



Dependence on a human structure influences the extinction of a non-native lizard population after a major environmental change

Daniel A. Warner · Joshua M. Hall · Amélie Fargevielle ·
Austin C. Hulbert · Sarin Tiatragul · Jenna E. Pruett · Timothy S. Mitchell

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Abstract Human activity causes major changes in natural landscapes via introduction of non-native species, development on natural habitat, and alteration of local weather patterns. These factors contribute to global change and may interact to affect local populations of plants and animals. We studied a viable, non-native lizard population (*Anolis sagrei*) in southeast Alabama, USA that has depended upon thermal conditions inside a greenhouse nursery during the winter for at least 10 years. Using Capture-Mark-Recapture surveys, we compared population

parameters and movement patterns of this introduced *A. sagrei* population to a native lizard population (*Sceloporus undulatus*) that also inhabits our study site. The population size of both species fluctuated over time, but that of *A. sagrei* was considerably larger than *S. undulatus*. *Anolis sagrei* was relatively philopatric and confined within the greenhouse and its immediate vicinity, whereas the *S. undulatus* population extended into the surrounding forest habitat. The thermal landscape within the greenhouse was substantially altered after the roof was removed due to winds from a tropical storm. Indeed, temperatures of all microhabitats commonly used by lizards frequently dropped below the critical thermal minimum for *A. sagrei* and below freezing during winter. Post-winter surveys revealed that no *A. sagrei* individuals survived, indicating that the temperature change in the greenhouse resulted in extinction. The native *S. undulatus* population, however, was still present after winter. Our study provides rare documentation of an extinction of an established introduced population and illustrates the role that human-made structures and natural weather events play in the process of biological invasion.

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D. A. Warner (✉) · J. M. Hall · A. Fargevielle ·
A. C. Hulbert · S. Tiatragul · J. E. Pruett · T. S. Mitchell
Department of Biological Sciences, Auburn University,
Auburn, AL 36849, USA
e-mail: daw0036@auburn.edu

A. C. Hulbert
Department of Environmental Sciences, University of
Toledo, Toledo, OH 43606, USA

S. Tiatragul
Division of Ecology and Evolution, Research School of
Biology, Australia National University, Canberra,
ACT 2601, Australia

T. S. Mitchell
Department of Ecology, Evolution and Behavior,
University of Minnesota, St. Paul, MN 55108, USA

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Introduction

Human activity has altered natural ecosystems in numerous ways, and thus is a major contributor to global change. Several notable human-driven impacts involve biological invasion, urbanization, and climate change (Walther 2010; Lockwood et al. 2013; Alberti 2015); how these influence populations is a core focus of global change biology. Although different types of human-driven global change can affect biological systems in unique ways, their biotic and abiotic effects on local environments may interact. For example, urban areas are often considered a conduit for biological invasion (Hufbauer et al. 2012; Cadotte et al. 2017), and a contributor to climate change (Kalnay and Cai 2003). Altered weather patterns and increased frequency of extreme events (e.g., hurricanes) due to climate change cause major disturbances to natural and urban habitats (Savage et al. 2018; Rogers 2019) and can influence population establishment of native and non-native species (Sergio et al. 2018; van den Burg et al. 2020). Additionally, increases in temperature along rural to urban gradients mirror future increases predicted from global warming (i.e., increases across space vs. through time; Youngsteadt et al. 2015). Therefore, studies must consider interactions among a range of anthropogenically-induced factors to better understand how populations respond to these drivers of global change.

Invasive species are particularly useful for addressing these issues because they experience novel environments upon introduction and create novel interactions for native wildlife (e.g., new competitors, prey sources; Phillips and Shine 2006; Stroud et al. 2017). However, despite the utility of invasive species in addressing these issues, the factors that contribute to their establishment and persistence in novel environments are not fully understood. Populations pass through several stages during the invasion process before being considered invasive (Williamson and Fitter 1996; Blackburn et al. 2011); i.e., reaching a size large enough to have an ecological or economic impact in the new environment (Crooks and Soule 2001). For instance, once individuals are introduced to a non-native landscape and overcome potential barriers to reproduction, the population will typically undergo a period of slow growth, and consequently, detection of non-native populations during this “lag phase” is difficult due to small numbers of individuals

(Mack et al. 2000; Crooks 2005; Larkin 2012). In many cases, however, founding populations may go extinct before they are noticed or reported (Willson et al. 2011). Consequently, non-native populations are typically detected when they are in late stages of exponential growth and spreading across the landscape. At this point they are difficult to manage and considered invasive (Mack et al. 2000). Additionally, the likelihood of early detection is greater in areas of increased human activity (i.e., urban areas) because (1) these are typical ports of entry for non-natives (Latella et al. 2011), (2) many non-natives thrive around anthropogenic structures (Sacchi et al. 2002; Locey and Stone 2006; Gavier-Pizarro et al. 2010; Gonzalez-Bernal et al. 2016), and (3) increased human presence likely facilitates detection. Given these biases in detection (e.g., mostly in urban areas at late stages of population growth), the number of species introductions that are successful relative to those that fail remains unknown in many cases. Thus, documentation of failed introductions or extinctions can provide useful insight into the factors that contribute to invasion success and will increase our understanding of population establishment and invasion dynamics.

The literature is full of examples of invasive species establishing in centers of human activity (reviewed in Lockwood et al. 2013) and examples of extreme weather events influencing population establishment and persistence (e.g., Frederiksen et al. 2008; Mazzotti et al. 2011; Meshaka 1993; Tinsley et al. 2015). Studies of *Anolis* lizards are prime examples: several *Anolis* species thrive in urban environments (e.g., Latella et al. 2011; Kolbe et al. 2016; Winchell et al. 2016; Tiatragul et al. 2019), and in some cases, rely on human structures (Hulbert et al. 2020). Indeed, invasive populations may become so dependent upon human structures that movement away from these areas may be detrimental (Locey and Stone 2006; Hulbert et al. 2020). Moreover, urbanization may have also contributed to their invasion success in locations well outside native ranges (Suzuki-Ohno et al. 2017; Stroud et al. 2019), and several studies have examined the impacts of extreme weather events (e.g., hurricanes, winter storms) on population dynamics and phenotypic selection (Spiller et al. 1998; Schoener et al. 2004; Tinsley et al. 2015; Campbell-Staton et al. 2017; Donihue et al. 2018; Reagan 2019). The brown anole (*Anolis sagrei*) is the subject of many such

studies. This species is native to Cuba and the Bahamas but has been introduced to several locations around the world (e.g., California, Hawaii, Singapore, Taiwan; Goldberg and Bursley 2000; Norval and Chen 2012; Mahrtdt et al. 2014) where it is known to alter the behavior and density of native species (Huang et al. 2008; Edwards and Lailvaux 2012; Stuart et al. 2014). Most notably, *A. sagrei* is well established in Florida, USA and its range has extended considerably throughout the state (and neighboring states). Several disjunct populations are established further north of the continuous invasive range (Parmley 2002), but few of these populations have been systematically studied to understand the factors that facilitate persistence in these areas (despite large differences in climate between these areas and their continuous invasive range; Hulbert et al. 2020).

We studied a disjunct, introduced population of *A. sagrei* in southeast Alabama, USA that inhabits a human-made structure (greenhouse nursery), which appears to thermally buffer individuals from exposure to lethally cold winter temperatures (Steffen and Birkhead 2007; Hulbert et al. 2020). We have three primary objectives. First, we quantify parameters relevant to establishment and persistence (e.g., population size, age class/body size variation, sex ratio) and compare these parameters to those of a sympatric native species (eastern fence lizard, *Sceloporus undulatus*) to assess the impact of natural winter temperatures on population persistence. These demographic parameters provide an indication of population health and recruitment. Additionally, because *S. undulatus* is adapted to the local climate and occupies the same habitat as *A. sagrei* at our study site, this comparison provides useful insight into the importance of the greenhouse structure to populations of non-native species, such as *A. sagrei*. Second, because the greenhouse shields lizards from potentially lethal winter temperatures, we examine movement of individuals within the greenhouse, lizard distributions outside the greenhouse, and among-individual variation in cold tolerance. Given that lizards can readily move indoors and outdoors, we expect that frequent long-distance movements (i.e., greater than the length of the greenhouse) provide lizards with a greater capacity to travel away from the greenhouse than short-distance movements. Long-distance movements at our site could result in exposure to lethal winter temperatures for *A. sagrei*. Thus, quantifying

movement behavior and physiology will provide insight into the level of exposure and tolerance to cold temperatures, respectively. Third, after major damage to the greenhouse roof from a tropical storm (and thus a change in winter thermal environments), we examine the persistence of these populations when the protection of this human structure has been removed. This major environmental change provided a rare opportunity to examine interactions among anthropogenic structures and extreme weather events on the persistence of an established non-native population.

Methods

Study system

Our study populations of the non-native brown anole (*A. sagrei*) and native fence lizard (*S. undulatus*) reside in and around a greenhouse at a plant nursery in Opelika, Alabama (Fig. 1). The area surrounding the greenhouse is mostly rural with a mix of forest, creeks, farmland, and residential properties. The immediate vicinity outside the greenhouse contains ornamental shrubs and trees, concrete cinderblocks, grassy areas, and a few storage sheds. *Sceloporus undulatus* is commonly observed in forest edge and human-disturbed habitat like that surrounding the greenhouse (Supplemental Fig. S1). Additionally, *A. sagrei* is well known to occupy human-disturbed areas and multiple records of this species in plant nurseries have been documented (Wiley 2005; Tay 2019; Fisher et al. 2020); this species likely arrived at our site via shipments of ornamental plants (Steffen and Birkhead 2007). The first record of *A. sagrei* at this site reports a minimum of 50 adults of both sexes observed over just one hour of searching (Steffen and Birkhead 2007), which suggests that this population was present for several generations prior to 2006. Given the short lifespan (1–3 years) and time to maturity (~ 6 months) of this species, it is likely that this population has been present for at least 10 generations. Other native squamate species are present at this site (*Anolis carolinensis*, *Plestiodon fasciatus*, *P. laticeps*, *Coluber constrictor*, *Pantherophis spiloides*), but their population densities are very low compared to *A. sagrei* and *S. undulatus*, and therefore, are not of focus here.

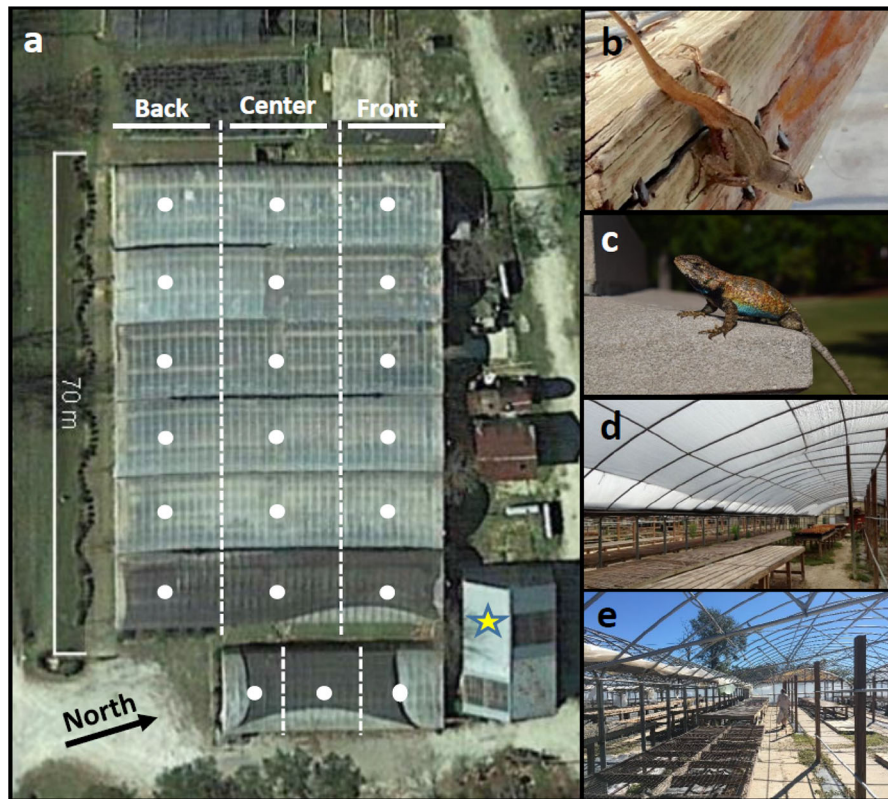


Fig. 1 Photographs of our study site. **(a)** Satellite image of the greenhouse, which is divided into seven interconnected sections; each section was visually divided into thirds (front, center, and back, denoted by dashed lines), which provided 21 locations where lizards were captured. The straight-line distance between capture locations (estimated at each white point) was used to estimate the distance that lizards travelled. The yellow

star shows an indoor structure that remained intact after the roof was removed from the greenhouse. **(b)** Adult male brown anole (*Anolis sagrei*) inside the greenhouse. **(c)** Adult male eastern fence lizard (*Sceloporus undulatus*). **(d)** Inside view of the greenhouse before and **(e)** after the roof was removed in September 2017

The greenhouse consisted of seven interconnected sections that comprised an area of 3300 m² (Fig. 1a). The greenhouse frames were mostly metal with some wood, while the roof and walls were polycarbonate plastic, which increased indoor temperature and humidity and likely kept indoor winter temperatures relatively high compared to the surrounding area (Hulbert et al. 2020). In addition, the lack of airflow within the greenhouse, due to nonfunctional ventilation fans during our study, contributed to high indoor temperatures. Center aisles within each greenhouse section consisted of tables made from a combination of wood, metal wire, and/or cinderblocks (Fig. 1). Plastic pots and flattened cardboard boxes were scattered on the tables and ground, which were often used as retreat sites for lizards. Two concrete walkways extended along the length of each section. The

substrate was a mix of concrete, exposed soil, and weed mat overtop soil. Many hollow steel pipes provided structural support for tables and served as retreat sites for lizards, allowing them to move below ground. Many of these materials absorb heat and likely contributed to relatively high indoor temperatures during winter. Indeed, temperatures inside unheated greenhouses can be as high as 30 °C greater than the immediate outside temperature during winter when heat-absorbing materials are present (Beshada et al. 2006). Low vegetation was abundant in areas with exposed soil that received water from leaks in the roof. The greenhouse structure had many gaps that enabled lizards and other animals to move in and out. Invertebrate prey (e.g. ants, grasshoppers, moths) were highly abundant (pers. observation).

Population parameters

From 2016 to 2018, we surveyed lizard populations in and around the greenhouse, attempting to capture all individuals sighted across eleven capture events that were grouped into four seasons (Supplemental Table S1). Three capture events were concentrated during summer of 2016 and two events in spring/summer 2017. On 22 September 2017, we noticed that the roof of the greenhouse was completely gone (Fig. 1d), presumably due to strong winds from a storm 18 days prior (these winds were from Hurricane Irma after it was downgraded to a tropical storm when it hit Alabama). Thus, in anticipation for a major temperature change inside the greenhouse over winter, we conducted six intense capture events: three before (autumn 2017) and three after winter (Summer 2018) (Supplemental Table S1). Importantly, this *A. sagrei* population exhibits no signs of thermal adaptation to this northern climate (Hulbert et al. 2020), and thus our capture efforts prepared us to examine changes in population demographics and physiology after winter without the thermal buffer of the greenhouse roof.

During each capture event, we visually searched the entire greenhouse and the surrounding immediate vicinity. On average, concerted capture efforts during autumn 2017 were 1.57 person hours (± 1.4 SE) greater than those after winter in 2018, but this difference was not statistically significant ($F_{1,7} = 1.25$, $P = 0.301$; Supplemental Table S1). Outside the greenhouse, we searched most intensively within 10 m of the external walls but also searched much farther during some surveys. Only two brown anoles were found more than 10 m from the greenhouse (see Supplemental Fig. S1), but fence lizards (and other native species) were commonly captured far from the greenhouse. Lizards were temporarily placed in bags, measured later that day (snout-vent length [SVL], tail length, mass), and their sex identified by their dorsal pattern (Cox and Calsbeek 2010) and the presence (male) or absence (female) of enlarged scales near the cloaca. Lizards were uniquely marked via toeclips and most were returned to their location of capture within 48 h. Ninety-two *A. sagrei* were kept for 3–5 days to measure cold tolerance prior to release (details below), and 27 *S. undulatus* (11 males, 16 females) collected in May and June 2017 were kept in captivity for another study and only the females were later returned to the site.

Using Capture–Mark–Recapture (CMR) data, we parameterised multi-event statistical models based on a Cormack–Jolly–Seber model, estimating survival and detection probabilities (Lebreton et al. 1992). Our initial analyses distinguished between juvenile and adult individuals; for *A. sagrei*; individuals < 39 and < 34 mm SVL were defined as juveniles for males and females, respectively, and larger individuals were classified as adults (Lee et al. 1989). For *S. undulatus*, individuals of both sexes < 50 mm SVL were defined as juveniles, and larger individuals were classified as adults (Crenshaw 1955; Pounds and Jackson 1983). Preliminary models indicated no difference in survival rate or detection probabilities between adults and juveniles, but these models were limited by unbalanced and small sample sizes, leading to convergence issues. Therefore, we reduced our analyses to ignore potential differences between adults and juveniles in their probability to survive to the next capture event and in their probability of detection. This parameterisation was entered into the E-SURGE program (Choquet et al. 2009).

We used a model-selection procedure (i.e., Akaike information criteria (QAICc); Anderson and Burnham 2002) to decide which covariates to include when estimating survival and detection probabilities. We first tested whether grouping capture events and/or grouping time lapse by season (e.g., June and July capture events regrouped as “Summer”) (Supplemental Table S2) would provide a better model than differentiating every capture event and/or time lapse (Supplemental Table S3). Then we tested different models including “season”, “sex” and “species” as potential covariates with detection probability or survival probability. Models including two-way interactions among factors were also tested (Supplemental Table S3). We then extracted estimates and 95% confidence intervals for survival and detection probabilities (Supplemental Table S4, S5) to estimate population size at each capture event. Estimated population size for each species at each capture event was calculated by dividing the number of captured individuals during a capture event by the estimated detection probability associated with that capture event.

Population densities were calculated by dividing population size estimates by the area of the greenhouse (3300 m²). This approach was justified for calculating the density of *A. sagrei* because all but two individuals

were found within the greenhouse or in the near vicinity. This approach may have slightly overestimated the density of *S. undulatus* because seven individuals were caught well outside the greenhouse area (Supplemental Fig. S1).

Variation in body size (SVL and mass) across seasons was examined with general linear models. Individuals were grouped into four seasons as described above (i.e., summer 2016, spring/summer 2017, autumn 2017, summer 2018) to ensure suitable sample sizes for comparisons. Because several individuals were recaptured multiple times within each season, we only included new individuals captured to avoid pseudoreplication (i.e., no individual was in the data set more than once). Separate tests were used to examine size differences among seasons for juveniles, adult females and adult males. Sample sizes were suitable for *A. sagrei* (Supplemental Table S6), but low sample sizes in some season/age class/sex combinations for *S. undulatus* (Supplemental Table S7) precluded meaningful analysis. Additionally, we calculated overall biomass as the average mass of new individuals captured multiplied by the estimated population size for each species; biomass was calculated separately for each season prior to 2018.

Distance travelled by lizards

We recorded the general location of each lizard captured in the greenhouse by noting the greenhouse section and whether it was in the front, center, or back area of each section ($n = 21$ locations; Fig. 1a). For lizards captured outside (within ~ 10 m) of the greenhouse, we recorded the nearest section and whether it was in the front or back of that section. Most surveys occurred during morning and early afternoon hours which is when lizards are most active (Supplemental Table S1). The distance travelled by lizards was measured using the central points of the sections of the greenhouse where lizards were captured (central points are represented by white dots in Fig. 1a). The central point within each section was used as a capture location even if an individual was captured away from that central point. The straight-line distance between central points of each section was then calculated for individuals that were captured two or more times; if an individual was captured in the same section, it was given a zero for distance travelled. Importantly,

because we did not record the exact location of lizards within each section, our measurements of distance travelled may be inaccurate by at most 18.2 m, which is a distance typically travelled within the home range of *S. undulatus* (Ferner 1974), but larger than the distance often travelled by *A. sagrei* (Schoener and Schoener 1982).

Data for distance travelled were available for 119 *A. sagrei* and 27 *S. undulatus*. We calculated the distance travelled between the first and last capture for each individual. Because many individuals were repeatedly captured in a given section of the greenhouse, distance data were heavily skewed towards zero. Thus, distance travelled was log transformed ($\log(1 + x)$) prior to analysis. Regression analyses tested for a relationship between distance travelled and the number of days between the first and last capture. Differences in distance travelled between species was quantified with Analysis of Covariance using the number of days between first and last capture as a covariate.

Cold tolerance and winter temperatures

In October 2017, our initial intention was to measure the critical thermal minimum (CT_{min}) of *A. sagrei*, to quantify how population CT_{min} might change over winter (i.e., in the absence of thermal buffering from the greenhouse roof), but post-winter measures never occurred due to population extinction (see Results); although we could not achieve this objective, we still report CT_{min} as an index of cold tolerance which provides insight into the likelihood of population persistence when exposed to winter temperatures. To measure CT_{min} , we placed each lizard ($n = 92$ individuals of both sexes) in a small, plastic container (GladWare Designer Series Rectangular Containers with Lids, UPC:0001258778514), which was kept floating inside a VWR circulating water bath for ~ 60 min at 16°C ; this temperature is 6.3°C warmer than the mean CT_{min} of brown anoles measured at our population in 2016 (Hulbert et al. 2020). We then removed each lizard and threaded a thermocouple wire through a small hole drilled in a transparent waterproof case (Pelican 1040 Micro Case Series, Model Number: 1040-025-100). The thermocouple probe was inserted 1 cm into each lizard's cloaca and held in place with surgical tape (Gunderson and Leal 2012; Campbell-Staton et al. 2016). We cooled lizard body

temperatures by approximately 1 °C per minute by placing and submerging the waterproof case (containing the lizard) in a cooler filled with ice such that the lizard was not in direct contact with the ice. Each time the lizard's temperature decreased by 1 °C, the lizard was flipped on its back by turning the container upside down quickly. CT_{\min} was considered the temperature at which the lizard had no natural inclination to right itself within 30 seconds. If the lizard righted itself before 30 seconds, we continued to decrease body temperature (Kolbe et al. 2014; Campbell-Staton et al. 2016). We recorded cloacal temperatures every 15 seconds. This procedure was performed once for each individual. CT_{\min} was not measured for *S. undulatus*.

On 17 November 2017, we placed 36 temperature loggers (Thermochron iButtons, Embedded Data Systems) in different microhabitats across the greenhouse to measure hourly winter temperature. The iButtons were waterproofed by placing them in a water balloon and wrapping them with parafilm. Each of the seven sections of the greenhouse contained 4–6 iButtons, and two iButtons were placed in an enclosed room adjacent to the greenhouse (this room retained its tin roof over winter and likely had a different thermal profile than the greenhouse; denoted with a star on Fig. 1a). Loggers were strategically placed to assess the overall thermal environments of different microhabitats within each section of the greenhouse, and associated air temperatures (~ 2.5 m above ground). The microhabitats included areas that were frequently observed as retreat sites for lizards (e.g., under wood boards, inside pipes, crevices in tables, under weed mat, in plant pots; Hulbert et al. 2020). We retrieved iButtons on 9 February 2018. Temperatures were similar among the various cover objects and, thus, we combined thermal data from iButtons placed under these objects. Consequently, analyses compared five microhabitat types: air temperature ($n = 5$), under cover ($n = 16$), in wooden crevices ($n = 8$), inside metal pipes ($n = 5$), and inside an enclosed room with a roof ($n = 2$). Minimum, maximum, and mean temperatures of each iButton were extracted for each day and used as dependent variables in three separate general linear mixed models that quantified differences in winter temperatures among microhabitats (including air temperature); iButton was included as a random effect. Ambient temperatures within the greenhouse were not measured during the winters prior to removal of the roof. However, monthly

temperature data from previous years (2005–2018) were obtained from a weather station (available via the National Climatic Data Center) located 10.8 km from the greenhouse and were used to determine if outside air temperatures during winter without the greenhouse roof (2017/2018) differed from previous years (Supplemental Fig. S2).

Results

Population parameters

Estimated population sizes of *A. sagrei* and *S. undulatus* fluctuated across the study period, but population size was consistently larger for *A. sagrei* than *S. undulatus* across all time periods before the 2017/2018 winter (Fig. 2). Population density of *A. sagrei* ranged from 0.073 to 0.236 individuals per m^2 , but upper estimates suggest that density may have reached as high as 0.361 individuals per m^2 (Table 1). Based on population estimates for males and females, the average sex ratio of the adult *A. sagrei* population was 44.1% male (ranging from 39.1 to 49.3% male). Population density of *S. undulatus* ranged from 0.019 to 0.056 individuals per m^2 , but upper estimates indicate that density may have reached as high as 0.139 individuals per m^2 (Table 1). Based on population estimates for males and females, the average sex ratio of the adult *S. undulatus* population was 39.5% male (ranging from 35.3 to 52.4% male) (Table 1).

Prior to the 2017/2018 winter, population sizes (sexes combined) were 779 individuals for *A. sagrei* (lower estimate = 563, upper estimate = 1192) and 62 individuals for *S. undulatus* (lower estimate = 39, upper estimate = 123). After winter, no *A. sagrei* were found (except for one carcass), providing strong evidence that the *A. sagrei* population went extinct. Indeed, survival rates across time remained between 0.46 and 0.81 but dropped to zero in the 2017/2018 winter (Fig. 3). For *S. undulatus*, the population size after winter did not differ appreciably from before (i.e., 95% confidence intervals overlap for Autumn 2017 and Summer 2018; Fig. 2b). Survival rates for *S. undulatus* were greater than 0.41 over most of the study, but survival dropped to 0.26 in spring 2017 and to 0.18 in the 2017/2018 winter; survival the following summer in 2018 (0.99) was similar to several previous estimates (Fig. 3). Both sexes and age classes for *S.*

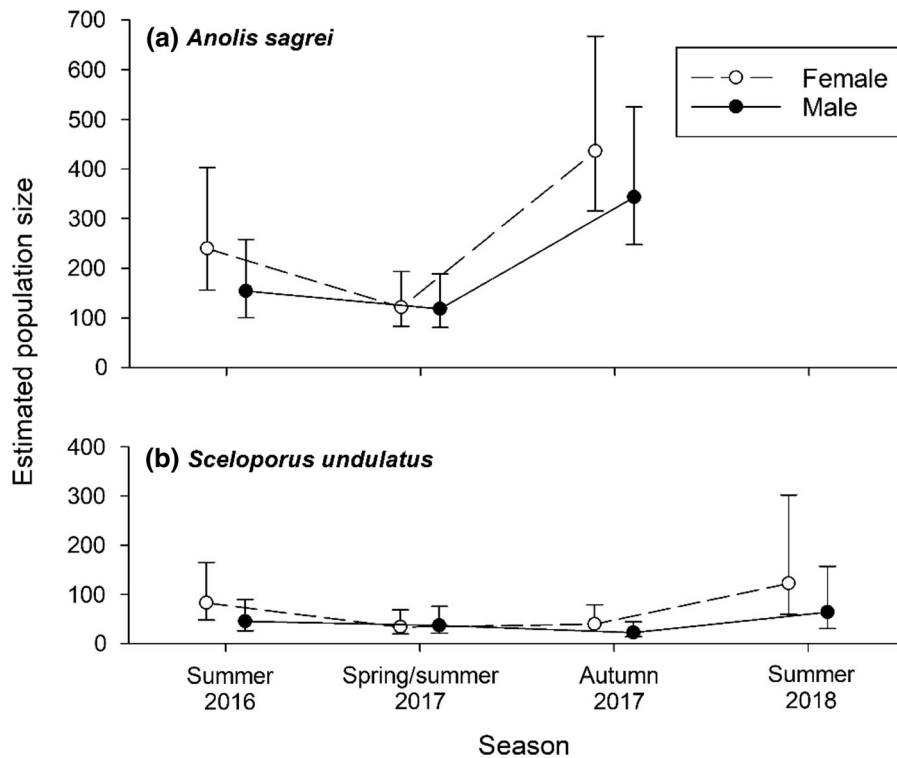


Fig. 2 Sex-specific estimates of population size across multiple seasons for (a) *Anolis sagrei* and (b) *Sceloporus undulatus*. Population size estimates for *A. sagrei* in summer 2018 were not

estimated because no individuals were present at this time. Bars represent the upper and lower estimates for the population size in each season

Table 1 Estimated population size, detection probability, population density (individuals/m²) and adult sex ratio (% male) for *Anolis sagrei* and *Sceloporus undulatus*

Species	Year	Season	Population size estimate	Detection probability (upper-lower)	Density estimate (upper-lower)	Adult sex ratio (%)
<i>A. sagrei</i>	2016	Summer	394	0.279 (0.166–0.429)	0.119 (0.078–0.200)	39.1
<i>A. sagrei</i>	2017	Spring/summer	240	0.313 (0.196–0.460)	0.073 (0.049–0.116)	49.3
<i>A. sagrei</i>	2017	Autumn	779	0.420 (0.274–0.581)	0.236 (0.171–0.361)	44.0
<i>A. sagrei</i>	2018	Summer	–	–	–	–
<i>S. undulatus</i>	2016	Summer	128	0.266 (0.133–0.460)	0.039 (0.022–0.077)	35.3
<i>S. undulatus</i>	2017	Spring/summer	70	0.299 (0.145–0.516)	0.021 (0.012–0.044)	52.4
<i>S. undulatus</i>	2017	Autumn	62	0.403 (0.203–0.643)	0.019 (0.012–0.037)	36.0
<i>S. undulatus</i>	2018	Summer	187	0.204 (0.083–0.421)	0.056 (0.027–0.139)	34.2

Population size is the sum of the estimated male and female populations. To calculate density estimates, population size values were divided by greenhouse area (3300 m²), and sexes and age classes were combined

undulatus were present during our final surveys in August 2018.

Body size varied among seasons for both species (Supplemental Tables S6, S7). For *A. sagrei*, juveniles

in autumn 2017 were 20.3% and 26.3% longer in SVL than those in the summer of 2016 and 2017, respectively ($F_{2,100}=12.4$, $P < 0.001$; Fig. 4). Similarly, juveniles in autumn 2017 were on average 73.5%

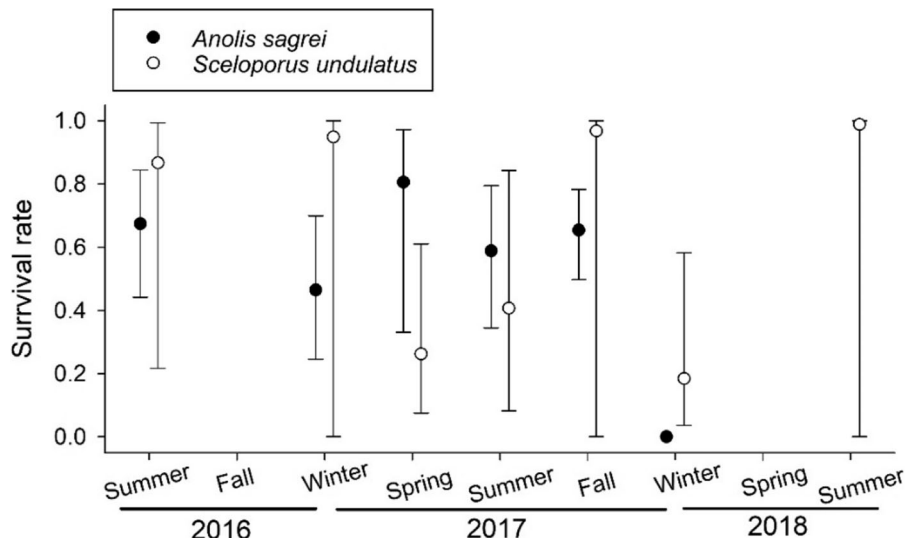


Fig. 3 Estimated survival rates between sampling periods for brown anoles (*Anolis sagrei*) and eastern fence lizards (*Sceloporus undulatus*) at the greenhouse. No brown anoles were present in summer 2018. No capture effort was made in

Fall 2016 or Spring 2018. Bars show the 95% confidence limits. Asymmetrical confidence limits are due to 0–1 survival rate boundaries and large uncertainty associated with survival rate for *Sceloporus undulatus*

and 110.7% heavier than those in summer 2016 and 2017, respectively ($F_{2,99} = 9.5, P < 0.001$). These patterns were reversed for adults; the average SVL of adult males and females in autumn 2017 was 16.3% and 14.6% shorter than in the previous summer 2017, respectively (all P values < 0.001). Body mass of adult males and females in autumn 2017 was 44.7% and 41.5% lighter than in the previous summer 2017, respectively (all P values < 0.001 ; see Supplemental Table S6 for effect sizes and other descriptive

statistics). For *S. undulatus*, juveniles in summer and autumn 2017 did not differ in SVL ($P = 0.112$), but were significantly larger than those in summer 2016 and 2018 ($F_{3,49}=16.5, P < 0.001$); juvenile body mass showed a similar trend ($F_{3,49} = 15.3, P < 0.001$). Adult size also varied among seasons, but low sample sizes precluded meaningful statistical comparisons; see Supplemental Table S7 for effect sizes and other descriptive statistics. Biomass for *A. sagrei* (ranged from 942 to 1580 g) was substantially greater than that

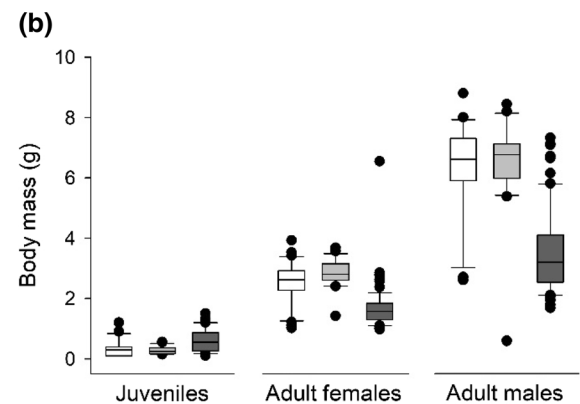
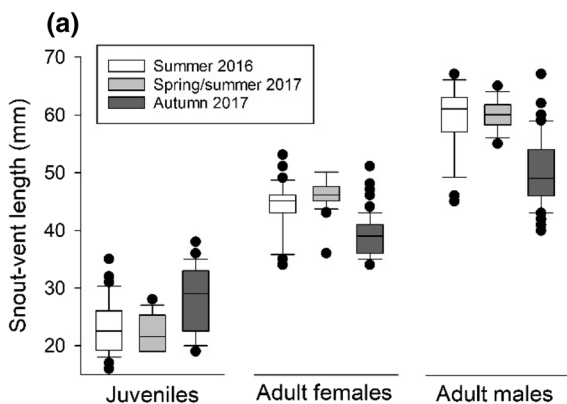


Fig. 4 Snout-vent length (a) and body mass (b) of *Anolis sagrei* across three seasons. These seasonal trends in body size provide evidence of recruitment to the adult population over the study. In all cases, the difference in average body size of individuals from autumn 2017 from that in the other two seasons is statistically

clear (P values < 0.001); all descriptive and test statistics are in Supplemental Table S6. Box plots show the median value (line within box), middle 50% of data (box), the 10th and 90th percentiles (whiskers), and outlying data (points)

for *S. undulatus* (ranged from 182 to 713 g) across the three seasons of this study before 2018.

Distance travelled by lizards

Lizards of both species were captured in all sections of the greenhouse (Supplemental Table S8) and individuals exhibited considerable variation in the distance they travelled during the study. On average, *A. sagrei* travelled 8.53 m (± 2.74 SE) less than *S. undulatus* ($F_{1,144} = 5.90$, $P = 0.016$). For *A. sagrei*, the average distance travelled was 10.6 m (SD = 12.4; range = 0–66.9 m); nearly half of the individuals recaptured (44%, $n = 119$) had a distance of zero (i.e., recaptured in the same location as their first capture), and 43% travelled less than 20 m. The relationship between distance travelled and the number of days between capture was not statistically clear for neither transformed ($r^2 = 0.014$, $P = 0.202$) nor raw data ($r^2 = 0.028$, $P = 0.069$); for every day between captures, individuals travelled a distance of 0.016 m (± 0.009 SE) (Fig. 5a). For *S. undulatus*, the average distance travelled was 19.1 m (SD = 14.9, range = 0–50.2); 26% ($n = 27$) travelled a distance of zero, and an additional 26% travelled less than 20 m. Nearly half (48%) of the *S. undulatus* recaptured travelled over 20 m. The relationship between distance travelled and the number of days between capture for *S. undulatus* was not statistically clear using transformed data ($r^2 = 0.066$, $P = 0.195$), but was statistically significant using raw data ($r^2 = 0.233$, $P = 0.011$); for

every day between captures, individuals travelled a distance of 0.037 m (± 0.013 SE) (Fig. 5b).

Cold tolerance and winter temperatures

Minimum and maximum winter temperatures differed among microhabitats inside the greenhouse, but mean winter temperature did not (Table 2). Despite differences among microhabitats in minimum temperatures, all microhabitats frequently exhibited temperatures far below CT_{\min} for *A. sagrei* (mean \pm SD: 10.2 ± 2.21 °C, range = 6–16 °C) and below freezing (Fig. 6). Although locations under cover objects (Fig. 6a) and inside an enclosed room (Fig. 6d) were slightly buffered from cold winter temperatures (mean minimum temperature of ~ 5 °C above air temperature; Table 2), the temperature of these microhabitats also dropped below freezing multiple times during winter. Air temperatures during the 2017/2018 winter were very similar to those recorded over the previous 13 years (Supplemental Fig. S2). Additionally, minimum temperatures dropped below that recorded in 2017/2018 in four of the 13 previous winters.

Discussion

The factors that influence establishment of non-native populations are challenging to identify. In our study, we show that a key factor responsible for both establishment and extinction of a non-native lizard

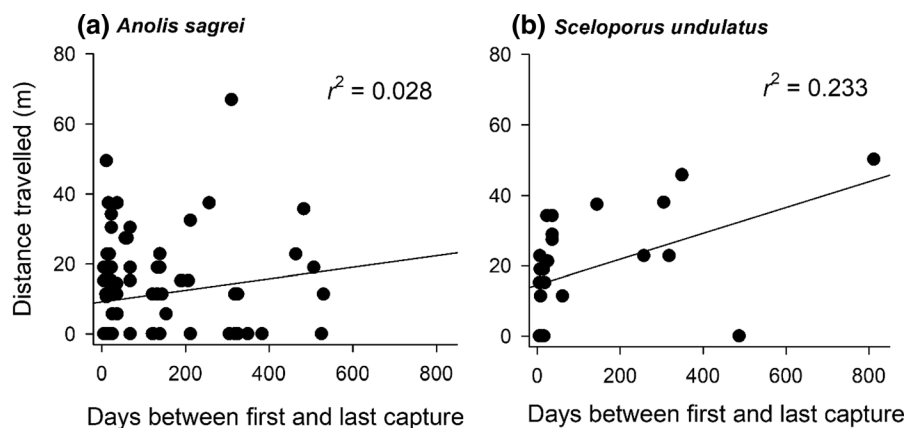


Fig. 5 Relationship between distance travelled from original capture location and the number of days between captures for *Anolis sagrei* (a) and *Sceloporus undulatus* (b). The average movement distance by *A. sagrei* (mean = 10.6 m) suggests that

this non-native species generally stays within the confines of the greenhouse. Analyses were performed using both transformed and raw data (see text). This figure illustrates results using raw data

Table 2 Microhabitat differences in thermal variables

Microhabitat	Minimum temperature (°C)			Mean temperature (°C)			Maximum temperature (°C)		
	$\beta \pm SE$	Mean	Range	$\beta \pm SE$	Mean	Range	$\beta \pm SE$	Mean	Range
Air	–	1.13	– 11.0–22.0	–	7.92	– 5.2–22.2	–	16.71	– 0.5–29.0
Cover	4.18 ± 0.996	5.32*	– 10.5–22.0	0.89 ± 0.280	8.82	– 5.3–22.2	– 3.39 ± 0.859	13.32*	– 2.0–30.0
Crevice	0.76 ± 1.109	1.90	– 12.5–22.5	0.29 ± 0.476	8.22	– 5.2–22.5	0.18 ± 0.956	16.89	– 1.0–34.0
Pipe	– 0.02 ± 1.230	1.12	– 12.0–22.0	0.70 ± 0.528	8.63	– 4.3–22.0	3.62 ± 1.061	20.34*	3.5–38.5
Indoor	4.24 ± 1.627	5.38*	– 6.0–22.0	1.09 ± 0.699	9.02	– 1.0–22.0	– 1.94 ± 1.403	14.77	2.5–44.0
Statistical test	$F_{4,3060} = 9.03, P < 0.0001$			$F_{4,3060} = 1.61, P = 0.1696$			$F_{4,3060} = 19.18, P < 0.0001$		

All microhabitat types experienced below freezing temperatures during winter. Effect sizes (β) were calculated using air temperature as the reference. Asterisks next to mean values denote statistically significant (all P values < 0.01) differences from the air temperature

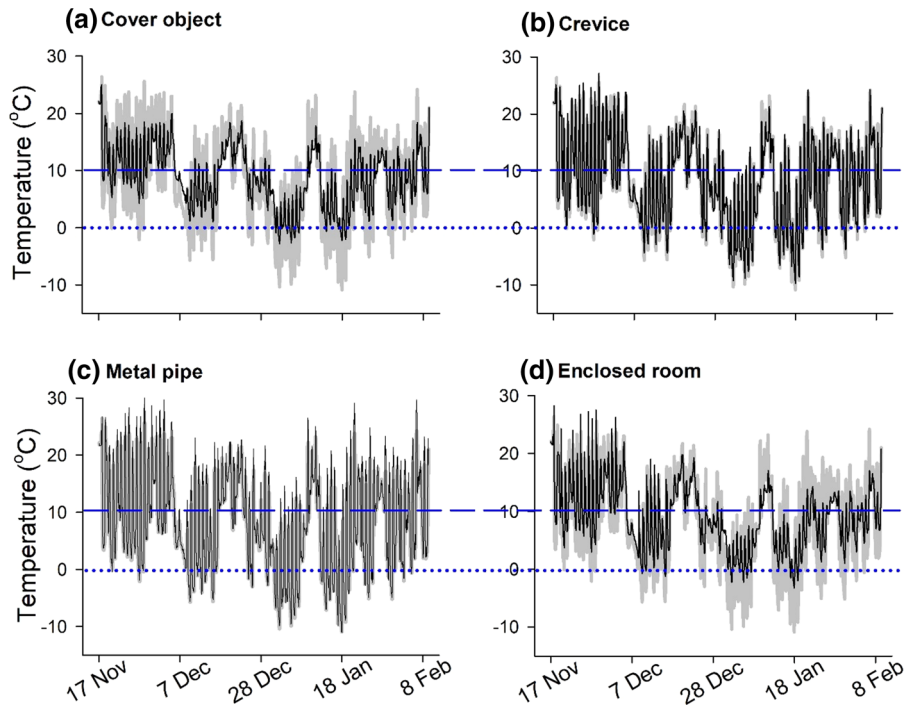


Fig. 6 Average hourly temperature profiles of different microhabitats in the greenhouse during winter 2017/2018. The thick gray lines in the background represent the air temperature. The dotted horizontal line represents the freezing temperature and dashed horizontal line represents the mean critical thermal

minimum for the *Anolis sagrei* population. The solid black lines represent the average temperature profile (a) under cover objects, (b) in crevices, (c) inside metal pipes, and (d) inside an enclosed room. See Methods for descriptions of each of these microhabitats

population was dependence on a human structure. With respect to our three primary objectives, we first demonstrate that the greenhouse contained sustainable populations of native (*S. undulatus*) and non-native (*A. sagrei*) lizards. Secondly, *S. undulatus* moved greater distances and were often found farther from the

greenhouse than *A. sagrei*; brown anoles were considerably more philopatric and almost always within or very close to the greenhouse. Long distance movement from the greenhouse would be detrimental to *A. sagrei*, as thermal buffering by the greenhouse may be necessary for this population to persist during

winter months when the roof was present (Hulbert et al. 2020). Third, extreme weather induced by a tropical storm likely influenced the winter thermal environment inside the greenhouse (via the loss of the roof). Consequently, populations experienced below freezing temperature, which likely drove the non-native *A. sagrei* population to extinction, whereas the native *S. undulatus* population persisted. Overall, our data provide evidence that human structures can facilitate biological invasion in areas far outside the native range of ectotherms (Sacchi et al. 2002; Locey and Stone 2006; Gavier-Pizarro et al. 2010; Gonzalez-Bernal et al. 2016), but established populations are still highly vulnerable to major environmental change.

Population biology

The *A. sagrei* population at our site has been present for at least 10 generations before our study. Clearly, this was a sustainable population, which is further supported by the presence of younger age classes and other evidence of reproduction (e.g., several hatched eggs found underneath cover objects throughout the greenhouse; pers. obs.). Indeed, 10.6% of juveniles were between 16 and 22 mm which indicates they were recently hatched neonates (Warner et al. 2012). The only time juveniles were not present was in April 2017, which is expected considering that eggs have likely not yet hatched this early in the season (Hall et al. 2020) and the previous year's offspring would have already grown to adult size (Cox et al. 2009). Additionally, five *A. sagrei* captured as juveniles in 2016 were later recaptured as adults, providing direct evidence of recruitment into the adult population. The seasonal trends in juvenile and adult body size also provide evidence of recruitment into the adult age class. For example, juveniles captured in autumn 2017 had more time to grow compared to those captured in summer (in 2016 and 2017), which explains the relatively large size of juveniles at that time period (Fig. 4); a similar trend in juvenile body size among seasons was observed in *S. undulatus* (albeit, this pattern was less pronounced than in *A. sagrei*, possibly due to species-specific differences in growth rates). Similarly, the reduced body size of adult *A. sagrei* in autumn was likely due to recruitment of young lizards into the adult size class, thereby driving the average adult size down, whereas recruitment into the adult size class was not expected in the summer season.

The conspicuous and philopatric behavior of *A. sagrei* (Calsbeek 2009) facilitates accurate population estimates for this species. However, the estimated population densities at the greenhouse were generally lower than those within the native and continuous non-native range of *A. sagrei*, even on islands that are considerably smaller than the greenhouse (Schoener and Schoener 1980; Lee et al. 1989; Kustra et al. 2019). For example, native population densities average 0.375 individuals/m² (range 0.077–0.969) in areas only about 100 m² (Schoener and Schoener 1980). In the greenhouse (3300 m²), estimated population densities ranged from 0.073 to 0.236 prior to the 2017/2018 winter, but were still within the lower density values reported for some natural populations (Schoener and Schoener 1980). The estimated sex ratios of the greenhouse population remained relatively stable and were also well within the range of native populations (Schoener and Schoener 1980; Muralidhar and Johnson 2017). Although populations of *A. sagrei* can reach considerably larger sizes (and densities) than those reported here (Kustra et al. 2019), population growth at this site may be constrained for a variety of reasons (e.g., cool winters, food limitation, habitat structure, isolation from other populations, competition with native species).

The *S. undulatus* population size and density were considerably smaller than those of *A. sagrei*, which is consistent with population studies of these species (cf., Ferguson et al. 1980; Schoener and Schoener 1980). Nevertheless, the estimated population density of *S. undulatus* in the greenhouse was larger than density estimates reported for many other *S. undulatus* populations (Ferguson et al. 1980; Parker 1994), even though a small number of individuals were permanently removed. For example, our estimated average population density (mean: 0.033; range: 0.019–0.059 lizards/m²) at the greenhouse was 14 times greater than the average across nine other populations (mean: 0.002; range: 0.0002–0.048 lizards/m²; Crenshaw 1955; Tinkle and Ballinger 1972; Vinegar 1975; Ferguson et al. 1980; Parker 1994). Importantly, although the *S. undulatus* population appears relatively large compared to most others, we point out two important caveats. First, most of our surveys were confined to the greenhouse where density may have been abnormally high. Indeed, the density of *S. undulatus* is considerably lower in forest habitat than in open areas with rocks and logs (Parker 1994), which

is similar to the greenhouse habitat. Moreover, the greenhouse may have provided unnaturally high prey abundance and lizard predators may have been excluded by the greenhouse walls and roof.

Our second caveat concerning relatively high densities for *S. undulatus* relate to how density estimates were calculated. Some individuals ($n = 7$) were captured far from the greenhouse (Supplemental Fig. S1), but density estimates were calculated using the area of the greenhouse, which would inflate estimates. Consequently, the population estimates at the greenhouse may have been more like those of other populations had we intensively and consistently surveyed the surrounding forest habitat. Furthermore, given the movement patterns of *S. undulatus* (Hein and Whitaker 1997; Angilletta et al. 2009), individuals likely travel between the surrounding forest habitat and the greenhouse, which could affect the accuracy of population size estimates when surveys are confined to smaller areas. In contrast, published densities for other populations may have been underestimated, as these studies did not account for detectability as we did (Tinkle and Ballinger 1972; Vinegar 1975; Ferguson et al. 1980; Parker 1994). Our density estimates for *S. undulatus* should be interpreted with these caveats in mind. Nevertheless, despite the relatively high densities that we report for *S. undulatus* compared to other studies, the overall biomass of this species was still considerably lower than that of *A. sagrei* at our site, even with lower individual body mass of the non-native species.

Population persistence and extinction

Several factors contribute to the persistence and extinction of populations—some of which have been identified for *Anolis* lizards. For example, *A. sagrei* has broad physiological tolerances (Kolbe et al. 2014; Hall and Warner 2019) and exhibits an impressive capacity to rapidly adapt to novel environments (Losos et al. 1997; Kolbe et al. 2012; Campbell-Staton et al. 2020). The multiple introductions of *A. sagrei* in Florida have also increased genetic diversity due to admixture which likely facilitates establishment (Kolbe et al. 2004). Although not documented at the greenhouse, it is possible that multiple introductions (via repeated ornamental plant shipments) further facilitated establishment at this site due to genetic admixture and repeated introductions (i.e., high

propagule pressure; Lockwood et al. 2013). Additionally, their rapid egg production, long reproductive season, and robust eggs/embryos also enhance their success as a biological invader (Warner et al. 2012; Tiatragul et al. 2017; Hall et al. 2020). All these features may have contributed to their persistence at the greenhouse.

Despite the persistence of *A. sagrei* at this site over at least 10 generations, we previously found no evidence for thermal adaptation or changes in cold tolerance in this population (Hulbert et al. 2020). This lack of adaptation could be due to a variety of factors. First, the thermal buffering of the greenhouse during winter may have dampened the strength of selection on thermal physiology (e.g., cold or heat tolerance). Second, this population may exhibit too little additive genetic variance for cold tolerance for this trait to rapidly respond to selection. Indeed, heritable genetic variation for thermal physiology traits is low in other *A. sagrei* populations (Logan et al. 2018). Third, if multiple introductions have occurred, repeated mixing of alleles from southern populations would slow the pace of adaptation (Slatkin 1987; Lenormand 2002), though some gene flow can facilitate adaptive divergence (Garant et al. 2007). Nevertheless, the greenhouse provided suitable conditions for sustaining the population, even in the absence of adaptation.

Because outdoor winter temperatures frequently drop below the CT_{\min} and the lethal limit (i.e., freezing) for *A. sagrei* (Supplemental Fig. S2), individuals that remain in the greenhouse during winter months are important for population stability. Dispersal away from the greenhouse is likely detrimental, and winter temperatures likely exert strong selection against dispersal in this population. We show that *A. sagrei* does not move far from their initial capture location; only about 20% of individuals travelled over 20 m within the greenhouse, only 6.5% of captures (36 of 557 captures) occurred outside the greenhouse (within ~ 10 m), and only two individuals were found at greater distances (~ 30 m) (Supplemental Fig. S1). Moreover, the average distance that these lizards moved was substantially shorter than the length of the greenhouse, which suggests that likelihood of movement far from the greenhouse is low. These short movements are consistent with the short dispersal distances measured in native populations (Schoener and Schoener 1982; Calsbeek 2009; Calsbeek et al. 2014). Dispersal is an important component of life

history for many organisms (Clobert et al. 2012), but this behavior can be costly (Bonte et al. 2012) and particularly detrimental at our study site since surrounding habitat is not thermally tolerable for *A. sagrei* during winter. Although the rural setting of our study population likely limits the potential spread of *A. sagrei* into the surrounding landscape, the documented dispersal across unsuitable habitat is usually human-mediated and has certainly been important for its spread across its near global range (Norval et al. 2002; Kolbe et al. 2004; Fisher et al. 2020). In the case of the present study, however, human structures that thermally buffer individuals from winter temperatures are likely required for populations to spread to higher latitudes, which will restrict the poleward spread of *A. sagrei* to urban areas or human structures within rural areas. A similar dependency on human structures has been observed in other lizard species, which is likely responsible for their persistence at high latitudes (Locey and Stone 2006; Platt et al. 2008).

The extinction of the *A. sagrei* population documented here was almost certainly due to a change in the greenhouse (loss of the roof) that exposed individuals to lethal winter temperatures, rather than dispersal of individuals or lack of detectability. For example, the presence of a large population across years, short movement distances of individuals, and non-significant relationship between time and distance travelled, suggest that the disappearance of this population after winter was not because the lizards moved elsewhere or that we could not find them. Moreover, the lack of post-winter detectability of surviving *A. sagrei* in 2018 is unlikely given detectability of *S. undulatus* at this time (Supplemental Table S5a). Indeed, although *S. undulatus* travels further distances (Angilletta et al. 2009; this study) and was considerably less abundant than *A. sagrei* prior to winter, numerous individuals were still found post-winter (in addition to native anoles, Table S1). This further supports our conclusion that the disappearance of *A. sagrei* was caused by exposure to freezing temperatures that previous generations were shielded from while inside the greenhouse. Moreover, external air temperature during the winter without the roof was not unusually cold: seven previous years reached similar or colder temperatures than those reported at our site in winter 2017/2018 (Supplemental Fig. S2), yet the *A. sagrei* population persisted across these winters. This observation supports the assertion

that the change in indoor temperature (due to the loss of the roof) drove the extinction rather than a particularly cold winter. Importantly, however, although our results point towards changes in winter temperature (due to changes in human-constructed thermal refugia) as being the driver of population extinction, a replicated experimental study is critical to demonstrate this causal relationship.

The rapid extinction of this *A. sagrei* population suggests that behavior and physiological adaptation were insufficient to sustain this non-native population without the thermal buffering of the greenhouse roof. Although overwinter survival of *A. sagrei* has been reported at other plant nurseries (in southeast Louisiana), minimum temperatures at those sites did not drop below 10 °C (Wiley 2005). At our site, temperatures of all microhabitats frequently dropped below freezing, and thus, behavioral choice of overwinter microhabitat did not shield individuals from lethal temperatures (as in native anoles; Bishop and Echternacht 2004). Although extreme winter events can place strong selection on cold tolerance and generate local adaptation in native *Anolis carolinensis* (Campbell-Staton et al. 2017), standing genetic variance for tolerance of sub-freezing temperatures was unlikely present in this *A. sagrei* population. Unlike *A. sagrei*, native species at our study site (e.g., *S. undulatus* and *A. carolinensis*) are physiologically adapted to local temperatures and can tolerate freezing (Lowe et al. 1971; Pauly 2012), which explains their overwinter survival. Although the number of individuals captured for both these native species were similar before vs. after winter 2017/2018 (Supplemental Table S1), reduced winter survival rate for *S. undulatus* (Fig. 3; Supplemental Table S5b) implies some benefit from the greenhouse for this native population.

Hurricane-induced extinctions have been documented previously for island populations of *A. sagrei* (Spiller et al. 1998; Kolbe et al. 2012), but to our knowledge, such extinctions have never been reported for established mainland populations. Rather, anecdotal evidence suggests that mainland *A. sagrei* in Florida may indirectly benefit from hurricanes because fallen trees create an abundance of preferred habitat (i.e., open-canopy, sunny patches; Meshaka 1993). Our study population was a special case because hurricane force winds indirectly caused the extinction of a mainland population by partially destroying the human structure upon which the

population depended. Although mainland populations of *A. sagrei* in Florida also experience freezing temperatures in winter, their persistence is likely due to their proximity to substantially larger and continuous populations, as well as far more suitable refuge sites than present at our greenhouse. Thus, even if some populations in Florida are reduced by freezing temperatures, their high reproductive rates will likely enable populations to quickly recover even with few survivors (Kolbe et al. 2012). Although we did not experimentally identify the causal links among the loss of the greenhouse roof, change in microhabitat winter temperature, and extinction of this population, our data strongly suggest that human structures produce thermally-suitable habitat, thereby facilitating establishment and persistence of non-native populations, and that subsequent changes in these structures can then rapidly drive populations to extinction.

Conclusions

This study provides a unique examination of interactions among three elements of global change – biological invasion, human modified habitat, and extreme weather events. Specifically, we show that human structures can enhance establishment of introduced species, but once established, non-native populations may depend upon those structures for survival. Evidence for this dependency was demonstrated by the disturbance caused by an extreme weather event (which are expected to increase under climate change; Mann et al. 2017; Stott 2016) that rapidly altered the environment, indirectly driving this population to extinction. Many non-native species depend on human-made structures for persistence, but due to future climate warming, established populations might move into the surrounding landscape. Such a possibility illustrates the complex interactions among different aspects of global change with respect to invasion biology. Because extinctions of established non-native populations are rarely documented, our study provides unique insight into the factors that facilitate or hinder biological invasion. Although non-native populations like the one reported here may eventually reach relatively large sizes, these populations are still highly vulnerable to environmental

perturbation, especially when environmental conditions drop below physiological tolerances.

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References

- Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol Evol* 30:114–126. <https://doi.org/10.1016/j.tree.2014.11.007>
- Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. *J Wildl Manag* 66:912–918
- Angilletta MJ, Sears MW, Pringle RM (2009) Spatial dynamics of nesting behavior: lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology* 90:2933–2939
- Beshada E, Zhang Q, Boris R (2006) Winter performance of a solar energy greenhouse in southern Manitoba. *Can Biosyst Eng* 48:5.1–5.8
- Bishop D, Echternacht A (2004) Emergence behavior and movements of winter-aggregated green anoles (*Anolis carolinensis*) and the thermal characteristics of their crevices in Tennessee. *Herpetologica* 60:168–177
- Blackburn T, Pysek P, Bacher S et al (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Bonte D, Van Dyck H, Bullock JM et al (2012) Costs of dispersal. *Biol Rev* 87:290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>
- Cadotte MW, Yasui SLE, Livingstone S, MacIvor JS (2017) Are urban systems beneficial, detrimental, or indifferent for

- biological invasion? *Biol Invasions* 19:3489–3503. <https://doi.org/10.1007/s10530-017-1586-y>
- Calsbeek R (2009) Sex-specific adult dispersal and its selective consequences in the brown anole, *Anolis sagrei*. *J Anim Ecol* 78:617–624
- Calsbeek R, Duryea MC, Parker E, Cox RM (2014) Sex-biased juvenile dispersal is adaptive but does not create genetic structure in island lizards. *Behav Ecol* 25:1157–1163. <https://doi.org/10.1093/beheco/aru102>
- Campbell-Staton S, Edwards S, Losos J (2016) Climate-mediated adaptation after mainland colonization of an ancestrally subtropical island lizard, *Anolis carolinensis*. *J Evol Biol* 29:2168–2180. <https://doi.org/10.1111/jeb.12935>
- Campbell-Staton S, Chevignon Z, Rochette N et al (2017) Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science* 357:495–498. <https://doi.org/10.1126/science.aam5512>
- Campbell-Staton S, Winchell K, Rochette N et al (2020) Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat Ecol Evol* 4:652–658
- Choquet R, Rouan L, Pradel R (2009) Program E-SURGE: a software application for fitting multievent models. Springer, New York
- Clobert J, Baguette M, Benton T, Bullock J (2012) Dispersal ecology and evolution. Oxford University Press, Oxford
- Cox RM, Calsbeek R (2010) An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. *J Evol Biol* 24:343–353. <https://doi.org/10.1111/j.1420-9101.2010.02171.x>
- Cox RM, Stenquist DS, Calsbeek R (2009) Testosterone, growth and the evolution of sexual size dimorphism. *J Evol Biol* 22:1586–1598. <https://doi.org/10.1111/j.1420-9101.2009.01772.x>
- Crenshaw J (1955) The life history of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille. *Am Midl Nat* 54:257–298. [https://doi.org/10.1674/0003-0031\(2001\)146](https://doi.org/10.1674/0003-0031(2001)146)
- Crooks J (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Écoscience* 12:316–329. <https://doi.org/10.2980/i1195-6860-12-3-316.1>
- Crooks J, Soule M (2001) Lag times in population explosions of invasive species: causes and implications. In: Sandlund O, Johan Schei P, Viken A (eds) *Invasive species and biodiversity management*. Kluwer Academic, Dordrecht, pp 103–125
- Donihue C, Herrel A, Fabre A et al (2018) Hurricane-induced selection on the morphology of an island lizard. *Nature* 560:88–91. <https://doi.org/10.1038/s41586-018-0352-3>
- Edwards JR, Lailvaux SP (2012) Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. *Ethology* 118:494–502. <https://doi.org/10.1111/j.1439-0310.2012.02037.x>
- Ferguson G, Bohlen C, Woolley H (1980) *Sceloporus undulatus*: comparative life history and regulation of a Kansas population. *Ecology* 61:313–322
- Ferner JW (1974) Home-range size and overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae). *Copeia* 1974:332–337. <https://doi.org/10.2307/1442527>
- Fisher S, Del Pinto L, Fisher R (2020) Establishment of brown anoles (*Anolis sagrei*) across a southern California county and their interactions with a native lizard species. *PeerJ* 8:1–12. <https://doi.org/10.7717/peerj.8937>
- Frederiksen M, Daunt F, Harris M, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *J Anim Ecol* 77:1020–1029
- Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct Ecol* 21:434–443. <https://doi.org/10.1111/j.1365-2435.2006.01228.x>
- Gavier-Pizarro GI, Radeloff VC, Stewart SI et al (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecol Appl* 20:1913–1925. <https://doi.org/10.1890/09-2168.1>
- Goldberg SR, Bursley CR (2000) Transport of helminths to Hawaii via the brown anole, *Anolis sagrei* (Polychrotidae). *J Parasitol* 86:750–755. <https://doi.org/10.2307/3284959>
- Gonzalez-Bernal E, Greenlees M, Brown G, Shine R (2016) Toads in the backyard: why do invasive cane toads (*Rhinella marina*) prefer buildings to bushland? *Popul Ecol* 58:293–302. <https://doi.org/10.1007/s10144-016-0539-0>
- Gunderson AR, Leal M (2012) Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. *Funct Ecol* 26:783–793. <https://doi.org/10.1111/j.1365-2435.2012.01987.x>
- Hall JM, Warner DA (2019) Thermal tolerance in the urban heat island: thermal sensitivity varies ontogenetically and differs between embryos of two sympatric ectotherms. *J Exp Biol*. <https://doi.org/10.1242/jeb.210708>
- Hall J, Mitchell T, Thawley C et al (2020) Adaptive seasonal shift towards investment in fewer, larger offspring: evidence from field and laboratory studies. *J Anim Ecol*. <https://doi.org/10.1111/1365-2656.13182>
- Hein EA, Whitaker SJ (1997) Homing in eastern fence lizards (*Sceloporus undulatus*) following short-distance translocation. *Gt Basin Nat* 57:348–351
- Huang SC, Norval G, Wei CS, Tso IM (2008) Effects of the brown anole invasion and betelnut palm planting on arthropod diversity in southern Taiwan. *Zoolog Sci* 25:1121–1129. <https://doi.org/10.2108/zsj.25.1121>
- Hufbauer RA, Facon B, Ravigné V et al (2012) Anthropogenically induced adaptation to invade (AIAD): contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evol Appl* 5:89–101. <https://doi.org/10.1111/j.1752-4571.2011.00211.x>
- Hulbert AC, Hall JM, Mitchell TS, Warner DA (2020) Use of human-made structures facilitates persistence of a non-native ectotherm. *Biol Invasions*. <https://doi.org/10.1007/s10530-020-02236-2>
- Kalnay E, Cai M (2003) Impact of urbanization and land-use change on climate. *Nature* 423:528–532. <https://doi.org/10.1038/nature01649.1>
- Kolbe JJ, Glor RE, Schettino LR et al (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–181. <https://doi.org/10.1038/nature02807>
- Kolbe JJ, Schoener TW, Spiller DA, Losos JB (2012) Founder effects persist despite adaptive differentiation: a field experiment with lizards. *Science* 335:1086–1089
- Kolbe J, Ehrenberger J, Moniz H, Angilletta M (2014) Physiological variation among invasive populations of the brown

- anole (*Anolis sagrei*). *Physiol Biochem Zool* 87:92–104. <https://doi.org/10.1086/672157>
- Kolbe JJ, Vanmiddlesworth P, Battles AC et al (2016) Determinants of spread in an urban landscape by an introduced lizard. *Landsc Ecol* 31:1795–1813. <https://doi.org/10.1007/s10980-016-0362-1>
- Kustra M, Kahl A, Reedy A et al (2019) Sperm morphology and count vary with fine-scale changes in local density in wild lizard population. *Oecologia* 191:555–564
- Larkin DJ (2012) Lengths and correlates of lag phases in upper-Midwest plant invasions. *Biol Invasions* 14:827–838. <https://doi.org/10.1007/s10530-011-0119-3>
- Latella IM, Poe S, Giermakowski JT (2011) Traits associated with naturalization in *Anolis* lizards: comparison of morphological, distributional, anthropogenic, and phylogenetic models. *Biol Invasions* 13:845–856. <https://doi.org/10.1007/s10530-010-9873-x>
- Lebreton J-D, Burnham K, Clobert J, Anderson D (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lee JC, Clayton D, Eisenstein S, Perez I (1989) The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989:930–937. <https://doi.org/10.2307/1445979>
- Lenormand T (2002) Gene flow and the limits to natural selection. *Trends Ecol Evol* 17:183–189. <https://doi.org/10.1111/j.1365-2184.1976.tb01248.x>
- Locey K, Stone P (2006) Factors affecting range expansion in the introduced Mediterranean gecko, *Hemidactylus Turcicus*. *J Herpetol* 40:526–530
- Lockwood J, Hoopes M, Marchetti M (2013) *Invasion ecology*, 2nd edn. Wiley, Hoboken
- Logan ML, Curlis JD, Gilbert AL et al (2018) Thermal physiology and thermoregulatory behaviour exhibit low heritability despite genetic divergence between lizard populations. *Proc R Soc B Biol Sci*. <https://doi.org/10.1098/rspb.2018.0697>
- Losos JB, Warheitt KI, Schoener T (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73
- Lowe C, Lardner P, Halpern E (1971) Supercooling in reptiles and other vertebrates. *Comp Biochem Physiol A* 39:125–135
- Mack R, Simberloff D, Lonsdale W et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Mahrdr CR, Ervin EL, Nafis G (2014) Geographic distribution: *Anolis sagrei*. *Herpetol Rev* 45:658–659
- Mann ME, Rahmstorf S, Kornhuber K et al (2017) Influence of anthropogenic climate change on planetary wave resonance and extreme weather events. *Sci Rep*. <https://doi.org/10.1038/srep45242>
- Mazzotti FJ, Cherkiss MS, Hart KM et al (2011) Cold-induced mortality of invasive Burmese pythons in south Florida. *Biol Invasions* 13:143–151. <https://doi.org/10.1007/s10530-010-9797-5>
- Meshaka W (1993) Hurricane Andrew and the colonization of five invading species in South Florida. *Florida Sci* 56:193–201
- Muralidhar P, Johnson MA (2017) Sexual selection and sex ratios in *Anolis* lizards. *J Zool* 302:178–183. <https://doi.org/10.1111/jzo.12446>
- Norval G, Chen CK (2012) The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russ J Herpetol* 17:131–138
- Norval G, Mao J, Chu H, Chen L (2002) A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zool Stud* 41:332–335
- Parker WS (1994) Demography of the fence lizard, *Sceloporus undulatus*, in northern Mississippi. *Copeia* 1994:136–152
- Parmley D (2002) Northernmost record of the brown anole (*Anolis sagrei*) in Georgia. *Geog J Sci* 60:191–193
- Pauly GB (2012) Evidence for freeze tolerance in the eastern fence lizard (*Sceloporus undulatus*). *Southwest Nat* 57:472–473. <https://doi.org/10.1894/0038-4909-57.4.472>
- Phillips BL, Shine R (2006) Allometry and selection in a novel predator-prey system: Australian snakes and the invading cane toad. *Oikos* 112:122–130. <https://doi.org/10.1111/j.0030-1299.2006.13795.x>
- Platt S, Rainwater T, Miller S (2008) Geographic distribution, *Hemidactylus turcicus*. *Herpetol Rev* 39:238
- Pounds J, Jackson J (1983) Utilization of perch sites by sex and size classes of *Sceloporus undulatus undulatus*. *J Herpetol* 17:287–289
- Reagan DP (2019) The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. *Biotropica* 23:468–474
- Rogers CS (2019) Immediate effects of hurricanes on a diverse coral/mangrove ecosystem in the U.S. Virgin Islands and the potential for recovery. *Diversity*. <https://doi.org/10.3390/d11080130>
- Sacchi R, Gentilli A, Razzetti E, Barbieri F (2002) Effects of building features on density and flock distribution of feral pigeons *Columba livia* var. *domestica* in an urban environment. *Can J Zool* 54:48–54. <https://doi.org/10.1139/Z01-202>
- Savage AM, Youngsteadt E, Ernst AF et al (2018) Homogenizing an urban habitat mosaic: arthropod diversity declines in New York City parks after Super Storm Sandy. *Ecol Appl* 28:225–236. <https://doi.org/10.1002/eap.1643>
- Schoener T, Schoener A (1980) Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *J Anim Ecol* 49:19–53
- Schoener T, Schoener A (1982) Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* 63:809–823
- Schoener TW, Spiller DA, Losos JB (2004) Variable ecological effects of hurricanes: the importance of seasonal timing for survival of lizards on Bahamian islands. *Proc Natl Acad Sci* 101:177–181
- Sergio F, Blas J, Hiraldo F (2018) Animal responses to natural disturbance and climate extremes: a review. *Glob Planet Change* 161:28–40. <https://doi.org/10.1016/j.gloplacha.2017.10.009>
- Slatkin M (1987) Gene flow and the geographic structure of natural populations. *Science* 236:787–892
- Spiller DA, Losos JB, Schoener TW (1998) Impact of a catastrophic hurricane on island populations. *Science* 281:695–698

- Steffen J, Birkhead R (2007) *Norops sagrei* (Brown Anole). *Herpetol Rev* 38:353
- Stott P (2016) How climate change affects extreme weather events. *Science* 352:1517–1518. <https://doi.org/10.1126/science.aaf7271>
- Stroud JT, Giery ST, Outerbridge ME (2017) Establishment of *Anolis sagrei* on Bermuda represents a novel ecological threat to critically endangered Bermuda skinks (*Plestiodon longirostris*). *Biol Invasions* 19:1723–1731. <https://doi.org/10.1007/s10530-017-1389-1>
- Stroud JT, Colom M, Ferrer P et al (2019) Behavioral shifts with urbanization may facilitate biological invasion of a widespread lizard. *Urban Ecosyst* 22:425–434. <https://doi.org/10.1007/s11252-019-0831-9>
- Stuart Y, Campbell T, Hohenlohe P et al (2014) Rapid evolution of a native species following invasion by a congener. *Science* 346:463–466
- Suzuki-Ohno Y, Morita K, Nagata N et al (2017) Factors restricting the range expansion of the invasive green anole *Anolis carolinensis* on Okinawa Island, Japan. *Ecol Evol* 7:4357–4366. <https://doi.org/10.1002/ece3.3002>
- Tay A (2019) Brown anole in a plant nursery at Thomson Road. *Singapore Biodivers Rec* 2019:82
- Tiatragul S, Kurniawan A, Kolbe JJ, Warner DA (2017) Embryos of non-native anoles are robust to urban thermal environments. *J Therm Biol* 65:119–124. <https://doi.org/10.1016/j.jtherbio.2017.02.021>
- Tiatragul S, Hall JM, Pavlik NG, Warner DA (2019) Lizard nest environments differ between suburban and forest habitats. *Biol J Linn Soc* 126:392–403. <https://doi.org/10.1093/biolinnean/bly204>
- Tinkle D, Ballinger R (1972) *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53:570–584
- Tinsley RC, Stott LC, Viney ME et al (2015) Extinction of an introduced warm-climate alien species, *Xenopus laevis*, by extreme weather events. *Biol Invasions* 17:3183–3195. <https://doi.org/10.1007/s10530-015-0944-x>
- van den Burg MP, Brisbane JLK, Knapp CR (2020) Post-hurricane relief facilitates invasion and establishment of two invasive alien vertebrate species in the Commonwealth of Dominica, West Indies. *Biol Invasions* 22:195–203. <https://doi.org/10.1007/s10530-019-02107-5>
- Vinegar MB (1975) Life history phenomena in two populations of the lizard *Sceloporus undulatus* in Southwestern New Mexico. *Am Midl Nat* 93:388. <https://doi.org/10.2307/2424171>
- Walther GR (2010) Community and ecosystem responses to recent climate change. *Philos Trans R Soc B Biol Sci* 365:2019–2024. <https://doi.org/10.1098/rstb.2010.0021>
- Warner D, Moody MA, Telemeco R, Kolbe JJ (2012) Egg environments have large effects on embryonic development, but have minimal consequences for hatchling phenotypes in an invasive lizard. *Biol J Linn Soc* 105:25–41. <https://doi.org/10.1111/j.1095-8312.2011.01778.x>
- Wiley M (2005) Population density and over-wintering of an exotic lizard, the brown anole *Anolis sagrei*, and an evaluation of anole distribution in LaFourche and Terrebonne parishes, Louisiana. MS thesis, Nicholls State University
- Williamson M, Fitter A (1996) The varying success of invaders. *Ecology* 77:1661–1666
- Willson J, Dorcas M, Snow R (2011) Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida. *Biol Invasions* 13:1493–1504. <https://doi.org/10.1007/s10530-010-9908-3>
- Winchell KM, Reynolds RG, Prado-Irwin SR et al (2016) Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution* 70:1009–1022. <https://doi.org/10.1111/evo.12925>
- Youngsteadt E, Dale A, Terando A et al (2015) Do cities simulate climate change? A comparison of herbivore response to urban and global warming. *Glob Chang Biol* 21:97–105. <https://doi.org/10.1111/gcb.12692>

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