Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Bite or flight? Behavioral interactions between bark anoles and brown anoles in their nonnative range

I. T. Clifton[1], N. D. Gripshover[1], A. G. Amador[1], W. Aquino[1], J. Fernandez[1], M. Mathieu[1], A. Menendez[1], C. Quintana[1], S. Rhoades[1], G. Suarez[1] & C. L. Cox[1,2]

[1]Department of Biological Sciences, Florida International University, Miami, FL, USA
[2]Institute of the Environment, Florida International University, Miami, FL, USA

Keywords
aggression; behavior; community structuring; florida; invasive species.

Correspondence
Ian T. Clifton, Department of Biological Sciences, Florida International University, 11200 SW 8th St., Miami, FL 33199, USA.
Email: iclifton@fiu.edu

Editor: Matthew Hayward
Associate Editor: Diego Astúa

Received 29 December 2022; revised 19 March 2023; accepted 23 May 2023

doi:10.1111/jzo.13094

Abstract

Both intra- and interspecific interactions play crucial roles in defining the structure of ecological communities. However, the specific behavioral processes underlying this structuring are often unclear and must be inferred from contemporary interactions. Rapid spread of nonnative species has resulted in increasingly homogenized communities, and this homogenization provides an excellent opportunity to study the behavioral processes that lead to stable communities of introduced species in novel habitats. Here, we compared the behavior of brown anoles (*Anolis sagrei*) and bark anoles (*A. distichus*) when faced with an incursion by an unknown brown anole to examine the intra- and interspecific interactions underlying the structuring of novel communities in South Florida, USA. We found that brown anoles were consistently more aggressive toward intruders than bark anoles, and this pattern was accentuated when they encountered intruders of the same sex. Conversely, bark anoles were likely to flee when they encountered intruder brown anoles. We also found that brown anoles were likely to attack intruders regardless of whether they engaged in aggressive behavioral displays while bark anoles were likely to flee regardless of whether the intruder engaged in behavioral displays. Our findings suggest that behavioral interactions could play a significant role in structuring the novel *Anolis* communities in South Florida and demonstrate the importance of aggressive interactions both within and between species.

Introduction

Interactions between individuals play a key role in the ecological and evolutionary dynamics of communities, defining space use (e.g., Grenier-Potvin et al., 2021; Sinervo & Lively, 1996), niche partitioning (Finke & Snyder, 2008; Hutchinson, 1959), and ultimately, community structure (Connell, 1983; Savolainen & Vepsäläinen, 1988). Agonistic interactions between conspecifics (i.e., intraspecific competition) are crucial for establishing dominance hierarchies and defending resources (Nakano & Furukawa-Tanaka, 1994). Additionally, agonistic interactions between heterospecifics (i.e., interspecific competition) can drive divergence in resource use (Krijger et al., 2001; Pacala & Roughgarden, 1982). While both intra- and interspecific interactions are important, the relative contribution of these interactions to the structuring of novel and introduced ecological communities remains unclear.

Behavioral interactions are critical in defining the spatial distribution of individuals (Hobbs & Munday, 2004; Svanbäck et al., 2008). For example, smaller, less aggressive individuals are sometimes excluded from ideal microhabitats and instead forced to make do in less suitable environments (e.g., Keren-Rotem et al., 2006; Moreira et al., 2008; Stamps, 1983). This can have important fitness consequences as exclusion from the most suitable conditions may diminish performance (Iglesias-Carrasco et al., 2020). Similarly, interference competition, a form of interspecific competition resulting from agonistic interactions between competing species, drive divergence in resource use and can eventually lead to the evolution of divergent phenotypes (i.e., character displacement; Brown Jr. & Wilson, 1956; Grant & Grant, 2006). Character displacement then facilitates the coexistence of previously competing species in the same habitat (Grether et al., 2017). Indeed, the relatively low degree of niche overlap in stable ecological communities is often attributed to historic character displacement (i.e., the ghost of competition past; Schluter, 2000). Because males have historically been considered more aggressive than females, much of the historical literature around both intra- and interspecific aggression has focused on male–male conflict, often in the context of mate guarding (Kamath & Losos, 2017). However, recent work suggests females can be more aggressive toward intruders than males (Bentz et al., 2019; Edwards & Lailvaux, 2013; Pröhl et al., 2019; Reedy et al., 2017). Regardless of the aggressor, these interactions are key to structuring the spatial distribution of individuals within a population and defining the composition of ecological communities.

Recent human activities have resulted in increasing homogenization of ecological communities as nonnative species gradually replace and displace native species, diminishing regional distinctions in biodiversity (McKinney & Lockwood, 1999; Olden, 2006). For example, human-mediated introductions of nonnative species into the Great Lakes of North America has resulted in increasingly homogenized fish communities since the late 1800s with the extirpation of more than 20 native species and the establishment of more than 30 nonnative species in at least one of the five lakes (Campbell & Mandrak, 2019). Similarly, the lizard communities of South Florida, USA are now dominated by nonnative species (Krysko et al., 2016). Anole lizards, particularly nonnative brown anoles (*Anolis sagrei*) and bark anoles (*A. distichus*) have become ubiquitous across much of South Florida, especially in urban habitats (King & Krakauer, 1966). Anole lizards are an excellent example of both the increasing homogenization of communities and the role of competitive interactions in structuring ecological communities. Anoles of the Greater Antilles have repeatedly evolved characteristics that minimize competitive interactions, allowing multiple closely related species to coexist in the same space (Losos et al., 1998). In the absence of congeners, native green anoles, *A. carolinensis*, have adopted a generalist lifestyle (Jenssen et al., 1998). However, the introduction of brown anoles precipitated behavioral and morphological changes in the native green anole reminiscent of the patterns observed throughout the Greater Antilles, including the selection of higher perch sites and changes in limb lengths (Kamath et al., 2013; Stuart et al., 2014). Changes in community assemblages driven by anthropogenically mediated introductions of nonnative species in established communities provides a unique opportunity to investigate the behavioral interactions that structure novel communities.

Throughout the mid-20th century, brown anoles (*Anolis sagrei*) and bark anoles (*A. distichus*) have spread throughout South Florida (King & Krakauer, 1966; Kolbe et al., 2004), where they encounter new native and nonnative lizard species. The establishment of these new lizard communities likely alters behavioral interactions and understanding these altered interactions may illuminate mechanisms underlying community structuring. We evaluated the behavioral responses of brown anoles and bark anoles to simulated intrusions of unknown brown anoles, and we compared the differences in responses between species and sexes. We also compared whether specific behaviors from intruders elicited specific behaviors from the resident lizards. Because previous investigators have found considerable interspecific aggression in brown anoles (e.g., Tokarz & Beck, 1987), we predicted that brown anoles would be more aggressive toward intruders than bark anoles would be. We also predicted that males and females of both species would be more aggressive toward intruders of the same sex than intruders of the opposite sex due to their perceived threat as a competitor for reproductive resources (e.g., mates, nest sites, etc.). Finally, because many lizard species are thought to defend territories from potential competitors, we predicted that aggressive displays from intruders would elicit aggressive displays from focal (i.e., resident) lizards, up to and including combat. We further predicted that brown anoles, a famously territorial species, would be more likely to attack intruders while bark anoles would be more likely to flee when encountering these displays from brown anoles.

Materials and methods

Study system

We performed behavioral assays on brown anoles and bark anoles, both of which can be found in high densities (61 and 29% of lizards observed on transect surveys, respectively; Table 1). Both species are native to islands of the Greater Antilles and were introduced to South Florida in the early to mid-20th century (King & Krakauer, 1966). Lizards of both species often engage in stereotypical behavioral displays when they encounter other lizards that are generally meant to avoid escalation to combat (Stamps, 1977). These behaviors include extension of the dewlap, a colorful flap of skin on the neck, rapid, short headbobs, and deep pushups facilitated by full engagement of the forelimbs (Paterson, 1999, 2002).

Activity surveys

In Spring 2021, we walked survey transects to assess the presence and densities of lizards in the urban habitats at the Modesto A. Maidique Campus of Florida International University, Miami, FL, USA (hereafter referred to as MMC). We walked pre-determined time-constrained (15 min) survey routes across campus either individually or in pairs to find lizards. We recorded the total number of individuals of each species we observed, and when possible, we recorded the sex of the individuals. All activity surveys occurred between 1100 and 1800 h.

Behavioral assays

We performed behavioral assays at MMC on 18 March 2021, 25 March 2021, and 1 April 2021, between 1500 and 1730 h. Prior to performing assays, we collected adult male and female brown anoles to act as stimulus lizards (i.e., the brown anole introduced to stimulate behavioral responses in the focal lizard) from a different part of campus from the assays to ensure focal and stimulus lizards had no prior interactions. We collected a broad size range of stimulus lizards, measuring SVL (male range: 48–69 mm; female range: 38–49 mm) at the time of capture, to encompass the distribution of body sizes focal lizards would likely encounter across MMC. We captured lizards using a long pole with a slipknot loop tied to the end of the pole and housed animals in a cloth bag prior to experimental procedures. Lizards were only retained for the few hours of the study each day and then released at their site of capture. We randomly chose the order of species for observations by a coin toss, and when we encountered an individual of the target species, we designated that individual the focal lizard (i.e., the lizard whose behaviors were being assayed in response to an intruder brown anole). We then tethered a stimulus lizard,

Table 1 Results of campus-wide surveys of MMC for *Anolis* lizards

Species	Sex			Total
	Male	Female	Unknown	
Brown Anole (*Anolis sagrei*)	136 (29.6%)	107 (23.3%)	35 (7.6%)	278 (60.6%)
Bark Anole (*Anolis distichus*)	20 (4.4%)	1 (0.2%)	114 (24.8%)	135 (29.4%)
Green Anole (*Anolis carolinensis*)	12 (2.6%)	9 (2%)	23 (5%)	44 (9.6%)
Knight Anole (*Anolis equestris*)	1 (0.2%)	0 (0%)	1 (0.2%)	2 (0.4%)

A total of 459 *Anolis* lizards of four species were observed across 26 survey transects between 11 March 2021 and 7 April 2021. All surveys were conducted between 1100 and 1800 h. The number in parentheses indicates the percentage of the total sample represented by each species and sex.

alternating between male and female stimulus lizards, to a long, slender pole (~4 m) by fastening a slipknot around the right hind leg of the lizard and tying it to the pole. We switched localities between assays to avoid collecting data from the same animal multiple times, a feasible strategy due to the high density of lizards in the study area and low movement rates of the focal lizards. We attempted to standardize the trials within the constraints of a moving focal lizard by placing the stimulus lizard approximately 1–10 cm away from the focal lizard at either the same height or slightly below the focal lizard and retreated approximately 10 m to observe their interactions through binoculars. Florida Fish and Wildlife does not require permits for the use of these nonnative species, and all experimental procedures were approved by the Florida International University Institutional Animal Care and Use Committee (protocol # IACUC-21-010).

We conducted behavioral trials until the focal lizard attacked, fled, or 10 min elapsed without the focal lizard attacking or fleeing. During each trial, we recorded the combined number of headbobs and pushups and the number of dewlap extensions for both the focal and stimulus lizards. We combined headbobs and pushups in our count because it can be difficult to distinguish between the two behaviors because they usually occur simultaneously. We also recorded the latency between introduction of the stimulus lizard and attack or flee. When possible, we captured the focal lizard at the conclusion of the behavioral trial to measure SVL and mass and mark them with a paint pen to avoid repeated observations.

Statistical analyses

Identifying focal lizards to sex was not always possible from a distance, especially in the absence of conspicuous dewlap extensions during observation. While dewlaps are present in females, they are considerably smaller than male dewlaps and, unlike male dewlaps, are not typically visible during displays. Logistic regressions revealed no differences between the probability of attack ($\chi^2 = 0.62$, $P = 0.43$) or flee ($\chi^2 = 0.78$, $P = 0.38$) between the known focal females and the unknown focal lizards. Therefore, we combined non-displaying lizards and females into a single category in our analyses. Pooling these unidentified individuals with females provides a more conservative estimate of intersexual differences while facilitating a more robust comparison of the two species.

We used four global logistic regression models to test for differences in the likelihood of the focal lizards doing headbobs and/or pushups, extending their dewlaps, attacking, and fleeing from the intruder *A. sagrei*. The outcome of the interaction (1 = behavior occurred, 0 = behavior did not occur) was used as the dependent variable for all four models and, with the exception of the model for dewlap extension, focal species, focal sex, and their interaction were used as the independent variables. The presence of a conspicuous dewlap is a diagnostic secondary sexual characteristic of males; therefore, we only included focal species in our model comparing the likelihood of extending the dewlap in response to an intruder. Because we found no evidence of a significant sex effect, nor interaction between sex and species, on attack or flee frequency (Table 2), we followed up with two logistic regressions considering only species to better understand the difference between bark anoles and brown anoles. We tested for differences in the latency to attack and flee (i.e., the time between intrusion and the behavioral response) between the bark and brown anoles using two linear models. We also compared the responses of focal lizards when they encountered intruders of the same sex and when they encountered intruders of the opposite sex with eight logistic regression models. Finally, we compared the probability of a focal lizard displaying a specific behavior given the behavior of a stimulus lizard with 8 independent logistic regressions with the focal lizard's behavior as the dependent variable and the stimulus lizard's behavior as the independent variable. We performed all analyses in R 4.2.1 (R Core Team, 2022) using the package 'arm' (Gelman & Su, 2022).

Results

Activity surveys

We performed 26 activity surveys from 11 March 2021 and 7 April 2021, during which we observed 538 lizards across the FIU MMC campus (Table S1). We observed 459 anole lizards during these surveys (Table 1). Brown anoles were by far the most abundant anole species observed during surveys, making up nearly 61% of the survey total. The second most abundant anole species was the bark anole, which accounted for nearly 30% of the survey total.

Table 2 Results of logistic regressions comparing the probability of a behavior occurring based on the species, sex, and their interaction

	Species		Sex		Species*Sex	
Response	χ^2	P	χ^2	P	χ^2	P
Headbob or Pushup	0.902	0.342	0.820	0.365	1.98	0.159
Dewlap extension	**4.58**	**0.0323**				
Attack	**3.86**	**0.0494**	3.38	0.0660	0.0005	0.983
Flee	**4.53**	**0.0333**	0.303	0.582	0.311	0.577

Significant effects are denoted in bold. The dewlap extension response is excluded from the between-sex comparison and its interaction with species because only males extended dewlaps.

Behavioral differences between species and sexes

We performed a total of 94 unique behavioral assays split between 49 focal bark anoles (23 males and 26 females) and 45 focal brown anoles (29 males and 16 females). We found no evidence of interspecific or intersexual differences in the frequency of headbob and/or pushup displays, nor was there a significant interaction between species and sex (Table 2). We found that male bark anoles were more likely to extend their dewlaps than male brown anoles (Table 2). We also found that brown anoles were more likely to attack the stimulus lizards than bark anoles regardless of sex (χ^2 = 5.2, P = 0.023; Fig. 1a). Conversely, bark anoles were more likely to flee from the stimulus lizards than brown anoles regardless of sex (χ^2 = 6.0, P = 0.014; Fig. 1b). However, there was no evidence of a difference between the two species in the latency to attack ($t_{1,29}$ = 1.6, P = 0.13; Fig. 1c) or flee ($t_{1,50}$ = 0.73, P = 0.47; Fig. 1d).

When encountering a male brown anole intruder, males of both species attacked more frequently than females (χ^2 = 7.6, P < 0.01; Fig. 2a). Females fled more frequently than males when they encountered male brown anole intruders (χ^2 = 4.2, P = 0.041; Fig. 2b); however, this pattern was primarily driven by the relatively low frequency at which male brown anoles fled in response to male intruders (31.6% of encounters), as male bark anoles fled nearly as frequently as females of both species (73.3% of encounters). There was no difference in the frequency at which male and female bark anoles and brown anoles attacked or fled when they encountered female brown anole intruders (P > 0.05; Fig. 2c,d). Brown anoles attacked more frequently when they encountered intruders of the same sex than bark anoles (χ^2 = 5.5, P = 0.019; Fig. 2e). Bark anoles of both sexes were more likely to flee when they encountered intruders of the same sex than were brown anoles (χ^2 = 6.9, P < 0.01; Fig. 2f). Males of both species were more likely to attack a female intruder than females were to attack a male intruder (χ^2 = 11.7, P < 0.01; Fig. 2g). Conversely, females of both species were more likely to flee when encountering a male intruder than males were to when encountering a female intruder (χ^2 = 4.6, P = 0.033; Fig. 2h).

Behavioral dependencies

We found that aggressive displays from intruder brown anoles were likely to elicit aggressive displays in focal lizards (Fig. 3a-d). We also found that regardless of whether intruder brown anoles performed an aggressive display, brown anoles were more likely to attack than bark anoles (Fig. 3e,f). Conversely, we found that bark anoles were likely to flee from intruder brown anoles regardless of whether they acted aggressively (Fig. 3g,h).

Discussion

We found that aggressive interspecific interactions were consistent with ecological abundance, with the most abundant species, brown anoles (Table 1), more likely to bite and less likely to flee than the next most abundant species, bark anoles (Fig. 1a,b). We found that males tended to be more aggressive than females in virtually all contexts we tested, but female

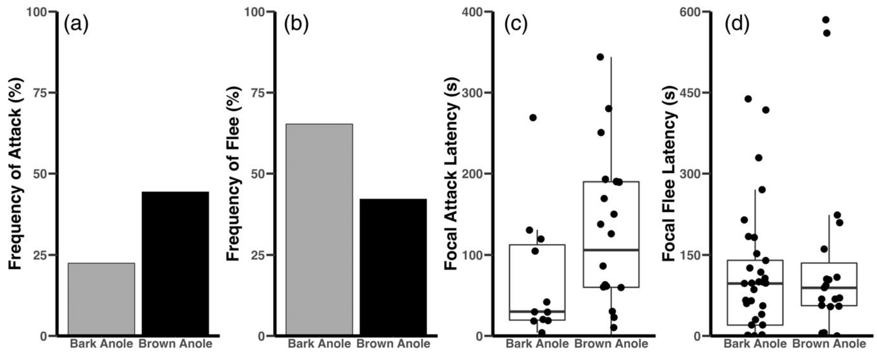

Figure 1 (a) Frequency of attack of bark anoles and brown anoles when confronted with an unknown intruder brown anole. (b) Frequency of fleeing of bark anoles and brown anoles when confronted with an unknown intruder brown anole. (c) Latency to attack of bark anoles and brown anoles when confronted with an unknown intruder brown anole. (d) Latency to flee of bark anoles and brown anoles when confronted with an unknown intruder brown anole.

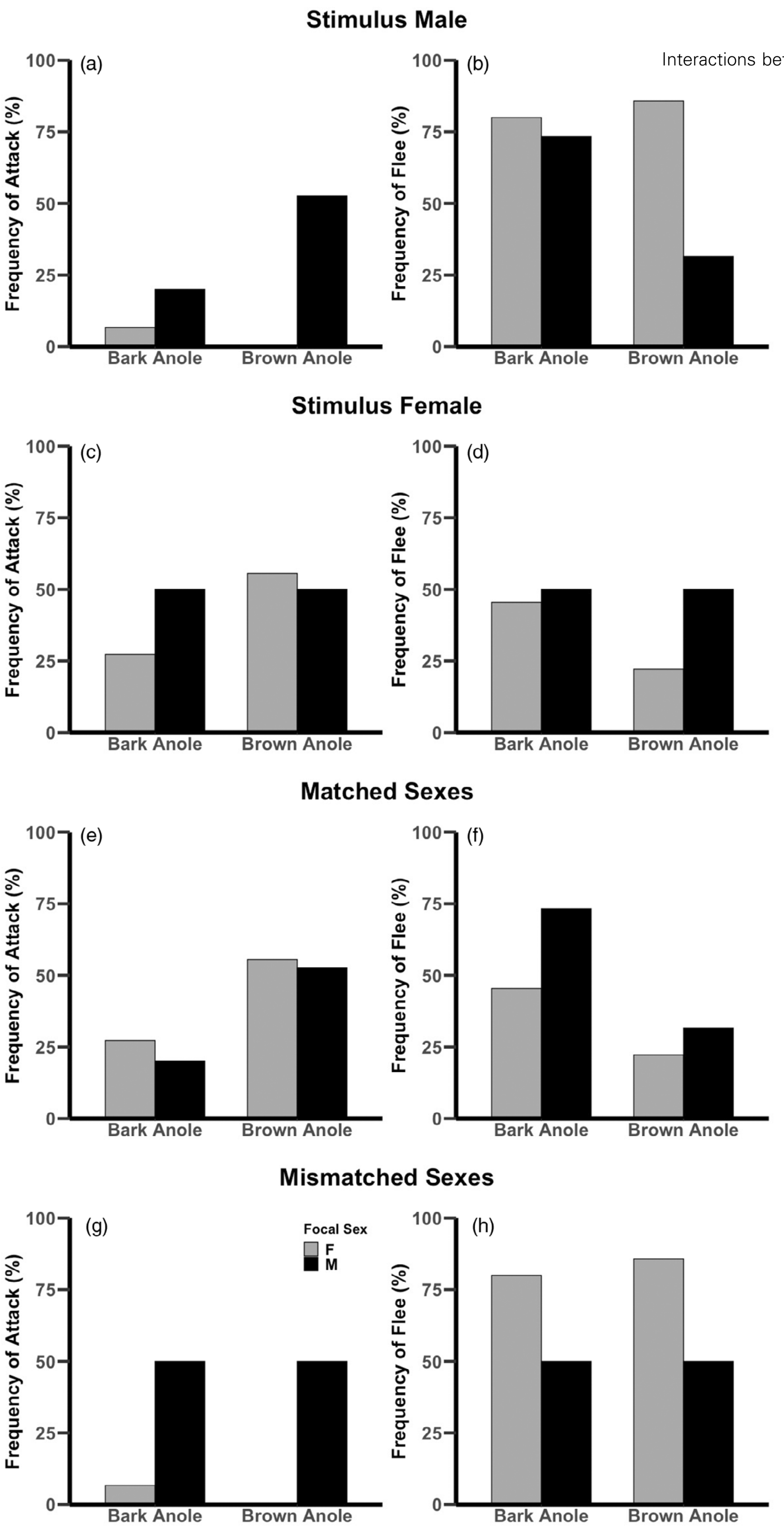

Figure 2 The frequency of attack and flee when bark anoles and brown anoles are confronted by an unknown male brown anole (a,b) compared to when they are confronted by an unknown female brown anole (c,d). The frequency of attack and flee when bark anoles and brown anoles are confronted by an unknown brown anole that matches their sex (e,f) compared to when they are confronted by an unknown brown anole of the opposite sex (g,h). Gray bars indicate female focal lizard attack frequency and black bars indicate male focal lizard attack frequency.

brown anoles were much more likely to attack when the intruder lizard was also a female (Fig. 2). Finally, we found evidence that the behavior of focal lizards was dependent on the behavior of stimulus lizards, with aggressive displays being met with aggressive displays (Fig. 3). The aggression that brown anoles displayed toward both conspecifics and heterospecifics suggests that they could play a significant role in structuring emerging novel communities and may continue to alter community composition and dynamics across their invasion front (Gotelli & Arnett, 2000; MacGregor-Fors et al., 2010).

Interspecific aggression, particularly toward more closely related species, has long been recognized as a spatial structuring mechanism in animal communities (e.g., Freeman et al., 2016; Jankowski et al., 2010; Robinson & Terborgh, 1995; Salzburg, 1984). For example, threespot damselfish (*Stegastes planifrons*) structure habitat use and population dynamics in congeners and have been shown to attack congeners further from their territory while ignoring more distantly related species closer to their territory (Myrberg Jr. & Thresher, 1974; Robertson, 1996). Regardless of the context, we found that bark anoles were significantly less likely to attack and more likely to flee than brown anoles. The fact that bark anoles typically fled when they encountered an intruder brown anole even when the intruder did not perform aggressive displays suggests the smaller, less abundant bark anoles see brown anoles as a threat. This finding may lend support to the idea that brown anoles are more aggressive than many of their congeners (e.g., Culbertson & Herrmann, 2019). Brown anole aggression toward heterospecifics likely plays a significant role in driving resource partitioning and may have contributed to the ecomorphological patterns we see in the native range of these lizards (Losos et al., 1998). Indeed, recent brown anole invasions in the United States have illustrated the behavioral and morphological impacts of more aggressive novel competitors on native congeners (e.g., Kamath et al., 2013; Stuart et al., 2014). The aggression brown anoles displayed toward heterospecifics may also explain their successful establishment in novel environments, including much of the Caribbean, the southeastern United States, Hawai'i, California, Taiwan, and Ecuador (Fisher et al., 2020; Kolbe et al., 2004; Narváez et al., 2020; Norval et al., 2011).

Previous work in fish has suggested that animals tend to display more aggression toward conspecifics than heterospecifics in complex, behaviorally structured communities (Eurich et al., 2018; Little et al., 2013). Indeed, aggressive interactions between male lizards of the genus *Plestiodon* appear to be almost exclusively restricted to conspecifics (Cooper & Vitt, 1987). However, this pattern is likely species- and context-dependent, as the invasive Asian house gecko (*Hemidactylus frenatus*) displayed little aggression toward conspecifics while the native Australian house gecko (*Gehydra dubia*) was highly aggressive toward conspecifics (Cisterne et al., 2018). Here, we found evidence of strong intraspecific aggression, particularly in male brown anoles, which were more likely to bite and less likely to flee than female brown anoles. The strong intraspecific aggression we observed here is consistent with the prevailing hypothesis that species coexistence depends on stronger intraspecific competition than interspecific competition (Chesson, 2000).

Previous studies found evidence for relatively high female–female aggression in both intraspecific interactions (Reedy et al., 2017) and interspecific interactions (Edwards & Lailvaux, 2013). Similarly, we found that female brown anoles were just as likely to attack female intruders as males were to attack male intruders (Fig. 2e), further evidence that the dominant perception of male-biased aggression may be inconsistent with the reality of behavioral interactions (Kamath & Losos, 2017). While we did not observe a similar pattern in female bark anoles, this may be, at least in part, a consequence of our experimental design. It is possible that female bark anoles would have displayed more aggression toward a conspecific rather than a heterospecific, especially a heterospecific already thought to be more aggressive. Thus, further investigations targeting intraspecific interactions in bark anoles would help us elucidate the behavioral processes underlying community structuring. Indeed, studies explicitly exploring the behavioral ecology of bark anoles appear to be relatively scarce, even in their native range (but see Paterson, 2002).

As we predicted, aggressive displays (i.e., headbobs and/or pushups and dewlap extensions) from brown anole intruders increased the likelihood that focal lizards would respond with aggressive displays (Fig. 3a-d). Similarly, aggressive behaviors of focal Australian house geckos have been shown to be affected by the magnitude of aggression displayed by intruder conspecifics and heterospecifics (Cisterne et al., 2018). Contrary to our predictions, brown anoles were likely to attack intruders regardless of whether an aggressive display occurred (Fig. 3e,f) while bark anoles were likely to flee from intruder brown anoles even when no aggressive displays occurred (Fig. 3g,h). Previous research suggests lizards are more likely to engage in aggressive displays and combat when competitors are viewed from their left side due to the lateralization of aggression (Deckel, 1995; Hews et al., 2004; Hews & Worthington, 2001). In this study, we were unable to maintain or consistently document the position and field of view of the focal and stimulus lizards due to their rapid and frequent movement, which may be an important consideration when examining patterns of aggression in these species. However, Reedy et al., 2017 found no evidence of this left-side bias in aggression in brown anoles. Our results support the idea that brown anoles are highly aggressive toward conspecifics and demonstrate that behavioral displays are not necessary or even likely before escalation to combat (Lailvaux & Irschick, 2007). Similarly, while the behavioral mechanisms remain unclear, bark anoles appear reluctant to engage in aggressive interactions with brown anoles, suggesting brown anoles are typically dominant when combat occurs.

There are specific aspects of our study that should be considered when interpreting our results. First, it is also possible these interactions are a function of body size rather than a difference in aggression. Body size is an important predictor of the outcome of aggressive interactions between individuals (Tokarz, 1985). Unfortunately, we were unable to capture many of the focal animals we observed for this study to better understand the influence of body size in interspecific interactions.

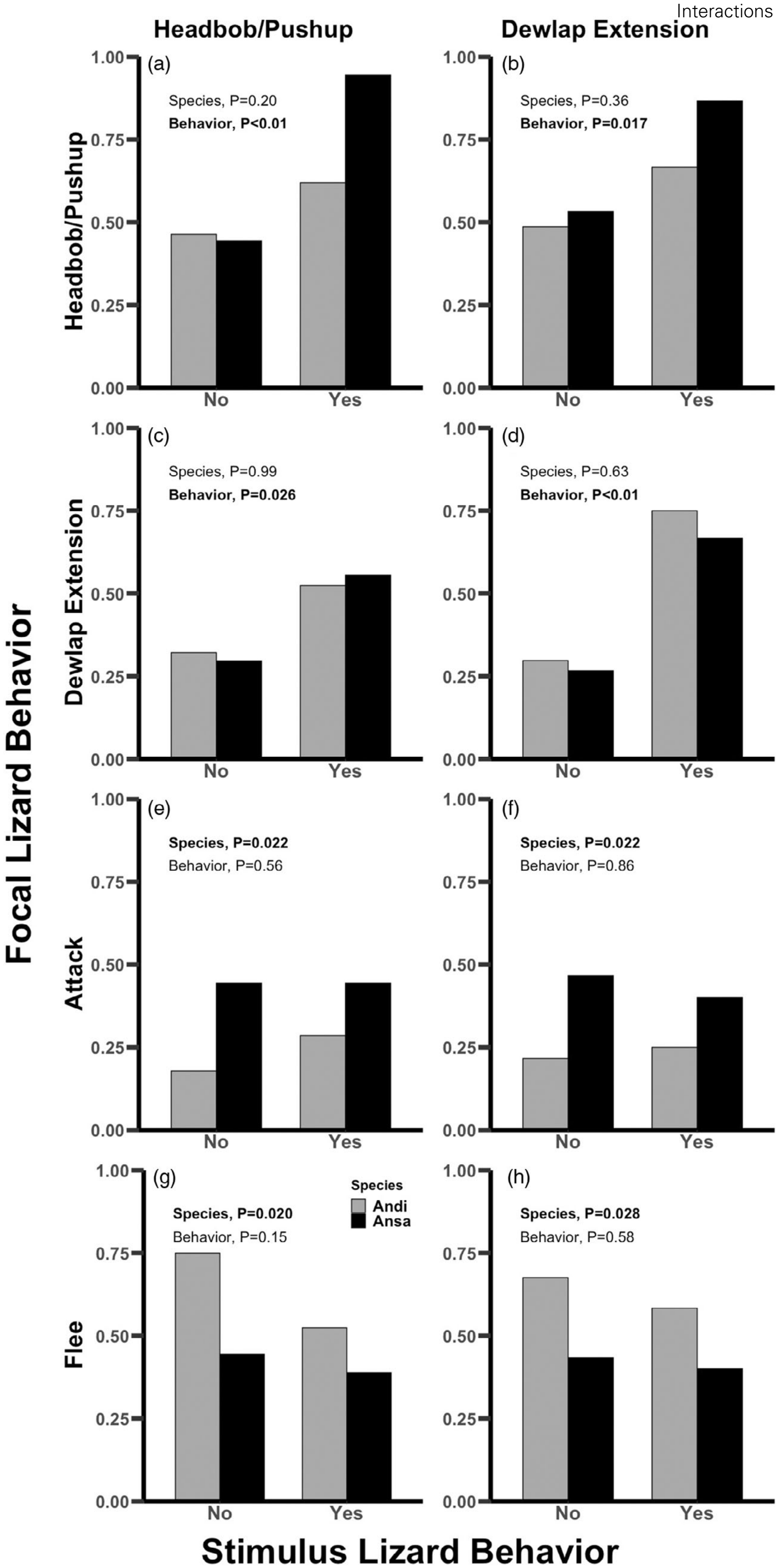

Figure 3 The probability of a behavior occurring based on whether the stimulus lizard (*x*-axis) engaged in the behavior. Gray bars indicate probability of bark anole focal response and black bars indicate probability of brown anole focal response. Significant factors are denoted in bold.

However, adult brown anoles are substantially larger than most bark anoles (Krysko et al., 2019), and this may partially explain why bark anoles were much more likely to flee than brown anoles when confronted by intruders. Second, our study was specifically designed to test how focal lizards responded to unknown intruders; however, lizards are embedded within neighborhoods. It is likely that previous interactions would influence later encounters (Jaeger, 1981; McMann & Paterson, 2012; Paterson, 2002). Regardless, the high aggression toward both conspecifics and congeners displayed here by brown anoles suggests they play a significant role in structuring these novel lizard communities in South Florida.

Much of the literature around invasive species focuses on behavioral interactions between the invader and target native species (e.g., Bush et al., 2022; Tokarz & Beck, 1987). Characterizing the behavioral interactions within and among introduced species in a highly homogenized community, such as those of South Florida, may provide valuable insight into the processes underlying the evolution of stable community structures. Our results suggest brown anoles are highly aggressive toward one another, particularly when encountering potential competitors of the same sex. The proclivity of bark anoles to flee from brown anole intruders regardless of sex or aggressive displays suggests that behavioral interactions with brown anoles could alter the distribution of bark anoles. We suggest future research focus on assessing behavioral interactions within and among the broader introduced and native *Anolis* community in South Florida. Importantly, we only compared the two most abundant *Anolis* species in the area. Examining the interactions between larger crested anoles (*A. cristatellus*) and brown anoles or native green anoles and smaller bark anoles would allow us to further disentangle the roles of body size and behavior in structuring novel anoline communities. Similarly, a study design that facilitates multispecies comparisons would further illuminate mechanisms underlying the evolution of stable community structures in a novel context.

ACKNOWLEDGEMENTS

This research took place as a class project for the Herpetology course at Florida International University. We thank members of the Cox Laboratory (K. Wuthrich and L. Bakewell) for helpful comments on previous iterations of this manuscript.

REFERENCES

Bentz, A. B., Philippi, K. J., & Rosvall, K. A. (2019). Evaluating seasonal patterns of female aggression: Case study in a cavity-nesting bird with intense female–female competition. *Ethology*, **125**, 555–564. https://doi.org/10.1111/eth.12881

Brown, W. L., Jr., & Wilson, E. O. (1956). Character displacement. *Systematic Zoology*, **5**, 49–64.

Bush, J. M., Ellison, M., & Simberloff, D. (2022). Impacts of an invasive species (*Anolis sagrei*) on social and spatial behaviours of a native congener (*Anolis carolinensis*). *Animal Behaviour*, **183**, 177–188. https://doi.org/10.1016/j.anbehav.2021.06.006

Campbell, S. E., & Mandrak, N. E. (2019). Temporal dynamics of taxonomic homogenization in the fish communities of the Laurentian Great Lakes. *Diversity and Distributions*, **25**, 1870–1878. https://doi.org/10.1111/ddi.12986

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Cisterne, A., Schwarzkopf, L., & Pike, D. A. (2018). Australian house geckos are more aggressive than a globally successful invasive Asian house gecko. *Behavioral Ecology*, **30**, 107–113. https://doi.org/10.1093/beheco/ary156

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist*, **122**, 661–696. https://doi.org/10.1086/284165

Cooper, W. E., & Vitt, L. J. (1987). Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces*: Chemical detection of conspecific sexual competitors. *Herpetologica*, **43**, 7–14.

Culbertson, K. A., & Herrmann, N. C. (2019). Asymmetric interference competition and niche partitioning between native and invasive *Anolis* lizards. *Oecologia*, **190**, 811–820. https://doi.org/10.1007/s00442-019-04466-1

Deckel, A. W. (1995). Laterality of aggressive responses in *Anolis*. *The Journal of Experimental Zoology*, **272**, 194–200. https://doi.org/10.1002/jez.1402720304

Edwards, J. R., & Lailvaux, S. P. (2013). Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *A. sagrei*. *Biological Journal of the Linnean Society*, **110**, 843–851. https://doi.org/10.1111/bij.12180

Eurich, J. G., McCormick, M. I., & Jones, G. P. (2018). Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes. *Marine Ecology Progress Series*, **587**, 201–215. https://doi.org/10.3354/meps12458

Finke, D. L., & Snyder, W. E. (2008). Niche partitioning increases resource exploitation by diverse communities. *Science*, **321**, 1488–1490. https://doi.org/10.1126/science.1160854

Fisher, S. R., Del Pinto, L. A., & Fisher, R. N. (2020). Establishment of brown anoles (*Anolis sagrei*) across a southern California county and potential interactions with a native lizard species. *PeerJ*, **8**, e8937. https://doi.org/10.7717/peerj.8937

Freeman, B. G., Class Freeman, A. M., & Hochachka, W. M. (2016). Asymmetric interspecific aggression in new Guinean songbirds that replace one another along an elevational gradient. *Ibis*, **158**, 726–737. https://doi.org/10.1111/ibi.12384

Gelman, A., & Su, Y.-S. (2022). *Arm: Data analysis using regression and multilevel/hierarchical models*. https://CRAN.R-project.org/package=arm

Gotelli, N. J., & Arnett, A. E. (2000). Biogeographic effects of red fire ant invasion. *Ecology Letters*, **3**, 257–261. https://doi.org/10.1046/j.1461-0248.2000.00138.x

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, **313**, 224–226. https://doi.org/10.1126/science.1128374

Grenier-Potvin, A., Clermont, J., Gauthier, G., & Berteaux, D. (2021). Prey and habitat distribution are not enough to explain predator habitat selection: Addressing intraspecific interactions, behavioural state and time. *Movement Ecology*, **9**, 12. https://doi.org/10.1186/s40462-021-00250-0

Grether, G. F., Peiman, K. S., Tobias, J. A., & Robinson, B. W. (2017). Causes and consequences of behavioral interference between species. *Trends in Ecology & Evolution*, **32**, 760–772. https://doi.org/10.1016/j.tree.2017.07.004

Hews, D. K., Castellano, M., & Hara, E. (2004). Aggression in females is also lateralized: Left-eye bias during aggressive courtship rejection in lizards. *Animal Behaviour*, **68**, 1201–1207. https://doi.org/10.1016/j.anbehav.2003.11.024

Hews, D. K., & Worthington, R. A. (2001). Fighting from the right side of the brain: Left visual field preference during aggression in free-ranging male tree lizards *Urosaurus ornatus*. *Brain, Behavior and Evolution*, **58**, 356–361. https://doi.org/10.1159/000057576

Hobbs, J. P. A., & Munday, P. L. (2004). Intraspecific competition controls spatial distribution and social organisation of the coral-dwelling goby *Gobiodon histrio*. *Marine Ecology Progress Series*, **278**, 253–259. https://doi.org/10.3354/meps278253

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159. https://doi.org/10.1086/282070

Iglesias-Carrasco, M., Brookes, S., Kruuk, L. E. B., & Head, M. L. (2020). The effects of competition on fitness depend on the sex of both competitors. *Ecology and Evolution*, **10**, 9808–9826. https://doi.org/10.1002/ece3.6620

Jaeger, R. G. (1981). Dear enemy recognition and the costs of aggression between salamanders. *The American Naturalist*, **117**, 962–974. https://doi.org/10.1086/283780

Jankowski, J. E., Robinson, S. K., & Levey, D. J. (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, **91**, 1877–1884. https://doi.org/10.1890/09-2063.1

Jenssen, T. A., Hovde, K. A., & Taney, K. G. (1998). Size-related habitat use by nonbreeding *Anolis carolinensis* lizards. *Copeia*, **1998**, 774–779. https://doi.org/10.2307/1447814

Kamath, A., & Losos, J. (2017). The erratic and contingent progression of research on territoriality: A case study. *Behavioral Ecology and Sociobiology*, **71**, 89. https://doi.org/10.1007/s00265-017-2319-z

Kamath, A., Stuart, Y. E., & Campbell, T. S. (2013). Behavioral partitioning by the native lizard *Anolis carolinensis* in the presence and absence of the invasive *Anolis sagrei* in Florida. *Breviora*, **535**(1), 1–10.

Keren-Rotem, T., Bouskila, A., & Geffen, E. (2006). Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). *Behavioral Ecology and Sociobiology*, **59**, 723–731. https://doi.org/10.1007/s00265-005-0102-z

King, W., & Krakauer, T. (1966). The exotic herpetofauna of Southeast Florida. *Quarterly Journal of the Florida Academy of Sciences*, **29**, 144–154.

Kolbe, J. J., Glor, R. E., Rodríguez Schettino, L., Lara, A. C., Larson, A., & Losos, J. B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181. https://doi.org/10.1038/nature02807

Krijger, C. L., Peters, Y. C., & Sevenster, J. G. (2001). Competitive ability of neotropical drosophila predicted from larval development times. *Oikos*, **92**, 325–332.

Krysko, K. L., Enge, K. M., & Moler, P. E. (2019). *Amphibians and reptiles of Florida*. University of Florida Press.

Krysko, K. L., Somma, L. A., Smith, D. C., Gillette, C. R., Cueva, D., Wasilewski, J. A., Enge, K. M., Johnson, S. A., Campbell, T. S., & Edwards, J. R. (2016). New verified nonindigenous amphibians and reptiles in Florida, 1976 through 2015, with a summary of over 152 years of introductions. *Reptiles & Amphibians*, **23**, 110–143.

Lailvaux, S. P., & Irschick, D. J. (2007). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist*, **170**, 573–586. https://doi.org/10.1086/521234

Little, K., Draud, M., & Itzkowitz, M. (2013). Interspecific aggression in two highly similar *Stegastes* damselfish. *Ethology Ecology and Evolution*, **25**, 227–242. https://doi.org/10.1080/03949370.2012.745451

Losos, J. B., Jackman, T. R., Larson, A., Queiroz, K., & Rodriguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of Island lizards. *Science*, **279**, 2115–2118. https://doi.org/10.1126/science.279.5359.2115

MacGregor-Fors, I., Morales-Pérez, L., Quesada, J., & Schondube, J. E. (2010). Relationship between the presence of house sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. *Biological Invasions*, **12**, 87–96. https://doi.org/10.1007/s10530-009-9432-5

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453. https://doi.org/10.1016/s0169-5347(99)01679-1

McMann, S., & Paterson, A. (2012). Display behavior of resident brown anoles (*Anolis sagrei*) during close encounters with neighbors and non-neighbors. *Herpetological Conservation and Biology*, **7**, 27–37.

Moreira, P. L., López, P., & Martín, J. (2008). Discrimination of conspecific faecal chemicals and spatial decisions in juvenile Iberian rock lizards (*Lacerta monticola*). *Acta Ethologica*, **11**, 26–33. https://doi.org/10.1007/s10211-007-0038-6

Myrberg, A. A., Jr., & Thresher, R. E. (1974). Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *American Zoologist*, **14**, 81–96. https://doi.org/10.1093/icb/14.1.81

Nakano, S., & Furukawa-Tanaka, T. (1994). Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars. *Ecological Research*, **9**, 9–20. https://doi.org/10.1007/BF02347237

Narváez, A. E., Ghia, T., Moretta-Urdiales, M. M., & Moreira, N. M. (2020). Feeding habits of *Anolis sagrei*, an introduced species, in urban ecosystems of Guayas Province. *Urban Ecosystem*, **23**, 1371–1376. https://doi.org/10.1007/s11252-020-00979-3

Norval, G., Bursey, C. R., Goldberg, S. R., Mao, J.-J., & Slater, K. (2011). Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), Southwestern Taiwan. *Pacific Science*, **65**(5), 383–390.

Olden, J. D. (2006). Biotic homogenization: A new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x

Pacala, S., & Roughgarden, J. (1982). Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science*, **217**, 444–446. https://doi.org/10.1126/science.217.4558.444

Paterson, A. V. (1999). Effects of prey availability on perch height of female bark anoles, *Anolis distichus*. *Herpetologica*, **55**, 242–247.

Paterson, A. V. (2002). Effects of an individual's removal on space use and behavior in territorial neighborhoods of brown anoles (*Anolis sagrei*). *Herpetologica*, **58**, 382–393. https://doi.org/10.1655/0018-0831(2002)058[0382:Eoairo]2.0.Co;2

Pröhl, H., Scherm, M. G., Meneses, S., Dreher, C. E., Meuche, I., & Rodríguez, A. (2019). Female–female aggression is linked to food defence in a poison frog. *Ethology*, **125**, 222–231. https://doi.org/10.1111/eth.12848

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.R-project.org/

Reedy, A. M., Pope, B. D., Kiriazis, N. M., Giordano, C. L., Sams, C. L., Warner, D. A., & Cox, R. M. (2017). Female anoles display less but attack more quickly than males in response to territorial intrusions. *Behavioral Ecology*, **28**, 1323–1328. https://doi.org/10.1093/beheco/arx095

Robertson, D. R. (1996). Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology*, **77**, 885–899. https://doi.org/10.2307/2265509

Robinson, S. K., & Terborgh, J. (1995). Interspecific aggression and habitat selection by Amazonian birds. *The Journal of Animal Ecology*, **64**, 1–11. https://doi.org/10.2307/5822

Salzburg, M. A. (1984). *Anolis sagrei* and *Anolis cristatellus* in southern Florida: A case study in interspecific competition. *Ecology*, **65**, 14–19. https://doi.org/10.2307/1939453

Savolainen, R., & Vepsäläinen, K. (1988). A competition hierarchy among boreal ants: Impact on resource partitioning and community structure. *Oikos*, **51**, 135–155.

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *The American Naturalist*, **156**, S4–S16. https://doi.org/10.1086/303412

Sinervo, B., & Lively, C. M. (1996). The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, **380**, 240–243. https://doi.org/10.1038/380240a0

Stamps, J. A. (1977). The relationship between resource competition, risk, and aggression in a tropical territorial lizard. *Ecology*, **58**, 349–358. https://doi.org/10.2307/1935609

Stamps, J. A. (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behavioral Ecology and Sociobiology*, **12**, 19–33. https://doi.org/10.1007/bf00296929

Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., & Losos, J. B. (2014). Rapid evolution of a native species following invasion by a congener. *Science*, **346**, 463–466. https://doi.org/10.1126/science.1257008

Svanbäck, R., Eklöv, P., Fransson, R., & Holmgren, K. (2008). Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos*, **117**, 114–124. https://doi.org/10.1111/j.2007.0030-1299.16267.x

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

Tokarz, R. R., & Beck, J. W. (1987). Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: An experimental test for behavioural interference. *Animal Behaviour*, **35**, 722–734. https://doi.org/10.1016/S0003-3472(87)80108-2

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Results of campus-wide surveys of MMC for lizard species. A total of 538 lizards were observed across 26 survey transects between 11 March 2021 and 7 April 2021. All surveys were conducted between 1100 and 1800 h. The number in parentheses indicates the percentage of the total sample represented by each species and sex.