable insight into the role of competition in diversification and community structure (e.g. Pacala and Roughgarden 1982, 1985, Leal et al. 1998). Our study species, *A. sagrei* and *A. cristatellus*, were also the subject of a removal experiment early in the invasion history of *A. cristatellus* in South Florida (Salzburg 1984). Salzburg showed that in a study plot in which *A. cristatellus* was

removed, *A. sagrei* shifted its habitat use in ways that suggested that *A. sagrei* was being excluded from certain parts of the habitat when *A. cristatellus* was present.

Unfortunately, three shortcomings of Salzburg's approach limit its utility in terms of understanding the intensity of competition between these species. First, there was no *A. sagrei*-removal treatment, so only the competitive effects of *A. cristatellus* on *A. sagrei* were evaluated – not the reverse. Second, the anoles in Salzburg's study were not individually marked, so it is not possible to determine whether observed shifts in *A. sagrei* habitat use represent changes in individual behavior, or the arrival of new individuals to fill vacancies left by the removed *A. cristatellus.* Finally, there were no formal statistical comparisons between experimental and control plots; instead, habitat use was compared between the pre- and post-removal intervals, and these tests were performed separately in the removal and control treatments. Therefore, while a significant habitat shift was reported in the experimental plots, the analyses do not show that the shift observed in the experimental plot differs significantly from that of the control plot. We attempted to address these shortcomings in our own removal experiment.

To assess the importance of competition in the ecology and evolution of sympatric *A. sagrei* and *A. cristatellus* in Miami, we performed a reciprocal removal experiment designed to evaluate the effects of both exploitative and interference competition between species. We established experimental plots in sympatric field sites in South Miami and monitored marked populations of male *A. sagrei* and *A. cristatellus* before and after implementing a large-scale ecological manipulation, which we accomplished by removing individuals of each species from different experimental plots. We focused on males because they are the more territorial sex, and they are most often involved in aggressive interactions, both within and between species (N. Losin, *pers. obs.*). We collected data on prey abundance, anole body condition, and anole growth

rate to test for interspecific exploitative competition, and data on each male's habitat use, home range, and movements to test for interspecific interference competition.

Because *A. sagrei* and *A. cristatellus* belong to the same ecomorph and had no ecological interactions prior to their recent introduction into Florida, we tested the hypothesis that the two species compete at sympatric sites through both exploitative and interference mechanisms. This hypothesis enabled us to make several predictions. Based on the hypothesis of exploitative competition, we predicted that in both con- and heterospecific removal treatments: 1) Anole body condition and growth rate would increase following the removals, and this effect would be accompanied by 2) Increased prey abundance following the removals. As a consequence of interference competition between species, we predicted that in the removal treatments: 3) After the removals, the habitat use of each species would shift toward the pre-removal habitat use of the other species, and 4) Individual anoles would move more and occupy larger home ranges after the removals. While Predictions 3 and 4 are not inconsistent with exploitative competition, we reasoned that if these predictions were met without concomitant shifts in body condition or prey abundance (i.e., if Predictions 1 and 2 were not met), this combination of results would implicate behavioral interference underlying competition. We did not make specific predictions about the relative effects of removing con- versus heterospecific rivals. If removal effects were to differ in magnitude, however, we expected that the removal of conspecific males would have a greater effect on each species' home range size, movement, body condition, and growth, because intraspecific competition is generally considered stronger than interspecific competition (Connell 1983, Gurevitch et al. 1992). In contrast, we expected that the removal of heterospecific rivals would have a greater effect on habitat use, because in sympatry the species seem to occupy somewhat different microhabitats (Salzburg 1984).

Methods:

Study system and study locations: Anolis sagrei and *A. cristatellus* are Caribbean lizard species that have been introduced and become established in Florida. *A. sagrei*, a native of Cuba, was first introduced into Florida in the late 19th century and has since spread throughout peninsular Florida and into neighboring states (Kolbe et al. 2004, Meshaka 2011). *A. cristatellus*, native to Puerto Rico, was introduced to Key Biscayne and mainland South Miami in the 1970s, and has become abundant in those areas, although its geographic range in Florida remains restricted to the Miami area (Kolbe et al. 2007, Krysko et al. 2011, Meshaka 2011).

The study sites were located in a sympatric zone in South Miami, where both species were abundant. Study plots were established in well-vegetated riparian habitat on the east and west banks of Snapper Creek, a wide, deep channel that runs from north to south along SW 57th Avenue (Red Road) and drains into Biscayne Bay. Our sites partly overlapped with the study plots used in Salzburg's (1984) *A. cristatellus*-removal experiment. Study plots were long (80-220m) and narrow (5.5-16.75m), and were bordered on their long sides by Snapper Creek on one side, and by a road (Red Road on the west bank of Snapper Creek; Banyan Drive on the east bank of Snapper Creek) on the other. In past experiments with *Anolis*, removal plots have either been enclosed by a dispersal barrier (e.g. Pacala and Roughgarden 1982, Pacala et al. 1983, Pacala and Roughgarden 1985) or left open (e.g. Leal et al. 1998). The borders of our study plots were primarily along the canal or road, which would hinder anole immigration or emigration, so we elected not to erect a costly and disruptive barrier. Anoles were not observed to cross Snapper Creek or either road during this experiment (N. Losin *pers. obs.*).

Marking male anoles: Since one of the limitations of Salzburg's (1984) experimental approach was that anoles were unmarked, we began by marking as many male anoles as possible within our study sites. Beginning in April 2011, we caught male anoles by hand or with a nylon noose at the end of a fishing pole. We marked a total of 319 males (147 sagrei and 172 cristatellus) with unique combinations of colored beads, affixed at the base of the tail with a loop of stainless steel surgical suture (Knapp and Moore 1996). These markings did not impede their movements, and marked males were observed exhibiting normal behaviors, including courtship and copulation, within 24 hours after capture. The markings remained in place for the duration of the experiment in all but three cases, and in two of these three cases, morphometric data allowed us to identify the male with the missing beads with a high degree of confidence, and re-mark it appropriately.

During marking, we also collected morphological measurements on each male: snout-vent length, tail length, hindlimb span, body mass, head length, head width, and head depth. These measurements were compared with subsequent recapture records to assess body condition and growth rates throughout the experiment.

Removal treatments: We divided the available area into seven plots, each of which had both *A. sagrei* and *A. cristatellus* present. Since the two species were not present in equal numbers in any plot, we designated two plots with a majority of *A. cristatellus* males as *A. cristatellus*-removal plots, and two plots with a majority of *A. sagrei* males as *A. sagrei*-removal plots. In each of the removal plots, we aimed to reduce the total density of male trunk-ground anoles (i.e., both male *A. sagrei* and *A. cristatellus*) by 50% by removing males of *only* the more abundant species. This design would leave males of both species remaining in each removal plot, allowing us to test the effects of each species' removal on both conspecifics and heterospecifics.

After collecting baseline habitat use data and mapping the home ranges of each male for at least three weeks (survey protocols detailed below), we randomly selected a subset of marked males in each removal plot to be removed, and over the course of one week, we captured and removed as many of these males as possible. During this period, we also re-captured and re-measured as many males as possible to assess their body condition and growth at the end of the pre-removal phase of the experiment. We removed all unmarked males encountered during the removals, and we continued to remove new unmarked arrivals, both in the removal and control plots, through the rest of the experiment. Males removed from the study site were donated to a reptile distributor in Miami. Following the removals, control and removal plots were surveyed regularly for 7-8 weeks to observe the effects of the treatments. This is a reasonable interval in which to observe effects of the species removals on arthropod density (Pacala and Roughgarden 1984, Dial and Roughgarden 1995), body condition, and growth rates (Licht 1974, Stamps 1984). At the end of the study, we re-captured and measured as many marked males as possible to assess their body condition and growth during the post-removal phase of the experiment.

Surveys: Four times weekly, we performed surveys of each experimental plot to record the presence, location, and habitat use of each male anole. Two or three observers worked together to conduct each survey, walking slowly through the plot and searching visually for anoles on all possible anole perches. When a male anole was detected, we first recorded its bead colors using binoculars. Then, we noted its location by using a measuring tape to determine its north-south coordinate (measured along a steel guard rail on the side of Red Road or Banyan Drive) and east-west coordinate (displacement from the guard rail). We also measured each male's perch height, perch diameter, and whether the male was in shade, part sun, or full sun. The same series of

habitat measurements was taken if an unmarked male was seen, and the locations of unmarked males were used to target our ongoing removal efforts. During at least one survey per week, we also took canopy photographs at each anole perch site. Canopy images were captured with a Panasonic LX-3 digital camera with a circular fisheye lens attachment to capture a full 180-degree circular image. These images were processed with Photoshop® CS3 (Adobe Systems, Inc.) and Gap Light Analyzer (Frazer et al. 1999) to calculate percent canopy cover from the anole perch location.

Measuring prey abundance: We collected arthropods weekly using pitfall traps and suspended sticky traps throughout the experiment. Pitfall traps were 1-quart plastic Gladware® tubs, filled approximately 2 cm deep with slightly soapy water. We buried the traps to their rims in the soil, and covered them with a plywood roof held about 2.5 cm above the substrate with small rocks at the corners. Sticky traps were transparent adhesive insect traps (Catchmaster 904-12) affixed to transparent acrylic rectangles and suspended 1.5 m above the ground. For one week, we could not obtain the same sticky traps as used in the remainder of the experiment; a different brand was used, and the difference in adhesive surface area between the two brands was used to adjust the prey counts for that week. Pitfall and sticky traps were deployed for 48 hours once per week. After collection, the pitfall trap samples were filtered through filter paper, dried, and each sample on filter paper was photographed alongside a size standard using a high-resolution digital camera (Canon 5D Mark II, 21 megapixels). Sticky traps were photographed against a white background using the same equipment. All samples were analyzed using NIH ImageJ software (Rasband 2011) to measure the body length of each arthropod, which was recorded along with basic

taxonomic information (usually to the level of order). We deployed 20 pitfall and 20 sticky traps for 3-4 weeks before the removals and 7-8 weeks following the removals (Table 3.2a).

Analysis: Habitat-use data were analyzed using mixed-effects ANOVA in the R package *nlme* (Pinheiro et al. 2012). Dependent variables were log-transformed when necessary to meet the distributional assumptions of ANOVA. To test for baseline differences in habitat use between species, we restricted the analysis to pre-removal re-sight records and included *species* as a fixed effect and *individual* as a nested random effect. To test whether each species' habitat use shifted following the removals, we included *experimental treatment* (i.e. *A. sagrei*-removal, *A. cristatellus*-removal, or control) and *time interval* (i.e. pre- or post-removal) as fixed effects, and *individual* as a nested random effect. If present in these models, effects of the removals would be manifested as significant *experimental treatment* * *time interval* interaction terms.

Within the removal treatments, we also calculated the distance from each male to the nearest removed male (i.e., the distance between the centroids of each male's pre-removal re-sighting records). We included this variable as a covariate in ANOVA models and tested for *removed neighbor distance* * *time interval* interactions. If such interactions occurred, they would suggest that males closer to removed conspecific or heterospecific males were affected to a different degree by the removals than males more distant from the removed individuals.

We used the "kernelUD" function in the R package *adehabitat* to calculate home range size estimates using the kernel estimation method (Calenge 2006). The 75-percent kernel usage distribution was used as a proxy for home range size in our analyses. We performed an ANOVA on each species' home range size with *experimental treatment* and *time interval* as fixed effects.

As with the habitat analyses described above, we also asked whether *removed neighbor distance* mediated any effects of the removal treatments on home range size.

Next, we asked whether the removals affected the movements of marked males. Using mean and maximum distance between consecutive re-sighting records as the dependent variable, we tested for interaction effects between *experimental treatment* and *time interval*. We also fitted models that included *removed neighbor distance* as a covariate as described above. Finally, we calculated the centroids of each male's re-sighting records, pre- and post-removal, and used a circular correlation test [found in R package *circular* (Agostinelli 2011)] to ask whether males shifted their home ranges toward vacancies left by their nearest removed neighbors.

Male body condition was estimated at three time points: initial capture, the end of the pre-removal interval, and the conclusion of the experiment. We collected morphological data for all males at the time of capture, and for a subset of males (as many as could be re-captured) at each subsequent time point. We calculated a regression of body mass against $(\text{snout-vent length})^3$ and tail length, and used the residuals of this regression as a proxy for body condition. Again, we used a mixed-effects ANOVA, with *individual* as a nested random effect, to test for the influence of *experimental treatment*, *time interval*, and their interaction on body condition for each species. Growth rates [mass (g) per day and SVL (mm) per day] were calculated over two intervals – initial marking to pre-removal ("pre"), and pre-removal to the end of the experiment ("post") – and we asked whether growth rates differed between time intervals or among treatments. Anoles' initial body size was included as a covariate, because larger individuals were found to grow more slowly than smaller individuals.

To analyze the arthropod data, we first excluded prey items below 2mm in total length, as we did not observe adult male trunk-ground anoles eating items this small (N. Losin *pers. obs.*).

We also excluded from our analysis certain taxonomic groups not typically eaten by trunk-ground anoles in our study area, including millipedes, isopods, and ants. Then, we used mixed-effects ANOVA to test the effects of *experimental treatment* and *time interval* on arthropod abundance, with *trap site* as a nested random effect. We asked whether these factors influenced the total number of prey items captured and the mean size of prey items captured in each trap.

Results:

Efficacy of marking efforts, surveys, and removals: We marked a total of 319 male anoles (147 *A. cristatellus*, 172 *A. sagrei*) in our study plots (Table 3.1a). A total of 228 marked males (112 *A. cristatellus*, 116 *A. sagrei*) were re-sighted at least once (Table 3.1b). Males were re-sighted from 1 to 26 times (mean = 8.00, sd = 6.17; Table 3.1c). Each plot was surveyed 13 to 14 times in the pre-removal phase (with the exception of the plot "Church", a control plot that was not surveyed during the pre-removal period), and 22-27 times in the post-removal phase (Table 3.1d). On each survey, from 1-20 individual males were observed (mean = 8.35, sd = 4.07; Table 3.1e). Across all surveys (n = 2156 sight records of male anoles), 1879 re-sighting records involved marked males (> 87% of all re-sightings), suggesting that our marking efforts (and continuous removal of unmarked males following the removals) were effective.

Comparing pre- and post-removal survey data, we found that our removals were effective at reducing the density of male trunk-ground anoles in removal plots. Three of the four removal plots showed a significant decrease in the average number of males detected per survey after the removals (Banyan: $F_{1,34} = 4.34$, $p = 0.04$; Red Road 2: $F_{1,39} = 20.91$, $p < 0.001$; Red Road 4: $F_{1,39} = 9.39$, $p = 0.004$), and the fourth removal plot showed a trend in the same direction (South Red Road: $F_{1,35} = 1.76$, $p = 0.19$; Table 3.1e). Neither of the two control plots showed a significant

decline in re-sighting records following the removals (Table 3.1e). Fewer unique males were observed in the removal plots during the post-removal phase than during the pre-removal phase. While none of our removals reached our goal of a 50% reduction in the density of male trunk-ground anoles (actual reductions ranged from 32.4 to 43.2%), we substantially reduced the number of resident males in each removal plot (Table 3.1f).

Finally, we predicted that the distance between the centroid of any given male's re-sighting records and the nearest centroid of a male of the "removal" species would increase following the removals. Our data support this prediction: in the *A. cristatellus*-removal plots, males of both species were significantly farther from their nearest *A. cristatellus* neighbors after removals than before removals ($F_{1,26} = 47.33$, $p < 0.001$). In *A. sagrei*-removal plots, males were

Table 3.1: Summary statistics on male anoles marked and re-sighted, surveys conducted, and the effects of our removals. In section (e), bold type indicates a significant decrease in the number of re-sight records per survey from the pre- to post-removal phase of the experiment.

	***A. cristatellus* removal**		***A. sagrei* removal**		**Control (no removal)**		
	Red Rd 2	**Banyan**	**Red Rd 4**	**S Red Rd**	**Red Rd 1**	**Red Rd 3**	**Church**
(a) Males marked							
A. cristatellus	44	24	19	8	30	17	4
A. sagrei	34	15	39	34	25	6	18
(b) Males re-sighted							
A. cristatellus	33	22	13	8	23	10	3
A. sagrei	12	13	19	31	18	5	18
(c) Re-sights per male							
A. cristatellus	7.9 ± 5.3	7.2 ± 5.1	7.5 ± 5.8	14.5 ± 8.3	10.9 ± 7.4	10.2 ± 9.1	12.3 ± 3.2
	(1 – 21)	(1 – 18)	(1 – 19)	(1 – 23)	(1 – 25)	(1 – 26)	(10 – 16)
A. sagrei	6.2 ± 4.8	3.2 ± 2.6	5.2 ± 3.2	8.7 ± 6.5	7.1 ± 5.9	5.0 ± 4.7	9.1 ± 6.0
	(1 – 18)	(1 – 9)	(1 – 13)	(1 – 26)	(1 – 20)	(1 – 11)	(1 – 17)
(d) Surveys conducted							
Pre-removal	14	13	14	13	14	14	0
Post-removal	27	23	27	24	26	27	22
(e) Re-sights per survey							
Pre-removal	**12.2 ± 4.7**	**9.8 ± 3.3**	**7.5 ± 2.8**	13.5 ± 3.3	10.2 ± 3.3	3.1 ± 1.2	n/a
	(3 – 19)	**(3 – 12)**	**(3 – 13)**	(9 – 18)	(2 – 15)	(1 – 5)	
Post-removal	**7.3 ± 2.3**	**7.8 ± 2.3**	**4.7 ± 2.8**	12.0 ± 3.1	10.5 ± 3.0	4.1 ± 1.4	9.8 ± 2.3
	(3 – 11)	**(3 – 15)**	**(1 – 16)**	(6 – 20)	(6 – 19)	(1 – 7)	(5 – 14)
(f) Unique males per plot							
Pre-removal	44	34	29	42	41	14	n/a
Post-removal	25	23	18	26	35	17	24
Percent change	- 43.2 %	- 32.4 %	- 37.9 %	- 38.1 %	- 14.6 %	+ 21.4 %	n/a

significantly farther from their nearest *A. sagrei* neighbors after removals than before removals ($F_{1,27}$ = 12.84, p = 0.001), although the latter effect was somewhat greater in *A. cristatellus* than *A. sagrei* residents (interaction $F_{1,27}$ = 4.86, p = 0.036). In contrast, in both removal treatments, the distance between males and their nearest neighbors of the non-removed species did not change between the pre-removal and post-removal phase of the experiment (both $p > 0.5$).

Species differences in habitat use and spatial metrics: We used the pre-removal surveys to evaluate species differences in habitat use and two spatial measures: home range size (estimated by the 75% usage kernel calculated from re-sight records) and individual movements. We found that male *A. cristatellus* perched higher than male *A. sagrei* ($F_{1,174}$ = 45.22, $p < 0.001$; Fig. 3.1a), occupied perches of larger diameter than *A. sagrei* ($F_{1,174}$ = 47.48, $p < 0.001$, Fig. 3.1b), and were observed on shaded perches more often than male *A. sagrei* (X^2 = 60.51, df = 2, $p < 0.001$; Fig. 3.1c). Consistent with the latter result, male *A. cristatellus* were also found on perches with

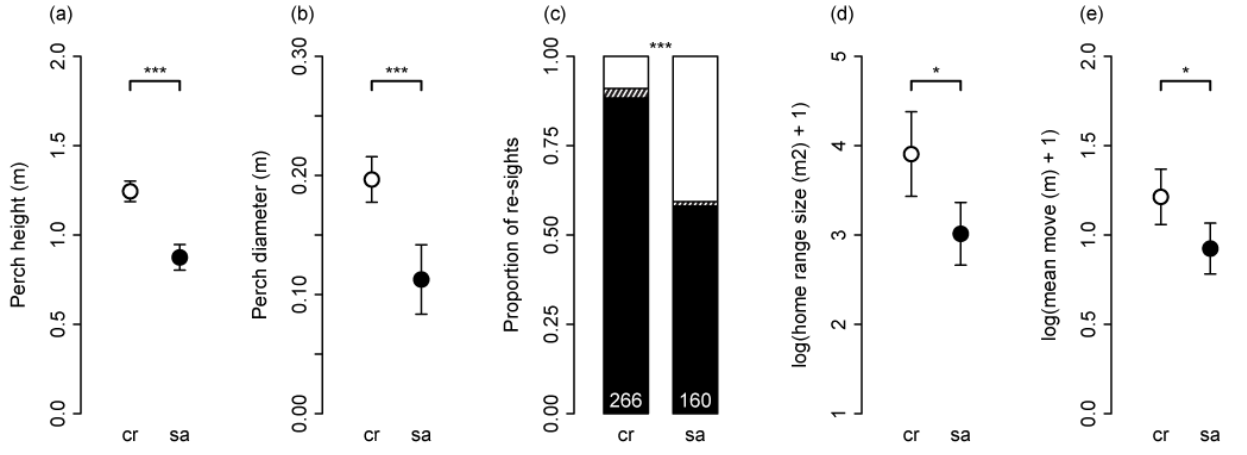


Figure 3.1. *Anolis cristatellus* and *A. sagrei* differ in habitat use. All data shown is from the pre-removal phase of the experiment. "cr" and unfilled circles = *Anolis cristatellus*; "sa" and filled circle = *A. sagrei*. (a) Perch height. (b) Perch diameter. (c) Insolation (black fill = shade, hatched fill = part sun; white fill = full sun). Numbers in bars indicate total sample size. (d) Home range size. (e) Mean movement between re-sightings. All means are shown with 95% confidence intervals. Key to significance symbols: n.s. not significant; † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$.

more canopy cover than *A. sagrei* ($F_{1,33}$ = 45.47, p < 0.001). Male *A. cristatellus* generally had larger home ranges than male *A. sagrei* ($F_{1,62}$ = 4.09, p = 0.048; Fig. 3.1d), though this effect became marginally non-significant after removing one outlier, a male *A. cristatellus* ("AKK") that moved substantially during the pre-removal phase and therefore had an unusually large estimated home range ($F_{1,61}$ = 3.66, p = 0.061). Finally, *A. cristatellus* had larger mean and maximum movements between re-sightings than *A. sagrei* (mean movement: $F_{1,138}$ = 5.90, p = 0.016, Fig. 3.1e; maximum movement: $F_{1,138}$ = 10.26, p = 0.002).

Effects of the removals: Next, we tested for interactions between *experimental treatment* (i.e. *A. sagrei*-removal, *A. cristatellus*-removal, or control) and *time interval* (i.e. pre-removal or post-removal). Such interactions can potentially reveal the unique effects of each treatment on the resident males that remain after the removal of potential competitors. For brevity, we hereafter refer to all such interactions as *treatment*time* effects.

For males of both species, there was no treatment*time effect on perch height (*A. sagrei*: $F_{2,676}$ = 0.54, p = 0.58; *A. cristatellus*: $F_{2,906}$ = 1.31, p = 0.27). Male *A. cristatellus*, however, perched lower post-removal than pre-removal ($F_{1,906}$ = 5.64, p = 0.018), regardless of treatment. For male *A. sagrei*, there was a marginally non-significant treatment*time effect on perch diameter ($F_{2,624}$ = 2.69, p = 0.069). We investigated this interaction further by analyzing each treatment separately. Male *A. sagrei* shifted to larger perches post-removal in *A. sagrei*-removal plots ($F_{1,285}$ = 10.95, p = 0.001), but not in *A. cristatellus*-removal ($F_{1,81}$ = 0.24, p = 0.63) or control plots ($F_{1,258}$ = 0.031, p = 0.861; Fig. 3.2). Visual inspection of the data suggested that one male *A. sagrei* ("GWB") that habitually perched on a very large Australian Pine during the post-removal phase of the experiment may have driven this nearly significant treatment*time effect.

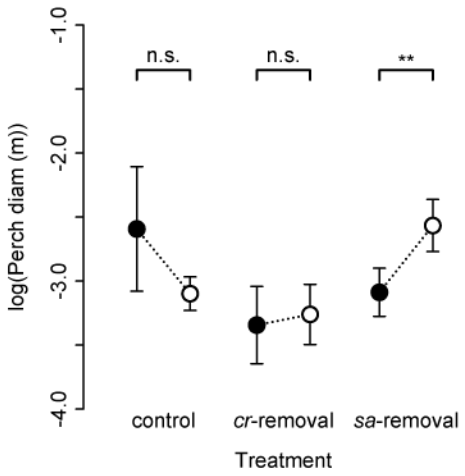


Figure 3.2: *Anolis sagrei* perch diameter. Filled circles represent the pre-removal phase of the experiment; unfilled circles represent the post-removal phase of the experiment. *cr*-removal = *A. cristatellus* removal. *sa*-removal = *A. sagrei* removal. Means are shown along with 95% confidence intervals. Key to symbols: n.s. not significant; † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$.

We therefore excluded this male and re-ran the analysis; although mean *A. sagrei* perch diameter was still greater post-removal than pre-removal in *A. sagrei*-removal plots ($F_{1,276} = 6.98$, $p = 0.009$), the treatment*time effect was not close to significant any longer ($F_{2,615} = 1.76$, $p = 0.17$). Like *A. sagrei* males, *A. cristatellus* males showed no treatment*time effect on perch diameter ($F_{2,880} = 1.59$, $p = 0.20$), although there was an overall decrease in perch height in the post-removal interval across experimental treatments ($F_{1,880} = 11.57$, $p < 0.001$).

To analyze whether the removals influenced each species' tendency to perch in sunny or shady locations, we calculated a mean degree of insolation for each male in the pre- and post-removal phases of the experiment. Insolation was recorded in the field based on whether the anole's body was in shade, part sun, or full sun. Ignoring surveys in which skies were overcast, we calculated the mean insolation for each male by treating the categorical variables as numeric: shade = 0, part sun = 0.5, and full sun = 1. We found no treatment*time effect on insolation for male *A. sagrei* ($F_{2,34} = 0.99$, $p = 0.38$) or *A. cristatellus* ($F_{2,43} = 0.69$, $p = 0.51$). The pre- versus post-removal canopy cover estimates for *A. cristatellus* residents did not differ among treatments

($F_{2,125}$ = 0.99, p = 0.37), but there was a significant treatment*time effect for *A. sagrei* ($F_{2,83}$ = 3.42, p = 0.038). This effect seemed to be driven by a difference in pre- versus post-removal canopy cover between control and *A. sagrei*-removal treatments ($F_{1,72}$ = 6.48, p = 0.013). Male *A. sagrei* were found on perches with greater canopy cover following the removal of *A. sagrei* males, while the canopy cover at *A. sagrei* re-sighting locations in control plots did not change following the removal treatments. This difference could be caused by a shift in *A. sagrei* habitat use, or a difference among plots in vegetation characteristics (e.g. seasonal shifts in leaf cover).

Next, we asked whether the removal experiments influenced male home range size. We used the 75% usage kernel as an estimate of home range size for each male, both pre- and post-removal; this measure could only be calculated robustly when there were at least five re-sighting records per male in the pre- or post-removal phases, so this approach necessarily reduced the sample size of these analyses. Because relatively few individuals had enough re-sighting records to estimate a home range size in both the pre- *and* post-removal phases (n = 6 *A. sagrei*, n = 14 *A. cristatellus*), we did not use a repeated-measures design for these analyses. We found that the number of re-sighting records for a male was positively correlated with the home range size estimate (b = 0.10, t = 2.55, df = 154, p = 0.012), so we included the total number of re-sightings as a covariate in each model. We did not find any evidence of a treatment*time effect on the home range size of either species (*A. sagrei*: $F_{2,61}$ = 0.37, p = 0.69; *A. cristatellus*: $F_{2,81}$ = 0.50, p = 0.61), although estimated home range sizes tended to increase following the removals across all treatments ($F_{1,61}$ = 4.43, p = 0.039).

Finally, we asked whether the removals influenced males' movements. For each male, we calculated the mean and maximum distance between successive re-sighting records. For male *A. cristatellus*, there was no treatment*time effect on mean ($F_{2,41}$ = 0.79, p = 0.46) or maximum

movements ($F_{2,41}$ = 0.67, p = 0.51), although both mean and maximum movement distance increased following the removals, regardless of treatment (mean: $F_{1,41}$ = 6.88, p = 0.012; maximum: $F_{1,41}$ = 16.81, $p < 0.001$). For *A. sagrei* males, we found no treatment*time effect on the mean ($F_{2,18}$ = 1.28, p = 0.30) or maximum movements ($F_{2,18}$ = 0.77, p = 0.47). Like the *A. cristatellus* movements, however, we found that *A. sagrei* movements increased post-removal across all treatments (mean: $F_{1,18}$ = 26.98, $p < 0.001$; maximum: $F_{1,18}$ = 45.69, $p < 0.001$).

Effects of the distance to nearest removed neighbor: In addition to testing the effects of the removal treatments compared to controls, we also tested whether the distance between a male and its nearest removed rival influenced its shift in habitat or space use following the removals. We predicted that differences in habitat or space use between pre- and post-removal intervals would be greatest for males that began the experiment close to a male who was later removed. Interaction effects – in this case, interactions between *removed neighbor distance* and *time interval* (i.e. pre- or post removal) – would potentially reveal effects of one species on another. We hereafter refer to such interactions as *distance*time* effects for brevity.

In *A. cristatellus*-removal plots, there were no distance*time effects on *A. cristatellus* or *A. sagrei* perch height, perch diameter, or insolation (all p > 0.15). In *A. sagrei*-removal plots, there were no distance*time effects on *A. sagrei* or *A. cristatellus* perch height, perch diameter, or insolation (all $p > 0.15$), except a marginally non-significant effect on *A. sagrei* perch diameter, $F_{1,197}$ = 2.91, p = 0.089). This marginal effect, however, was in the opposite direction from our prediction (i.e., there tended to be a greater difference between pre- and post-removal perch diameter in males with *more distant* nearest removed neighbors), and seemed to be driven by a male *A. sagrei* ("GWB") that was far from its nearest *A. sagrei* neighbor, and often perched

on a very large Australian pine during the post-removal phase. When this outlier was excluded from the analysis, the effect was no longer close to significant ($F_{1,188} = 0.40$, $p = 0.53$).

We then asked whether the distance to the nearest removed rival mediated removal effects on home range size and individual movement. In the *A. cristatellus*-removal plots, we found no distance*time effects on *A. cristatellus* or *A. sagrei* home range size ($p > 0.25$). In the *A. sagrei*-removal plots, we found no distance*time effect on *A. cristatellus* home range size ($p > 0.4$), and there were not enough data to test for such an effect on *A. sagrei* home range size. There was a marginally non-significant distance*time effect of *A. cristatellus* removal on *A. cristatellus* mean movement ($F_{1,2} = 8.74$, $p = 0.098$), but it was in the opposite direction from our prediction (i.e., males who were farther from their nearest removed rival had *smaller* differences between pre- and post-removal movements). The same *A. cristatellus* that was an outlier in our analysis of species differences in home range size ("AKK") was an outlier in this analysis as well, and when excluded from the analysis, there was no distance*time effect of *A. cristatellus* removal on *A. cristatellus* movements ($F_{1,2} = 2.58$, $p = 0.2493$). There was not enough data to test for a distance*time effect of *A. cristatellus* removal on *A. sagrei* movements. There were also no distance*time effects of *A. sagrei* removal on the mean or maximum movements of either resident species (both $p > 0.5$).

Finally, we asked whether males moved toward vacancies left by removed rivals. We calculated the compass bearing between each male's pre-removal and post-removal re-sighting centroid, and tested for a circular correlation between this bearing and one calculated between the male's pre-removal centroid and that of the nearest removed male. There were no significant correlations between these two compass bearings in any combination of experimental treatment (*A. cristatellus*-removal or *A. sagrei*-removal) and resident male species (all $p > 0.15$).

Body condition and growth rates: To evaluate possible effects of the removals on males' body condition and growth, we first calculated an index of condition by fitting a model to predict body mass that included *species*, *(snout-vent length)*^{3}, and *tail length*, as well as the interaction terms between species and each of the morphometric variables. This model's main and interaction terms significantly predicted variation in body mass (species: $F_{1,446} = 3099.29$, $p < 0.001$; SVL^3: $F_{1,446} = 2912.07$, $p < 0.001$; tail length: $F_{1,446} = 5.51$, $p = 0.019$; species * SVL^3: $F_{1,446} = 15.54$, $p < 0.001$; species * tail length: $F_{1,446} = 6.43$, $p = 0.012$). We used the residuals from this model as an index of condition. Therefore, males with body masses larger than the model's prediction had positive body condition scores, while those with masses smaller than the model's prediction had negative condition scores. We tested the effects of time (i.e., initial marking, the end of the pre-removal phase, and the end of the experiment) and experimental treatment on body condition. The average body condition of both *A. sagrei* and *A. cristatellus* males did change with time interval (*A. sagrei*: $F_{2,43} = 5.85$, $p = 0.006$; *A. cristatellus*: $F_{2,80} = 5.57$, $p = 0.005$), but these changes were unrelated to treatment; the treatment*time interactions were non-significant; (*A. sagrei*: $F_{4,43} = 0.44$, $p = 0.78$; *A. cristatellus*: $F_{4,80} = 1.36$, $p = 0.26$).

Next, we aimed to ask whether the removals affected males' growth rates. To estimate growth rates, however, we required morphological data from multiple time points. We measured every male in the study at the time of initial capture, and a subset of males at the end of the pre-removal phase and the end of the experiment. Post-removal growth rate estimates required measurements at the second and third sampling times, and we did not have enough male anoles measured at all three time points to test our predictions about growth rates. We did find that the initial snout-vent length influenced the rate of mass gain and snout-vent length growth; larger

Table 3.2: Summary statistics on arthropod traps collected and prey items counted.

	A. cristatellus removal	*A. sagrei* removal	Control (no removal)
(a) Traps collected			
Pitfall (pre-removal)	27	28	12
Pitfall (post-removal)	57	58	32
Sticky (pre-removal)	28	28	12
Sticky (post-removal)	59	60	32
(b) Prey items (pitfall traps)			
Pre-removal	0.8 ± 1.4 (0 – 7)	**1.5 ± 1.5 (0 – 6)**	4.8 ± 8.4 (0 – 27)
Post-removal	0.6 ± 0.9 (0 – 4)	**0.4 ± 0.7 (0 – 3)**	2.3 ± 7.2 (0 – 41)
(c) Prey items (sticky traps)			
Pre-removal	2.2 ± 2.3 (0 – 8)	2.7 ± 2.0 (0 – 7)	3.1 ± 2.8 (0 – 8)
Post-removal	1.7 ± 1.4 (0 – 5)	2.0 ± 1.6 (0 – 7)	2.0 ± 1.5 (0 – 5)

males grew more slowly than smaller males (mass gain: $F_{1,11} = 166.46$, $p < 0.001$; snout-vent length growth: $F_{1,11} = 167.97$, $p < 0.001$). Starting body condition also influenced growth rates; males in better condition gained mass more quickly ($F_{1,11} = 42.00$, $p < 0.001$), but unexpectedly, grew in snout-vent length more slowly than males in poorer condition ($F_{1,11} = 6.07$, $p = 0.031$).

Prey abundance: We predicted that the removals would cause an increase in prey availability. A total of 20 pitfall and 20 sticky traps were deployed at 20 trapping sites (n = 4 in control plots, n = 8 in *A. sagrei*-removal plots, and n = 8 in *A. cristatellus*-removal plots) for 3-4 weeks before and 7-8 weeks after the removals (Table 3.2a). We counted from 0 to 41 potential prey items per trap (Table 3.2b-c). We analyzed the data from these traps to test whether arthropod abundance varied among treatments and time intervals.

In the pitfall traps, we found a significant decline in prey abundance following the removals ($F_{1,191} = 15.04$, $p < 0.001$) and a nearly significant treatment*time interaction ($F_{2,191} = 2.99$, $p = 0.053$; Fig. 3.3). To investigate this possible interaction further, we inspected the data and observed that, contrary to the overall downward trend, no post-removal decline in abundance was evident in the *A. cristatellus*-removal plots. There was no treatment*time interaction

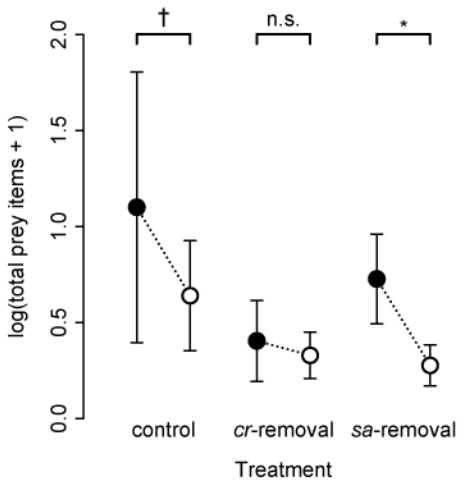


Figure 3.3: Prey collected in pitfall traps. Filled circles represent the pre-removal phase of the experiment; unfilled circles represent the post-removal phase of the experiment. Means are shown along with 95% confidence intervals. Key to symbols: n.s. not significant; † $p < 0.1$; * $p < 0.05$.

between the *A. sagrei*-removal and control plots ($F_{1,116} = 0.19$, $p = 0.66$). When the data from these plots were pooled, there was a significant treatment*time interaction effect when compared with the *A. cristatellus*-removal plots ($F_{1,192} = 5.64$, $p = 0.018$). In terms of prey size, prey captured in pitfall traps were larger after the removals than before them ($F_{1,228} = 10.71$, $p = 0.001$), but there was no treatment*time interaction ($F_{2,228} = 2.33$, $p = 0.10$).

On the sticky traps, we found a marginally non-significant effect of time interval on prey abundance, with fewer prey collected post-removal than pre-removal ($F_{1,196} = 3.72$, $p = 0.055$). This effect, however, was consistent across experimental treatments (interaction $F_{2,196} = 0.31$, $p = 0.74$). We also did not detect any difference in the mean body size of prey items collected based on time interval, experimental treatment, or their interaction (all $p > 0.4$).

Discussion: We performed a reciprocal removal experiment involving two recently sympatric Caribbean lizards, *Anolis sagrei* and *A. cristatellus*, in suburban South Miami. Consistent with previous studies on these species, we found clear differences in microhabitat use between

species. We found only weak evidence, however, for interspecific exploitative or interference competition, even though our manipulations significantly reduced the abundance of the removed species. We also found scant evidence of intraspecific competition; contrary to expectations, a substantial reduction in density of one species had little effect on the ecology or behavior of either conspecifics or heterospecifics. We discuss the implications of these findings below.

Although *A. cristatellus* and *A. sagrei* both belong to the trunk-ground ecomorph and occupy similar habitats in their native ranges (Puerto Rico and Cuba, respectively), they showed significant differences in microhabitat use in a sympatric site in South Miami. *A. cristatellus* was found on higher, larger-diameter, and shadier perches than *A. sagrei*. These trends are consistent with larger-scale patterns in the distribution of *A. cristatellus* in South Miami as a whole; while *A. sagrei* can be found nearly everywhere in South Florida and seems at home in sunny edge habitats with sparse vegetation, *A. cristatellus* seems to be restricted to areas with large trees and dense canopy cover (N. Losin *pers. obs.*). Male *A. cristatellus* also had larger home ranges and more movements than *A. sagrei*, which may be a consequence of their larger overall body size – male *A. cristatellus* typically outweigh male sagrei by a ratio of nearly 2 to 1. The larger body size of *A. cristatellus* may necessitate a larger home range for foraging. These differences in habitat use between the species seem to allow them to coexist stably in structurally complex habitats (such as our study sites), although in more homogeneous habitats (such as large patches of undisturbed hardwood hammock), one species or the other may predominate.

Our data provided some hints of inter- and intraspecific interference competition, but overall the evidence for interference competition between males was slim. We observed, for example, that *A. sagrei* shifted to larger-diameter perches following the removal of *A. sagrei.* Despite an absence of such an effect in *A. cristatellus*-removal or control plots, however, there

was no statistical difference between the *A. sagrei*-removal effect and the pre- to post-removal shifts in the other treatments. There was also no evidence of any effect of our manipulations on perch height, diameter, insolation, home range size, or individual movements. Furthermore, we tested for an effect of nearest-removed-neighbor distance on the magnitude of the removal effect. If such neighbor-distance effects existed, they would constitute strong evidence for interference competition. We found no evidence, however, that neighbor distance mediated any effects of the removals. In sum, our evidence for inter- and intraspecific competition was weak.

We also collected data on the abundance of arthropod prey and anole body condition to detect possible inter- and intraspecific exploitative competition. Using pitfall traps to measure the abundance of terrestrial prey, we found that *A. cristatellus*-removal plots did not follow the same pattern of pre- versus post-removal prey abundance as the other treatments. While there was a general decline in prey abundance from the pre- to post-removal phases of the experiment, there was no such decline in the *A. cristatellus*-removal plots. This finding may indicate that the removal of *A. cristatellus* males resulted in greater prey abundance than otherwise expected. If true, we would predict an increase in the body condition or growth of anoles individuals in the *A. cristatellus*-removal plots following the removals. While we did not have enough pre- and post-removal recapture data to test for an effect on growth rate, we found no evidence of differences in body condition across treatments. If the variation we observed in the temporal pattern of prey abundance was a consequence of our *A. cristatellus* removal, that variation was not great enough to be reflected in the body condition of the anoles in our experiment.

Naturally, we wanted to compare our results to those of Salzburg (1984), who performed an *A. cristatellus*-removal experiment in South Miami in the early 1980s. Salzburg's data, which compared *A. sagrei* habitat use before and after the removal of *A. cristatellus*, suggested that the

presence of *A. cristatellus* limited *A. sagrei* to sunnier, more peripheral perches than they would otherwise have occupied. While we collected similar data to Salzburg, we found no evidence of either species influencing the habitat use of the other. There are several reasons that the two sets of results may differ. First, in our dataset it was not uncommon to see pre- to post-removal shifts in various habitat-use measures, including shifts that met the threshold for statistical significance in some treatments and not in others. For example, we found that male *A. cristatellus* perched lower post-removal than pre-removal – a shift toward the pre-removal habitat use of *A. sagrei* – in *A. sagrei*-removal plots ($F_{1,190} = 5.04$, $p = 0.026$), but not in *A. cristatellus*-removal ($F_{1,338} = 1.81$, $p = 0.18$) or control plots ($F_{1,378} = 0.82$, $p = 0.37$). These effects, however, did not differ statistically between treatments (interaction $F_{2,906} = 1.31$, $p = 0.27$). Salzburg's study did not include formal tests to evaluate the difference between *A. cristatellus*-removal and control plots, so it is not clear whether the shifts observed in his removal plots differ significantly from controls. Second, we tried to maintain the anole densities achieved via the removals through the rest of the experiment by removing all incoming unmarked individuals from the study plots. Salzburg, in contrast, continued to remove *A. cristatellus* arriving in the removal plots, but did not remove newly arriving *A. sagrei*. Since Salzburg's anoles were not marked, apparent shifts in habitat use could result from new individuals settling in areas formerly occupied by *A. cristatellus*, rather than individual behavioral shifts by non-removed males. Third, Salzburg attempted to remove all *A. cristatellus* (male and female), while we only attempted to reduce the total density of male trunk-ground anoles (regardless of species) by 50%. We think the removal of females is unlikely to affect the habitat use by males; male anoles are usually aggressive only toward other males. Nevertheless, while no pre-removal densities are provided in Salzburg's paper, it is possible that his removal of *A. cristatellus* constituted a more dramatic manipulation

of rival density than our own. Fourth, the intensity of competition between the two species may have diminished in the thirty years that have passed between Salzburg's study and our own. Such a decline could occur through shifts in morphology or habitat preference (i.e. ecological character displacement) or reduced behavior interference (i.e. agonistic character displacement). Finally, changes in the overall density of trunk-ground anoles or the availability of prey could also mediate the competitive relationship between species. From Salzburg's data on the number of *A. cristatellus* he removed, however, the overall density of *A. cristatellus* at the time of his study seems to be somewhat *lower* that the densities observed in our study, consistent with the recent arrival of that species, making density differences an unlikely explanation for less evidence of competition being observed in 2011.

Regardless of the source of the difference between our findings and those of Salzburg (1984), the present data shows only weak evidence for interspecific competition between *A. sagrei* and *A. cristatellus*. It is possible that the summer (May through August), when this study was conducted, differ substantially from other times of year in terms of food availability. Had we performed a similar experiment at another time of year, perhaps we would have gotten a different result. Indeed, the extent of niche overlap between species can vary seasonally along with food abundance (e.g. Smith 1991). If prey is less abundant at other times of year, competition within and between species might also be greater during these "food-lean" times (Schoener 1983, Smith 1991). It is also possible that, had the experiment been continued longer, the effects of competition may have become apparent. This is particularly true if competition were to cause a reduction in the reproductive rate of one or both species. Field experiments designed to evaluate competition, however, often cannot be maintained long enough to document the effects of competition on population growth, and it is common to use proxy measures such as growth rate,

feeding rate, or other variables related to per-capita population growth (Schoener 1983). In past removal studies with anoles, for example, the competitive effects of one species on another have been documented by measuring growth and feeding rates (Pacala and Roughgarden 1982, 1985) in studies with closed plots, and by monitoring population density (Leal et al. 1998) in a study with open plots. In this study, although our study plots were not enclosed, we removed all newly arriving individuals of both species, so we took an approach similar to that taken in closed-plot studies, measuring prey abundance and lizards' body condition and growth rates, and failed to find strong evidence of interspecific competition.

The apparent lack of detectable exploitative competition, if in fact reflective of levels of competition throughout the year, suggests that selection for further phenotypic divergence (i.e. ecological character displacement) should be weak or non-existent in established sympatric zones. This could be a result of the two species being sufficiently divergent before secondary contact, or could result from divergence following contact (see Ch. 1). In more recent contact zones, where the species have not been interacting for long, there may be greater selection for divergence. If exploitative competition is weak, then selection may favor reduced interspecific aggression, assuming interspecific encounters are costly. At least for *A. sagrei*, the species with a smaller body size and weaker bite force (cf. Tokarz 1985, Lailvaux and Irschick 2007), it is likely that aggressive encounters with larger rivals are costly, so we might expect reduced interspecific aggression from *A. sagrei* in sympatry (see Ch. 2). It is not yet clear why our experiment yielded no evidence of *intra*specific competition; the densities of anoles in our study plots were high compared to other sites in South Miami (N. Losin *pers. obs.*), though lower than the densities used in classic field-enclosure experiments that have documented interspecific competition (Pacala and Roughgarden 1982, 1985). Anoles in our study showed high site

fidelity, many often occupying only a few perches for the duration of the study. It is possible, therefore, that the benefits of being familiar with a territory outweighed the potential benefits of dispersing to a new area, making it difficult to detect any competitive release in the form of space use following removals.

Although we did not detect interspecific competition in our study, this finding does not entail that the ongoing spread of *A. cristatellus* in Miami will be without consequence for *A. sagrei*. In a complex, patchy matrix of habitats, the two species currently seem to coexist without strong evidence of competition. In other habitats, however, one species or the other may prevail. Experiments with a variety of taxa show that intensity of interspecific competition, whether through interference or exploitation, may be mediated by habitat (e.g. Reed 1982, Rummel and Roughgarden 1985, Gibb 2011). Indeed, in south Miami, there are already areas within the zone of sympatry in which *A. cristatellus* predominate, and others where *A. sagrei* are more common, suggesting that habitat influences the competitive impacts of each species on the other.

Despite belonging to the same ecomorph and not having a history of ecological interactions, *A. cristatellus* and *A. sagrei* appear to coexist in South Miami without substantial competition, either through interference or exploitation mechanisms. Our results underscore the importance of appropriate controls in removal experiments designed to measure competition. A population's habitat use, spatial ecology, body condition, and other behavioral and ecological attributes frequently vary seasonally and spatially (even on small temporal and spatial scales), so comparing pre- and post-removal data with parallel data from non-removal control plots is critical. Moreover, experiments that follow marked individuals may yield different conclusions about the effects of an ecological manipulation than experiments that simply average behavior or habitat use across all individuals encountered. The evident lack of competition between *A. sagrei*

and *A. cristatellus* in Florida suggests that although they share a similar niche in allopatry, they have sufficiently divergent habitat preferences to coexist stably in sympatry. Other work in this system (see Ch. 1, Ch. 2) suggests that evolutionary or plastic shifts in morphology and behavior may account for the ongoing coexistence of these closely related species.

Chapter 4: Ecological and evolutionary correlates of interspecific territoriality: A comparative study of wood-warblers (Aves: Parulidae)

Abstract: Interspecific territoriality (IT) is widespread in nature, but the ecological and evolutionary factors that cause IT are poorly understood. Some authors have argued that adaptive IT is widespread and plays an important role in structuring natural communities, while others have suggested that IT is not stable over evolutionary timescales and that IT usually represents misdirected intraspecific territoriality. Comparing the incidence of IT among species or habitats may be a fruitful way to test hypotheses about the factors that underlie IT, but this comparative approach is underutilized. In this study, we performed a comparative analysis of the factors underlying IT in a diverse family of North American birds, the wood-warblers (Parulidae). We searched the literature for records of IT involving parulids; wherever IT was documented, we compared species exhibiting IT with other species that were present at the site but did not exhibit IT. We found that over half of North American parulids have been observed to show IT with one or more species. Using a diverse group of potential rivals for comparison, we found that species exhibiting IT were more similar to one another in morphology, feeding guild, and habitat use than were other species at the same sites. When we considered the warblers alone, we also found that genetic distance significantly predicted IT; species involved in IT were more closely related than expected by chance. In multivariate models, genetic distance was a better predictor of IT than morphology, feeding guild, or habitat preferences, highlighting the impact of evolutionary history on contemporary ecological interactions. We propose that future studies of IT should consider the evolutionary history of the taxa involved as well as the current adaptive value of IT.

Introduction: Territoriality is a widespread behavioral tactic for partitioning space and defending food sources, mates, and other resources against rivals (reviewed in Maher and Lott 2000, Adams 2001). Intraspecific territoriality has been well studied in a wide range of taxa, but interspecific territoriality (hereafter IT) has received much less attention (reviewed in Grether et al. 2009). In particular, the ecological and evolutionary factors causing interspecific territoriality are still poorly understood, and to our knowledge there have been no comparative studies aimed at assessing these factors. Here we present a comparative analysis of the factors underlying IT in North American wood-warblers (Aves: Parulidae).

Simmons (1951) proposed the following definition of "interspecific territorialism":

> "A territory holder of one species exhibits persistent aggressive behaviour to an intruding [individual] of a second species, showing to it some, if not all, of the reactions usually forthcoming in intraspecific encounters. Aggression is related to the territory as a whole and not merely to a particular part of it… The result of this interspecific aggression is the exclusion of the second species from the territory."

This definition captures the elements of IT that distinguish it from other forms of aggressive behavior between species. First, the agonistic behaviors observed during IT are similar, if not identical, to those exhibited during intraspecific territoriality. Second, these agonistic behaviors are not limited to interactions at foraging sites, nest sites, or other spatially restricted or ephemeral resources; instead, the entire territory is defended against heterospecific rivals. Finally, the outcome of IT is a more or less complete spatial segregation of the two species, with little or no territorial overlap between them.

The occurrence of IT raises a basic ecological and evolutionary question: What benefits do individuals gain by excluding heterospecifics from their territories? Classic ecological theory suggests that sympatric species must differ in habitat or food preferences to avoid competitive exclusion (Gause 1934, Lack 1947), and many avian communities seem to fit this model, with each species using a different foraging method or specializing on a different microhabitat (e.g. MacArthur 1958). Nevertheless, IT has been observed among many bird species, prompting questions about its adaptive significance (Simmons 1951, Orians and Willson 1964).

There remains no clear consensus regarding whether IT is adaptive. Orians and Willson (1964) suggested that many instances of IT were adaptive, and that adaptive IT would typically occur in one of three ecological scenarios: 1) in structurally simple habitats, such as marshes or grasslands; 2) among species that share a highly specialized feeding niche; and 3) in species-rich communities where further interspecific divergence in resource use is unlikely. What these three scenarios have in common are barriers to ecological divergence; thus, Orians and Willson argued that IT might enable species to coexist where such divergence was impossible. Cody (1973) showed, using a simple model in which travel between the nest and feeding areas is costly, that IT could be adaptive even when two species do not overlap completely in their feeding niche. Mikami and Kawata (2004) took an analytical modeling approach, and showed that IT is most likely to be adaptive when niche overlap with a potential rival is high (i.e., the fitness cost of *not* excluding a rival is large) and when the fitness and time costs of excluding a rival are low. These predictions have not been adequately tested in natural systems, however.

The primary alternative hypothesis is that IT is a transitory phenomenon resulting from recent secondary contact between species that share similar recognition systems (Murray 1971, 1976). Under this hypothesis, IT is interpreted as misdirected intraspecific territoriality. Murray

(1971) argued that one of the interacting species would inevitably be dominant over the other and eventually replace it. This hypothesis has not been formally modeled, and Murray's verbal model relied on several assumptions that may or may not be met in nature (e.g., that one type of habitat is optimal for both species, and that one species is behaviorally dominant to the other under all ecological conditions). Some recent models, however, have also failed to show species coexistence under interspecific interference competition (e.g. Amarasekare 2002).

Most hypotheses proposed to explain IT require comparative tests, yet to date, studies of IT have considered only a single pair of interacting species. In this study, our objective is to use a comparative approach to evaluate the effects of ecological and evolutionary factors on the occurrence of IT. We use birds in our analysis; Simmons (1951) cites several examples of IT in birds, and many others have been documented in the decades since (Orians and Willson 1964, Grether et al. 2009, Peiman and Robinson 2010, Ord et al. 2011). Birds are often a focus of IT studies – and of studies of territoriality more generally – because avian territorial behaviors, such as song and aggressive displays, are easy to observe and quantify. In this paper, we restrict our comparative analyses to the wood-warblers (Parulidae), a speciose family of North American passerines in which several well-documented cases of IT occur.

We aim to test the hypothesis that IT is an adaptive consequence of ecological overlap in wood-warblers. If our hypothesis is true, species exhibiting IT should be more similar to one another in body size, bill size, feeding guild, and habitat preferences than species not exhibiting IT. Furthermore, we predict that IT more frequently between closely related species than more distantly related species, because close relatives often share similar morphological and ecological attributes as a result of shared ancestry. We use a comparative approach to test the influence of morphology, ecology, and relatedness on the occurrence of IT. We first search the literature for

known cases of IT. At each study site where IT has been documented, we compare the pair of species involved in IT with randomly selected species pairs at the same location. We also aim to test Orians and Willson's first two ecological hypotheses about IT: namely, that IT most often occurs between species living in structurally simple environments, or between species using a highly stratified food source in a more complex environment.

Methods:

Literature review: We selected the North American wood-warblers (Parulidae) for this comparative analysis because it is a species-rich family (51 extant species in North America) in which several well-known cases of IT occur (Appendix 1). As currently defined, the Parulidae is monophyletic with respect to other passerine groups (Lovette and Bermingham 2002, Lovette et al. 2010). We began by using *The Birds of North America Online* (hereafter "BNA") species accounts (Poole 2005) to gather data on all documented cases of interspecific territoriality for each of the 51 species of North American parulids, along with their body mass and bill length.

The BNA species accounts provided the starting point for our own literature search. We began by consulting papers cited under the "Agonistic Behavior," "Spacing," and "Social and Interspecific Behavior" sections of BNA species accounts to evaluate whether putative cases of IT met our criteria for inclusion in this study. We included only cases that were unambiguously territorial in nature. In the absence of further supporting information, we did not consider cases of interspecific aggression over food and other ephemeral resources as IT. If the BNA citations were insufficient to verify a putative case of IT, we searched the primary literature using the Zoological Records database. We carefully evaluated the literature for reports of IT, noting the intensity and frequency of interspecific encounters. Isolated or anecdotal reports of IT made in

the absence of systematic observation were disregarded, as were any reports that appeared to be observations of non-territorial interspecific aggression (which we found was often conflated with IT the BNA species accounts). Examples of true IT typically included records of chases and territorial displays or songs directed at heterospecifics, particularly at known territorial boundaries, as well as partial or complete spatial segregation of territories.

After determining which species exhibited IT, we gathered additional information on all warbler species from a variety of sources. First, we used the BNA habitat descriptions for each species to assign the species a habitat complexity score. We created a 3-point scale of habitat complexity: 1 represented simple habitats, such as tundra or grassland, 2 represented habitats of intermediate complexity, such as chaparral or forest edge, and 3 represented the most complex habitats, such as coniferous and deciduous forest. Data on feeding guild were gathered from de Graaf and colleagues (1985), which classifies North American birds on three feeding niche axes: food type, feeding substrate, and method of food collection. Finally, since closely related species were likely to share ecological and morphological attributes, we asked whether phylogenetic relatedness influenced the occurrence of IT. As a measure of relatedness, we used mitochondrial (mtDNA) genetic distances (cf. Lovette and Hochachka 2006) from a well-resolved species-level phylogenic study of the Parulidae (Lovette et al. 2010). Finally, we examined all hybridization records among parulid species to assess whether species that hybridize in nature are more likely to show IT than species that do not (McCarthy 2006).

Identifying potentially interacting species: To test whether species that exhibited IT were more similar in their ecology, morphology, or relatedness than species that did not exhibit IT, we first identified species that were sympatric with each known IT species pair. We used the USGS

Breeding Bird Survey (BBS) dataset (Sauer et al. 2011) to determine which species were sympatric with each IT species pair.

We began by recording the latitude and longitude of each study in which IT was observed; when the latitude and longitude were not provided in the source paper, we inferred the coordinates as precisely as possible using other locality information provided and Google Earth. Then, at each study location we found the 20 closest BBS routes that were run within ±5 years of the conclusion of the study that reported IT. Within these 20 BBS routes, we restricted our search to routes at which both IT species were reported, and used up to three of the closest routes in the list to generate a list of sympatric species at each locality. Since wood-warblers are not likely to compete with species with very different ecological niches (e.g., raptors, ducks), we restricted these sympatric species lists to passerines and a selected group of ecologically similar taxa (i.e. Columbiformes, Cuculiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes; this list was narrowed further in subsequent analyses, see below).

The BBS provides a unique opportunity not only to assess landscape-scale sympatry, but also "microsympatry" or syntopy. Each BBS count route comprises 50 stops, with a standardized 3-minute point count is performed at each stop. Therefore, we can ask whether a pair of species occurs at the same stop (i.e., the species are syntopic) more or less often than we would expect if their distributions were fully independent. BBS data is summarized into 10-stop bins for much of the history of the survey, but the full 50-stop data is available for most routes from 1997 to present. We used these data to calculate an index of syntopy for each pair of sympatric species at each study location. We began by finding all routes within 250km of each study site. Within each route, we calculated the total number of survey stops in the 50-stop dataset, the number of stops occupied by species 1, by species 2, and by both species. Across all routes within 250km of each

study site, we calculated two indices of syntopy. In the first index (the "proportion metric") we calculated the proportion of stops occupied by the less abundant species that were also occupied by the more abundant species. In the second (the "observed/expected metric"), we calculated a ratio of the observed number of stops where both species were found, divided by the expected number of stops at which both species would be found if their distributions were independent.

Analysis: We tabulated warbler species by habitat complexity and IT (present or not present) and used a Fisher's exact test to assess Orians and Willson's first hypothesis (that IT would be most prevalent in structurally simple habitats). To allay possible concerns that IT was only detected in well-studied species, we used a t-test to compare the number of studies conducted on species known to exhibit IT and species in which IT was not recorded.

To test whether IT species were more similar to one another than species that did not exhibit IT, we used a randomization approach. We compared each pair of IT species with a randomly selected pair that included one of the two IT species, calculated a mean difference between all IT and non-IT species pairs, and repeated this process 10,000 times to generate a distribution of mean differences. During each iteration of this process, if there was more than one study location where IT was observed for a given IT species pair, we selected one study location at random. At this location, we selected a non-IT species pair by randomly choosing one of the two IT species and one species not involved in IT. We assumed that each species known to be involved in IT was sufficiently well studied that randomly pairing it with a species in which IT was not documented would result in a true non-interspecifically-territorial pair (i.e. that there were no undetected cases of IT involving either of the known IT species at each study location). Finally, we recorded the variable of interest (e.g. mass difference, genetic distance, syntopy) for

each IT and non-IT species pair and calculated a mean difference between IT and non-IT species pairs. Using the distribution of these mean differences, we perform 1-tailed tests of significance by asking what proportion of the distribution lay above (or below) zero, depending on the direction of our *a priori* predictions.

We performed three sets of analyses using the strategy described in the preceding paragraph; these three approaches differed only in the set of species considered to be potential rivals of the parulid species that exhibited IT. In the most liberal approach, we used the broadest list of potential rivals, including all passerine birds and some ecologically similar taxa. Next, we restricted this list based on size. Using the criterion of a 2:1 mass ratio permitting coexistence of sympatric species at the same trophic level (Hutchinson 1959), for each IT species we selected pair a list of potential rivals within a range of one-half the mass of the smaller IT species (lower bound) to twice the mass of the larger IT species (upper bound). Finally, in the third approach, we restricted the list of potential rivals to parulids only.

These three analytical approaches allowed us to ask different ecological questions. With the broadest approach, we could ask in very general terms whether ecological or morphological similarity predisposes species to show interspecific territoriality. With the size-limited approach, we excluded species that occupy very different niches and asked wither, among potential rivals of a similar size, feeding guild and syntopy still predict the occurrence of IT. The third, within-family analysis allows us to avoid the potentially confounding influence of shared phylogenetic history at the family level, and focus instead on factors that influence IT among species sharing a common evolutionary history. To explore the effect of common descent further, we assembled a list of all sympatric parulid species pairs from the study locations considered in this survey, and

used logistic regression to evaluate the effects of genetic distance alongside morphological and ecological variables that were predicted to influence the occurrence of IT.

Results:

Descriptive statistics: Out of 51 wood-warbler species that breed regularly in North America, 27 exhibit IT, primarily with other parulids (although one was interspecifically territorial with an *Empidonax* flycatcher; see Appendix 1). Most parulids (44 species) fell into our third habitat category (habitats of high structural complexity), and many of these exhibited IT with one or more species (Table 4.1). Our data did not support Orians and Willson's (1964) hypothesis that IT would occur primarily in structurally simple habitats (Fisher's Exact Test, $p = 0.67$).

There was substantial variation in the amount of research effort dedicated to different parulid species. Therefore, we asked whether research effort predicted the incidence of IT. Using the number of records returned by a Zoological Records search on the species' Latin name as a measure of research effort, we found that species known to exhibit IT were not studied any more intensely than species not known to show IT ($t = 0.93$, $df = 49$, $p = 0.36$).

Comparisons between IT and non-IT species: First, we considered a broad list of species, both warblers and non-warblers (see above), as potential rivals of parulids. Using the randomization approach described above, we tested whether species exhibiting IT were more similar to one another in morphology and ecology than species not exhibiting IT. We found that IT species were more similar in mass ($p < 0.0001$; Fig. 4.1a) and bill length ($p = 0.023$; Fig. 4.1b) than species selected at random. IT species pairs also shared more feeding guild attributes than non-IT species pairs ($p < 0.0001$; Fig. 4.1d). We tested each guild attribute (attributes are *food type*,

Table 4.1: Number of parulid species exhibiting IT in simple vs. complex habitats. There is no significant association between IT and habitat complexity (Fisher's exact test, p = 0.67).

Habitat complexity:	1 (simple)	2 (intermediate)	3 (complex)
IT observed	0	2	22
IT not observed	1	4	22

feeding substrate, and *feeding technique*) separately and found that all three guild attributes were more often shared between IT species than non-IT species (food type: $p < 0.0001$; feeding substrate: $p = 0.008$; feeding technique: $p < 0.0001$). Finally, regardless of the syntopy metric used, IT species were more syntopic than non-IT species ($p = 0.023$ using the proportion metric, Fig. 4.1c; $p = 0.011$ using the observed/expected metric; see Methods for details).

Next, we restricted the list of potentially interacting species to include only species of similar size to the IT species pair, and performed the same set of analyses again. The effect of mass similarity persisted in the size-restricted analysis; IT species were still, on average, more similar in size than randomly selected species ($p = 0.0007$; Fig. 4.1a), but were not more similar in bill length ($p = 0.52$; Fig. 4.1b). IT species pairs still shared more guild attributes than non-IT pairs ($p = 0.0002$; Fig. 4.1d); this result is striking because certain food types and feeding strategies are limited to taxa much larger than wood-warblers. As in the non-size-restricted analysis, all three guild attributes were more likely to be shared between IT species than non-IT species (food type: $p < 0.0001$; feeding substrate: $p = 0.020$; feeding technique: $p = 0.0004$). Finally, the effect of syntopy observed in the broadest analyses persisted in the size-restricted analyses; IT species are more syntopic than randomly selected species ($p = 0.033$ using the proportion metric, Fig. 4.1c; $p = 0.013$ using the observed/expected metric).

Finally, we conducted a similar set of analyses in which only parulids were considered potential rivals of the IT species. Again, we found that IT species were more similar in mass ($p = 0.048$; Fig. 4.1a), but not in bill length ($p = 0.86$; Fig. 4.1b), than randomly selected warbler

species. Although there is little variation in feeding guild among parulids, we still found that IT species were more similar in feeding guild than randomly selected warbler species ($p = 0.025$; Fig. 4.1d); this effect was driven by similarity in feeding substrate ($p = 0.025$) rather than similarity in food type or feeding technique, which are nearly invariant among warblers. Consistent with the other analyses, IT species tended to be more syntopic than randomly selected species. This effect was non-significant using the proportion metric of syntopy ($p = 0.12$; Fig. 4.1c), but significant using the observed/expected metric ($p = 0.0002$). Finally, we used mtDNA distances to ask whether IT species were more closely related to one another than were randomly selected pairs of wood-warblers. As predicted, we found that IT species are more closely related to one another than expected by random pairing ($p = 0.0004$; Fig. 4.1e).

Using the same warbler-only dataset, we then asked whether body mass, bill dimensions, and guild overlap (in this case, overlap in feeding substrate) influenced the occurrence of IT

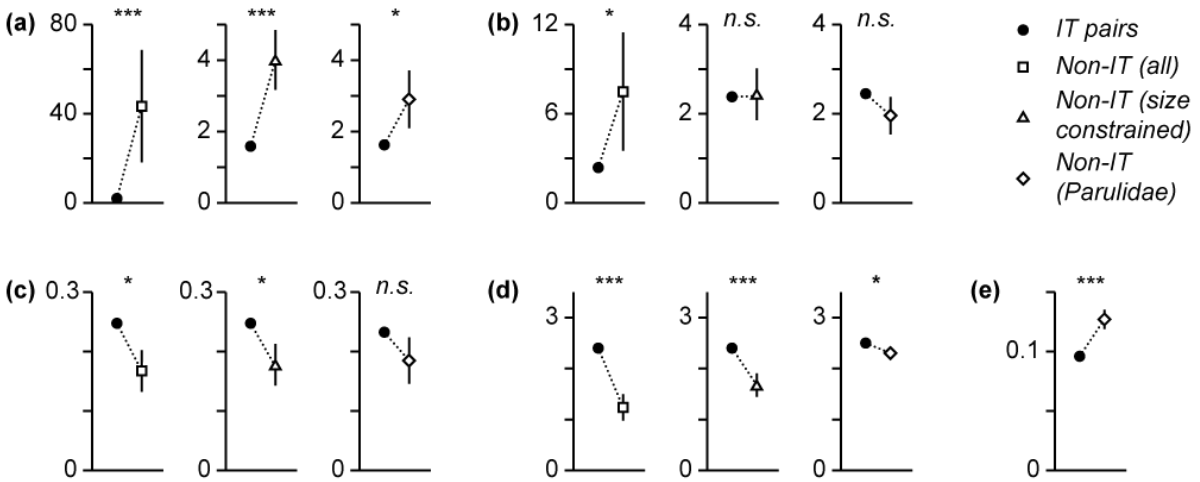


Figure 4.1: Interspecifically territorial (IT) species are more similar to one another in morphology and ecology than are non-IT species. (a) Mass difference (g); (b) bill length difference (mm); (c) proportion metric of syntopy; (d) feeding guild overlap; (e) mtDNA distance. Mean differences between IT species are represented by filled circles; mean differences between non-IT species are shown with unfilled symbols and error bars (± SE). Unfilled squares represent mean differences in non-IT species pairs selected randomly from a broad set of potentially interacting passerine and non-passerine species; unfilled triangles represent mean differences in non-IT pairs selected from a size-limited set of potentially interacting species; unfilled diamonds represent mean differences in non-IT pairs of parulid species. Key to significance symbols: *n.s.* not significant; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

when we controlled for genetic distance. We assembled a complete list of warbler species pairs that both (a) occurred near the study sites where IT was reported, and (b) included one or both IT species at the site. Then, we built logistic regression models to evaluate the effects of genetic distance, morphology, and feeding guild on IT. Genetic distance significantly predicted the occurrence of IT in a univariate analysis (b = -30.59, $p < 0.001$), and remained a significant predictor in all two-factor models (all $p < 0.05$). None of the other factors, however, predicted IT when genetic distance was included in the model (mass difference: b = -0.19, p = 0.33; bill length difference: b = 0.43, p = 0.063; shared feeding substrate: b = 0.65, p = 0.26).

Discussion: We performed a comparative analysis to investigate the ecological and evolutionary factors that promote interspecific territoriality in birds, using the North American wood-warblers (Parulidae) as the focal taxon. Our survey of the literature showed that more than half of North American parulids (27 of 51) exhibit IT in some part of their geographic range. We were surprised by how common IT was among warblers; more than half of North American warbler species exhibited IT with at least one other species, and some with several sympatric species. We have not surveyed the literature on any other passerine families, so we cannot say for certain whether the parulids have an unusually high incidence of IT. It is possible, however, that the relatively recent diversification of the Parulidae into a species-rich group of ecologically similar, broadly sympatric species predisposes them to exhibit IT with one another (Price et al. 2000). One case of IT involved a warbler and an *Empidonax* flycatcher (Goossen and Sealy 1982), but all other cases involved two species of parulids. Species engaging in interspecific territoriality (IT) were more similar to each other in morphology and feeding guild, and were more syntopic than species not involved in IT. With an analysis restricted to only parulids as potential rivals,

genetic distance was a highly significant predictor of IT and the only factor that predicted IT in a multivariate logistic regression model. Shared ancestry has apparently played a substantial role in determining which species in this group are interspecifically territorial.

Orians and Willson (1964) proposed that IT primarily occurs (1) among species coexisting in structurally simple habitats, such as marshes or grasslands, and (2) among species that share a highly specialized feeding niche. We found no evidence that IT is more common in simpler habitats. Most parulids are found in complex habitats, such as coniferous and deciduous forests, and the incidence of IT appears to be unrelated to habitat complexity. Nor are any of the wood-warblers highly specialized in their feeding niche during the breeding season; all species are insectivorous, and insects are not a highly stratified food source. Therefore, our results do not appear to support Orians and Willson's predictions about the community ecological context of IT. We are not aware of any prior attempts to test Orians and Willson's (1964) predictions.

Using the broadest set of potentially interacting species, which included all North American passerines and a few ecologically similar non-passerine taxa, we found that IT species were more similar to each other in mass, bill length, and feeding guild, and were more syntopic, on average, than were randomly selected species that did not show IT. Many of the species included in this analysis were distantly related to warblers and quite different in body size, however. Next, we restricted the set of potential rivals to those between 50% and 200% of the body mass of the IT species. A mass ratio of 2:1 is often considered a rough threshold below which two species in the same trophic level cannot persist sympatrically (Hutchinson 1959). By limiting the list of potential rivals in this way, we removed many of the ecological dissimilar and distantly related taxa from our analyses. Nevertheless, IT species were still more similar in mass and feeding guild and were more syntopic than non-IT species pairs of similar body size.

Finally, we limited the potential rivals to other species within the family Parulidae. This substantially limited the ecological variability among the species under consideration. Still, IT species were more similar in body mass and guild (specifically, feeding substrate), and more syntopic than were randomly selected species of sympatric warblers, suggesting that even among a morphologically and ecologically homogeneous group like the wood-warblers, the occurrence of IT is not haphazard. While it was clear from the outset that IT was more frequent between warbler species than it was between warblers and other groups, our analysis of IT among the Parulidae allowed us to ask whether phylogenetic relatedness (mtDNA distance) predicted the occurrence of IT within the family. Warbler species pairs exhibiting IT were significantly more closely related than pairs not involved in IT. When we controlled for genetic distance, body mass and feeding substrate were not significant predictors of IT. Therefore, in wood-warblers, it appears that phylogenetic relatedness is a better predictor of IT than either body size or feeding guild. We do not interpret this result to mean that ecology is unimportant, however. Indeed, it is possible that genetic distance is a better measure of overall similarity than either body mass or feeding guild alone; phylogenetic niche conservatism plays a significant role in the distributions and community ecology of North American Parulids (Lovette and Hochachka 2006).

The challenge of isolating the influence of ecology and morphology from that of shared ancestry has key implications for the question of whether IT is adaptive. Traditionally, adaptive hypotheses of IT have predicted that IT will occur between species that occupy similar niches. The expected benefits of excluding heterospecifics from a territory depend largely on the extent of niche overlap between species (Lorenz 1962, Johnson 1963, Cody 1969, Grether et al. 2009). Our finding – that closely related species are more likely to exhibit IT – is consistent with these predictions, because closely related species often occupy similar niches. The misdirected

*intra*specific territoriality hypothesis of IT (Murray 1971, 1976), however, also predicts that species involved in IT will often be closely related. Closely related species often share the traits used to recognize conspecific competitors (e.g. songs, coloration; Grether 2011), and this may lead to maladaptive interspecific aggression where species ranges overlap. As a result, distinguishing between adaptive and non-adaptive causes of IT, as they have traditionally been defined, is an empirical challenge.

Historically, the literature on IT was dominated by a debate about its adaptive value (e.g. Cody 1969, Murray 1971, Cody 1973, Murray 1976). We think this dichotomy oversimplifies the problem; interspecific interactions, including IT, are shaped by processes occurring over ecological and evolutionary timescales. This is not a new idea (e.g. Johnson 1963), and we are encouraged that recent empirical studies of IT have taken a more nuanced approach (e.g. Tobias and Seddon 2009, Anderson and Grether 2010b, a). We propose that current and future studies of IT should continue to move beyond the classic adaptive-versus-non-adaptive debate and acknowledge that current ecology, evolutionary history, and the duration and geographic extent of contact between species may all affect interspecific interactions (Grether et al. 2009, Peiman and Robinson 2010, Grether 2011). When two species first come into contact, their behavioral responses toward one another may largely be governed by how similar they are in appearance and territorial signals. Whether IT evolves (or is maintained) is likely to depend not only on the initial degree of niche overlap, but also on the rate of gene flow from allopatric populations, whether the species coexist broadly in syntopy or only in a narrow zone of contact, and whether they are able to diverge in resource use in sympatry, either through facultative or developmental shifts or through ecological character displacement. Both the signals on which competitor recognition depends and the ecological overlap between species may be influenced by

phylogeny. Therefore, IT is both an ecological and evolutionary problem, and this complexity should be reflected in the integrative approaches used to study it. Alongside traditional empirical approaches used to study IT, both modeling and comparative approaches (like the approach taken in the present study) will provide additional insight.

We performed, to our knowledge, the first comparative analysis of the factors underlying IT in complex natural communities. The North American wood-warblers are, both in ecology and morphology, a relatively homogeneous group. Shared traits among warbler species make separating the influence of ecology, morphology, and common evolutionary history a challenge. To disentangle possible drivers of IT further, it would be fruitful to consider one or more groups that encompass greater ecological and morphological variation, particularly variation that is not tightly linked to phylogeny. Despite the homogeneity of the wood-warblers, however, we found evidence that shared ancestry, similarity in body size and feeding guild, and a high degree of syntopy contribute to the occurrence of IT. We acknowledge that some of these factors may be interrelated as a result of phylogeny. Nevertheless, our results demonstrate that a comparative approach can be effective in testing hypotheses about the ecological and evolutionary processes underlying interspecific territoriality. We recommend that such an approach be taken with other study taxa to test the generality of our conclusions.

Appendix 1: List of all cases of interspecific territoriality in North American wood-warblers.

Species 1	Species 2	Dominance	Study Location	Year(s)	References
Bay breasted Warbler *Setophaga castanea*	Cape May Warbler *Setophaga tigrina*	n/a	Aroostook Valley, Maine	1976	(Morse 1978)
Prairie Warbler *Setophaga discolor*	Bachman's Warbler *Vermivora bachmanii*	Bachman's Warbler	Saint Andrews Parish, SC	1958	(Dawn 1958)
Prairie Warbler *Setophaga discolor*	Blue-winged Warbler *Vermivora cyanoptera*	Prairie Warbler	Monroe County and Bloomington, IN	1952-1965	(Nolan 1978)
Yellow-throated Warbler *Setophaga dominica*	Pine Warbler *Setophaga pinus*	Pine Warbler	Shad Landing/Cedarville State Forest, MD; Shad Landing State Park, MD	1967-1968; 1963-1966	(Morse 1974) (Ficken et al. 1968)
Blackburnian Warbler *Setophaga fusca*	Black-throated Green Warbler *Setophaga virens*	n/a	Hog Island, Maine	1966-1974	(Morse 1976)
Kirtland's Warbler *Setophaga kirtlandii*	Northern Waterthrush *Parkesia noveboracensis*	n/a	Baptiste, Ontario	1951-1975	(Brown 1975)
Chestnut-sided Warbler *Setophaga pensylvanica*	Yellow Warbler *Setophaga petechia*	n/a	Webster, Damariscotta, and Bremen, ME	1963-1965	(Morse 1966)
Yellow Warbler *Setophaga petechia*	Least Flycatcher *Empidonax minimus*	n/a	Assinobine River Diversion (Lake Manitoba) Canada	1974-1976	(Goossen and Sealy 1982)
Yellow Warbler *Setophaga petechia*	American Redstart *Setophaga ruticilla*	n/a	Wreck, Fankland and Haddock Islands, ME	1967-1970	(Morse 1973)
Yellow Warbler *Setophaga petechia*	Pine Warbler *Setophaga pinus*	n/a	Webster, Damariscotta, and Bremen, ME	1963-1965	(Morse 1966)
Townsend's Warbler *Setophaga townsendi*	Hermit Warbler *Setophaga occidentalis*	Townsend's Warbler	Olympic Mt, WA	2001-2002	(Owen-Ashley and Butler 2004)
Black -throated Green Warbler *Setophaga virens*	Yellow-rumped ("Myrtle") Warbler *Setophaga coronota*	n/a	Hog Island, Maine	1966-1974	(Morse 1976)
Black -throated Green Warbler *Setophaga virens*	Magnolia Warbler *Setophaga magnolia*	n/a	Hog Island, Maine	1966-1974	(Morse 1976)
Black -throated Green Warbler *Setophaga virens*	Northern Parula *Setophaga americana*	n/a	Hog Island, Maine	1966-1974	(Morse 1976)
Kentucky Warbler *Geothlypis formosa*	Hooded Warbler *Setophaga citrina*	Kentucky Warblers	Front Royal, VA	2000-2009	(Mcdonald 1998), M. V. Mcdonald, *pers. comm.*

Species 1	Species 2	Dominance	Study Location	Year(s)	References
Orange-crowned Warbler *Oreothlypis celata*	Virginia Warbler *Oreothylpis viginiae*	Orange-crowned Warbler	Mogollan Rim, AZ	1995-1998	(Martin and Martin 2001)
Golden-winged Warbler *Vermivora chrysoptera*	Blue-winged Warbler *Vermivora cyanoptera*	Blue-winged Warbler	Varna, NY and Thurmnot, MD	1961-1966	(Ficken and Ficken 1968)
Hooded Warbler *Setophaga citrina*	Swainson's Warbler *Limnothylpis swainsonii*	n/a	Arkansas County, AK; Canebrakes, GA; Dismal Swamp and Nansemond County, VA	1966-1967	(Meanley 1969)

Literature cited:

Abrams, P. A. 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. Theoretical Population Biology **29**:107-160.

Abrams, P. A. 1987. Alternative models of character displacement and niche shift. 2. Displacement when there is competition for a single resource. American Naturalist **130**:271-282.

Abrams, P. A., C. Rueffler, and G. Kim. 2008. Determinants of the strength of disruptive and/or divergent selection arising from resource competition. Evolution **62**:1571-1586.

Adams, E. S. 2001. Approaches to the study of territory size and shape. Annual Review of Ecology and Systematics **32**:277-303.

Agostinelli, C., Lund, U. 2011. R package 'circular': Circular statistics (version 0.4-3).

Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1994. Male coloration and species recognition in sympatric flycatchers. Proceedings of the Royal Society B: Biological Sciences **256**:113-118.

Allen, J. A. 1877. The influence of physical conditions in the genesis of species. Radical Review **1**:108-140.

Amarasekare, P. 2002. Interference competition and species coexistence. Proceedings of the Royal Society B: Biological Sciences **269**:2541-2550.

Anderson, C. N. and G. F. Grether. 2010a. Character displacement in the fighting colours of *Hetaerina* damselflies. Proceedings of the Royal Society B: Biological Sciences **277**:3669-3675.

Anderson, C. N. and G. F. Grether. 2010b. Interspecific aggression and character displacement of competitor recognition in *Hetaerina* damselflies. Proceedings of the Royal Society B: Biological Sciences **277**:549-555.

Anderson, R. A., L. D. Mcbrayer, and A. Herrel. 2008. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. Biological Journal of the Linnean Society **93**:709-720.

Angetter, L.-S., S. Lötters, and D. Rödder. 2011. Climate niche shift in invasive species: the case of the brown anole. Biological Journal of the Linnean Society **104**:943-954.

Bartlett, R. D. and P. B. Bartlett. 1999. A field guide to Florida reptiles and amphibians.

Bateman, P. W. and P. A. Fleming. 2011. Frequency of tail loss reflects variation in predation levels, predator efficiency, and the behaviour of three populations of brown anoles. Biological Journal of the Linnean Society **103**:648-656.

Beuttell, K. and J. B. Losos. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs **13**:1-28.

Boker, S. M., M. C. Neale, H. H. Maes, M. J. Wilde, M. Spiegel, T. R. Brick, R. Estabrook, T. C. Bates, P. Mehta, T. von Oertzen, R. J. Gore, M. D. Hunter, D. C. Hackett, J. Karch, and A. Brandmaier. 2012. OpenMx 1.2 User Guide.

Boker, S. M., M. C. Neale, H. H. Maes, M. J. Wilde, M. Spiegel, T. R. Brick, J. Spies, R. Estabrook, S. Kenny, T. C. Bates, P. Mehta, and J. Fox. 2011. OpenMx: An open source extended structural equation modeling framework. Psychometrika **76**:306-317.

Brach, V. 1977. Notes on the introduced population of *Anolis cristatellus* in south Florida. Copeia **1977**:184-185.

Broennimann, O., U. A. Treier, H. Müller-Schärer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters **10**:701-709.

Brown, R. D. 1975. A Comparative Study of the Vocalizations and Associated Behavior of *Seiurus* Warblers (Parulidae). Ohio State University, Ohio.

Brown, W. L., Jr. and E. O. Wilson. 1956. Character displacement. Systematic Biology **5**:49-64.

Byers, J. E. 2000. Competition between two estuarine snails: Implications for invasions of exotic species. Ecology **81**:1225-1239.

Calenge, C. 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Calsbeek, R. and E. Marnocha. 2006. Context dependent territory defense: The importance of habitat structure in *Anolis sagrei*. Ethology **112**:537-543.

Calsbeek, R., T. B. Smith, and C. Bardeleben. 2007. Intraspecific variation in *Anolis sagrei* mirrors the adaptive radiation of Greater Antillean anoles. Biological Journal of the Linnean Society **90**:189-199.

Carroll, S. P. 2011. Conciliation biology: the eco-evolutionary management of permanently invaded biotic systems. Evolutionary Applications **4**:184-199.

Case, T. J. and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences **71**:3073-3077.

Cody, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor **71**:223-239.

Cody, M. L. 1973. Character covergence. Annual Review of Ecology and Systematics **4**:189-211.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition - Evidence from field experiments. American Naturalist **122**:661-696.

Cooley, J. R. 2007. Decoding asymmetries in reproductive character displacement. Proceedings of the Academy of Natural Sciences of Philadelphia **156**:89-96.

Dawn, W. 1958. An Anomalous Bachman's Warbler. Atlantic Naturalist **13**:229-232.

Dayan, T. and D. Simberloff. 2005. Ecological and community-wide character displacement: The next generation. Ecology Letters **8**:875-894.

de Graaf, R. M., N. G. Tilghman, and S. H. Anderson. 1985. Foraging guilds of North American birds. Environmental Management **9**:493-536.

Deitloff, J., J. O. Church, D. C. Adams, and R. G. Jaeger. 2009. Interspecific agonistic behaviors in a salamander community: Implications for alpha selection. Herpetologica **65**:174-182.

Dial, R. and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: Direct and indirect effects. Ecology **76**:1821-1834.

Dickman, C. R. 1991. Mechanisms of competition among insectivorous mammals. Oecologia **85**:464-471.

Dyer, W. G., L. Bunkley-Williams, and E. H. Williams, Jr. 2001. Some helminth parasites of *Anolis stratulus* and *Anolis cristatellus* (Sauria: Polychrotidae) in Puerto Rico. Transactions of the Illinois State Academy of Science **94**:161-165.

Ficken, M. S. and R. W. Ficken. 1968. Territorial relationships of blue-winged warblers, golden-winged warblers and their hybrids. Wilson Bulletin **80**:442-451.

Ficken, R. W., M. S. Ficken, and D. H. Morse. 1968. Competition and character displacement in two sympatric pine dwelling warblers (*Dendroica*, Parulidae). Evolution **22**:307-314.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software **27**:233-249.

Francis, R. C. 1988. On the relationship between aggression and social dominance. Ethology **78**:223-237.

Frazer, G. W., C. D. Canham, K. P. Lertzman, P. Sallaway, and D. Marinakis. 1999. Gap Light Analyzer (GLA). Pages Imaging software to extract forest canopy structure and gap light transmission indices from true-color hemispherical (fisheye) photographs. Institute of Ecosystem Studies, Simon Fraser University.

Gallagher, R. V., L. J. Beaumont, L. Hughes, and M. R. Leishman. 2010. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. Journal of Ecology **98**:790-799.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland, USA.

Gibb, H. 2011. Experimental evidence for mediation of competition by habitat succession. Ecology **92**:1871-1878.

Gill, D. E. 1974. Intrinsic rate of increase, saturation density, and competitive ability. II. The evolution of competitive ability. American Naturalist **108**:103-116.

Goossen, J. P. and S. G. Sealy. 1982. Production of young in a dense nesting population of yellow warblers, *Dendroica petechia*, in Manitoba. Canadian Field Naturalist **96**:189-199.

Grant, P. R. 1972. Convergent and divergent character displacement. Biological Journal of the Linnean Society **4**:39-68.

Gray, S. M. and B. W. Robinson. 2002. Experimental evidence that competition between stickleback species favours adaptive character divergence. Ecology Letters **5**:264-272.

Gray, S. M., B. W. Robinson, and K. J. Parsons. 2005. Testing alternative explanations of character shifts against ecological character displacement in brook sticklebacks (*Culaea inconstans*) that coexist with ninespine sticklebacks (*Pungitius pungitius*). Oecologia **146**:25-35.

Grether, G. F. 2011. The neuroecology of competitor recognition. Integrative and Comparative Biology **51**:807-818.

Grether, G. F., N. Losin, C. N. Anderson, and K. Okamoto. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biological reviews of the Cambridge Philosophical Society **84**:617-635.

Gröning, J. and A. Hochkirch. 2008. Reproductive interference between animal species. The Quarterly Review of Biology **83**:257-282.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. American Naturalist **140**:539-572.

Hairston, N. G. 1983. Alpha selection in competing salamanders: Experimental verification of an a priori hypothesis. American Naturalist **122**:105-113.

Hairston, N. G., K. C. Nishikawa, and S. L. Stenhouse. 1987. The evolution of competing species of terrestrial salamanders: Niche partitioning or interference? Evolutionary Ecology **1**:247-262.

Harris, D. B. and D. W. Macdonald. 2007. Interference competition between introduced black rats and endemic Galapagos rice rats. Ecology **88**:2330-2344.

Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, M. Holland, J. Lambrinos, U. Malvadkar, B. A. Melbourne, K. Moore, C. Taylor, and D. Thomson. 2004. The spatial spread of invasions: new developments in theory and evidence. Ecology Letters **8**:91-101.

Herrel, A., R. Joachim, B. Vanhooydonck, and D. J. Irschick. 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. Biological Journal of the Linnean Society **89**:443-454.

Herrel, A., L. D. Mcbrayer, and P. M. Larson. 2007. Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. Biological Journal of the Linnean Society **91**:111-119.

Hertz, P. E. 1992. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. Oecologia **90**:127-136.

Hess, N. E. and J. B. Losos. 1991. Interspecific aggression between *Anolis cristatellus* and *A. gundlachi*: comparison of sympatric and allopatric populations. Journal of Herpetology **25**:256-259.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal **50**:346-363.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? The American Naturalist **93**:145-159.

Huyghe, K., A. Herrel, D. Adriaens, Z. Tadić, and R. Van Damme. 2008. It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. Biological Journal of the Linnean Society **96**:13-22.

Jenssen, T. A., K. R. Decourcy, and J. D. Congdon. 2005. Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? Animal Behaviour **69**:1325-1336.

Jenssen, T. A., D. L. Marcellini, C. A. Pague, and L. A. Jenssen. 1984. Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. Copeia **1984**:853-862.

Johnson, M. A., L. J. Revell, and J. B. Losos. 2010. Behavioral convergence and adaptive radiation: Effects of habitat use on territorial behavior in *Anolis* lizards. Evolution **64**:1151-1159.

Johnson, N. K. 1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondii-oberholsi-wrighti* complex. University of California Publications in Zoology **66**:79-238.

Jones, E. I. and R. Gomulkiewicz. 2012. Biotic interactions, rapid evolution, and the establishment of introduced species. American Naturalist **179**:E28-E36.

Just, W. and M. R. Morris. 2003. The Napoleon complex: Why smaller males pick fights. Evolutionary Ecology **17**:509-522.

Just, W., M. R. Morris, and X. Sun. 2007. The evolution of aggressive losers. Behavioural processes **74**:342-350.

Knapp, R. and M. C. Moore. 1996. Male morphs in tree lizards, *Urosaurus ornatus*, have different delayed hormonal responses to aggressive encounters. Animal Behaviour **52**:1045-1055.

Kolbe, J. J., R. E. Glor, L. Rodríguez Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature **431**:177-181.

Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2007. Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. Conservation biology **21**:1612-1625.

Kolbe, J. J. and J. B. Losos. 2005. Hind-Limb Length Plasticity in *Anolis carolinensis*. Journal of Herpetology **39**:674-678.

Kolbe, J. J., P. S. VanMiddlesworth, N. Losin, N. Dappen, and J. B. Losos. *in press*. Climatic niche shift predicts thermal trait response in one but not both introductions of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, USA. Ecology and Evolution.

Krysko, K. L., J. P. Burgess, M. R. Rochford, C. R. Gillette, D. Cueva, K. M. Enge, L. A. Somma, J. L. Stabile, D. C. Smith, J. A. Wasilewski, G. N. Keickhefer, III, M. C. Granatosky, and S. V. Nielsen. 2011. Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages. Zootaxa **3028**:1-64.

Lack, D. L. 1947. Darwin's Finches. Cambridge University Press., Cambridge, England.

Lailvaux, S. P., A. Herrel, B. Vanhooydonck, J. J. Meyers, and D. J. Irschick. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). Proceedings of the Royal Society B: Biological Sciences **271**:2501-2508.

Lailvaux, S. P. and D. J. Irschick. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. American Naturalist **170**:573-586.

Langkilde, T. and R. Shine. 2007. Interspecific conflict in lizards: Social dominance depends upon an individual's species not its body size. Austral Ecology **32**:869-877.

Leal, M. and L. J. Fleishman. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. Proceedings of the Royal Society B: Biological Sciences **269**:351-359.

Leal, M. and L. J. Fleishman. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. American Naturalist **163**:26-39.

Leal, M., J. A. Rodríguez-Robles, and J. B. Losos. 1998. An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. Oecologia **117**:273-278.

Licht, P. 1974. Response of *Anolis* lizards to food supplementation in nature. Copeia **1974**:215-221.

Liu, H. and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions **8**:1535-1545.

Lorenz, K. 1962. The function of colour in coral reef fishes. Proceedings of the Royal Institute of Great Britain **39**:282-296.

Losos, J. B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. Copeia **1985**:905-910.

Losos, J. B. 1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: An evolutionary analysis. Ecological Monographs **60**:369-388.

Losos, J. B. 1990b. The evolution of form and function: Morphology and locomotor performance in West Indian *Anolis* lizards. Evolution **44**:1189-1203.

Losos, J. B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Annual Review of Ecology and Systematics **25**:467-493.

Losos, J. B. 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles.

Losos, J. B., D. A. Creer, D. Glossip, R. Goellner, A. Hampton, G. Roberts, N. Haskell, P. Taylor, and J. Ettling. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. Evolution **54**:301-305.

Losos, J. B., T. R. Jackman, A. Larson, K. De Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science **279**:2115-2118.

Losos, J. B., T. W. Schoener, R. B. Langerhans, and D. A. Spiller. 2006. Rapid temporal reversal in predator-driven natural selection. Science **314**:1111.

Losos, J. B., T. W. Schoener, and D. A. Spiller. 2004. Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. Nature **432**:505-508.

Losos, J. B., T. W. Schoener, K. I. Warheit, and D. Creer. 2001. Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards. Genetica **112-113**:399-415.

Losos, J. B. and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. Journal of Experimental Biology **145**:23-30.

Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature **387**:70-73.

Lovette, I. J. and E. Bermingham. 2002. What is a wood-warbler? Molecular characterization of a monophyletic Parulidae. Auk **119**:695-714.

Lovette, I. J. and W. M. Hochachka. 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. Ecology **87**:S14-S28.

Lovette, I. J., J. L. Pérez-Emán, J. P. Sullivan, R. C. Banks, I. Fiorentino, S. Córdoba-Córdoba, M. Echeverry-Galvis, F. K. Barker, K. J. Burns, J. Klicka, S. M. Lanyon, and E. Bermingham. 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). Molecular phylogenetics and evolution **57**:753-770.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**:599-619.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications **10**:689-710.

Maher, C. R. and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. The American Midland Naturalist **143**:1-29.

Marnocha, E., J. Pollinger, and T. B. Smith. 2011. Human-induced morphological shifts in an island lizard. Evolutionary Applications **4**:388-396.

Martin, P. R. and T. E. Martin. 2001. Behavioral interactions between coexisting species: Song playback experiments with wood warblers. Ecology **82**:207-218.

McCarthy, E. M. 2006. Handbook of Avian Hybrids of the World. Oxford University Press, New York, New York, USA.

Mcdonald, M. V. 1998. Kentucky Warbler (*Geothlypis formosus*).*in* A. Poole, editor. The Birds of North America Online. The Cornell Lab of Ornithology, Ithaca, New York, USA.

Meanley, B. 1969. Pre-nesting and nesting behavior of the Swainson's warbler. Wilson Bulletin **81**:246-257.

Meshaka, W. E., Jr. 2011. A runaway train in the making: The exotic amphibians, reptiles, turtles, and crocodilians of Florida. Herpetological Conservation and Biology **6**:1-101.

Metzger, K. A. and A. Herrel. 2005. Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. Biological Journal of the Linnean Society **86**:433-466.

Mikami, O. K. and M. Kawata. 2004. Does interspecific territoriality reflect the intensity of ecological interactions? A theoretical model for interspecific territoriality. Evolutionary ecology research **6**:765-775.

Morrell, L. J., J. Lindström, and G. D. Ruxton. 2005. Why are small males aggressive? Proceedings of the Royal Society B: Biological Sciences **272**:1235-1241.

Morse, D. H. 1966. The context of songs in the yellow warbler. The Wilson Bulletin **78**:444-455.

Morse, D. H. 1973. The foraging of small populations of yellow warblers and American redstarts. Ecology **54**:346-355.

Morse, D. H. 1974. Foraging of pine warblers allopatric and sympatric to yellow-throated warblers. The Wilson Bulletin **86**:474-477.

Morse, D. H. 1976. Hostile encounters among spruce-woods warblers (*Dendroica*, Parulidae). Animal Behavior **24**:764-771.

Morse, D. H. 1978. Populations of bay-breasted and Cape May warblers during an outbreak of the spruce budworm. The Wilson Bulletin **90**:404-413.

Murray, B. G., Jr. 1971. The ecological consequences of interspecific territorial behavior in birds. Ecology **52**:414-423.

Murray, B. G., Jr. 1976. A critique of interspecific territoriality and character convergence. The Condor **78**:518-525.

Nolan, V., Jr. 1978. The Ecology and Behavior of the Prairie Warbler, *Dendroica discolor*. Ornithological Monographs **26**:1-595.

Ord, T. J. 2011. Receiver perception predicts species divergence in long-range communication. Animal Behaviour **83**:3-10.

Ord, T. J., L. King, and A. R. Young. 2011. Contrasting theory with the empirical data of species recognition. Evolution **65**:2572-2591.

Ord, T. J. and E. P. Martins. 2006. Tracing the origins of signal diversity in anole lizards: Phylogenetic approaches to inferring the evolution of complex behaviour. Animal Behaviour **71**:1411-1429.

Ord, T. J. and J. A. Stamps. 2009. Species identity cues in animal communication. American Naturalist **174**:585-593.

Orians, G. H. and M. F. Willson. 1964. Interspecific territories of birds. Ecology **45**:736-745.

Owen-Ashley, N. T. and L. K. Butler. 2004. Androgens, interspecific competition and species replacement in hybridizing warblers. Proceedings of the Royal Society B: Biological Sciences **271 Suppl.**:S498-S500.

Pacala, S. and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science **217**:444-446.

Pacala, S. and J. Roughgarden. 1984. Control of arthropod abundance by *Anolis* lizards on St . Eustatius (Neth. Antilles). Oecologia **64**:160-162.

Pacala, S. and J. Roughgarden. 1985. Population Experiments with the *Anolis* Lizards of St . Maarten and St . Eustatius. Ecology **66**:129-141.

Pacala, S., J. Rummel, and J. Roughgarden. 1983. A technique for enclosing *Anolis* lizard populations under field conditions. Journal of Herpetology **17**:94-97.

Paterson, A. V. and S. McMann. 2004. Differential headbob displays toward neighbors and nonneighbors in the territorial lizard *Anolis sagrei*. Journal of Herpetology **38**:288-291.

Pearson, S. F. and S. A. Rohwer. 2000. Asymmetries in male aggression across an avian hybrid zone. Behavioral Ecology **11**:93-101.

Peiman, K. S. and B. W. Robinson. 2007. Heterospecific aggression and adaptive divergence in brook stickleback (*Culaea inconstans*). Evolution **61**:1327-1338.

Peiman, K. S. and B. W. Robinson. 2010. Ecology and evolution of resource-related heterospecific aggression. The Quarterly Review of Biology **85**:133-158.

Perkins, T. A. 2012. Evolutionarily labile species interactions and spatial spread of invasive species. American Naturalist **179**:E37-E54.

Perry, G., K. Levering, I. Girard, and T. Garland, Jr. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. Animal Behaviour **67**:37-47.

Petren, K. and T. J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology **77**:118-132.

Pfennig, K. S. and D. W. Pfennig. 2009. Character displacement: Ecological and reproductive responses to a common evolutionary problem. The Quarterly Review of Biology **84**:253-276.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. D. C. Team. 2012. nlme: Linear and Nonlinear Mixed Effects Models.

Poole, A. E. 2005. The Birds of North America Online: http://bna.birds.cornell.edu/BNA/. Cornell Lab of Ornithology, Ithaca, New York, USA.

Prentis, P. J., J. R. U. Wilson, E. E. Dormontt, D. M. Richardson, and A. J. Lowe. 2008. Adaptive evolution in invasive species. Trends in plant science **13**:288-294.

Price, T., I. J. Lovette, E. Bermingham, H. L. Gibbs, and A. D. Richman. 2000. The imprint of history on communities of North American and Asian warblers. American Naturalist **156**:354-367.

Qualls, C. P. and R. G. Jaeger. 1991. Dear enemy recognition in *Anolis carolinenis*. Journal of Herpetology **25**:361-363.

Rasband, W. S. 2011. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, USA.

Reed, T. M. 1982. Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: Playback and removal experiments. Animal Behaviour **30**:171-181.

Rice, J. C. 1978. Behavioural interactions of interspecifically territorial vireos. I. Song discrimination and natural interactions. Animal Behaviour **26**:527-549.

Rohwer, S. A. 1973. Significance of sympatry to behavior and evolution of Great Plains meadowlarks. Evolution **27**:44-57.

Rummel, J. D. and J. Roughgarden. 1985. Effects of reduced perch-height separation on competition between two *Anolis* lizards. Ecology **66**:430-444.

Rychlik, L. and R. Zwolak. 2006. Interspecific aggression and behavioural dominance among four sympatric species of shrews. Canadian Journal of Zoology **84**:434-448.

Salzburg, M. A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: A case study in interspecific competition. Ecology **65**:14-19.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American Breeding Bird Survey: Results and Analysis 1966 - 2010. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist **156**:S4-S16.

Schluter, D. and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. American Naturalist **140**:85-108.

Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. Science **227**:1056-1059.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240-285.

Schwartz, A. and R. Thomas. 1975. A check list of West Indian amphibians and reptiles. Carnegie Museum of Natural History Special Publications **1**:1-216.

Simmons, K. E. L. 1951. Interspecific territorialism. Ibis **93**:407-413.

Simon, V. B. 2011. Communication signal rates predict interaction outcome in the brown anole lizard, *Anolis sagrei*. Copeia **2011**:38-45.

Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2012. Generalized linear mixed models using AD model builder.

Slatkin, M. 1980. Ecological character displacement. Ecology **61**:163-177.

Smith, T. B. 1991. Inter- and intra-specific diet overlap during lean times between *Quelea erythrops* and bill morphs of *Pyrenestes ostrinus*. Oikos **60**:76-82.

Spezzano, L. C., Jr. and B. C. Jayne. 2004. The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). Journal of Experimental Biology **207**:2115-2131.

Stamps, J. A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology **58**:349-358.

Stamps, J. A. 1984. Growth costs of territorial overlap: experiments with juvenile lizards (*Anolis aeneus*). Behavioral Ecology and Sociobiology **15**:115-119.

Stamps, J. A. and V. V. Krishnan. 1994a. Territory acquisition in lizards: I. First encounters. Animal Behaviour **47**:1375-1385.

Stamps, J. A. and V. V. Krishnan. 1994b. Territory acquisition in lizards: II. Establishing social and spatial relationships. Animal Behaviour **47**:1387-1400.

Stamps, J. A. and V. V. Krishnan. 1995. Territory acquisition in lizards: III. Competing for space. Animal Behaviour **49**:679-693.

Stamps, J. A. and V. V. Krishnan. 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Animal Behaviour **55**:461-472.

Stevens, R. D. and M. R. Willig. 2000. Community structure, abundance, and morphology. Oikos **88**:48-56.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? Ecology Letters **9**:357-374.

Suarez, A. V. and N. D. Tsutsui. 2008. The evolutionary consequences of biological invasions. Molecular Ecology **17**:351-360.

Therneau, T. 2011. coxme: Mixed effects Cox models.

Tobias, J. A. and N. Seddon. 2009. Signal design and perception in *Hypocnemis* antbirds: Evidence for convergent evolution via social selection. Evolution **63**:3168-3189.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Animal Behaviour **33**:746-753.

Tokarz, R. R. and J. W. Beck, Jr. 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test for behavioural interference. Animal Behaviour **35**:722-734.

Toro, E., A. Herrel, and D. J. Irschick. 2004. The evolution of jumping performance in Caribbean *Anolis* lizards: Solutions to biomechanical trade-offs. American Naturalist **163**:844-856.

Toro, E., A. Herrel, B. Vanhooydonck, and D. J. Irschick. 2003. A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. Journal of Experimental Biology **206**:2641-2652.

Török, J. and L. Tóth. 1999. Asymmetric competition between two tit species: A reciprocal removal experiment. Journal of Animal Ecology **68**:338-345.

Vallin, N., A. M. Rice, R. I. Bailey, A. Husby, and A. Qvarnström. 2011. Positive feedback between ecological and reproductive character displacement in a young avian hybrid zone. Evolution **66**:1167-1179.

Vanhooydonck, B., A. Herrel, and D. J. Irschick. 2006. Out on a limb: The differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. The Journal of experimental biology **209**:4515-4523.

Vellend, M., L. J. Harmon, J. L. Lockwood, M. M. Mayfield, A. R. Hughes, J. P. Wares, and D. F. Sax. 2007. Effects of exotic species on evolutionary diversification. Trends in Ecology & Evolution **22**:481-488.

Whitney, K. D. and C. A. Gabler. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: Challenges for predicting invasive potential. Diversity and Distributions **14**:569-580.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evolutionary Biology **6**:47-89.

Williams, E. E. and A. S. Rand. 1977. Species recognition, dewlap function and faunal size. American Zoologist **17**:261-270.

Wilson, L. D. and L. Porras. 1983. The ecological impact of man on the South Florida Herpetofauna. University of Kansas Museum of Natural History Special Publications **9**:1-89.

Yuan-Ting, J., T. Ren-rong, and L. Nai-Fa. 2006. Altitudinal variations of morphological characters of *Phrynocephalus* sand lizards: on the validity of Bergmann's and Allen's rules. Acta Zoologica Sinica **52**:838-845.