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Mechanisms of Invasion and Competition in Anolis sagrei and Anolis carolinensis lizards in southeastern Louisiana

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Mechanisms of Invasion and Competition in Anolis sagrei and Anolis carolinensis lizards in southeastern Louisiana

A Dissertation

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in
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By

Jessica R. Edwards

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Dedicated to my family and friends

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Abstract

Invasive species can have a variety of effects on the behavior and ecology of native species. Currently in New Orleans, Louisiana, both *A. sagrei* and *A. carolinensis* lizards are relatively abundant, but the *A. sagrei* population is expanding rapidly. I used a combination of laboratory and field studies to investigate factors that might be influencing local dominance of invasive *A. sagrei* over native *A. carolinensis* populations, including habitat use, display behavior, interspecific aggressive interactions, and plasticity. When comparing display behavior and habitat use in anole populations across three field sites in southern Louisiana, I found differences in male display behavior of both species, and also that *A. carolinensis* perched higher when *A. sagrei* was present. In staged interspecific interactions, I discovered that *A. sagrei* females achieved consistently higher aggressive scores than *A. carolinensis* females, suggesting that female interspecific behavior is probably more important than male behavior in driving changes in habitat use. Lastly, I studied plasticity in several morphological and whole-organism performance variables by rearing males and females of each species on two different perch diameters. I found that sprinting performance in *A. sagrei* was significantly different between treatment groups, although the morphological differences between perch treatments were subtler than those reported in previous studies. I also found that *A. carolinensis* females exhibited significant differences in both sprinting and clinging performance, despite no significant differences in male or female morphology between perch size treatments, highlighting the potential for both species-specific and sex-specific plasticity.

Key words: Display behavior; Habitat use; Interspecific interactions; Plasticity; Whole-organism performance

Chapter 1.
Dissertation Introduction

Introduction

Invasive species can have a variety of important impacts on native fauna (Kiesecker and Blaustein, 1998; Callaway and Ridenour, 2004; Dukes and Mooney, 2004). In some cases, these impacts can be direct and straightforward, such as non-native bullfrogs (*Rana catesbeiana*) competing with and predating on native *Rana boylinii* in western North America (Moyle, 1973; Kupferberg, 1997). In other cases, native species may primarily face competition from invaders over habitat, often forcing native fauna to alter their patterns of habitat use (Cadi and Joly, 2003). The resulting limited access to preferred habitats may have further negative effects in native species. For example, the invasive house gecko *Hemidactylis frenatus* is suspected of contributing to the fragmentation and extinction of native geckos by displacing local species from preferred positions close to refugia, thus exposing them to increased risk of predation (Cole, Jones and Harris, 2005).

The recent invasion and spread of *Anolis sagrei* throughout the southeastern United States has the potential to greatly impact the ecology and behavior of both *A. sagrei* and the native green anole, *Anolis carolinensis*. Currently in New Orleans, Louisiana, both *A. sagrei* and *A. carolinensis* are relatively abundant, but the *A. sagrei* population is expanding rapidly. Both species are similarly sized, eat similar diets, and even when naturally present together, experience slight niche overlap. However, when *A. sagrei* moves into an area previously dominated by *A. carolinensis*, *A. carolinensis* frequently exhibits shifts in habitat use and becomes rare within a period of just a few years (Echternacht, 1999). The factors allowing *A. sagrei* to displace and apparently out-compete *A. carolinensis* are currently unclear, and the current situation in New Orleans affords an ideal situation to study interactions between these two species in a natural setting. I used a combination of laboratory and field studies to investigate a variety of these factors, including habitat use, display behavior, interspecific aggressive interactions, and plasticity.

Background

Anoles are small, diurnal lizards native to the Caribbean, the southeastern United States, and parts of Central and South America. *Anolis carolinensis* is the only anole native to the United States, and locally, to New Orleans, Louisiana. The species is classified in the trunk-crown ecomorph, meaning that it is morphologically adapted to exploit the trunks and crown areas of trees. When no other anoles are present, *A. carolinensis* will frequently expand its niche to include crown-trunk-ground habitat (Echternacht, 1999). *A. sagrei* is native to Cuba and the Bahamas, and has been introduced multiple times to the U.S. (Kolbe *et al.*, 2004), including New Orleans, Louisiana. Population density has dramatically increased in New Orleans over the past five to ten years (Lailvaux, unpublished data). *A. sagrei* is a trunk-ground ecomorph and known to adapt very well to new habitats, especially disturbed habitats (Marnocha, Pollinger and Smith, 2011).

Several previous studies have investigated interactions between *A. sagrei* and *A. carolinensis*, including male-male interactions, intra-guild predation, and changes in habitat use (Tokarz and Beck, 1987; Losos and Spiller, 1999; Campbell, 2000; Gerber and Echternacht, 2000). I built on this body of work by investigating the importance of bite force and dewlap size in predicting winners in interspecific fights, and the role of female territoriality in habitat shifts exhibited post- *A. sagrei* introductions. I also investigated potential effects of the presence of *A. sagrei* on the display behavior of *A. carolinensis*.

Phenotypic plasticity, or environmental responsiveness, is also likely to play an important role in whether *A. sagrei* is able to successfully displace *A. carolinensis* in New Orleans. Both species are known to exhibit phenotypic plasticity when raised in different habitats (Losos *et al.*, 2000; Kolbe and Losos, 2005), however little is known on how phenotypic plasticity can affect performance as adults, particularly whether differential phenotypic plasticity might influence local dominance of invasive *A. sagrei* populations over those of *A. carolinensis*. I examined the relative functional consequences of plasticity in each species with the intention of narrowing this gap in knowledge.

Display behavior

While competition over food sources and habitats between invasive and native species has been well documented, effects of the presence of novel heterospecifics on other aspects of native species ecology have received relatively less attention. One important area in this respect is display behavior. Animals may display for several reasons, including advertisement of territory ownership, mate attraction, and to deter predators (MacDonald *et al.*, 2007). In many species, display behavior is explicitly tied to habitat use, as individuals may select particular perches or other areas for display in order to enhance signal propagation (Baker, 2001; Barker and Mennill, 2009). If habitat availability is altered by the presence of an invasive species, then this may have a secondary effect of altering native display behavior as well. Alternatively, the presence of invasives may impact native display behavior independently of habitat use, for example by simply soliciting more frequent aggressive displays from native fauna (Holway and Suarez, 1999). However, despite the importance of display behaviors to the reproductive and behavioral ecology of many species, the effects of invasive taxa on the displays of native fauna, either by directly affecting the types and frequency of display types or indirectly via altering habitat use, are seldom considered.

Previous studies have suggested that the presence of *A. sagrei* affects the perch height of *A. carolinensis,* causing the green anole to restrict its habitat use in response (Losos and Spiller, 1999), but relatively little is known about how the introduction of novel congeners affects anole display behaviors (but see Hess & Losos 1991; Ord & Stamps 2009 for examples). Visual displays in anoles can be affected by a variety of factors, including habitat use, habitat visibility, predation risk, and density of conspecifics (Persons et al. 1999; Fleishman 2000; Orrell & Jenssen 2003; Leal & Fleishman 2004; Leal & Rodriguez-Robles 1997). If any of these factors are altered by the presence of other invasive anoles, then those effects may ultimately be manifested as a difference in display behavior between allopatric and sympatric anole populations.

Interspecific aggression

Perhaps more important than indirect effects on display behavior might be the direct interactions between the species themselves. Males of both species are highly territorial, and use similar displays consisting of push-ups, bobbing, and dewlap extensions to advertise territory ownership and gain mates. A previous study of staged interactions between *Anolis carolinensis* and *Anolis sagrei* demonstrated that both species display more vigorously at conspecifics rather than heterospecifics, and suggested that male-male interactions are unlikely to be a key component of competition (Tokarz and Beck, 1987). However, male interspecific interactions do nonetheless occur, and it is likely that the same factors that affect the outcomes of interspecific interactions in anoles (i.e. bite-force and dewlap size) may affect the outcome of fights between these heterospecifics as well. There is also evidence that females of some *Anolis* species may defend resources and demonstrate territoriality towards similarly sized congeners more so than males (Rand, 1967a; Rand, 1967b), so additionally I investigated the outcome of female interspecific interactions in a similarly staged setting. Female interspecific interactions could affect habitat use and offer an explanation to the changes in perch height demonstrated in previous studies.

Phenotypic plasticity

In addition to display behavior, phenotypic plasticity (i.e. the capacity of a genotype to produce different phenotypes in response to environmental variation) has potentially important implications for several aspects of animal ecology and evolution, including survival and invasiveness. Studies have demonstrated repeatedly that organisms that are able to alter their phenotype in response to environmental variation have a greater chance of survival in changing environments (Fagen, 1987; Sorci, Clobert and Belichon, 1996; Rodgers and Hughes, 2002; Peperkorn, Werner and Beyschlag, 2005; Engel, Tollrian and Jeschke, 2011). Within *Anolis,* hind limb length can vary greatly, even between two species of comparable body size (Losos 1990). This variation is reflective of different habitat uses (Williams, 1983). Species using narrow surfaces such as those living in bushes, branch tips, or grasses tend to have shorter hind limbs, while those using broad surfaces (large tree trunks, ground, or buildings) tend to have much longer hind limbs relative to body size. Longer hind limbs will give better sprinting ability on a broad surface, while shorter limbs aid in careful movements on narrow surfaces, such as twigs (Losos & Sinervo 1989).

Recent studies have documented phenotypic plasticity in hind limb length in both *A. sagrei* and *A. carolinensis*, with hatchlings developing longer or shorter legs depending on the width of the perches on which they were raised (Losos et al. 2000; Kolbe & Losos 2005). Given the importance of hind-limb length to locomotion in *Anolis*, it is plausible that plasticity in limb length over ontogeny will affect adult locomotion. This may influence fitness by determining which lizards perform well enough in a given environment to survive and produce offspring. Determining the effects of the relative degree of plasticity in *A. carolinensis* and *A. sagrei* and the resultant morphology and performance relationships for each species in different habitats could therefore shed light on the changes in habitat use and ecology occurring within the New Orleans anole populations.

Objectives

I proposed three projects to investigate several behavioral and life-history factors potentially influencing the ecology and interactions of *Anolis carolinensis* and *Anolis sagrei*, addressing the following hypotheses:

1) The presence of *A. sagrei* affects both the habitat use and display behavior of *A. carolinensis*.
2) *A. sagrei* exhibits a higher degree of phenotypic plasticity than *A. carolinensis*, and thus performs better in novel habitats.
3) Outcomes of aggressive interactions between male *A. sagrei* and *A. carolinensis* are predicted by larger dewlap size and stronger bite forces among species.
4) Aggressive interactions between female *A. sagrei* and *A. carolinensis* have asymmetrical outcomes in favor of *A. sagrei*.

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Chapter 2.

Display Behavior and Habitat Use in Single and Mixed Populations of *Anolis carolinensis* and *Anolis sagrei* Lizards

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Abstract

Introduced species can have a variety of effects on the behavior and ecology of native species. We compared display behavior and habitat use of introduced *Anolis sagrei* and native *Anolis carolinensis* lizards across three sites in Southern Louisiana. The chosen sites were similar in that they were all located in urban settings with clumped vegetation. The first site contained only *A. sagrei*, the second supported sympatric *A. sagrei* and *A. carolinensis* populations, and the third site harbored only *A. carolinensis*. We found that (1) *A. carolinensis* perched significantly higher when *A. sagrei* was present, consistent with previous studies, whereas perch height of *A. sagrei* was not altered by the presence of *A. carolinensis*; (2) *A. carolinensis* in single and mixed sites exhibited different proportions of display types, with individuals at the mixed Tulane site performing significantly more C displays than those at the single site; and (3) *Anolis sagrei* at the Tulane mixed site exhibited less push- ups than those in the site with *A. sagrei* alone. These data suggest that the arrival of congeners can affect display behavior of anoles, although such effects are different for the natives and the invaders.

Introduction

Invasive species can have a variety of important impacts on native fauna (Kiesecker & Blaustein 1998; Callaway & Ridenour 2004; Dukes & Mooney 2004; Pimentel et al. 2005). In some cases, these impacts can be direct and straightforward; for example, non-native bullfrogs (*Rana catesbeiana*) are commonly known to both compete with and prey upon native *Rana boylinii* in western North America (Moyle 1973; Kupferberg 1997). In other cases, native species may primarily face competition from invaders over habitat, often forcing native fauna to alter their patterns of habitat use (Cadi & Joly 2003), and the resulting limited access to preferred habitats may have further negative effects on native species. European starlings (*Sturnus vulgaris*), for instance, are suspected to have contributed to the decline of the purple martin (*Progne subis*) by taking over available nest cavities (Small 1994). Similarly, the invasive house gecko *Hemidactylus frenatus* is suspected of contributing to the fragmentation and extinction of native geckos by displacing local species from preferred positions close to refugia, thus exposing them to increased risk of predation (Cole et al. 2005).

While competition over food sources and habitats between invasive and native species has been well documented, effects of the presence of novel hetero- specifics on other aspects of native species ecology have received relatively less attention. One important area in this respect is display behavior. Animals may display for several reasons, including advertisement of territory ownership, mate attraction, and to deter predators (MacDonald et al. 2007). In many species, display behavior is explicitly tied to habitat use, as individuals may select particular perches or other areas for display to enhance signal propagation (Baker 2001; Barker & Mennill 2009). If habitat availability is altered by the presence of an invasive species, then this may have a secondary effect of altering native display behavior as well. Alternatively, the presence of invasives may impact native display behavior independently of habitat use, for example, by simply soliciting more aggressive displays from native fauna (Holway & Suarez 1999). However, despite the importance of display behaviors to the reproductive and behavioral ecology of many species, the effects of invasive taxa on the displays of native fauna, either by directly affecting the types and frequency of display types or indirectly via altering habitat use, are seldom considered.

Just as invasive species might affect native displays, the display behaviors of invasives can potentially be affected by the new ecological milieu as well. Given that newly arrived species may often face competition with ecologically similar natives, one might expect successful invaders, when faced with a novel species assemblage, to exhibit behavioral traits that would tend to bias any interspecific interactions in their own favor, such as increased aggressive behaviors or displays (Holway & Suarez 1999). For example, invasive red-eared sliders typically initiate aggressive encounters directed toward native heterospecifics and consequently ingest a greater percentage of the available food (Polo-Cavia et al. 2011). Thus, altered display on the part of natives may be a response to elevated aggression from invaders. Any consideration of the effects of invasive species on native displays should therefore ideally consider the behavioral dynamic from the perspective of the invaders as well.

The recent invasion and spread of *Anolis sagrei* throughout the southeastern United States has the potential to greatly impact the ecology and behavior of both *A. sagrei* and the native green anole, *Anolis carolinensis*. In the absence of other *Anolis* species, the trunk-crown anole *A. carolinensis* is known to commonly expand its habitat use to ground-level vegetation, including habitats favored by the trunk- ground anole *A. sagrei* (Losos & Spiller 1999; Campbell 2000). Previous studies have suggested that the presence of *A. sagrei* affects the perch height of *A. carolinensis*, causing the green anole to restrict its habitat use in response (Losos & Spiller 1999), but relatively little is known about how the introduction of novel congeners affects anole display behaviors (but see Hess & Losos 1991; Ord & Stamps 2009 for examples). Visual displays in anoles can be affected by a variety of factors, including habitat use, habitat visibility, predation risk, and density of conspecifics (Leal & Rodriguez-Robles 1997; Persons et al. 1999; Fleishman 2000; Orrell & Jenssen 2003; Leal & Fleishman 2004). If any of these factors are altered by the presence of other invasive anoles, then those effects may ultimately be manifested as a difference in display behavior between allopatric and sympatric anole populations.

We tested whether the presence of a congener affects display behaviors in both *A. sagrei* and *A. carolinensis* by examining male lizard displays in an area where both species co-occur, as well as in areas where only one of each species is present. *Anolis carolinensis* males exhibit highly conserved, stereotyped display forms (A, B, and C) comprising various combinations of head-bobbing patterns combined with dewlap extensions (Decourcy & Jenssen 1994; Lovern et al. 1999; Jenssen et al. 2000; Orrell & Jenssen 2003). Although researchers have thus far been unable to assign context-dependent labels to these display types, they appear to serve different functions and hence may be used at different proportions in different ecological contexts. These displays (and more specifically the different proportions of displays used) are therefore most likely to be affected by the presence of another anole species. *Anolis sagrei* are also known to exhibit a species- specific signature display consisting of head-bob and dewlap displays that is highly variable and used in multiple contexts, including aggression and court- ship (Scott 1984). Recent work on *A. sagrei* display has noted that higher signal rates may predict better territorial defense and mating success in this species (Simon 2011). Given that many *Anolis* species exhibit territoriality toward congeners in addition to conspecifics (Ortiz & Jenssen 1982; Hess & Losos 1991; Leal et al. 1998), we examined the frequencies of head-bobs and dewlap displays in areas with and without *A. carolinensis* to test the prediction that the presence of a congener would elicit additional aggressive displays from *A. sagrei*. We also predicted that both *A. carolinensis* and *A. sagrei* would display at higher rates and for longer in the mixed population compared with those populations with only a single species. Finally, we examined habitat use of both species in those sites to determine whether *A. sagrei* affect *A. carolinensis* habitat use, as has been shown in previous studies (Losos & Spiller 1999). We predicted that *A. carolinensis* would alter their perch height upward in areas where *A. sagrei* are present, and we tested for an interaction between habitat use and display behavior to determine whether any observed differences might be driven by exclusion from preferred habitat types in either species.

Methods

Study Site

We measured adult male lizard behavior in three different urban sites in the greater New Orleans area: City Park (latitude = 29.986433, longitude = 90.094832), La Freniere Park (29.998059, 90.208893), and Tulane University campus (29.939481, 90.121968). The *A. sagrei* populations present in New Orleans seem to center around urban areas that have experienced frequent landscaping, in particular public parks such as City Park and Audubon Park (which is adjacent to Tulane University). Surrounding neighborhoods do have *A. sagrei* present, but not in as high density (J. R. Edwards, pers. obs.). City Park's Sculpture Garden was chosen because it currently supports a thriving population of *A. sagrei*, and *A. carolinensis* are scarce or absent. Tulane's campus has recently experienced an invasion of *A. sagrei*, in addition to the *A. carolinensis*, which were already established. La Freniere Park was selected because at the time this study was conducted (May/June 2009) it supported *A. carolinensis* only and had superficially similar habitat structure to the other two sites (all three sites consisted of isolated clumps of vegetation in urban settings).

Display Behavior

We used similar methods to those of Bloch & Irschick (2006) for videotaping and analyzing displays. Focal data were collected for free-ranging *A. carolinensis* and *A. sagrei* males from each population during May 15 through July 15 2009 for a total of 21 *A. carolinensis* and 28 *A. sagrei* males from Tulane (mixed population), 29 *A. sagrei* males from City Park, and 23 *A. carolinensis* males from La Freniere Park. Individuals were videotaped using a Sony HandyCam digital camera with a tripod for 5–20 min or until they were out of sight. To ensure consistency, only one investigator (J. Edwards) videotaped and analyzed all the videos. Videotapes were reviewed multiple times at half speed to identify specific behaviors and displays as described by Orrell & Jenssen (2003). The duration and number of both displays and dewlap extensions were recorded for both species, as well as display type (A, B, or C, or variants for *A. carolinensis* and the number of bobs and push-ups for *A. sagrei*). For *A. sagrei*, a bob was defined as a single up and down head movement, and similarly, a push-up was defined as a single up and down torso movement. For *A. carolinensis*, each display was also determined to be either a single or part of a volley of displays (with displays in the same volley being less than 2 s apart). The initial perch height of each lizard was also recorded. The following variables were calculated for each focal video: the percentage of time displaying relative to total observation time; display frequency; total number of dewlap extensions; duration of dewlap extensions; and for *A. carolinensis*, the proportion of A, B, and C displays relative to total number of displays. For *A. sagrei*, the proportions of head-bobs and push-up displays were used instead of A, B, and

C displays. Because display behaviors may also be affected by the density of individuals at a given site, male lizard density was estimated by measuring the areas sampled at each site and dividing by the number of male lizards observed at each site by species.

Actual And Random Habitat Analysis

We quantified the availability of structural habitat in all three sites by measuring the availability of perches at regular intervals within the sampled areas following the methods of Irschick et al. (2005). We used 1.5-m-long rods placed parallel to the ground and perpendicular to the transect at heights of 0.5, 1, and 2 m, so that the center points were roughly in the middle of the vegetation. A perch was defined as any surface between two nodes (ca. Irschick et al. 2005). Any perches within 5 cm of the rods were measured, and for each perch, diameter, length, distance to nearest perch (Dnp), taken from the middle of each perch, and the diameter of the nearest perch were measured. Habitat was sampled every 10 m, or at least once for every clump of vegetation, for a total of 33 total sample points for the three sites. We also measured the total number of perches available at each height to compare for each site. For actual habitat use, the perch of every lizard videotaped was measured for the following: substrate type, height, diameter, length, distance to nearest perch, and diameter of nearest perch. Total habitat area sampled was measured to be 149.83 m^2 for City Park, 309.47 m^2 for La Freniere Park, and 289.72 m^2 for Tulane University, for an overall total of approximately 749 m^2 for all three sites.

Statistical Analyses

We used a generalized linear model with Poisson errors to compare the frequencies of A, B, and C displays across populations. We used a similar model with perch height as a factor and quasi-Poisson errors (to account for over-dispersion) to test for an interaction effect between population and perch height for display frequency across single and mixed *A. carolinensis* populations. We compared the percent time displaying across both *A. carolinensis* and A*. sagrei* populations using a Kruskal–Wallis test. We used unpaired t-tests to compare the perch heights in both *A. carolinensis* and *A. sagrei* in each site. We compared the frequencies of single and volley displays across *A. carolinensis* populations and frequencies of dewlap extensions and push-ups across *A. sagrei* populations using a X^2 test.

Finally, we compared random vs. actual patterns of habitat use with pair-wise Kolmogorov–Smirnov tests. We conducted the following comparisons: (1) within Tulane (actual *A. carolinensis* vs. random); (2) within Tulane (actual *A. sagrei* vs. random); (3) within City Park (actual vs. random); (4) within La Freniere Park (actual vs. random); (5) Tulane-City Park for *A. sagrei* (actual vs. actual); (6) Tulane-City Park for *A. sagrei* (random vs. random); (7) Tulane-La Freniere Park for *A. carolinensis* (actual vs. actual), and (8) Tulane-La Freniere Park for *A. carolinensis* (random vs. random)(Table 3). We also used pair-wise Kolmogorov–Smirnov test to compare perch availability between the three sites (Table 4). All analyses were conducted using R v. 2.8.1 and SPSS v.16.

Results

We filmed a total of 44 adult *A. carolinensis* males and 58 adult *A. sagrei* throughout the three sites. Densities of adult male *A. carolinensis* at La Freniere Park and Tulane University were comparable (0.0808 m^2, and 0.0724 m^2, respectively), whereas the density of adult male *A. sagrei* was higher at City Park (0.1934 m^2) compared with Tulane (0.0931 m^2) (Table 1).

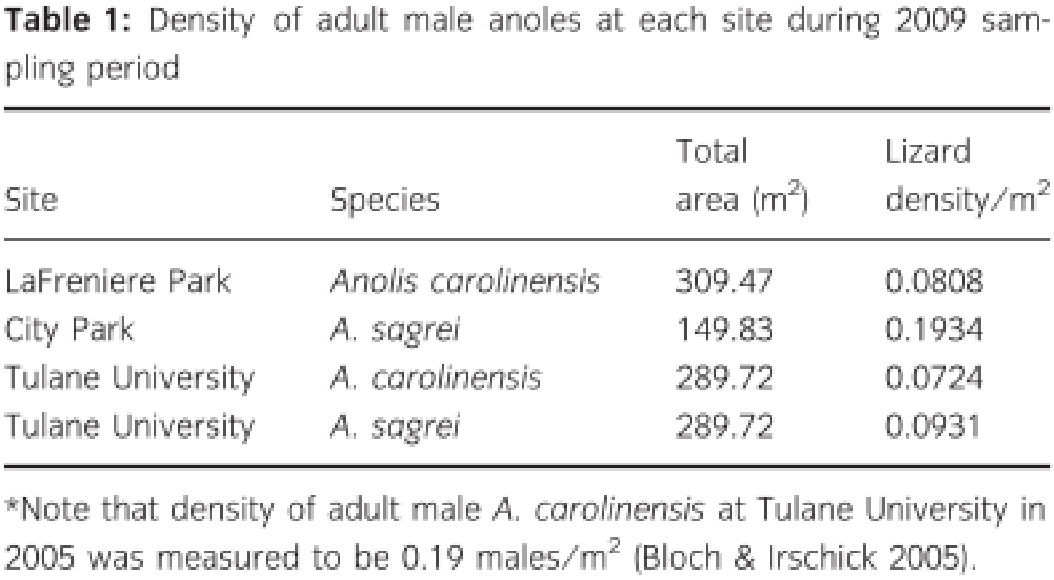

Table 1: Density of adult male anoles at each site during 2009 sampling period

Site	Species	Total area (m^2)	Lizard density/m^2
LaFreniere Park	*Anolis carolinensis*	309.47	0.0808
City Park	*A. sagrei*	149.83	0.1934
Tulane University	*A. carolinensis*	289.72	0.0724
Tulane University	*A. sagrei*	289.72	0.0931

*Note that density of adult male *A. carolinensis* at Tulane University in 2005 was measured to be 0.19 males/m^2 (Bloch & Irschick 2005).

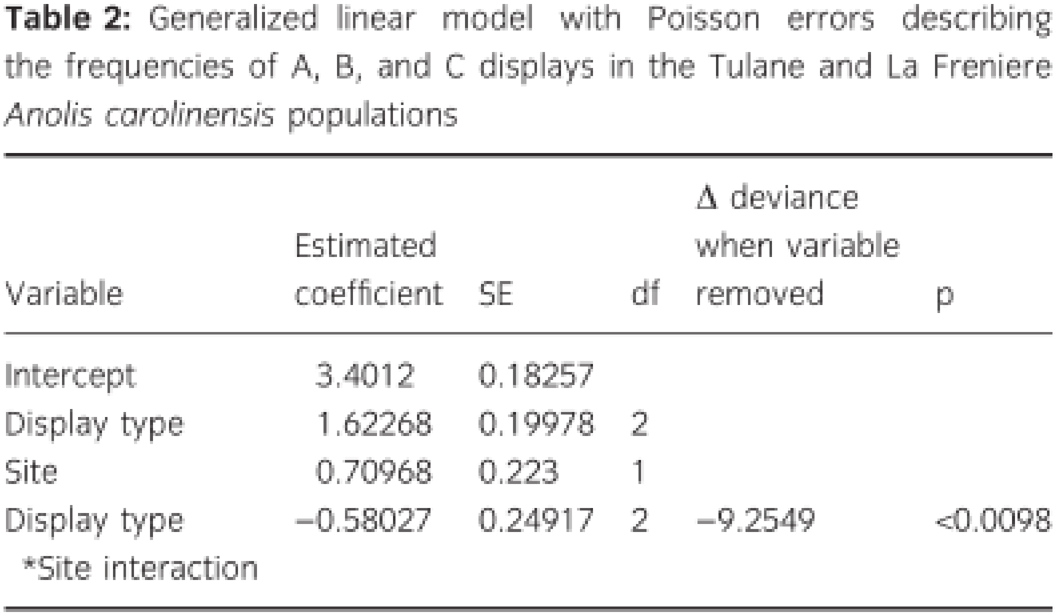

Table 2: Generalized linear model with Poisson errors describing the frequencies of A, B, and C displays in the Tulane and La Freniere *Anolis carolinensis* populations

Variable	Estimated coefficient	SE	df	Δ deviance when variable removed	p
Intercept	3.4012	0.18257			
Display type	1.62268	0.19978	2		
Site	0.70968	0.223	1		
Display type *Site interaction	−0.58027	0.24917	2	−9.2549	<0.0098

Consistent with previous studies (Losos & Spiller 1999), our data show that *A. carolinensis* perched significantly higher in the mixed as opposed to the single site (t = 2.52, df = 62, p < 0.0145), whereas the perch heights of *A. sagrei* are not altered by the presence of *A. carolinensis*, as shown by comparison with a predominantly *A. sagrei* population in New Orleans (t = 0.902, df = 61, p = 0.371) (Fig. 1). In addition to altering their perch height, male green anoles at the mixed (Tulane) site used significantly different proportions of A, B, and C displays compared with the single population (La Freniere) site (significant interaction between site and display type in the GLM; df = 2, change in deviance = 9.2549, p < 0.0098) (Table 2) driven largely by a higher number of C displays in the mixed as opposed to the single population (Fig. 2). However, the two *A. carolinensis* populations did not differ significantly in the observed frequencies of single or volley displays (X^2 = 0.729, p = 0819), and the interaction between perch height and population was non-significant for display frequency (df = 40, change in deviance = 16.32, p = 0.18) (Table 3). *A. carolinensis* populations at the two sites also did not differ significantly in time spent displaying (Kruskal–Wallis X^2 = 0.514, df = 1, p = 0.473)(Table 4); however, we note that the current observed display time for *A. carolinensis* at Tulane is almost half of that recorded for this population in 2005, prior to the arrival of *A. sagrei* (% time displaying in

2005 = 9.31 ± 0.84, compared with % time displaying in 2009 = 4.89 ± 0.70)(Bloch & Irschick 2006).

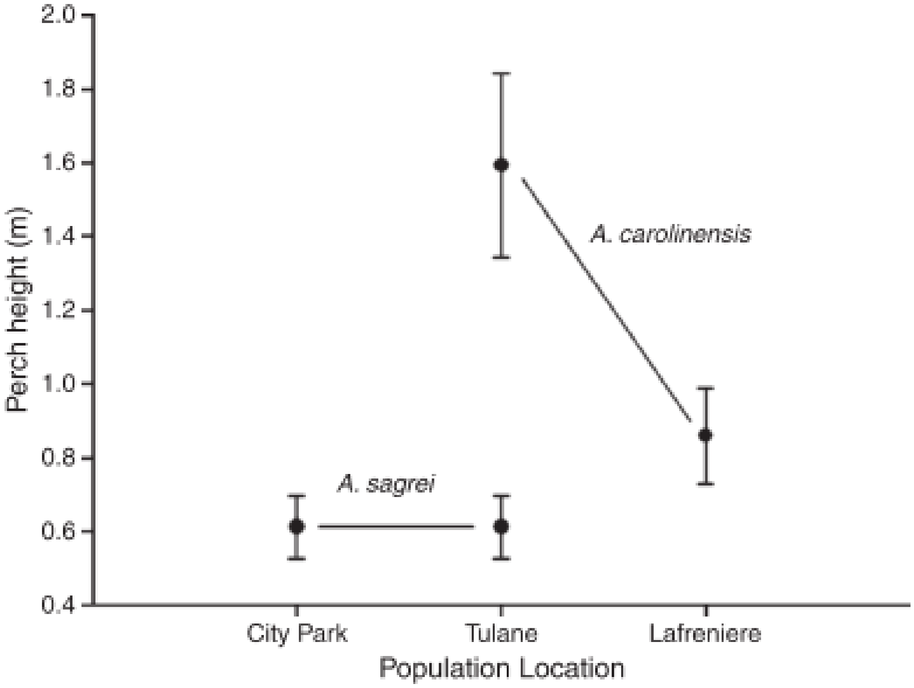

Fig. 1: Perch Height of *Anolis carolinensis* and *A. sagrei* in single and mixed populations. Values are means ± SE.

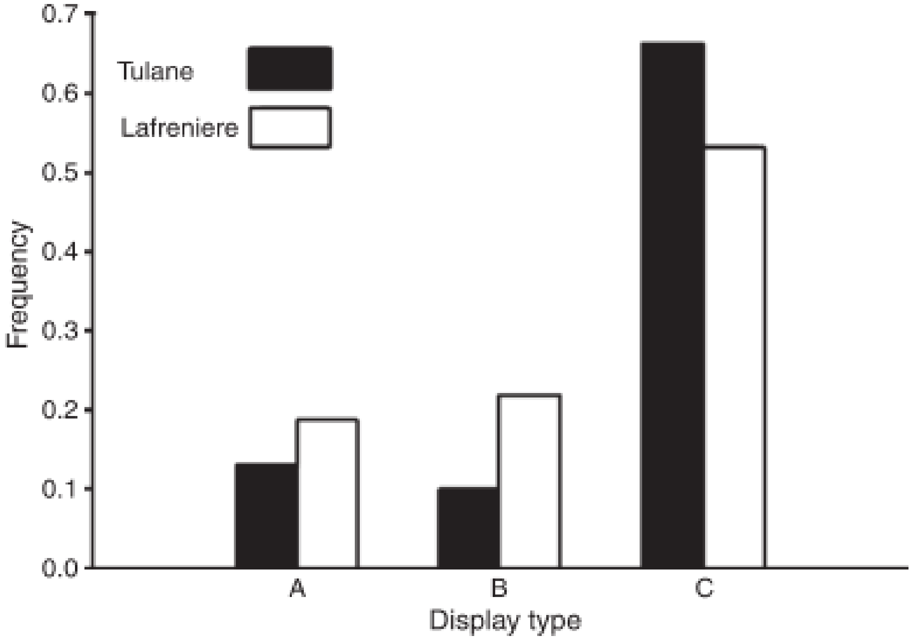

Fig. 2: Display type frequencies in single (La Freniere) and mixed (Tulane) populations.

We found no significant difference in perch height between *A. sagrei* males at the single (City Park) and mixed (Tulane) sites (Fig. 1). Thus, our data show that the presence of *A. carolinensis* has no effect on *A. sagrei* perch height, consistent with Losos & Spiller (1999). Male *A. sagrei* did not differ significantly in either time spent displaying between sites or in dewlap display frequency (Table 4). However, the frequency of push- up displays was significantly higher in the City Park population (p = 0.0413) (Table 4; Fig. 3). The random habitat analyses show that the habitats at the three sites, while superficially similar, were nonetheless different in terms of perch structure availability (Table 5). However, actual habitat usage distributions were almost always significantly different from random for both species (Table 5), and thus, anoles were clearly selecting habitat and perches. Furthermore, actual habitat use across populations showed several differences, but also some similarity, across populations, with *A. carolinensis* choosing perches of similar length at each site and *A. sagrei* always selecting less open habitats (Table 5).

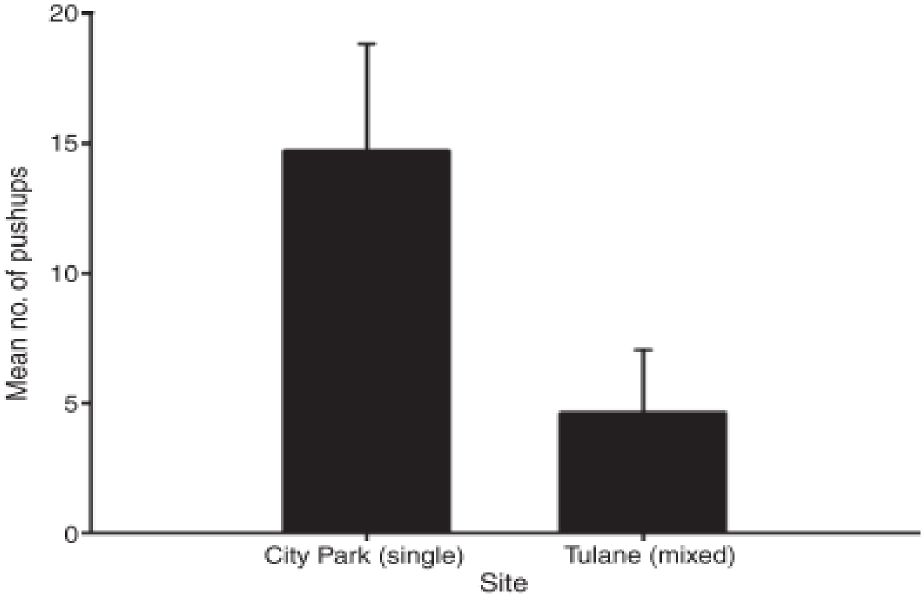

Fig. 3: Mean number of *A. sagrei* push-ups by site.

Table 3: Generalized linear model with quasi-Poisson errors (to correct for over dispersion) describing the overall display frequencies in the Tulane and La Freniere *Anolis carolinensis* populations.

Variable	Estimated coefficient	SE	df	Δ deviance when variable removed	p
Intercept	3.4012	0.18257			
Perch height	0.04823	0.11480	1		
Site	−0.15283	0.41881	1		
Perch height *Site interaction	0.32518	0.23780	1	−16.32	0.18

Table 4: Mean (±SE) values for various display variables in the Tulane, City Park, and La Freniere Park *Anolis carolinensis* and *Anolis sagrei* populations

	Anolis carolinensis		*Anolis sagrei*	
Variable	Tulane	La Freniere	Tulane	City Park
% time displaying	4.89 ± 0.70	6.3 ± 0.97	15.52 ± 1.66	11.7 ± 1.2
Average time exposing dewlap (s)	21.90 ± 1.80	22.4 ± 2.12	56.07 ± 8.97	37.58 ± 5.61
Average ABC display duration (s)	3.57 ± 0.17	3.51 ± 0.18	NA	NA
Average no. of head-bobs (*A. sagrei* only)	NA	NA	69.89 ± 13.72	62.41 ± 7.82
Average no. of push-ups (*A. sagrei* only)	NA	NA	4.62 ± 2.43	14.70 ± 4.13

Table 5: D_{max} values from Kolmogorov–Smirnov tests comparing random and actual habitat distributions for Tulane, City Park, and La Freniere Park

Comparison	Kind of Comparison	PH	PD	PL	Dnp	PDnp	df
Within La Freniere (*A. carolinensis*)	Actual–random		3.746***	2.280***	2.117***	3.746***	146
Within Tulane (*A. carolinensis*)	Actual–random		22.485***	3.482***	4.068***	1.507*	148
Within Tulane (*A. sagrei*)	Actual–random		2.072***	3.451***	3.347***	0.320	145
Within City Park (*A. sagrei*)	Actual–random		1.474*	3.328***	1.525*	3.907***	98
Tulane-La Freniere (*A. carolinensis*)	Actual–actual	1.581*	1.526*	0.908	2.348***	1.667**	63
Tulane-La Freniere (*A. carolinensis*)	Random–random		3.803***	4.549***	5.077***	3.602***	231
Tulane-City Park (*A. sagrei*)	Actual–actual	0.640	2.176***	2.432***	1.168	2.452***	62
Tulane-City Park (*A. sagrei*)	Random–random		4.108***	2.099***	4.263***	3.785***	179

$^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

PH, perch height; PD, perch diameter; PL, perch length; Dnp, distance to nearest perch; PDnp, diameter of nearest perch.

Discussion

The presence of invasive species can affect the behavior and ecology of native taxa in a variety of ways. Here, we show that both the display behavior and habitat use of *A. carolinensis* lizards are altered in sites where they co-occur with a recent invader, *A. sagrei*. We also show asymmetric effects of both of these variables on *A. carolinensis* and *A. sagrei*, suggesting that *A. carolinensis* is overall more affected by the presence of *A. sagrei* than *A. sagrei* is by the presence of *A. carolinensis*.

We quantified several aspects of *A. carolinensis* display and predicted higher display rates for this species in the presence of *A. sagrei* relative to the population where *A. sagrei* was absent. This prediction was only partially upheld. Time spent displaying did not differ significantly between the single (La Freniere) and mixed (Tulane) *A. carolinensis* populations nor did *A. carolinensis* in the Tulane population exhibit higher average dewlap display times (Table 4). However, we did find a significant interaction between display type and site across the single and mixed *A. carolinensis* populations, pointing to a significant alteration of the frequencies of the A, B, and C displays used by *A. carolinensis* males in the mixed Tulane population relative to the single La Freniere population (Table 2). Specifically, this effect appears to be driven by a clear increase in the frequency of C displays in the Tulane population where *A. sagrei* is also present (Fig. 2). This differential increase in C display frequency (relative to the frequencies of A and B displays) between the two green anole populations could be caused by multiple factors. Firstly, C displays have previously been shown to be used most often in long distance signaling in this species, whereas A and B displays are proportionally increased at shorter signaling distances (Orrell & Jenssen 2003). Previous studies have noted that *A. carolinensis* shift their mean perch height upwards in the presence of *A. sagrei* (e.g., Losos & Spiller 1999), and we document a similar significant upward shift in *A. carolinensis* perch height in the Tulane population relative to the La Freniere population harboring green anoles only (Fig. 1). The significant change in habitat use (perching higher) for *A. carolinensis* in the Tulane population may result in more vertical distance between individuals, and thus, a higher proportion of C-type displays. Given that the increase in mean perch height for the Tulane *A. carolinensis* appears to be driven by the presence of *A. sagrei* at this site, the green anole males might be directing relatively more C displays in the mixed population at invasive *A. sagrei* which occupy significantly lower, and hence further away, perches (Fig. 1). Indeed, previous studies have shown that other anole species may respond just as aggressively to conspecifics as to heterospecifics (Ord & Stamps 2009), and it is therefore possible that these displays are being directed specifically at *A. sagrei* (but see Tokarz & Beck 1987). However, this explanation is not fully supported by our results, as the interaction between perch height and population for overall *A. carolinensis* display frequency was not significant (Table 3).

Another possibility is therefore that the shift in perch height also results in a shift in distribution (although not density) of lizards, leading to more intraspecific communication at long range. Alternatively, perhaps, the perch height shift alters habitat complexity, which might require different display forms. A more likely explanation for the increased frequency of C displays exhibited by the Tulane green anoles relative to those at La Freniere is an apparent difference in age structure between the two populations. Whereas 15 large ‘heavyweight’ (64 mm SVL and up; Lailvaux et al. 2004) adult male *A. carolinensis* were observed at La Freniere Park, far fewer heavyweights were found at Tulane University (only 4 were >64 mm). Given that younger *A. carolinensis* individuals have also been reported to use a higher proportion of C displays (Lovern & Jenssen 2003), our results may therefore be partially explained by the lack of older males at Tulane. An additional line of evidence supporting this view comes from a previous study of *A. carolinensis* displays in the Tulane population prior to the arrival of *A. sagrei*. Bloch & Irschick (2006) found that green anoles at the same Tulane population that we studied used a high proportion of type A and B displays and suggested that this was owing to the high density of males present at Tulane. Specifically, Bloch & Irschick (2006) reported the density of adult male *A. carolinensis* at Tulane University in 2005 to be 0.19 males/m2, which is over twice the current density measured in 2009 (0.0724; Table 1). Furthermore, only heavy- weight *A. carolinensis* males over 64 mm SVL length were video-taped by Bloch & Irschick (2006); however, in 2009, few large males were present, and so, adult males as small as 50 mm SVL were recorded for display data instead. Even as recently as 2007, the Tulane population was found to harbor substantially more heavyweight males than in the current study (Husak et al. 2009). The recent arrival of

A. sagrei in the Tulane population therefore roughly coincides with drastic changes in both the density and, very likely, the age structure of the native *A. carolinensis* population, and in particular with a lower frequency of larger *A. carolinensis* males. This finding mirrors those of Leal et al. (1998) who showed that an experimental reduction in the density of *Anolis gundlachi* at sites in Puerto Rico led to a significant increase in the abundance of the sympatric *Anolis evermanni*. Indeed, a further point of interest in this regard is that the current overall display time of *A. carolinensis* at Tulane is also markedly reduced compared with display times reported by Bloch & Irschick (2006), and again, this is likely the result of changes in the density and, potentially, age structure of green anoles coinciding with the arrival of *A. sagrei* at this site. (It should be noted that Hurricane Katrina occurred shortly after the completion of Bloch and Irschick's study in 2005, but this population was monitored both before and after the hurricane and no significant changes in demographic structure were noted at the time (see Husak et al. 2007, 2009). However, because we only included three sites in the current study, we nonetheless urge caution in generalizing these results beyond those sites. Future studies might benefit from considering other sites where both species co-occur. Other future research might focus on the ecological context and utility of display sequences to more effectively understand and interpret any differences (or lack thereof), as well as further quantifying the changes in density and age structure that might occur in an *A. carolinensis* population as *A. sagrei* is introduced (possibly via experimental manipulations ca. Leal et al. 1998).

In addition to effects of *A. sagrei* on *A. carolinensis*, the behavior of the invasive *A. sagrei* was altered at the mixed-species Tulane site as well. This difference is manifested as significantly fewer push-up displays at the Tulane site, compared with City Park where *A. sagrei* occurs without *A. carolinensis* (Fig. 3). By contrast, no significant difference was found in A. sagrei head-bobbing displays or in dewlap display frequency. However, a potentially confounding factor in the present study is that the density of adult male *A. sagrei* at City Park was twice that of the Tulane site (Table 1), which may be affecting the display behaviors of this species (Bloch & Irschick 2006). A recent study on intraspecific interactions in *A. sagrei* showed that increased signal rates predict male combat outcomes in this species (Simon 2011). The lower rates of bobbing at the Tulane site therefore suggest that *A. sagrei* experience less intraspecific competition in the mixed site, which is to be expected given the lower density of the Tulane *A. sagrei*. However, this result also suggests that *A. sagrei* are not necessarily directing aggressive head-bob displays toward *A. carolinensis* in the field. Again, further work on the ecological contexts of these various display types would be helpful for interpreting our findings here.

Although we attempted to locate single and mixed sites that were similar in habitat structure, we were limited by the availability of appropriate sites, especially those where *A. sagrei* were completely absent. Consequently, our choice of sites was necessarily opportunistic, and the habitats of the three study sites are not identical (Table 5). Indeed, random habitat measures show that available habitat was significantly different between mixed site and single sites, with the La Freniere site offering significantly more high perch sites than both Tulane and City Park (Table 5). Importantly, however, despite the greater availability of high perches at La Freniere, *A. carolinensis* lizards nonetheless perched higher at the Tulane site, again likely due to the presence of sympatric *A. sagrei* at Tulane (ca. Losos & Spiller 1999). By contrast, *A. sagrei* maintained their lower perch preference at both City Park and Tulane populations, and the perch heights measured for *A. sagrei* are within the range of those previously reported for this species in other populations (Rand 1967; Schoener 1975). Thus, although the variation in habitat structure across the study sites is greater than might be considered ideal, the variation in the availability of the habitat axis that *A. sagrei* and *A. carolinensis* appear to most greatly segregate themselves along (i.e., perch height) is in the direction that lends our findings here greater confidence.

Conclusions

In conclusion, we document differences in display behavior in both native *A. carolinensis* and *A. sagrei* species across three sites where these species occur either in sympatry or alone. Furthermore, we present evidence suggesting that striking changes in both the density and the age structure of the previously studied Tulane University *A. carolinensis* population are likely a result of the recent invasion of *A. sagrei* at this site. These results both highlight the importance of considering the behavioral impacts of invasive species on native fauna and call for a greater understanding of the ecological contexts of anole displays.

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Chapter 3.

Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *Anolis sagrei*

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Abstract

An important goal in evolutionary ecology is to understand how and why coexisting closely related species partition habitat among themselves. Although studies of interspecific interactions typically focus on males, interactions between females may also play an important role in shaping habitat use within multi-species communities. The green anole (*Anolis carolinensis*) exhibits a wide range of habitat use in southeastern Louisiana, but its observed habitat use is restricted and altered in areas where it occurs with the introduced *Anolis sagrei*. We staged interactions between these two species in the laboratory to test the hypothesis that *A. sagrei* dominate *A. carolinensis* in contests over shared habitat. We examined whether species identity, bite force, dewlap size, and body size affected the outcome of interspecific interactions between both males and females, and tested the prediction that bite force and size would be the most important determinants of interaction outcomes in both sexes. In male interspecific interactions, we found that individuals with relatively larger dewlaps tended to score higher on aggressive behaviors regardless of species identity, and that interactions consisted of signalling and rarely escalated to physical combat. However, we found that *A. sagrei* females achieved higher aggressive scores than *A. carolinensis* females in almost all cases, lending support to the notion that female interspecific behavior is probably more important than male behavior in driving changes in habitat use.

Additional Keywords: behavior – dewlap – invasive species – performance – staged interactions.

Introduction

In areas where two or more ecologically similar species exploit a range of common resources, selection may drive each species to specialize on part of that range, thereby constraining each species' niche width and reducing potentially costly competitive interspecific interactions (Andrewartha & Birch, 1954; Schluter, 1994). For instance, in the well-known adaptive radiation of Galapagos finches, each of at least 13 species possesses particular characteristics (e.g. specialized beaks), allowing them to partition their resource use so that competition is minimized (Schluter, 2000). Similarly, the adaptive radiation of cichlid fish is also thought to be driven in part by specialization of the feeding apparatus to specific resource niches (Fryer, 1996; Sturmbauer, 1998; Takahashi & Koblmüller, 2011). This notion of ecological character displacement has undergone a revival in recent years (Stuart & Losos, 2013), but despite a great deal of interest in the evolutionary implications of such interspecific interactions, the proximate behavioral competitive mechanisms, such as aggressive behaviors, leading to specialization on key resources have received relatively little attention (Grether et al., 2009; but see Adams, 2004; Peiman & Robinson, 2007; Laiolo, 2013 for some examples).

The nature of the competitive interactions driving such resource specialization may vary among taxa or with the contested resource. In the case of direct interspecific competition over habitat use, aggressive signalling and physical confrontations are likely to be important in governing access to desirable habitat (Brawn, 1990). While aggression within a species generally arises as a result of male competition over resources or mates, interspecific aggression is often triggered by common resource overlap in sympatric species or poor species recognition (Nishikawa, 1987). Repetitive aggressive interspecific interactions over time, however, can result in almost complete separation of resource use, such that a given species may be asymmetrically constrained and consistently dominated by another (Robinson & Terborgh, 1995; Peiman & Robinson, 2010). This can make interpretations of observed current-day interactions (if any) difficult, because the historical factors leading to such ecological outcomes are often unclear (the 'ghost of competition past'; Connell, 1980). Indeed, a common hurdle facing researchers interested in studying the development of specialization within ecological communities is that they are often forced to start with complete species assemblages and reason backwards (Schluter, 2000; Losos & Mahler, 2010).

The flipside of specialization is ecological release, whereby a species entering a new environment is able to exploit a wider range of resources than in its native range (Cox & Ricklefs, 1977; Bolnick et al., 2010). Invasive species often experience such release as a result of introduction into a new ecological milieu, allowing them to make use of new or different resources, often at the expense of native species (e.g. Petren & Case, 1996; Shine, 2010). In doing so, invasive species can alter the resource use of natives, thereby imposing strong selection pressure for specialization upon those native species. These interactions between species may result in niche partitioning and/or ecological character displacement (Tynkkynen, Rantala & Suhonen, 2004; Peiman & Robinson, 2007, 2010; Grether et al., 2009; Anderson & Grether, 2010; Pearce, Pryke & Griffith, 2011), and could ultimately play a very important role in shaping ecological communities. Competitive interactions between invasive and native species that have occurred in sympatry for only a short period of time and that compete for shared resources therefore offer a unique opportunity to observe the proximate behavioral origins of specialization on a small scale (Hess & Losos, 1991; Losos & De Queiroz, 1997; Bolnick et al., 2010).

The invasion and advance of the lizard *Anolis sagrei* throughout the southeastern United States has the potential to greatly impact the ecology and behavior of both *A. sagrei* and the native green anole lizard, *Anolis carolinensis*. *Anolis carolinensis* is the only anole native to the United States and, locally, to New Orleans. The species is morphologically adapted to exploit the trunks and crown areas of trees, and thus is nominally a trunk–crown ecomorph. However, when no other anoles are present, *A. carolinensis* will frequently expand its niche to include crown–trunk–ground habitat (Echternacht, 1999). By contrast, *A. sagrei* is a trunk–ground ecomorph and is known to adapt very well to new habitats, especially disturbed habitats (Marnocha, Pollinger & Smith, 2011). Although native to Cuba and the Bahamas, *A. sagrei* has been introduced multiple times to the US (Kolbe et al., 2004), including New Orleans. In New Orleans, *A. sagrei* and *A. carolinensis* are both relatively abundant, but the *A. sagrei* population appears to be on the rise in recent years (Lailvaux, unpublished data). Both species share a similar diet, are similarly sized, and experience slight spatial niche overlap even when naturally present together (Campbell, 2000). However, when *A. sagrei* is introduced into an environment previously dominated by *A. carolinensis*, *A. carolinensis* commonly exhibits shifts in habitat use and often becomes rarer within a period of a few years (Echternacht, 1999; Campbell, 2000). Indeed, several studies, including a recent study of anoles in New Orleans, have found that *A. carolinensis* perches significantly higher when *A. sagrei* are present, suggesting that *A. sagrei* are actively displacing the native green anoles (Collette, 1961; Losos & Spiller, 1999; Edwards & Lailvaux, 2012). The factors behind this shift in habitat are currently unclear, but the population in New Orleans offers an ideal study situation to address this question.

We staged male–male and female–female interactions between *A. carolinensis* and *A. sagrei* to investigate the nature of the interspecific interactions that are likely to be driving shifts in habitat use by *A. carolinensis*. Males of both species are highly territorial, and use similar displays consisting of push- ups, bobbing, and dewlap extensions to advertise territory ownership and gain mates. Furthermore, previous studies have shown that bite force is an important determinant of intraspecific male combat outcomes in both of these species (Lailvaux et al., 2004; Lailvaux & Irschick, 2007b). A previous study of staged interactions between *A. carolinensis* and *A. sagrei* demonstrated that both species display more vigorously at conspecifics rather than at heterospecifics, and suggested that male–male interactions are unlikely to be a key component of competition (Tokarz & Beck, 1987). However, male interspecific interactions have previously been reported in nature (Collette, 1961; Losos, Marks & Schoener, 1993), and so we tested how bite force and relative dewlap size may affect the outcome of fights between these heterospecifics. Finally, while most studies of both inter- and intraspecific aggression focus on males, there is also evidence that females of some *Anolis* species may defend resources and demonstrate territoriality towards similarly sized congeners more so than males (Rand, 1967a, b). The documented *A. carolinensis* mating system is that of female defence polygyny (Ruby, 1984; Nunez, Jenssen & Ersland, 1997; Jenssen, Lovern & Congdon, 2001), whereby males defend territories containing females or resources that females require. If female green anoles are forced to alter their habitat use by the presence of *A. sagrei*, then the observed shift in green anole male habitat use may simply reflect males following females to their new habitat. We therefore investigated the outcome of female interspecific interactions in a similarly staged setting. However, while females of both species have significantly lower bite forces than males (Herrel, Mcbrayer & Larson, 2007; S. P. Lailvaux, unpubl. data) it is unclear whether females can bite hard enough to inflict significant injury, and bite force might therefore not be expected to be important to female contest resolution. We therefore tested the following specific hypotheses:

1. Outcomes of interspecific interactions between male *A. sagrei* and *A. carolinensis* would be predicted by larger body size and stronger bite force;

2. Outcomes of interactions between female *A. sagrei* and *A. carolinensis* will be predicted by larger body size.

Material And Methods

Adult male and female *A. carolinensis* and *A. sagrei* lizards (55 male and 38 female *A. sagrei*, 56 male and 40 female *A. carolinensis*) were captured from City Park in New Orleans, Louisiana, during April/May 2012. Because both species are present in City Park, location of capture of each individual was noted to avoid staging interactions between potentially familiar animals. Lizards were captured either by hand or with a noose attached to a pole by walking through the habitat during normal activity hours (09.00– 17.00 h), and capturing any lizard present. Lizards were then transported to the University of New Orleans to measure morphology, maximum bite force, and staged interactions.

Morphology

On the day of capture, we measured body mass to the nearest 0.01 g with a digital balance (Mettler Toledo PR8002 DeltaRange), and snout–vent length (SVL) to the nearest 0.01 mm with digital calipers. After staged interactions, we measured SVL, forelimb length, hind limb length, and head morphology with digital calipers. We measured dewlap size by first extending the dewlap, using forceps to grasp the ceratobranchial near the articulation with the basilhyoid, and then photographing the extended dewlap using a Canon Rebel T1i

SLR digital camera. The images were analysed using TPSDIG v. 2.15 to calculate dewlap area (Vanhooydonck et al., 2005; Huyghe et al., 2007; Lailvaux & Irschick, 2007b; Rohlf, 2010).

Bite Force

We measured in vivo bite force using an isometric Kistler force transducer (type 9023, Kistler) connected to a type 5058a Kistler charge amplifier (see Herrel et al., 1999, 2001 for a detailed description) using standard methods. Lizards were induced to bite a force plate by tapping their cheek until their mouth opened, then lining up the mouth with the centre of the force plate until the lizard bit forcefully. Bite trials were repeated every hour for a total of five trials per animal, and the largest bite force obtained was taken as the maximal bite force for that animal (Adolph & Pickering, 2008; Losos, Creer, & Schulte II, 2002). All lizards were placed in an incubator at 33 °C (approximately the preferred field body temperature for both species; see Huey & Webster, 1976; Lailvaux & Irschick, 2007a) for 1 h prior to trials, and during rest periods in between trials.

Staged Encounters

We staged interactions following methods consistent with those used in previous studies (Lailvaux et al., 2004; Perry et al., 2004; Henningsen & Irschick, 2012). We used a large 38-litre glass aquarium as a test arena, with the sides and back covered with opaque paper. Each end of the arena contained a brick to provide a raised platform for the displays, and each aquarium was initially divided with a clear plastic perforated aquarium divider. *Anolis carolinensis* lizards were paired randomly with *A. sagrei* lizards of the same sex, and one of each pair was placed randomly on either side of the divider. This allowed the animals to see and display to each other, but prevented them from physically interacting. After a 15-min acclimatization period, the divider was removed and we added one perch site beneath a suspended heat lamp (Henningsen & Irschick, 2012). The lizards were free to move throughout the arena for an additional 60 min. Sixty minutes of behavior was scored for each interaction, not including the acclimatization period, and encounters were recorded with a Sony Handycam digital camera and tripod. Each animal was used in only a single interaction.

We scored behavior using methods similar to those of Lailvaux et al. (2004). All observed agonistic behaviors were assigned positive scores using the following system: head bobs and push-ups, defined as a bout of rapid up-and-down movement of the head or body, and dewlap display bouts scored as 0.5. Lateral displays, chases, and bites were scored as 1. Lateral displays were defined as an animal turning its body perpendicular to the line of sight of the other animal combined with lateral compression and dorso-ventral expansion. Chases were defined as running towards an opponent. Retreats, defined as running away from an opponent, were scored as −1. Submissive nodding, as described for *A. sagrei* (Simon, 2011), was awarded −0.25. Scores were also awarded for first to perch and longest on perch (0.25 each) and hiding (−0.25). The member of the pair that has the higher cumulative score at the end of the observation period was considered the 'winner'.

Analysis

Male–Male Interactions

To analyse the effects of morphological characteristics (dewlap, head measurements, mass, SVL) and bite force differences on determining outcomes of staged male interactions, we selected one of the two individuals in each contest at random as the focal individual. If the focal individual exhibited the highest aggressive score, the outcome of the contest was coded as 1, and outcomes for focal males with the lowest score in a dyad were coded as 0. This coding was then entered into a generalized linear model as a binary dependent variable with a logit link (Hardy & Field, 1998; Lailvaux & Irschick, 2007b), using software R v. 2.13.2. Quasi-binomial errors were used to correct for over-dispersion identified in the model. The independent variables were the differences in morphological measurements and bite force between the focal individual and the other competitor, plus the interactions between each variable. We also included quadratic terms in the initial models to test for non-linear effects. Model simplification based on deletion tests using log-likelihood ratios allowed the creation of a 'minimum adequate model' to describe the data (Crawley, 1993; Hardy & Field, 1998). To visualize the interactions among variables, we used the fields package in R v. 2.13.2 to create three-dimensional response surfaces.

Female–Female Interactions

Due to the nature of the outcomes of the female- staged interactions (see Results), we did not perform similar modelling analyses on the female data. To test for differences between species in dewlap size, maximum bite force and SVL, we used a one-way MANOVA with species as a factor for both males and females.

Results

Male–Male Interactions

We filmed 55 male–male staged interactions. In five of these interactions, no behaviors were observed during the testing period; consequently, these bouts were excluded from analyses (Lailvaux & Irschick, 2007b). Of the 50 remaining matches, there were 30 *A. sagrei* 'winners' and 20 *A. carolinensis* 'winners'. None of the staged interactions escalated to physical combat. After randomly selecting a focal male from each pair for GLM analysis and removing non- significant terms from the saturated model, our simplest model had two significant two-way interactions, namely SVL/relative dewlap size and bite force/ relative dewlap size (Table 1). Because species identity did not explain a significant amount of variation in male contest outcomes in the overall model, either alone or in conjunction with other factors, we pooled data from the two species and estimated the response surface for winning or losing based on dewlap size, SVL, and bite force for all individuals. The resulting three-dimensional response surfaces reveal that individuals with large dewlaps relative to both maximum bite force (Fig. 1A) and SVL (Fig. 1B) accrued higher aggressive scores, regardless of species identity. These results are very robust, and hold whether *A. sagrei* and *A. carolinensis* are analysed together in a global model or in separate models.

Table 1. Results of the best-fitting minimum adequate model describing the outcomes, in terms of aggressive scores, of staged interactions between male *A. sagrei* and *A. carolinensis*

Variable	Est. coefficient	SE	*Z* value	*P*-value
Intercept	−0.825	0.453	−1.824	0.075
SVL	0.058	0.101	0.579	0.565
Bite	−0.160	0.179	−0.891	0.378
Dewlap	0.641	1.275	0.503	0.618
SVL:dewlap	0.910	0.405	2.248	0.030
Bite force:dewlap	−1.268	0.671	−1.891	0.065
AIC = NA				
Null deviance = 66.406 on 49 d.f				
Residual deviance = 49.262 on 44 degrees of freedom				
Number of Fisher scoring iterations: 6				
Dispersion parameter for quasibinomial family taken to be 1.291				

Table 2. Average body size (snout–vent length) and average dewlap size by sex and species; despite the shorter average body size of male *A. sagrei*, *A. carolinensis* males have a smaller average dewlap size

Species	Average SVL ± SE (mm)	Average dewlap size ± SE (mm^2)	Average bite force ± SE (N)
A. sagrei (male)	56.662 ± 0.393	1.943 ± 0.039	5.850 ± 0.163
A. carolinensis (male)	63.318 ± 0.555	1.693 ± 0.051	9.827 ± 0.372
A. sagrei (female)	42.021 ± 0.326	0.270 ± 0.010	1.369 ± 0.010
A. carolinensis (female)	50.426 ± 0.450	0.286 ± 0.010	2.936 ± 0.101

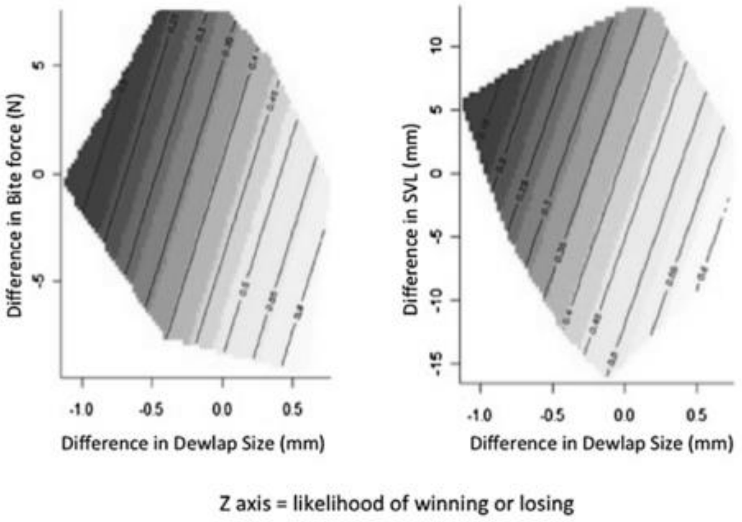

Figure 1. Non-parametric response surfaces of male interactions. These two models are three-dimensional response surfaces of the two significant two-way interactions. The *z*-axis represents the likelihood of winning a fight, where light colours are peaks, and the dark areas are valleys. Surface A shows the interactions between difference in maximum bite force (N) and difference in dewlap size (mm^2), while surface B demonstrates interactions between difference in snout–vent length/SVL (mm) and difference in dewlap size (mm^2).

Female–Female Interactions

We filmed 38 female–female staged interactions. In 36 of these *A. sagrei* scored higher based on observed behavior, again with no escalated combat occurring (Fig. 2).

We also compared body size, dewlap size, and maximum bite force for both males and females between the two species, *A. carolinensis* and *A. sagrei*, using a one-way MANOVA (Table 2). Differences in SVL, dewlap size, and bite force were all significantly different (Pillai's trace = 0.9974; SVL: F1,100 = 97.75, P < 0.001; dewlap size: F1,100 = 15.56, P < 0.001; bite force: F1,100 = 97.72, P < 0.001) between males of each species, while SVL and bite force were significantly different between females of each species (Pillai's trace = 0.9975; SVL: F1,74 = 249.28, P < 0.001; bite force: F1,74 = 133.89, P < 0.001). *Anolis sagrei* females have a larger relative dewlap size than *A. carolinensis* females in relation to SVL, although the difference was not statistically significant (Pillai's trace = 0.9975; F1,74 = 0.867, P = 0.354).

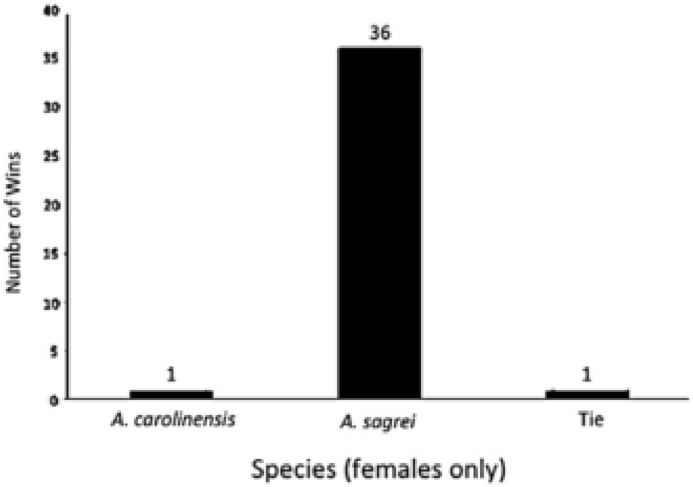

Figure 2. Of 38 female–female interactions, one was a tie, one was won by an *A. carolinensis* female, and the other 36 were won by *A. sagrei* females.

Discussion

Multiple factors can play a role in driving apart habitat use in sympatric species. Here we tested two specific hypotheses to investigate whether interspecific interactions between now-sympatric *A. sagrei* and *A. carolinensis* in southeastern Louisiana were a possible cause of observed shifts in habitat use by *A. carolinensis*. We found that in male–male interactions, individuals with the higher aggression scores were those with larger dewlaps relative to both dewlap size and body size, regardless of species identity (Fig. 1). The results for females, however, were strikingly different, with *A. sagrei* females scoring higher in almost every interspecific interaction with *A. carolinensis* females, despite female green anoles being larger, with stronger bite forces. Thus, our first hypothesis (i.e. that outcomes of aggressive interactions between male *A. sagrei* and *A. carolinensis* would be predicted by stronger bite forces among species) was not supported. Furthermore, our second hypothesis was also not supported, as our results indicate that species identity is the most important factor driving female–female interaction outcomes as opposed to size.

Males

Although *A. sagrei* scored higher in a majority of the staged interactions in this study (30 out of 50), they did not 'win' significantly more bouts *than A. carolinensis*, and indeed species identity was not a significant factor in the model (Table 1, Fig. 1). Instead, the response surfaces for males indicate that large dewlaps in combination with both small body size and low bite force relative to those of an opponent predict outcomes in interspecific interactions, strongly suggesting that relative dewlap size is the key trait in such competitive situations (Fig. 1). Although the ecology of anole dewlaps is poorly understood, previous studies have posited a role for the dewlap in interspecific recognition and signalling contexts (reviewed by Losos & Chu, 1998; Losos, 2009; Vanhooydonck et al., 2009); nonetheless, direct measures of the value of dewlap size in competitive interspecific contexts are few. Another possibility to be taken into account for future work is differences in dewlap colour or brightness, as several studies have shown that UV reflectance can influence either intraspecific contest outcomes (Bajer et al., 2011) or the likelihood of being challenged by rivals (Stapley & Whiting, 2006) in male *Lacerta viridis* and *Platysaurus broadleyi* lizards, respectively. Our results differ from those obtained for intraspecific anole male combat, which tend to show that dewlap size is less important than bite force for winning fights in territorial anoles (Lailvaux & Irschick, 2007b). However, in this study, as in previous studies using *A. sagrei* and *A. carolinensis* species (e.g. Tokarz & Beck, 1987), staged interactions consisted almost entirely of signalling and rarely escalated to physical combat. This result is in contrast with documented staged interspecific interactions between some other anole species where escalated aggression was observed (e.g. Losos, 1985). The lack of escalated physical interactions between male *A. carolinensis* and *A sagrei* is perhaps surprising given that each of these dimorphic, territorial species engages in physical confrontations with conspecific males (Lailvaux et al., 2004; Lailvaux & Irschick, 2007b). Furthermore, the shift in habitat use and lower population densities of *A. carolinensis* in the presence of *A. sagrei* (Losos & Spiller, 1999; Edwards & Lailvaux, 2012) is consistent with what one might expect if these species are competing over habitat resources. On the other hand, theory also predicts that interspecific interactions are likely to be less intense and physically aggressive than intraspecific interactions, especially in situations where mistaken identity and interbreeding are unlikely (Brunswick, 1979; but see Lailvaux, Huyghe & Van Damme, 2012). Both anole species exhibit female-defence polygyny, but given that male green and brown anoles are unlikely to mistake each other for the same species, and that the rate of inbreeding between these species is probably extremely rare if it occurs at all (Losos, 2004), our results therefore suggest that habitat separation between these two species is not driven by interspecific aggression between males, despite the appearance of competitive exclusion based on male habitat data (Hess & Losos, 1991).

Females

In contrast to the results from the male–male trials, where species identity was found not to be a significant factor predicting interspecific outcomes, we found that outcome of female interspecific interactions were heavily asymmetric in favour of *A. sagrei*. In fact, of the 38 female–female interactions staged, *A. sagrei* females received the highest aggressive score in all but two trials (Fig. 2). *Anolis sagrei* females appeared to have larger dewlaps relative to body size, as found in the male staged interactions, but due to the one-sided outcomes of the female– female trials, there is insufficient variation in contest outcomes to estimate the relative importance of dewlap size and species identity statistically (see Table 2, with female dewlap/SVL).

Based on our results, aggressive female interspecific outcomes appear to be based almost entirely on species identity rather than phenotypic trait values, with female *A. sagrei* scoring consistently more aggressive behavior than *A. carolinensis* regardless of differences in body size, dewlap size, or bite force. If this is true in natural settings as well, the observed shift in green anole habitat use is likely to be driven by *A. carolinensis* females moving higher in response to aggressive *A. sagrei* females with males following them in order to base their territories around female positions. Furthermore, *A. carolinensis* males also generally perch higher than females (Irschick et al., 2005), probably contributing further to the observed habitat shift.

It is not surprising that female interspecific behavior may be more important than male behavior in driving these changes in habitat use given the *A. carolinensis* and *A. sagrei* female defence polygyny mating system. In general, *Anolis* female territories are based around food availability, and territory size does not change seasonally like those of males (Losos, 2009). Females also maintain consistent levels of aggressive interactions and displays year-round in other anole species (Andrews, 1971; Schoener & Schoener, 1982; Nunez et al., 1997). As females are defending resources such as food and egg-laying sites, it would make sense for them to defend these resources against all intruders whenever possible. Note that many anoline species use communal egg- laying sites (Rand, 1967c), and it is possible that females may be trying to exclude other females for reasons other than egg-laying. What is surprising, however, is that the 'winning' species in these female interactions, *A. sagrei*, exhibits smaller body size, and a weaker maximum bite force than *A. carolinensis*, whereas in males body size and bite force are important combat outcome predictors in dimorphic, territorial anoles (Lailvaux & Irschick, 2007b). Unlike male–male combat, however, female combat has received very little attention, and the morphological and physiological factors that mediate the outcomes of female aggressive interactions are not understood [but see While, Sinn & Wapstra (2009), and Langkilde & Shine (2007), who showed that female aggression is unrelated to body size in the lizard *Egernia whiteii*]. Further studies investigating the nature of female combat would be useful for understanding these inter- actions. It would be particularly useful to examine female–female interspecific interactions year-round, and not just during breeding periods.

Conclusions

In conclusion, we found evidence that female interspecific behavior may possibly be more important than male behavior in driving the well- documented changes in habitat frequently occurring following introduction of *A. sagrei* into areas formerly occupied solely by *A. carolinensis*. This result offers potential insight into the factors driving apart species that use similar habitat resources in the early stages of ecological habitat displacement. However, further studies are required to test whether these behaviors observed in the lab are indicative of behavior that occurs during interactions between these two species in nature.

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Chapter 4.

Plasticity and whole-organism performance in invasive *Anolis sagrei* and native *Anolis carolinensis* lizards

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Abstract

Phenotypic plasticity may be beneficial to invasive species if young individuals are able to alter their phenotype to better fit novel habitats, thereby enjoying enhanced survival and potentially gaining a performance advantage over native species. We studied plasticity in several morphological and whole-organism performance variables in two species of lizards in New Orleans: the native, *Anolis carolinensis,* and recent invader, *Anolis sagrei*. Both species have previously exhibited some degree of phenotypic plasticity in hindlimb length. To test the hypothesis that *A. sagrei* and *A. carolinensis* differ in both morphological and performance plasticity, we reared males and females of each species on two different perch diameter sizes. We then measured limb morphology in response to the two perch treatments, as well as sprinting and clinging ability. Sprint performance in *Anolis sagrei* differed between treatment groups, although the morphological differences between perch treatments were subtler than those reported in previous similar projects. We also found that *A. carolinensis* females exhibited significant differences in both sprinting and clinging performance, despite no differences in male or female morphology between perch size treatments. This study is one of the first to examine the relationship between morphology and performance plasticity. Our findings also highlight the necessity for considering the environmental range that animals encounter in natural settings when designing plasticity experiments, as well as the potential for both species-specific and sex-specific plasticity.

Introduction

Phenotypic plasticity (i.e. the capacity of a genotype to produce different phenotypes in response to environmental variation) can have important implications for individual fitness and survival (West-Eberhard 2003). Consequently, understanding this potentially adaptive nature of plasticity has long been an important goal in evolutionary ecology, and studies of plasticity have shown both positive, adaptive (e.g. Waddington 1961; Suzuki & Nijhout 2006) and negative, non-adaptive relationships (e.g. Schaum & Collins 2014) between the directions of selection and plastic change. From an evolutionary perspective, the relationship between plasticity and adaptive evolutionary change is complex. For example, in Trinidadian guppies, non-adaptive plasticity facilitates more rapid adaptive evolution than adaptive plasticity because non-adaptive traits experience more intense directional selection (Ghalambor *et al.* 2015). However, from a proximate, individual perspective, the adaptive utility of plasticity is clearer, and individual organisms that are able to alter their phenotype appropriately in response to selection imposed by environmental variation are expected to enjoy enhanced survival in changing environments relative to organisms with more canalized phenotypes.

A related issue to that of adaptive utility is the potential contribution of plasticity to the success and competitive abilities of invasive species (Lee 2002; Richards *et al.* 2006). A recent meta-analysis showed that invasive plant species exhibit higher levels of phenotypic plasticity compared with natives, but that this plasticity is only sometimes associated with a fitness benefit (Davidson, Jennions & Nicotra 2011; but see Matzek 2012). Similarly, the success of invasive species relative to natives has been linked to plasticity in both life-history and physiological traits in some arthropods (Chown *et al.* 2007; Lardies & Bozinovic 2008). Given the known vulnerability of disturbed habitats to species invasions (reviewed in Dukes & Mooney 2004; Didham *et al.* 2007), one likely characteristic of successful invaders that enter such habitats is thus increased adaptive plasticity (at the individual level) relative to that of native species.

The green anole lizard (*Anolis carolinensis*) has long been the only species of anole commonly found in the mainland United States, but this status has recently been challenged by multiple (and in some cases, repeated) invasions of congeners. In particular, the brown anole (*Anolis sagrei*) in particular has spread rapidly through the southeast (Kolbe *et al.* 2004), and is presently abundant in areas that were once inhabited exclusively by green anoles. Previous studies have linked the presence of brown anoles to both shifts in habitat use and declines in population abundance of green anoles in several such regions (Echternacht 1999; Kamath, Stuart & Campbell 2013; Stuart *et al.* 2014), including New Orleans, Louisiana (Edwards & Lailvaux 2012). Potential explanations for the negative influence of *A. sagrei* on *A. carolinensis* include predation on *A. carolinensis* juveniles by adult *A. sagrei* (Gerber & Echternacht 2000); sex-specific variation in movement by *A. carolinensis* in response to the presence of *A. sagrei* (Kamath & Stuart 2015); and heightened interspecific aggression of *A. sagrei* females towards *A. carolinensis* females (Edwards & Lailvaux 2013). However, the potential for differential phenotypic plasticity to influence local dominance of invasive *A. sagrei* populations over those of *A. carolinensis* has never been rigorously assessed.

Within the genus *Anolis*, hind limb length can vary greatly, even between two species of comparable body size (Losos 1990) and reflects differential habitat use (Williams 1983). Species using narrow surfaces such as those living in bushes, branch tips, or grasses have shorter hind limbs, while those using broad surfaces (large tree trunks, ground, or buildings) exhibit much longer hind limbs relative to body size. Longer hind limbs confer better sprinting ability on a broad surface, while shorter limbs enable careful movements on narrow surfaces, such as twigs (Losos & Sinervo 1989; Irschick & Losos 1999). Morphological plasticity in hindlimb length has been reported in both *A. carolinensis* and *A. sagrei*. Juvenile *A. sagrei* experimentally reared on broader perches grew significantly longer hindlimbs than individuals reared on narrow perches (Losos *et al.* 2000), whereas Kolbe and Losos (2005) found that the hindlimbs of males were less plastic than those of female *A. carolinensis* under similar conditions. More recently, Langford *et al.* (2014) showed that *A. sagrei* individuals reared on different diameter perches all chose to perch on broad perches more often when given a choice. Thus, existing evidence suggests that *A. sagrei* exhibits greater morphological plasticity than *A. carolinensis*, and that such plasticity could affect habitat use in nature.

These findings are intriguing both because of the well-documented relationship between hindlimb length and sprint speed in anoles (Losos 1990; Losos & Irschick 1996).

Previous studies have also reported a close fit between limb length and perch diameter in these lizards, with longer-limbed individuals being faster sprinters on broad perches, but more sensitive to perch diameter than short-limbed anoles, which are equally slow on all perch types (Losos & Sinervo 1989; Irschick & Losos 1998). Anoles consequently avoid perch types on which locomotor performance is submaximal (Irschick & Losos 1999). Plasticity in the direction of selection could be immediately useful if young individuals were able to alter their limb length to fit common or preferred local perch types, with the generally more plastic *A. sagrei* invaders then also able to realize a performance advantage over native *A. carolinensis*.

Although sprint speed is an important and commonly-measured determinant of survival (Calsbeek & Irschick 2007), it is not the only metric of whole-organism performance (defined as any dynamic, ecologically relevant task such as running, jumping, or biting; Bennett & Huey 1990; Lailvaux & Irschick 2006) for arboreal anoles. Most *Anolis* lizards also possess toepads, which enhance their locomotor capacities when moving on vertical surfaces (Irschick *et al.* 1996; Elstrott & Irschick 2004). Bloch & Irschick (2005) showed that toe-clipping reduces the surface area of the adhesive lamellae and significantly reduces clinging ability of *A. carolinensis*. Kolbe (2015) reported increased clinging ability on *Anolis cristatellus* lizards reared on narrow perches as opposed to broader ones. Because toepads are potentially useful for navigating horizontal perches, any tests of relative plasticity in performance and perch use in *A. sagrei* and *A. carolinensis* should consider plasticity in clinging ability as well. Furthermore, previous studies of anole plasticity have inferred sprint performance from hindlimb length, but none have verified this relationship through measurement of performance. Doing so is important because any individual fitness benefits might stem from plasticity at multiple levels of biological organization. With regard to whole-organism performance, the eco-morphological paradigm states that morphology determines performance, which in turn determines fitness (Arnold 1983). Since this paradigm assumes that the ultimate target of selection is performance, tests of performance plasticity should ideally measure performance directly rather than inferring it from morphology.

The objectives of this study were to measure how limb length plasticity in *A. sagrei* and *A. carolinensis* is related to perch site and, and to test whether limb plasticity is related to both sprinting and clinging performance. While two-species comparison studies are generally considered problematic (see Garland Jr & Adolph 1994) in this particular case both species are sharing the same space in conjunction with shifts in both habitat use and population abundance, and appear to compete for habitat. We are not comparing *A. sagrei* and *A. carolinensis* with the goal of testing any evolutionary hypotheses, and therefore consider a two-species comparison to be appropriate for our study. We tested the following hypotheses:

1) When raised under identical experimental conditions, *A. sagrei* morphology is more responsive to perch treatments than *A. carolinensis*.
2) Plastic morphological responses prompt related changes in performance in both *A. sagrei* and *A. carolinensis*.

Methods

We hand-captured 150 small juveniles of both *A. sagrei* and *A. carolinensis* during September/October 2011 from two urban parks, City Park and Audubon Park, located in New Orleans, LA. To prevent stress mortality, lizards were immediately placed in a cooled dark container with vegetation for transportation to the laboratory at the University of New Orleans. We only used juveniles measuring less than 30mm snout-vent length (SVL), and did not sex them before randomly assigning them into four different developmental treatments: 75 *A. sagrei* reared on broad perches, 75 *A. carolinensis* on broad perches, 75 *A. sagrei* on narrow perches, and 75 *A. carolinensis* on narrow perches).

We used housing methods similar to Kolbe and Losos (2005). Lizards were housed in plastic cages (28.5cm x 17.5cm x 21cm) with the cage bottoms covered with Cyprus mulch, and we coated the cage sides with Fluon (Asahi Glass Co., Ltd.) to prevent lizards from clinging to cage walls. Each shelving rack of cages was provided with Repti-Sun 5.0 UVB 310 40 W Fluorescent Lamps to mimic natural sunlight. Animal room conditions were maintained at approximately 30^{o} C, 70% relative humidity, with a light:dark cycle of 12:12 hours.

Initially we housed 4 hatchling lizards per cage, then separated them into individual cages upon attaining SVLs of >30mm. Housing small juvenile lizards together promotes socialization and prevents stress (Sanger *et al.* 2008). We covered the exterior of each cage with newspaper to prevent lizards from viewing one another and to control for any potential effects of dominance on development.

Lizards were misted daily and fed size-appropriate crickets or termites dusted with mineral supplements every two days. The "narrow perch" treatment consisted of one narrow dowel 0.64 cm in diameter and 30cm long, and the "broad perch" treatment consisted of one broad dowel 2.54 cm long and 30 cm long. Perches were angled diagonally against the cage sides with the higher end towards the lamps. Cages were randomly rearranged on the shelves weekly to minimize placement effects.

Data Collection

Before assigning juveniles to a random perch treatment, we measured snout-vent length (SVL) and mass. We later measured morphology and sexed the animals at 5 months once the lizards had reached adulthood per Kolbe & Losos (2005). Adult minimum SVL for *A. sagrei* is 39-40 mm for males and 34-35 mm for females (Sexton & Brown 1977; Lee *et al.* 1989), and for *A. carolinensis* the adult minimum SVL is 45-48 mm for males and 40-41 mm for females (Hamlett 1952; Fox 1958). Bite force, sprint speed, and clinging ability were also measured at 5 months.

Morphology

Digital calipers were used to measure SVL, forelimb length, hindlimb length, and head morphology to the nearest 0.01mm. Body mass was measured with a digital balance (Mettler Toledo PR8002 DeltaRange) to the nearest .01g. Toe-pad size was measured by placing the lizard inside a flatbed scanner (HP Scanjet G3110), scanning the toe-pad area at 600 dpi, and then digitally measuring toe-pad size with tpsDIG (Rohlf 2010).

Bite Force

We included bite force as a control trait that should not be affected by perch diameter. We measured in vivo bite force using an isometric Kistler force transducer (type

9023, Kistler, Winterthur, Switzerland) connected to a type 5058a Kistler charge amplifier (see Herrel *et al*. 1999, 2001 for a detailed description). Lizards were induced to bite a force plate by tapping their cheek until their mouth opened, then lining up the mouth with the center of the force plate until the lizard bit forcefully. Bite trials were repeated every hour for a total of five trials per animal, and the largest bite force obtained was taken as the maximal bite force for that animal (Adolph & Pickering, 2008; Losos, Creer, & Schulte, 2002). All lizards were placed in an incubator at 33°C (approximately the preferred field body temperature for both species; see Huey & Webster, 1976; Lailvaux & Irschick, 2007) for one hour prior to trials, and during rest periods in between trials.

Sprint Speed

Sprint trials were conducted in a large closet warmed to 33^{o}C using similar methods to those of Losos and Irschick (1996). Lizards were given at least one hour to acclimate before each trial. Each lizard performed 4-5 trials on two different wooden rod sizes (diameter sizes 2.54cm and 0.64cm). Each rod was angled at 45^{o}, with distance marked at 0.1m intervals. Trials were videotaped with a Sony HandyCam digital camera with a tripod, and sprint speed was calculated for the fastest 0.2 meter interval for each trial, with the fastest sprint speed obtained taken as the maximal sprint speed for that animal (Braña 2003; Husak 2006). Trials in which the lizard ran sub-maximally were excluded, and any lizards that jumped off the rod were retested immediately. Rod order was randomized, with at least one-hour rest for lizards between trials.

Clinging Ability

Lizards were warmed in an incubator for one hour at 33^{o}C, then dragged backwards with both fore-limbs in contact with a piece of transparency paper taped to the top of a Kistler Z17097 piezoelectric force plate connected to a Kistler 9685 charge amplifier (Bloch & Irschick 2004; Elstrott & Irschick 2004). Digital traces were read from a Kistler 5691 DAQ-book into a Windows computer using Bioware software version 4.1.02. Because the force plate measures forces exerted in the x, y, and z planes, clinging force was measured as the force trace on the y-axis. Each trial was repeated 4-5 times, with the highest recorded score considered the maximum for clinging ability.

Data Analysis

All statistical analyses were performed using R v. 3.3.2 (R Development Core Team 2016).

Morphology

Initial juvenile morphological characteristics (SVL and mass) were tested for treatment differences using ANOVA for both species. Adult morphological characteristics (SVL, mass, head measurements, limb measurements, and toepad measurements) were transformed with Box-Cox power transformations as needed. MANOVA was used to analyze differences in SVL, head measurements, and mass. MANCOVA was used to test for differences in limb morphology elements, using head-length to control for size.

Performance

We tested for differences in cling force and bite force in both species with ANOVA, again using head-length to control for size. To compare maximum sprint performance of lizards on their "home" perch (the perch size they were reared on) versus the reciprocal perch, we used generalized linear mixed models using the lme function of the nlme package version 3.1–128 (Pinheiro *et al.* 2017) for R analytical software version 3.3.2 (R Core Team 2016). Each lizard had two maximum speed measurements: the maximum speed measured on the narrow perch, and the maximum speed measured on the broad perch. We used four different treatment codes to describe this in our analysis:

BB= reared on broad perch and tested on broad perch.

BN= reared on broad perch and tested on narrow perch.

NB= reared on narrow perch and tested on broad perch.

NN= reared on narrow perch and tested on narrow perch.

First, we used Box-Cox transformations (using the MASS package in R) to find the best transformation for sprint in both species (sprint^0.53 for sagrei, and sprint^0.12 for carolinensis). All models included a random intercept for each individual, as well as head length (to control for size) as a random slope. Treatment type, sex, and head length (to control for size) were fitted as fixed factors using maximum likelihood. We then performed model reduction using log-likelihood ratio tests, and refitted the final models using restricted-estimate maximum likelihood REML.

Results

Survival at the end of all experiments was 87.3% for *A. carolinensis* (131/150) and 82% for *A. sagrei* (123/150).

Morphology

Neither *A. carolinensis* head morphology nor limb morphology were significantly affected by perch size after controlling for body size, nor were there significant differences in toe-pad area in hindtoe or foretoe (Table 1). While there was no difference in *A. sagrei* head morphology between treatments, we found significant differences in hindlimb morphology after adjusting for body size (P<0.05). In subsequent univariate ANOVA analysis of individual elements of the hindlimb, both tibia length and hindtoe length was significantly longer (P < 0.005) in *A. sagrei* reared on broad perches than those reared on narrow perches (Table 2). There were no significant differences in toe-pad area in hindtoe or foretoe (Table 2).

Table 1. Mean (± 1 SE) morphological measures for male and female *A. carolinensis* reared on different perch sizes. N represents the sample size.

	***A. carolinensis* Morphology**			
Sex	Male		Female	
Perch type	Broad	Narrow	Broad	Narrow
N	23	26	41	41
Morphology				
Mass (g)	2.58 ± 0.87	2.33 ± 0.76	1.80 ± 0.34	1.72 ± 0.31
SVL (mm)	48.31 ± 5.49	48.54 ± 4.85	43.18 ± 3.13	43.34 ± 3.08
HL (mm)	16.25 ± 1.65	16.26 ± 1.43	14.18 ± 0.74	13.99 ± 0.76
Humerus (mm)	7.09 ± 0.82	7.05 ± 0.75	6.29 ± 0.54	6.38 ± 0.54
Radius (mm)	6.30 ± 0.69	6.36 ± 0.71	5.57 ± 0.45	5.49 ± 0.41

Hand (mm)	6.26 ± 0.60	6.13 ± 0.59	5.51 ± 0.36	5.44 ± 0.42
Foretoe area (mm^2)	2.11 ± 0.56	1.92 ± 0.51	1.53 ± 0.35	1.55 ± 0.44
Femur (mm)	9.87 ± 1.26	9.97 ± 1.15	8.83 ± 0.59	8.66 ± 0.78
Tibia (mm)	10.02 ± 0.92	9.99 ± 1.09	8.85 ± 0.44	8.82 ± 0.57
Metatarsal (mm)	6.07 ± 0.75	6.09 ± 0.65	5.41 ± 0.44	5.30 ± 0.41
Longtoe (mm)	6.37 ± 0.66	6.20 ± 0.62	5.52 ± 0.45	5.43 ± 0.53
Hindtoe area (mm^2)	2.68 ± 0.73	2.65 ± 0.65	2.17 ± 0.54	2.16 ± 0.49

Table 2. Mean (± 1 SE) morphological measures for male and female *A. sagrei* reared on different perch sizes. N represents the sample size. Values with asterisk were significantly different between treatments.

	A. sagrei Morphology			
Sex	Male		Female	
Perch type	Broad	Narrow	Broad	Narrow
Sample size	26	26	31	40
Morphology				
Mass (g)	2.84 ± 1.07	3.00 ± 1.32	1.77 ± 0.37	1.75 ± 0.57
SVL (mm)	47.37 ± 4.49	46.60 ± 6.06	40.37 ± 2.71	39.60 ± 3.11
HL (mm)	13.98 ± 1.35	13.95 ± 1.71	12.16 ± 0.73	12.03 ± 0.80
Humerus (mm)	7.93 ± 0.62	7.74 ± 0.90	6.58 ± 0.56	6.61 ± 0.64
Radius (mm)	7.00 ± 0.64	6.76 ± 0.82	5.72 ± 0.34	5.65 ± 0.54
Hand (mm)	6.46 ± 0.71	6.50 ± 0.76	5.30 ± 0.44	5.24 ± 0.58
Foretoe area (mm^2)	1.47 ± 0.42	1.57 ± 0.51	1.08 ± 0.30	1.16 ± 0.34
Femur (mm)	11.36 ± 1.19	10.94 ± 1.52	9.18 ± 0.57	9.10 ± 0.77
Tibia (mm)*	**11.51± 0.95***	**10.97 ± 1.51***	**9.47 ± 0.49***	**9.21 ± 0.73***
Metatarsal (mm)	7.53 ± 0.59	7.39 ± 0.89	6.17 ± 0.47	6.14 ± 0.52
Longtoe (mm)*	**7.46 ± 0.69***	**7.22 ± 1.05***	**6.19 ± 0.40***	**5.90 ± 0.56***
Hindtoe area (mm^2)	2.03 ± 0.70	2.01 ± 0.70	1.38 ± 0.34	1.41± 0.41

Performance

Bite Force

There were no significant treatment effects for maximum bite force in either *A. carolinensis* (Figure 1a) or *A. sagrei* (Figure 2a).

Cling Force

While *A. carolinensis* males showed no significant treatment effects in clinging performance, females did (P<0.05). Those reared on narrow perches clung more strongly than those reared on broad perches (Figure 1b). *A. sagrei* exhibited no significant differences in maximum cling force between treatments (Figure 2b).

Sprint Speed

Both sexes of *A. carolinensis* sprinted faster on broad perches and there was no significant difference in male *A. carolinensis* sprint speed between treatments. Females reared on narrow perches sprinted significantly faster on both perch types than did females reared on broad perches (Table 3, Figure 1c). While all *A. sagrei* sprinted faster on broad perches than narrow perches, lizards reared on narrow perches sprinted significantly faster on both perch types than those reared on broad perches (Table 4, Figure 2c).

Table 3. Best-fit models for sprinting as a function of treatment, sex, head-length, and treatment sex interaction in *A. carolinenis*. The baseline category for treatment is broad-reared lizards running on broad perches, and the baseline category for sex is female. Thus, the reported values give estimated change in sprint speed between the category named in the table and the baseline category.

Model Term	Coefficient	SE	p-value
Intercept	0.901	0.038	0.000
treatmentBN	-0.073	0.007	0.000
treatmentNB	0.014	0.009	0.135
treatmentNN	-0.053	0.009	0.000
Sexmale	0.009	0.012	0.474
Headlength (hl)	-0.002	0.003	0.379
treatmentBN:sexmale	-0.008	0.012	0.514
treatmentNB:sexmale	-0.003	0.015	0.859
treatmentNN:sexmale	-0.038	0.015	0.012*

Figure 1. *A. carolinensis* Performance

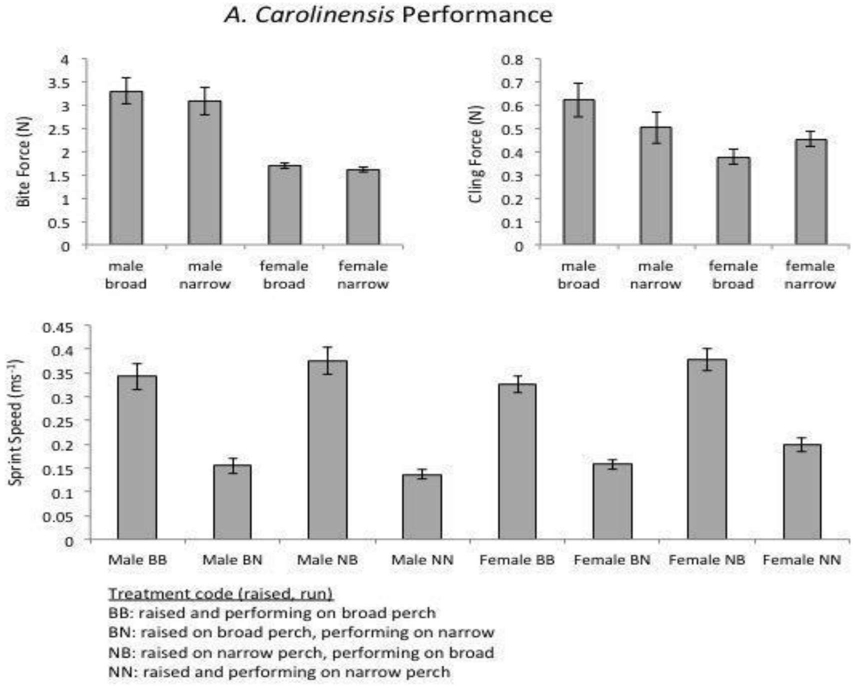
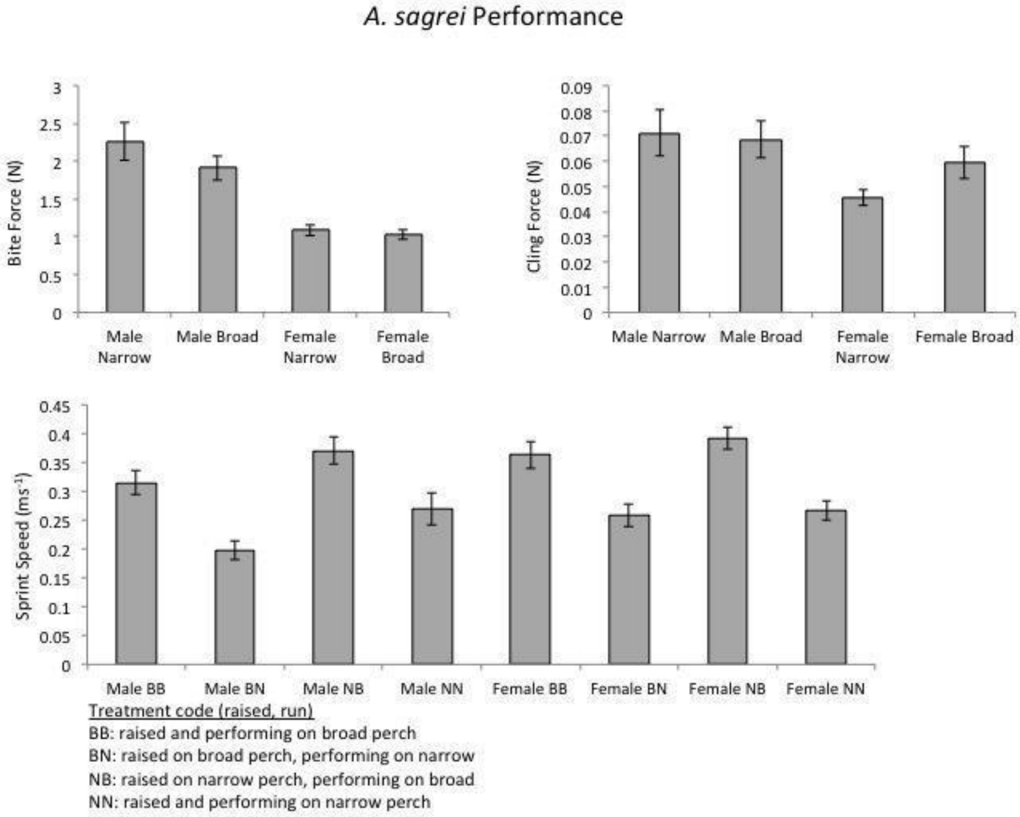


Table 4. Best-fit models for sprinting as a function of treatment and head-length in *A. sagrei*. The baseline category for treatment is broad-reared lizards running on broad perches. Thus, the reported values give estimated change in sprint speed between the category named in the table and the baseline category.

Model term	Coefficient	SE	p-value
Intercept	0.727	0.070	0.0000
treatmentBN	-0.109	0.018	0.0000
treatmentNB	0.034	0.020	0.090
treatmentNN	-0.078	0.020	0.0001
Headlength (hl)	-0.013	0.005	0.015

Figure 2. *A. sagrei* Performance



Treatment code (raised, run)
BB: raised and performing on broad perch
BN: raised on broad perch, performing on narrow
NB: raised on narrow perch, performing on broad
NN: raised and performing on narrow perch

Discussion

Although the role of plasticity in promoting or constraining evolutionary change is controversial, plasticity may enhance short-term fitness in ecological contexts such as invasion into novel habitats. We tested whether invasive *A. sagrei* and native *A. carolinensis* lizards showed similar degrees of plasticity in both limb morphology and in resultant whole-organism performance tasks when raised with substrates of two diameters. We found that *A. sagrei* showed significant treatment differences in sprint performance, although the morphological treatment differences were subtler than in previous investigations. We also found no evidence for morphological plasticity in *A. carolinensis* within the two perch diameters considered here. Despite finding no effect of perch diameter on morphology, we found significant treatment differences in sprint performance and clinging performance in *A. carolinensis* females, but not males. Our study is one of the first to measure tests of performance plasticity directly in addition to morphological/phenotypic plasticity.

Previous studies have documented a close fit between limb length and perch diameter in anoles (Losos & Sinervo 1989; Irschick & Losos 1998). Instead of measuring the entire limbs as in those studies, we measured elements of the hindlimb and forelimb separately. We found significant differences in two aspects of *A. sagrei* morphology: tibia length and long toe length. This suggests that at least for *A. sagrei*, there might be more plasticity in these components than in other parts of the limbs. Our morphology results were more subtle than previously reported for *A. sagrei* and *A. carolinensis* (Losos *et al.* 2000; Kolbe & Losos 2005). We found no significant morphological differences in *A. carolinensis*, and this was likely due to our more constrained treatment design. Both earlier studies used broad, flat wooden planks for the large diameter treatment, whereas we used a 2.54 cm diameter wooden dowel. Because anoles in nature are likely to encounter and use a wide range of substrate types (Losos 2009), both of these experimental approaches are valid. However, our results suggest that moderately broad substrates elicit less plasticity than that exhibited by anoles using tree trunks. Given that plasticity in anoles appears to occur within a narrow developmental window prior to sexual maturity, our results highlight the importance of the juvenile environment for influencing adult morphology and performance phenotypes (Royle, Lindstrom & Metcalfe 2006; Lailvaux, Breuker & Van Damme 2017; Garland, Cadney & Waterland 2017).

While all lizards sprinted faster on broader perches than narrow perches, and as noted in earlier studies (Losos & Sinervo 1989; Losos 1990; Irschick & Losos 1999; Spezzano *et al.* 2004; Calsbeek & Irschick 2007), broad treatment reared lizards were more sensitive to smaller perch diameters, all *A. sagrei* and *A. carolinensis* females reared in the narrow treatment group sprinted faster on both perch types than lizards in the broad treatment group. Finding no significant shifts in *A. carolinensis* morphology between treatments was unexpected and contrary to previous findings (Losos & Sinervo 1989; Losos & Irschick 1996; Irschick & Losos 1998). Potentially, perch treatments may have prompted changes in kinematics that affected perch performance. Foster and Higham (2012) found that *A. carolinensis* placed hindlimbs laterally on narrower perches while maintaining a medial forelimb position, suggesting that forelimbs may adopt a more propulsive role while the hindlimb assists in balance and stabilization. Narrow diameter perches increase the likelihood of falling due to sloped sides and narrow support base; this increases the proportion of the gravitational force acting tangentially to the perch, creating a toppling moment that increases with deflection of the center of mass away from the perch (Preuschoft 2002; Lammers & Biknevicius 2004; Lammers & Gauntner 2008). Foster and Higham (2012) suggested that lizards might place the rear foot more laterally on the perch to partially circumvent constraints of smaller perch diameter, thus increasing the angle of the arc subtended by the limbs and reducing the tangential component of the adduction force to aid with grip maintenance. They also noted that such foot placement would likely decrease the propulsive component of force because a greater proportion of force is directed medially to maintain grip (Lammers & Biknevicius 2004; Lammers 2007; Schmidt & Fischer 2010, 2011). While we did not measure kinematics in our study, it is plausible that lizards in the narrow treatment groups may have benefitted from previous experience using these narrower perches, and this could account for some of the differences in sprint speed between treatments. Yet a further possibility is that perch diameter may have affected hindlimb muscle morphology or function, which we do not consider in this study.

Clinging ability is generally tightly correlated with pad area in anole species (Irschick *et al.* 1996; Elstrott & Irschick 2004), but we found that *A. carolinensis* females reared on narrow perches demonstrated better clinging performance than those reared on broad perches, with no obvious morphological differences in toepad area or width. A separate 2005 study with nearby populations of *A. carolinensis* (Tulane University campus) also found evidence that toepad area did not change with differences in clinging performance (Irschick *et al.* 2005b). It therefore seems likely that some other variable besides toepad area is affecting treatment differences in cling performance. For instance, we did not measure claw morphology or count lamellae on toepads (known to correlate with cling performance (Glossip & Losos 1997)). However, claw morphology is not known to affect clinging ability on smooth surfaces (Zani 2000; Dai, Gorb & Schwarz 2002), and lamellae count seems to be fixed at hatching, although it can shift over generations in *A.*

carolinensis (Stuart *et al.* 2014). Finally, it is possible there were morphological and kinematic changes in the setae of the lamellae that we did not detect, and may warrant further study.

Our finding that treatment differences affect only female *A. carolinensis* performance may be due to sex differences in performance. For example, Irschick *et al.* (2005b) found that *A. carolinensis* females were better performers (relative to size) than males or juveniles for jumping velocity, acceleration, and clinging ability. Sexual dimorphism within *A. carolinensis* might partially account for differences in sprinting performance; females have relatively shorter limbs than males, which keeps the body closer to the perch surface to aid in stability and balance (Higham & Jayne 2004; Schmidt & Fischer 2010). This in turn might lead to fewer and less extreme changes in kinematics as perch diameter changes (Foster & Higham 2012). While we found no significant morphological differences with our treatment design, others have documented stronger female phenotypic plasticity responses than in male *A. carolinensis*. In an earlier study, females exhibited a larger hindlimb response range to perch size (Kolbe & Losos 2005), and Dill *et al*. (2013) found in the wild that adult females using broader perches had relatively longer limbs than females using narrower perches, but not in males. This could be related to habitat use. *Anolis* males typically use broader perches than females or juveniles (Schoener 1968; Schoener, *et al.* 1971; Irschick *et al.* 2000), but not always (Irschick *et al.* 2005a). Behavioral differences and habitat use between males and females may also be a factor, with males moving around more to defend territory (Dill *et al.* 2013), where broader perches allow for faster sprint performance (Losos & Sinervo 1989; Macrini & Irschick 1998). In addition, broad perches are typically less flexible, and anoles in nature selectively jump from perches that are relatively rigid, which improves performance (Gilman & Irschick 2013).

We found no significant treatment differences for *A. sagrei* cling performance, which was not surprising as this species does not have well-developed toe-pads (Irschick *et al.* 1996). Our experimental design for measuring cling performance is similar to Irschick *et al.* (1996) and relevant for measuring how well toepads adhere to smooth flat surfaces, but it does not take into consideration how claws, limbs, tendons, and toes contribute to clinging ability across different substrates (Zani 2000; Tulli *et al.* 2009; Tulli, Abdala & Cruz 2011). Kolbe (2015) used a whole-organism approach to measure cling performance, allowing lizards to wrap forelimbs and hindlimbs around different sized perches and measuring the force needed to pull them from perches. Lizards with shorter limbs relied more on compressive force from limb adduction to prevent slipping, while longer-limbed lizards were able to increase cling force substantially by forming a grip that encircled perches (Kolbe 2015). This likely would have been a more ecologically relevant method for testing cling performance for *A. sagrei* due to their less developed toepads. The ability to cling to a wooden perch without slipping could also contribute to sprinting performance, although tradeoffs have been noted in two species of chameleons where sprint speed decreased on narrower dowels while clinging ability increased (Losos *et al.* 1993).

One objective of this study was to explore the potential contribution of plasticity to local *A. sagrei* dominance over *A. carolinensis* populations. We found that *A. sagrei* demonstrated a greater range of morphological plasticity than *A. carolinensis*, plus plasticity in sprinting performance between perch treatments. While it is possible that morphological responses prompted the changes in performance, locomotor shifts in sprinting kinematics between different perch diameters could also affect the variation in sprint performance. One possible experimental design to separate the plasticity effects from the kinematic changes might be to take baseline measures of adult lizards with a "neutral" phenotype, and then train them (see Husak, Keith & Wittry 2015) on various size perches to see if practice and experience prompts shifts in running kinematics. Few studies have documented phenotypic plasticity in lizards in natural settings, and future experiments such as common garden and natural selection experiments would shed more light on plasticity hypotheses against other alternatives.

Conclusions

In conclusion, our results show that the relationship between morphology and performance plasticity is not straightforward, and emphasize that future experiments need to consider environmental ranges that animals encounter in natural settings, including species-specific and sex-specific differences in habitat usage. Future studies might extend these findings to test how these differences in plasticity and habitat use affect sympatric population densities of *A. carolinensis* and *A. sagrei*.

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Chapter 5.

Dissertation Conclusions

Anolis sagrei does displace *A. carolinensis* populations in southeastern Louisiana. Changes in *A. carolinensis* habitat use or shifts in population structure and density could potentially increase the distance or habitat complexity between individuals. *A. carolinensis* lizards might be altering their signaling displays to compensate for these changes in distance or habitat complexity.

Based on staged interactions in lab-controlled settings, it is possible that female interactions between *A. carolinensis* and *A. sagrei* might be a driving force behind shifts in habitat use. Based on the assumed historical mating systems for each species (female defense polygyny) males may have less reason to interact since interbreeding between the species in the wild is rare, and there are no known occurrences of hybrid offspring. However, females may have increased motive to interact if they are competing for resources such as food or nesting sites. Future research might examine nesting site selection criteria for the two species, and consider if the presence of *A. sagrei* might induce female *A. carolinensis* individuals to shift or alter their selection of nesting sites.

Plasticity is only one of several characteristics often found in invasive species. While our plasticity study should not be applied to long-term adaptation, our results suggest that *A. sagrei* could be benefitting from a plasticity advantage over *A. carolinensis*, at least in the short term. Future experiments such as common garden and natural selection experiments would shed more light on plasticity hypotheses against other alternatives. Based on personal observations and the initial results of pilot studies, I would additionally recommend that both propagule pressure and the range of temperature tolerances between the two species be further investigated.

Vita

The author was born in Cullman, Alabama. She obtained her Bachelor's degree in Biology from the University of Alabama at Birmingham in 2007. In 2008, she joined the University of New Orleans to pursue a PhD in Conservation Biology.