

Article

Meta-Analysis Reveals Behavioral Plasticity, Not Agonistic Behavior, Facilitates Invasion of Brown Anoles (*Anolis sagrei*) and Replacement of Green Anoles (*Anolis carolinensis*)

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Abstract: In a meta-analysis, we examined the behavioral portfolio of invasive brown anoles (*Anolis sagrei*) and native green anoles (*Anolis carolinensis*) in urban and non-urban environments. We hypothesized that invasive anoles would display more agonistic and bold signals (head bobbing, dewlap extensions, and pushups) than their native-range counterparts and their native competitors. We found that in urban settings, anoles of both species signaled more with dewlap extensions than with head bobs. Brown anoles displayed significantly more in non-urban habitats and their native range compared to urban habitats and invasive ranges. The outcome of our analysis suggests that brown anoles have plastic behavioral portfolios, whereas green anoles have relatively balanced preferences for head bobbing, irrespective of the habitat in which the populations were collected. We attribute the success of the brown anole invasion to the flexible strategy in the face of higher mate competition, higher predation risks, and less resource competition in both urban and invasive ranges. Lastly, we observed publication biases. More studies were conducted with urban and invasive brown anoles and specifically in manipulative mesocosm experimental settings—transplanting populations from native field settings. We show this altered the display rates across all studied signals.



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Keywords: communication; dewlap extension; pushups; head bob; territoriality; aggression; urban ecology

1. Introduction

Invasive species are considered one of the major drivers of biodiversity loss in the Holocene (Anthropocene) extinction period [1]. Many researchers have tried to categorize the underpinning traits of invasive species and highlight several adaptive traits that can be generalized as the drivers of these populations. Invasive populations tend to be r-selected, exhibit density-independent growth, and grow at a much faster rate than their native-range counterparts [2–4]. A generalist diet has been shown to favor invasive animal species, allowing them to forage opportunistically and maximize energetic intake to increase reproductive success [5–8]. Invasives are commonly described as disturbance-loving species that can adapt to constant turnover in environmental conditions brought on by human activity [8–10]. Lastly, the most “successful” invasive species are ones that are characterized by bold, risk-taking, and aggressive behaviors [11–14]. It is through these behavioral strategies that they manipulate resources and gain competitive advantage over the native species in the invaded communities [15].

The characteristics of invasive species alone cannot explain the establishment of invasive populations. The properties of the invaded community and its environment will influence whether a population exhibiting some of the above-mentioned traits will successfully be established. Two patterns emerge in communities that can be invaded [16]: either open-resource niches allow nonnative species to colonize, or the community’s competitors hold ecologically inferior resource-harvesting strategies compared to the newcomers. In

this review, we focus on the former, specifically urban communities, where resource niches are continuously vacated by anthropogenic disturbance [17]. Human activity in urbanized zones actively favors species that are bolder and more aggressive [9]. Specifically, humans inherently pose risks to wildlife, directly managing populations and indirectly generating community-wide reverberations. The active hunting of species perceived as direct threats and the mass culling of disease vectors changes the structure of communities [18,19]. Humans favor human-commensal and mutualistic mesocarnivores (pets) that hunt small vertebrate species [20–23]. Additionally, our technology, such as motorized vehicles and signal-interfering noise and light pollution, pose adaptive challenges to wildlife [24–26]. Coupled with attractive resources that humans discard into their environment, all the above risks generate ecological traps that cause native populations to decline [27]. Lastly, habitat fragmentation hinders the movement of wildlife, shrinking populations and driving sub-populations into extirpation [28], and thus frees resources for bold and aggressive species. They are able to monopolize the aforementioned abundant food resources in the form of trash (rubbish) [23,29,30] and byproducts of feeding pets [29,31,32]. These factors, along with others not discussed, indicate that invasive species can utilize urbanization patterns to establish populations and expand their invasive ranges through their behavior. We set out to test this hypothesis by conducting a meta-analysis of published behavioral assays of native North American Green Anoles (*Anolis carolinensis*, AC) and their invasive counterparts, the Cuban Brown Anoles (*Anolis sagrei*, AS), in their native and invasive ranges (Figure 1—distribution of study populations).

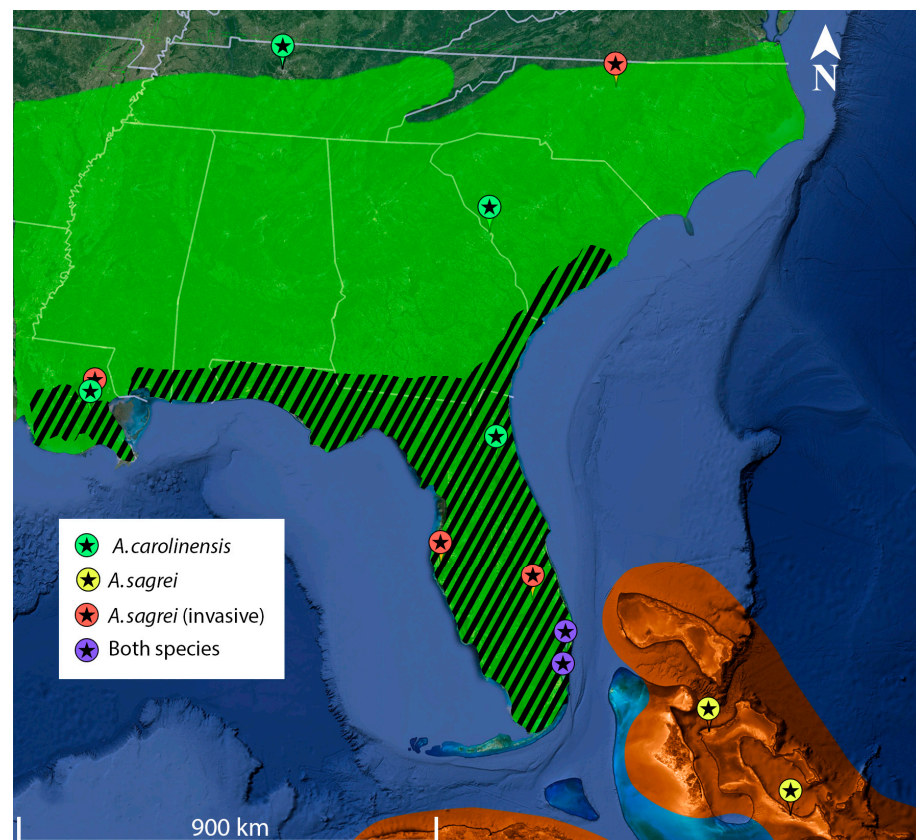


Figure 1. Map displaying sources of populations used in publications for this meta-analysis generated on Google Earth Pro (version 7.3.6.9796). Markers represent locations where populations were sampled and may represent various publications. The green shaded environment is the native range of the *Anolis carolinensis* (AC); the brown shaded zones are native ranges of *Anolis sagrei* (AS). Bahamian AS were considered native species in this review. The diagonal lines represent the invasive range of AS where they cohabitate with AC.

Anolis lizards have been used for decades as models for the study of evolutionary patterns, speciation, and the roles their behaviors play in their adaptability to habitats in varied island ecosystems [33–35]. Anoles have been shown to evolutionarily radiate based on microhabitat selection, where they choose resting perches based on branch size and elevation to balance safety, access to food, and thermoregulation [36,37]. Additionally they diversify based on predator avoidance strategies [38–40] and in response to environmental disturbance [11,41]. The elaborate record on anole evolution [33], including their phylogenetic relationships, historic adaptive radiations [40,42], and their tendency to undergo speciation following disturbance events and the isolation of subpopulations (founder effects) [43–45], makes them an ideal model organism for studying changes driven by anthropogenic disturbance [33]. Of all their evolutionary divergences, the strongest measures of differentiation rely on ethological (behavioral) variation in mate courting, territoriality, and agonistic displays towards conspecifics. While the ability of female anoles across many species to clone themselves, parthenogenesis, allows for rapid population establishment following natural catastrophes [46–49], their evolutionary radiation into various habitats depends more on their polygynous social structure [50–52]. This structure relies heavily on bold and aggressive male behaviors to establish territories and mate-guard.

Given these traits, we must dwell on the types of behaviors established as the arsenal used by anoles in adversarial interactions. These predominantly include the establishment and guarding of a territory (territorial behavior), signaling to conspecifics of agonistic intentions (a form of honest signaling), and, of course, mate-attracting signals that serve to display strength, virality, and the ability to take risks [53]. Being a sexually dimorphic genus, signaling behaviors reflect the reproductive tactics and pressures faced by males and females. While the same displays are used by both sexes, males exhibit them at significantly higher rates. In females, these behaviors are less vigorous and are often used to defend nesting sites and safer perches. As males frequently engage in intense mate guarding, territorial defense signals tend to also play a role in mate attraction to various extents. Given the mate attraction emphasis in males, some signals are associated with mate attraction over territorial defense, specifically dewlap extensions (Des; see below).

As polygynous lizards, *Anolis* males establish and guard territories with various females [50,54]. Territoriality refers to the agonistic behavior that anoles utilize to defend a specific area or territory, characterized by site fidelity (remaining in or returning to a fixed area) and exclusivity (the exclusion of individuals, specifically conspecifics of the same sex in that area) [54]. Male territories vary by species but range between 50 and 100 m² [55–57]. Meanwhile, females establish territories based on perches, dominance to control resources, and ideal locations for predator evasion [58]. While less studied, female territories, which exclude the need to defend mates from conspecifics, are smaller and estimated to be half the size of those of their male counterparts. Anoles will often avert physical altercations by signaling strength and aggression (discussed below as the major focus of this paper) but will often physically defend their territories by biting, wrestling, and same-sex copulations [59,60]. There is some debate on how territoriality and territory defense alter with captive anoles [58], but underlying aggression remains a focus of their behavioral repertoire in both natural conditions and mesocosm experiments.

The expression of aggressive behaviors and communication among members of the *Anolis* species shapes their social dynamics and evolutionarily constrains their interactions with members of the biological communities they inhabit. Anoles showcase a relatively extensive repertoire of behaviors in their communication, which has made them model organisms for both ethology and evolution [33]. For this meta-analytical review, we only focus on agonistic displays and ones that have a dual purpose with courtship and conspecific agonism—head bobs, dewlap extensions, and pushups. The length (display time) and rate of signaling (count of signals/minute), are honest signals of strength and stamina in energy-limited ectotherms. They can communicate the size and strength of the individual, its sexual receptiveness and level of arousal, and dominance in defending territories [57,61–63].

Head-bobbing (HB) displays are visual signaling mechanisms to convey dominance. This display is defined as a discontinuous series of up-and-down movements of the body and tail, where each individual upward movement is referred to as a bob [64]. Head bobbing serves to communicate the lizard's presence, size, and vigor to rivals and mates, thereby establishing dominance and minimizing the likelihood of harmful conflict. Predominantly exhibited by male anoles, these displays are essential for territorial defense and deterring intruders, indicating the male's readiness to defend his space [65,66]. Additionally, head bobbing has a lesser role in courtship [67].

Anoles unfold a dewlap, a brightly colored skin appendage from under their neck, which, in many species, includes specs and patterns, to startle competitors and attract mates [68–70]. In females, dewlaps appear smaller and are used less frequently than in males [71]. In males, the reproductive use of the display takes precedence during the mating season. These dewlaps, which are energetically expensive to make and sustain when combined with head bobbing, are a good indicator of a male's health and vitality. Dewlap extensions in males are strongly associated with the breeding season and the level of testosterone of the displayer. Higher testosterone is correlated with morphological changes, increased display rates of all signals, and greater stamina [72–74]. While remaining a topic of debate, we find it is easy to connect this behavior specifically with the “good gene hypothesis”, where females increase the likelihood of offspring quality and survivorship by choosing mates with higher-quality genes [75,76], and ones that are able to boldly take risks in the face of adversaries and predators (the handicap principle) [77,78].

Last, anoles use vertical gyration, resembling a human pushup (hence the name), to signal to individuals who enter their territory to step down. Pushup displays (PUs) are primarily employed by anoles as a visual communication tool to signal dominance, territorial defense, and, in a lesser role, attract potential mates. These actions convey fitness to prospective mates and provide the impression that the anole is bigger and more intimidating to predators and rivals. Male anoles exhibit pushup displays more than females [55,65]. By creating hierarchies through pushup displays, they play a critical role in intra-specific interactions—reducing the necessity for physical conflicts and injury [67]. By flexing and extending their forelimbs, anoles perform pushup displays, quickly raising and lowering their body, often in conjugation with head bobbing and extending their dewlaps [79].

Given the propensity of anoles for agonistic behaviors, they are ideal organisms to cohabitate with humans in urban zones. We hypothesize that the pressures imposed on their populations by human urban activity would directionally select for more agonistic populations. We expect that studies of urban populations will display more than “natural” populations. Additionally, given that invasive populations are expected to be more aggressive in interspecific interactions, and agonistic towards each other, we hypothesize that the same species would be bolder and more agonistic in the invasive range and especially at the frontline of the invasion. This follows a pattern in invasive bluebirds in the UK and aquatic invasives such as goby fish and crayfish [80–83]. Lastly, if aggression facilitates biological invasions, we expect that the overall signal of aggression in the invasive populations of anoles will be significantly stronger than that of native competing species in the same locations.

2. Materials and Methods

2.1. Study Organisms

In our study, we compared two species of anoles, AC and AS. AS is native to Cuba, Jamaica, and the Bahamas [36,84–86]. It has become invasive in several U.S. states expanding from Florida, north to Georgia, and as far west as Texas. Additional invasive populations, resulting from the exotic pet trade, are found in Hawaii, California, and Taiwan [87,88]. AC is native to North America, particularly the southeastern United States [89]. It too has been introduced as an invasive to Hawaii [90]. Both AS and AC adults typically measure (SVL (snout–vent length) + tail) between 12 and 22 cm, with AS leaning towards the upper

part of the range [90]. Both species are dimorphic, with males being 2–3 times larger than females [91,92]. Both species live an average of 18 months, but they can live up to five years in the wild [93,94]. Both species are insectivores, feeding primarily on small arthropods [73,95].

The species diverge in habitat preference and some morphological attributes. AS prefer sunny, exposed, and disturbed habitats with low vegetation cover [87,96], whereas AC prefer dense vegetation [97]. AC, formerly known as the American chameleon, apply color change for crypsis and mate attraction, while AS are fixed in a brown coloration [98]. AS lay 1–2 eggs at approximately 10-day intervals throughout the breeding season, which spans from May to September [62]. AC lay single-egg clutches at approximately 7- to 14-day intervals, totaling around 15 offspring for the entire breeding season [90].

2.2. Data Collection

Conducting research from a primarily undergraduate teaching institution, we had restricted access to databases. Therefore, we relied primarily on the limited access provided by Elsevier Science Direct, JSTOR, and Google Scholar. We relied heavily on Interlibrary Loan to supplement access to articles. We supplemented our database with studies identified in the bibliographies of articles we found helpful and by searching for articles from prolific research groups in the field (Losos, Lovern, Jenssen, Lailvaux, etc.). Our searches included species names (AS, AC, and the common names Brown Anole and Green Anole). We combined those with key words with focus behaviors (head bob and dewlap extension), and environmental key terms (urban vs. forest) to identify non-urban habitats. The latter was only relevant to the urban zones, identifying papers focusing on urbanization, especially in the context of the invasive AS.

2.3. Data Analyses

Using a couple of criteria, we narrowed our database to 23 publications (Supplementary Materials S1), which included peer-reviewed manuscripts and theses only. We narrowed our database for the needed information on the source of animal collection and the availability of all statistics for power analyses (sample sizes, mean display rates, standard deviation [SD] and/or standard error [SE]).

In addition, we collected descriptive information about each study—animal source (wild-caught or lab-bred), the environment of the collection site (urban zones defined as metropolitan areas with over 100,000 human inhabitants), and information regarding the experimental setup (field studies or mesocosm/agonistic exposure, male–male (MM), or reproductive scenarios with a male–female (MF) setup). Lastly, we noted the developmental state of the subjects of the studies (Juvenile/Adult) and the sex of the focal test subject.

Our data mining yielded a total of 111 comparable data. Ten papers yielded 26 data points for AC (excluding one study from the invasive range in Hawaii due to low replicability). The AS literature provided 85 data points, with 23 from the native range in Cuba and the Bahamas and the majority from the invasive range in the continental U.S. To facilitate comparability between grouping variables, we made sure that the amount of data for each category combination had at least five data (Table 1, Figure 1).

Table 1. Data mining results, exhibiting data collected by species, population source environment, sex of subjects, invasive status, and experimental setup. Summed and organized based on behavior observed. Each data point is a reported sub-population selected for specific attributes and appearing in the publications with complete information (mean behavior rate, sample size, and standardized error of the mean).

Category	Factor	Total				<i>A. carolinensis</i>				<i>A. sagrei</i>			
		(N)	DEs	HBs	PUs	(N)	DEs	HBs	PUs	(N)	DEs	HBs	PUs
Species	AC	26	16	7	3								
	AS	85	41	30	14								

Table 1. Cont.

Category	Factor	Total				<i>A. carolinensis</i>				<i>A. sagrei</i>			
		(N)	DEs	HBs	PUs	(N)	DEs	HBs	PUs	(N)	DEs	HBs	PUs
Environment	Non-Urban	36	18	12	6	4	2	2	ND	32	16	10	6
	Urban	75	39	25	11	22	14	5	3	54	25	21	8
Sex	Female	12	6	4	2	7	5	2	ND	5	1	2	2
	Male	99	51	33	15	19	11	5	3	81	40	29	12
Invasive stat.	Invasive	62	30	23	9					63	30	24	9
	Native	49	27	14	8	26	16	7	3	23	11	7	5
Setup	Field	49	22	20	7	1	1	ND	ND	48	21	20	7
	Mesocosm	62	35	17	10	25	15	7	3	38	20	11	7

Abbreviations: N—Data collected, DEs—Dewlap extensions, HBs—Head bobs, PUs—Pushups, ND—No data. AC—*Anolis carolinensis*, AS—*Anolis sagrei*.

2.4. Meta Analyses

Given the large scale of these meta-analyses, we ran weighted, means-based, random-effect meta-analyses models (i.e., assuming different general means, μ). We used grouping based on these predefined categories: environment, species, sex, and invasive status. We ran the meta-analyses based on the protocol published by Cummings [99] for large-scale meta-analyses. We used the ESCI package [100] on the Jamovi interface [101] running on the R platform [102]. Using this protocol, we generated forest plots [103], comparative distributions, and uncertainty plots [104]. In uncertainty plots, the distribution of difference values is generated through a normalization function using the standardized linear contrast of means [103]. The more spread out the original data sets for both moderator groups, the wider the distribution of the difference. The tighter the data sets are, the higher the confidence in the estimated difference.

3. Results

We narrowed our data based on the selection criteria and identified a subset of 23 peer-reviewed sources. These sources provided complete data, including sample sizes, observation times, behavior rates (counts/time unit), and either standard deviations or standard errors of the mean. Of the sources, 7 provided data for AC, and 18 provided data for AS (Table 2). Despite the relatively low number of studies, together, these generated 114 data (111 after removing juvenile individuals). Additionally, a publication bias was found. Significantly more publications were published on AS than on AC, with 75% compared to 29% (Tables 1 and 2), with several comparative studies addressing the overlap in percentages. Three additional biases were found: (1) more studies were published using urban anoles as subjects (55%) than ones collected in rural locations (45%); (2) the studies focusing on AS overwhelmingly used populations from the invasive range (79%) over the native range (21%); and (3) the lizards were predominantly brought into the lab for mesocosm experiments in terraria (54%).

Table 2. Data collected by publication designated by species, sex, behavior types, and the number of data mined from each publication (correlated with Supplementary Materials S1—alphabetical bibliography).

Publication	Species	Sex	Display			
			DEs	HBs	PUs	# of Data
Calsbeek & Marnocha, 2006 * [62]	AS	M	✓		✓	4
Cox et al., 2009 * [74]	AS	M	✓			2
Decourcy & Jenssen, 1994 [105]	AC	M		✓		2

Table 2. Cont.

Publication	Species	Sex	Display			# of Data
			DEs	HBs	PUs	
Driessens et al., 2014 * [106]	AS	Both	✓		✓	10
Edwards & Lailvaux, 2012 [107]	AS	M		✓	✓	4
Farrell et al., 2016 [108]	AC	M	✓		✓	4
Johnson & Wade, 2010 * [109]	AC	M	✓			1
Magaña, 2017 *‡ [110]	Both	Both	✓	✓		19
McMann & Paterson, 2003 [111]	AS	M		✓		1
McMann & Patterson, 2012 [64]	AS	M	✓	✓		4
Orrell, 2002 ‡ [57]	AC	Both	✓			6
Partan et al., 2011 * [112]	AS	Both	✓	✓	✓	6
Paterson, 1999 ‡ [113]	AS	M	✓	✓		10
Paterson, 2002 [114]	AS	M	✓	✓		6
Simon, 2002 *‡ [115]	AS	M	✓	✓	✓	10
Simon, 2007 * [68]	AS	M	✓	✓	✓	3
Simon, 2011 * [116]	AS	M	✓	✓		8
Stroud et al., 2019 [117]	AS	M	✓	✓		4
Tokarz & Beck, 1987 [118]	Both	M	✓			3
Tokarz et al., 2002 * [69]	AS	M	✓			1
Tokarz et al., 2003 [70]	AS	M	✓	✓		3
Tokarz et al., 2005 [119]	AS	M	✓			1
Yang & Wilczynski, 2002 * [120]	AS	M	✓		✓	2
Total						111

Abbreviations: DEs—dewlap extension, HBs—head bob, PUs—pushup, *—data estimated using calipers to measure values from printed figures, ‡—signifies a thesis, AS—*Anolis sagrei*, AC—*Anolis carolinensis*, M—male, ✓ represents a behavior studies in the corresponding publication.

Observing the entire data set, the two species differed in dewlap extension rates and in pushups but did not in their head-bobbing behavior, with p values of $p < 0.01$, $p = 0.03$, and $p = 0.89$, respectively (Figures 2 and 3A–C, Supplementary Materials S3). Only in the pushup behaviors did AC have a higher rate of signaling than AS. The anoles significantly signaled more in urban environments than in non-urban zones, with p values < 0.01 for both dewlap extension and head bobbing (Figure 3D,E). We suggest a caveat in the ratios expressed across habitats. Given imbalances in data availability for the two species and questionable biological relevance to the measure combining the two species, we caution against over-reliance on this comparison. These patterns may be statistically significant but biologically moot. Observing the nuances within each species can yield more complexity, even when signaling rate comparisons may not be significantly different between habitats (*cf.* Figure 2—HBs between urban and non-urban AS). Nonetheless, interesting patterns emerge when comparing the portfolios of behaviors expressed across the habitats. We defined behavioral portfolios as the ratios of different signals. Portfolios provide insight into the choices made by the populations sourced in urban and non-urban zones. Most importantly, these portfolios reflect energetic expenditure as expressed by the balance of different ritualistic signals and the functions they serve.

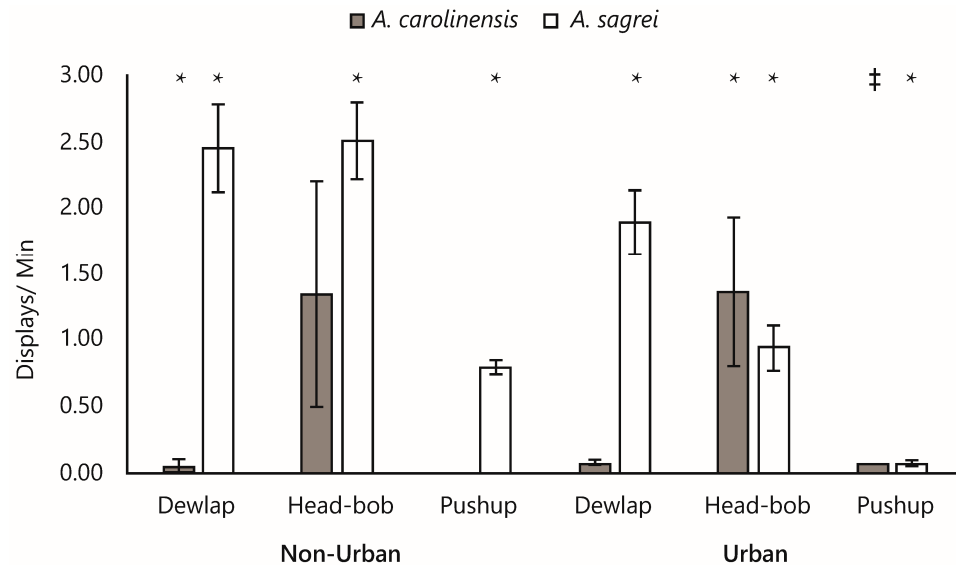


Figure 2. Visual comparison of mean display rates (per minute) generated by meta-analyses for each of the display behaviors for each species of anole in urban and non-urban populations. The * represents a significant power analysis for generated meta-analytical mean $\pm$ SE. ‡ represents an un-refined estimate for the purpose of visualization, not the outcome of statistical analysis. Overall display rates are greater for *Anolis sagrei* than *Anolis carolinensis*; however, the former show greater behavioral plasticity and reduction in display rates in urban populations.

AS signaled more than AC across all behaviors (Figure 2, $p < 0.01$ for DE and PU and 0.01 for HB). This variation is best observed in the behavioral portfolios. AC, regardless of the habitat, showed similar portfolios, with both urban and non-urban anoles favoring head bobbing over dewlap extensions. In urban populations, AC signaled with a ratio of 20:1 for HB to DE. In non-urban AC, this pattern was even more extreme, with a ratio of 32:1 for HB to DE. Pushup signals were excluded in AC due to the lack of data for non-urban populations. In AS, the portfolios were plastic, with pushups being the least favored and were thus used as the basis for ratio comparison. The rate of PU signaling in non-urban AS was 12 times higher than in urban AS, while still being a relatively rare behavior compared with HB and DE. Non-urban AS signaled at a ratio of 3:3:1 for DE, HB and PU, respectively. In urban environments, they signaled at a ratio of 28:14:1 for DE, HB, and PU, respectively, shifting emphasis to DE.

Data for AC were limited in comparison with AS, as mentioned above. We were thus limited in the moderator analyses we could run. The environment from whence the animals were collected did not significantly impact DE rates ($p = 0.62$), while sex had a marginally significant impact (one-tailed $p = 0.03$), with females signaling less than males (Supplementary Materials S4). The HB rates did not vary by urban environment ($p = 0.98$), nor by sex ($p = 0.85$, Supplementary Materials S4). We did not run a pushup meta-analysis for AC, given the limited sample size.

AS behavior shows significantly more variable behaviors than the behavior of its AC counterpart. The urban anoles' HB was at a fourth of the rate of non-urban anoles ($p < 0.01$, Figure 4A). For DE rates, the urban vs. non-urban environment comparison was not statistically significant ($p = 0.17$); however, a clear trend was visible, with urban anoles signaling more than their non-urban counterparts (Figure 4B). The invasive populations showed a trend of signaling more with DE than the anoles in the Caribbean native range ($p = 0.19$, Figure 4C). Meanwhile, HB displays were signaled by invasive populations at a third of the rate than in their native-range counterparts ($p < 0.01$, Figure 4D). Unsurprisingly, males signaled six times more than females ($p = 0.03$) with HB. We did not have enough data for sex-based comparison with DE. By comparing the signaling rates for AS, we were

able to observe a significant bias, where trials ran in captivity (mesocosms) showed lower display rates than in field settings (HB- $p < 0.01$, Figure 5A, DE- $p = 0.05$, Figure 5B).

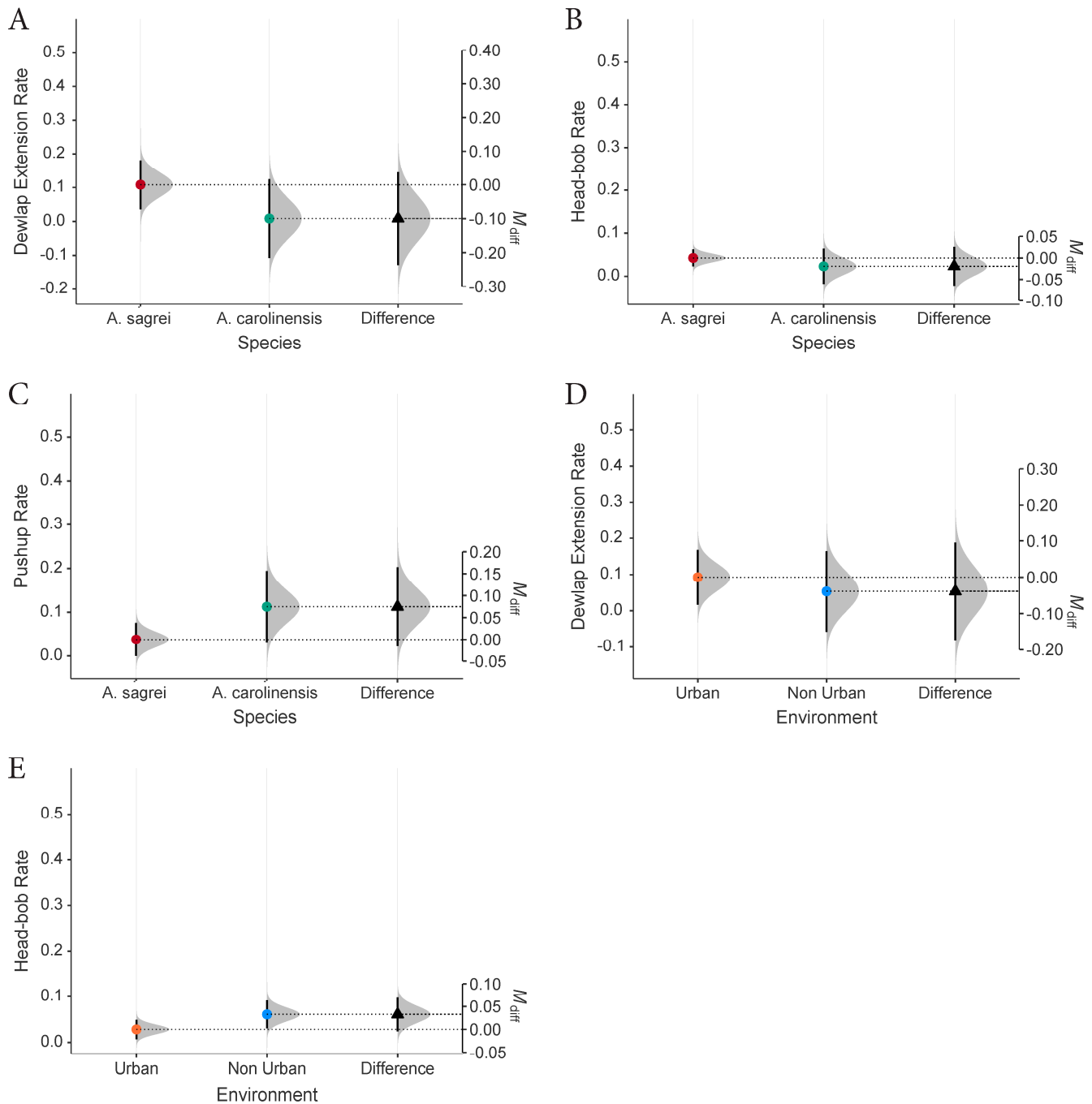


Figure 3. Distribution of means based on 95% CI generated from a large-scale meta-analysis for the combined data set ($N = 111$) as expressed in dichotomous moderator analyses of (A–C) display rates (per second) by species and (D,E) display rates/population environment. *Anolis sagrei* are shown to display more with dewlap extensions and head bobs. Meanwhile, *Anolis carolinensis* perform more pushups. Head-bobbing rates are lower, while dewlap extension rates are slightly elevated in urban-dwelling lizards. The distribution of comparative differences is represented by the black triangle, and distribution corresponds to the right axis.

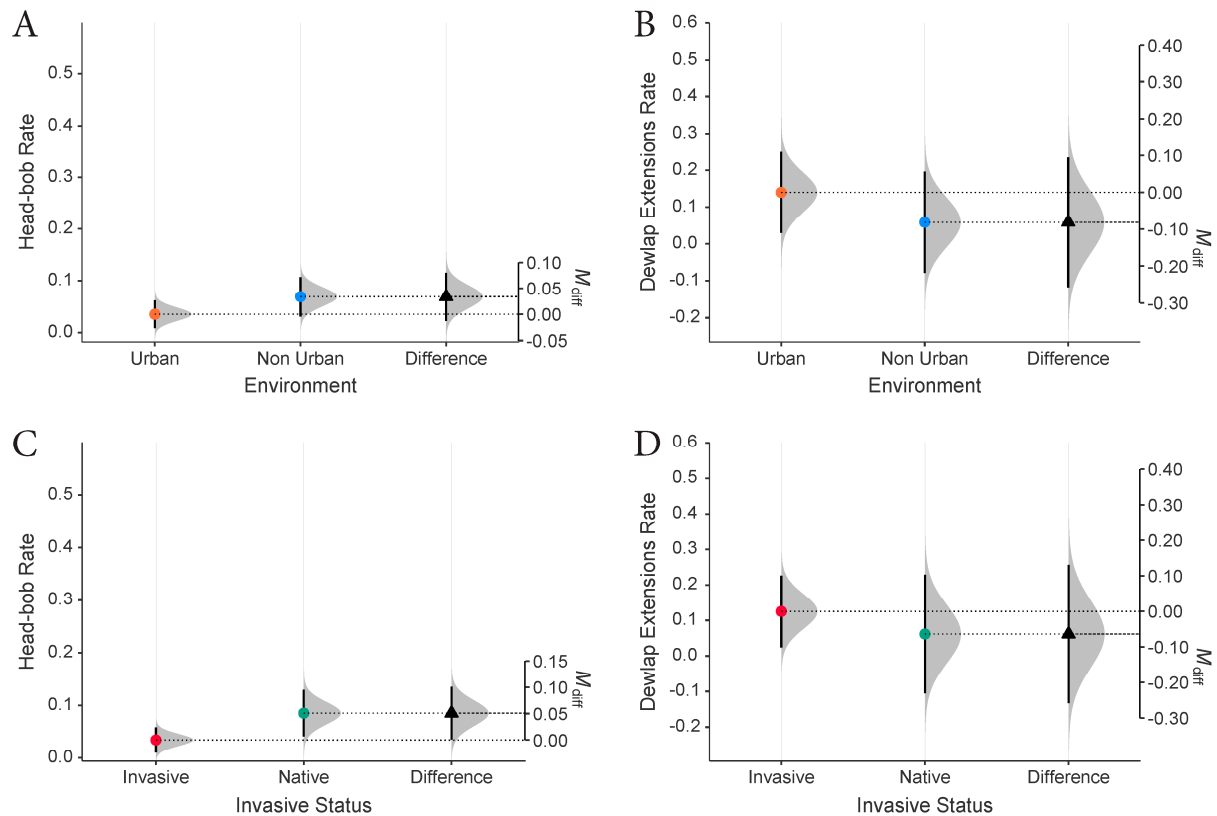


Figure 4. Distribution of mean display rates based on 95% CI generated from a large-scale meta-analysis for *Anolis sagrei*, showing dichotomous moderator analyses with dependent variables of each behavioral display rate (per second)—(A,B) comparing urban and non-urban populations and (C,D) comparing populations from native and invasive ranges. The patterns of elevated dewlap extension rates and lowered head bobbing are duplicated in urban environments and invasive populations. The distribution of comparative differences is represented by the black triangle, and distribution corresponds to the right axis.

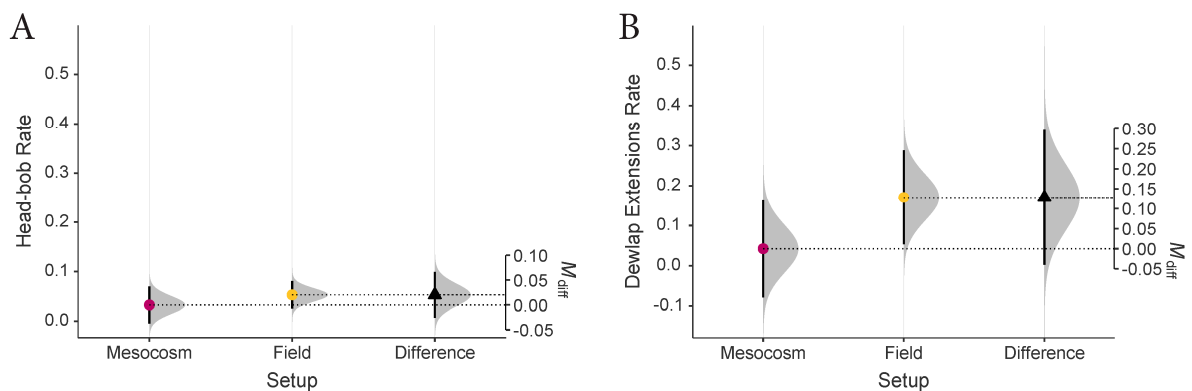


Figure 5. Distribution of mean display rates based on 95% CI generated from a large-scale meta-analysis *Anolis sagrei*, showing dichotomous moderator analyses with dependent variables of behavioral display rate (per second) comparing mesocosm experimental setups with field studies. (A) Head-bobbing display and (B) dewlap extension rates. Field studies record higher display rates than mesocosm experiments, suggesting experimental bias in experimental outcomes. The distribution of comparative differences is represented by the black triangle, and distribution corresponds to the right axis.

4. Discussion

Anoles, irrespective of species, appear to act more agonistically in urban zones. However, the two species of anoles vary greatly in their behaviors and reveal a more complex balancing act of ritualistic signaling. AS show plastic responses and appear to focus on signals that have dual use, mate attractions, and challenger deterrence. AC, on the other hand, favor territorial defense signals and do not vary in behavior based on population origin. We attribute the variations in behavioral portfolios we observed to three major factors: invasive population dynamics, density-dependent population dynamics, and habitat-dependent shifts in mating strategies.

4.1. Frontline of Invasion Compared with Established Invasive Communities

Addressing the behavior of these lizards cumulatively poses the challenge of comparing apples to oranges. The overall data suggest that AS signal more than AC; however, we suggest caution in relying on that specific interpretation. Given the weaker data set for AC, this comparison may be influenced by data availability bias. However, when comparing the balance or proportion of signals, distinct behavioral profiles can be identified for each species. AC, a widespread species, clearly focus on HB displays with significantly higher rates over DE and PU. These patterns persisted in our analysis independently of the habitat from which the populations were collected. We interpret the shape of this profile to suggest a high focus on terrestrial defense (excluding the PU data, which were not robust enough) and a secondary investment in mate-attracting signaling (primary focus of DE activity). Meanwhile, AS show flexibility in their behavioral preferences, suggesting flexible energetic allocation, a signature of species that has high invasion potential, and a record of successful invasions [121,122].

The decrease in territorial behavior seen in the invasive AS populations is surprising. We expected to observe a shift in the invasive populations; however, the significant decrease in HB rates surprised us, as we predicted an opposite pattern. Current trends suggest invasive populations express greater aggression, as this is what gives them an upper hand in the invaded territory [16]. With that in mind, we provide three hypotheses that likely factor into the explanation of this observed behavioral pattern of AS displaying less in their invasive range.

4.1.1. Courting over Territoriality

DE signals are higher in the invasive populations than in the native ones. This suggests that AS use this mate-attracting signaling in preference over HB, which are associated with competitor deterrence. While in some cases, the DE is also a warning signal, it is used in an agonistic fashion more by females than males [52]. We believe there is a high probability that invasive populations focus on courting over aggression for a couple of reasons. First, invasive populations are denser. This leads to lower competition for mates, as mate availability is greater. Second, invasive populations tend to have a higher rate of dispersal syndrome individuals, which prefer to disperse in search of new habitats over territorial defense [12,123,124]. Individuals that prefer dispersal will invest energy in quickly attracting mates, many times choosing sneaky copulations over defending a territory with a harem [12,50,123,124].

4.1.2. Invasion Front and Habituated Populations

As alluded to in the previous section, dispersal takes priority in invasive populations, and aggressive behaviors tend to be associated with these tendencies. Aggressive territorial behaviors are not always the same behaviors that would benefit invasive populations on the front of the invasion. Risk-taking decisions, more likely to support the invasion front, are not well surveyed in the *Anolis* literature. Nonetheless, we can build on observations from the study of some of the most infamous biological invasions, namely cane toads in Australia. The cane toad literature suggests that the behavioral syndromes in the range-expanding front of an invasion give way to shier, less aggressive, and less risk-taking populations once

populations are established [125,126]. Given that we do not have clear data on the age of the invasive population in each of the sampled populations, we do not have the ability to test whether the pattern we observed is a result of habituation of the invasive populations or if it is a factor of traits associated with range expansion. Correlating the behavioral profiles of populations with the historic record of invasion may reveal the answer to this question.

While we think this hypothesis has merit, we are also cautious in suggesting that this is the leading cause of reduced aggression. Putnam, Pauly and Blumstein [127] suggest that AS are less aggressive in California, where they have not been present as long as in some of the sampled studies in the southeastern U.S.

4.1.3. Marginal Costs of Territorial Defense

The final dynamic worth discussing is the tendency for invasive species to form denser populations in new ranges compared to their native ranges [128–130], a pattern also observed in invasive AS [131–133]. The energetic tradeoffs in denser populations shift, driving individuals to disperse [134,135] and occupy less rich habitats that experience less competition [136,137]. The inference we draw from ideal free distribution [134] is that organisms that inhabit areas of high density adapt their behavior in various ways to maximize fitness. We hypothesize that aggressive individuals with dispersal syndrome are found at the invasion front but that individuals that are more appeasing and invest less in aggressive behaviors are the ones that stay behind in higher-density populations. In such conditions, investing in territorial defense would be a constant energetic drain, and would therefore also explain the lower rate of aggressive behaviors we observed in the literature. In lieu of energetic investment in HB and PU, the established invasive AS use displays that have dual use—defense and courtship.

4.2. Tolerance as an Adaptive Trait to Higher Densities in Urban Zones

AC hardly differ in behavior between urban and non-urban environments. However, we observed an overall decrease in displays by urban AS. Lailvaux et al. [11] suggest that newly established urban populations tend to be less competitive than their non-urban counterparts, specifically due to the overabundance of forage and increased predatory risks from human commensal predators. As we suggest above, with the pattern of biological invasions, tolerance (lower aggression) in urban zones may be driven by the necessity of coexisting in overlapping and limited habitats where continuous agonistic behavior is energetically wasteful and thus maladaptive. Why is it maladaptive? Populations in urban environments are denser than in “natural” zones. Urban AS peaked at 0.97 individuals/m² in a study in urban zones in the Bahamas [138], compared with 0.2 in forested areas [139]. The same pattern is true for AC but at lower densities—0.14 individuals/m² individuals compared with 0.06 in forested zones [38,138]. Given the greater hazards in urban zones (predation, physiological disturbance related) the plastic response observed in AS is likely an adaptive change towards energetic efficiency [41]. Moreover, AS success as an urban invasive is attributed to their capacity to adapt and respond to external stimuli while minimizing conflicts in already hazardous zones [140].

4.3. Mating Strategies

As polygynous species, both agonistic and sexual signals have fitness tradeoffs in anoles. The analyses we conducted allowed us to glean insight into these tradeoffs and draw some conclusions about the importance of territoriality in the different species and across different habitats inhabited by the populations sampled. We observed a shift in priority in the invasive populations of AS, suggesting that they rely more heavily on sexual signaling and less on territoriality. We postulate that this is likely selective pressure due to population density, as discussed above. Two potential reasons may lead to the decline in territorial defense. First, a shift in life history tradeoffs in the invasive range, with supposed higher predation risks and resource competition in continental habitats [84], may increase the fitness value of sneaky copulations and outweigh the risk-taking behavior associated

with agonistic territorial defense. Alternately, the abundance of competition for mates would suggest that the defense of territories may become impossible with many sneaky competitor males around. In this scenario, the shift to high mate-attracting signals may be the better fecundity-producing strategy, as the energetic payoff of territorial defense becomes an energy sink. We do not have the analytical power to tease apart those two potential evolutionary paths. However, we can only suggest that it is these shifts in behavioral profiles that suggest that the invasive populations attract mates and guard them in different ways than the native populations in the Caribbean. It is likely that those shifts are responsible for the highly successful and expanding AS invasion across North America.

4.4. Publication Bias

One of the greatest benefits of meta-analysis is the ability to assess publication and research biases. Ecological research is always a balance of tradeoffs, and significant assumptions are made on the validity of studies under constraints. To correct for “noisy” data, ecological studies rely on larger data sets and normalization functions to clean databases and conform them to traditional analyses. Alternatively, many studies control for environmental noise using semi-natural arenas and mesocosm experiments. These experimentation practices give rise to a couple of observed biases in publication that we need to address in this review. (1) Despite having comparatively large sample sizes of studies, at least comparable to meta-analyses from the biomedical fields, the patterns of noisy data make the analysis for AC behavior less reliable. (2) The vast majority of the studies we were able to mine for data were conducted in laboratory settings.

These biases generate constraints that must be considered in the interpretation of behavioral studies on anoles. First and foremost, anoles in captive conditions signal at lower rates across the board than their counterparts in the field. Laboratory-based experiments offer various benefits, including the ability to source anoles from suppliers, control for environmental noise, and provide a high level of regulation of the experimental setup, to name a few. However, our analysis strongly shows that the setting greatly influenced how the animals responded, with free-range anoles signaling at higher rates.

Additionally, two more biases were observed, specifically in the source of experimental populations. Finding data from non-urban AC was a challenge; with effort, we were able to find some papers that represented under 16% of the data. Behavioral studies of AS in their native range represented 29% of the data collected. Urban bias was also evident for invasive AS, with over 60% of data being sourced in urban zones. We connected this bias to the ease of research near university campuses, the locations of animal suppliers, and the lower costs of trapping in urban environments. The native range of AS in Cuba, specifically, limits access to most researchers based in U.S. academic institutions, which provide the major funding sources for this research.

Last, as an ecological research community, we do not stress the reporting of data relevant to power analysis in numerical form. To estimate effect sizes, we used calipers to measure printed graphs to extract the needed information for this analysis and excluded many publications where the relevant data could not be estimated (missing sample sizes, means, or standard deviations). This reduced the accuracy of the meta-analyses. However, we trust that the signals we observed are still correct. We believe our conclusions to be representative of the patterns found in the environments where the studies were conducted by the well-established *Anolis* research community, but these would have had reduced noise given better reporting practices were enforced by journals.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16100620/s1>.

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