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

Jessica R. Edwards & Simon P. Lailvaux

Department of Biological Sciences, University of New Orleans, New Orleans LA, USA

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 vulgari*s), 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 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 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 courtship (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 video-taping 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 video-taped 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) video-taped 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 video-taped 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 overdispersion) 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 χ^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).

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 (LaFreniere) 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 ($\chi^2 = 0.729$, 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*
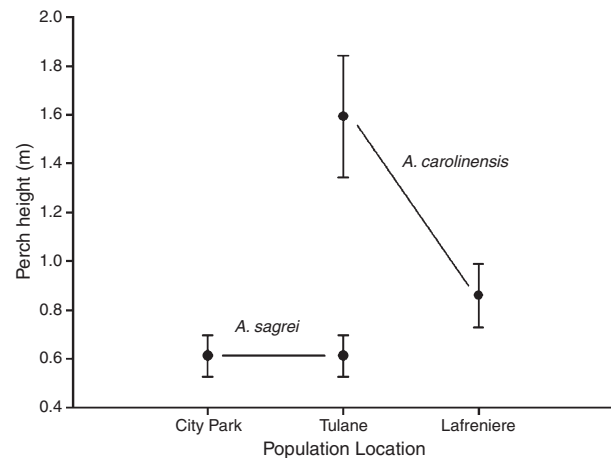
Fig. 1: Perch Height of *Anolis carolinensis* and *A. sagrei* in single and mixed populations. Values are means ± SE.

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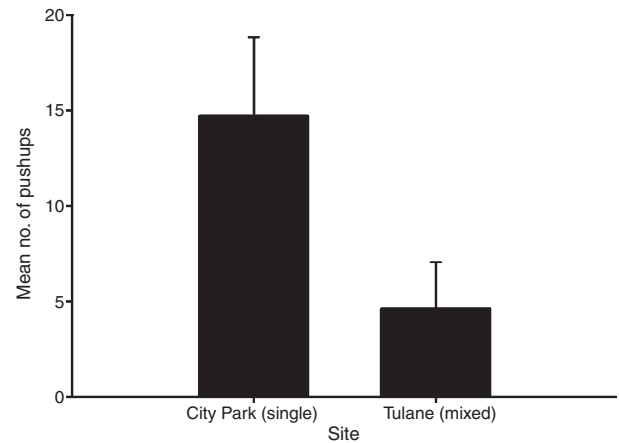
Table 2: Generalized linear model with Poisson errors describing the frequencies of A, B, and C displays in the Tulane and La Freniere *Anolis carolinensis* populations

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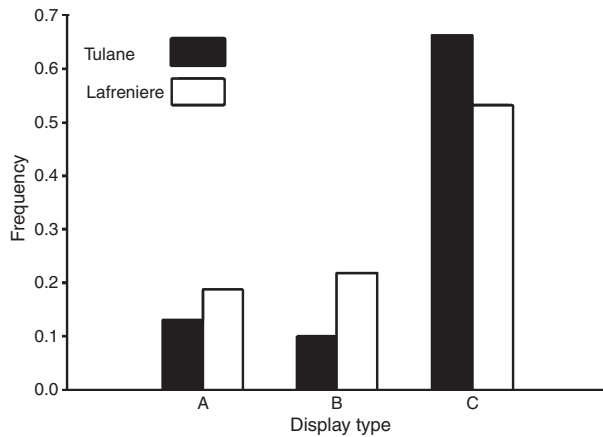
Fig. 2: Display type frequencies in single (La Freniere) and mixed (Tulane) populations.

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

populations at the two sites also did not differ significantly in time spent displaying (Kruskal–Wallis $\chi^2 = 0.514$, 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).

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).

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

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 heavyweight *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.

Acknowledgements

Literature Cited

Baker, M. C. 2001: Bird song research: the past 100 years. Bird Behav. **14**, 3—50.

Barker, N. K. S. & Mennill, D. J. 2009: Song perch height in Rufous-and-White Wrens: does behaviour enhance effective communication in a tropical forest? Ethology **115**, 897—904.

Bloch, N. & Irschick, D. J. 2006: An analysis of interpopulation divergence in visual display behavior of the green Anole Lizard (*Anolis carolinensis*). Ethology **112**, 370—378.

Cadi, A. & Joly, P. 2003: Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). Can. J. Zool. **81**, 1392—1398.

Callaway, R. M. & Ridenour, W. M. 2004: Novel weapons: invasive success and the evolution of increased competitive ability. Front. Ecol. Environ. **2**, 436—443.

Campbell, T. S., 2000: Analysis of the effects of an exotic lizard (*Anolis sagrei*) on a native lizard (*Anolis carolinensis*) in Florida, using islands as experimental units. Ph.D. Thesis, Univ. of Tennessee, Tennessee, USA.

Cole, N. C., Jones, C. G. & Harris, S. 2005: The need for enemy-free space: the impact of an invasive gecko on island endemics. Biol. Conserv. **125**, 467—474.

Decourcy, K. R. & Jenssen, T. A. 1994: Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. Anim. Behav. **47**, 251—262.

Dukes, J. S. & Mooney, H. A. 2004: Disruption of ecosystem processes in western North America by invasive species. Rev. Chil. Hist. Nat. **77**, 411—437.

Fleishman, L. J. 2000: Signal function, signal efficiency and the evolution of anoline lizard dewlap color. In: Animal Signals: Signaling and Signal Design in Animal Communication. (Epsmark, Y., Amundsen, T. & Rosenqvist, G., eds.) Tapir Academic Press, Norway, pp. 209—236.

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

Holway, D. A. & Suarez, A. V. 1999: Animal behavior: an essential component of invasion biology. Trends Ecol. Evol. **14**, 328—330.

Husak, J. F., Irschick, D. J., Meyers, J. J., Lailvaux, S. P. & Moore, I. T. 2007: Hormones, sexual signals, and performance of green anole lizards (*Anolis carolinensis*). Horm. Behav. **52**, 360—367.

Husak, J. F., Irschick, D. J., Henningsen, J. P., Kirkbride, K. S., Lailvaux, S. P. & Moore, I. T. 2009: Hormonal response of male green anole lizards (*Anolis carolinensis*) to GnRH challenge. J. Exp. Zool. **311**, 105—114.

Irschick, D. J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., VanHooydonck, B., Meyers, J. & Herrel, A. 2005: A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. Biol. J. Linn. Soc. **85**, 223—234.

Jenssen, T. A., Orrell, K. S. & Lovern, M. B. 2000: Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. Copeia **1**, 140—149.

Kiesecker, J. M. & Blaustein, A. R. 1998: Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth, and survival of native red-legged frogs (*Rana aurora*). Con. Bio. **12**, 776—787.

Kupferberg, S. J. 1997: Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology **78**, 1736—1751.

Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J. & Irschick, D. J. 2004: Performance capacity, fighting tactics, and the evolution of life-stage morphs in the green anole lizard (*Anolis carolinensis*). Proc. R. Soc. Lond. B Biol. Sci. **271**, 2501—2508.

Leal, M. & Fleishman, L. J. 2004: Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. Am. Nat. **163**, 26—39.

Leal, M. & Rodriguez-Robles, J. A. 1997: Signaling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. Anim. Behav. **54**, 1147—1154.

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

Losos, J. B. & Spiller, D. A. 1999: Differential colonization success and asymmetrical interactions between two lizard species. Ecology **80**, 252—258.

Lovern, M. B., Jenssen, T. A. & Orrell, K. S. 1999: Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: signal stability or lability? Herpetologica **55**, 222—234.

Lovern, M. B. & Jenssen, T. A. 2003: Form emergence and fixation in social signals: ontogeny of headbobbing displays in green anole lizards (*Anolis carolinensis*). J. Comp. Psychol. **17**, 133—141.

MacDonald, J., Roudez, R., Glover, T. & Weis, J. S. 2007: The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. Biol. Invas. **9**, 837—848.

Moyle, P. B. 1973: Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia **1**, 18—22.

Ord, T. J. & Stamps, J. A. 2009: Species identity cues in animal communication. Am. Nat. **174**, 585—593.

Orrell, K. S. & Jenssen, T. A. 2003: Heterosexual signaling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. Behaviour. **140**, 603—634.

Ortiz, P. R. & Jenssen, T. A. 1982: Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. Z. Tierpsychol. **60**, 227—238.

Persons, M. H., Fleishman, L. J., Frye, M. A. & Stimphil, M. E. 1999: Sensory response patterns and the evolution of visual signal design in anoline lizards. J. Comp. Physiol. A. **184**, 585—607.

Pimentel, D., Zuniga, R. & Morrison, D. 2005: Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. **52**, 273—288.

Polo-Cavia, N., Lopez, P. & Martin, J. 2011: Aggressive interactions during feeding between native and invasive freshwater turtles. Biol. Invas. **13**, 1387—1396.

Rand, A. S. 1967: The ecological distribution of the anoline lizards around Kingston, Jamaica. Breviora. **272**, 1—18.

Schoener, T. W. 1975: Presence and absence of habitat shift in some widespread lizard Species. Ecol. Monogr. **45**, 233—258.

Scott, M. P. 1984: Agonistic and courtship displays of male *Anolis sagrei*. Breviora. **479**, 1—22.

Simon, V. B. 2011: Communication signal rates predict interaction outcome in the brown anole lizard, *Anolis sagrei*. Copeia, **1**, 38—45.

Small, A. 1994: California Birds. Their status and Distribution. Ibis Publishing, Vista, California.

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