

Habitat structure mediates vulnerability to climate change through its effects on thermoregulatory behavior

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Abstract

Tropical ectotherms are thought to be especially vulnerable to climate change because they are thermal specialists, having evolved in aseasonal thermal environments. However, even within the tropics, habitat structure can influence opportunities for behavioral thermoregulation. Open (and edge) habitats likely promote more effective thermoregulation due to the high spatial heterogeneity of the thermal landscape, while forests are thermally homogenous and may constrain opportunities for behavioral buffering of environmental temperatures. Nevertheless, the ways in which behavior and physiology interact at local scales to influence the response to climate change are rarely investigated. We examined the thermal ecology and physiology of two lizard species that occupy distinct environments in the tropics. The brown anole lizard (*Anolis sagrei*) lives along forest edges in The Bahamas, whereas the Panamanian slender anole (*Anolis apletophallus*) lives under the canopy of mature forests in Panama. We combined detailed estimates of environmental variation, thermoregulatory behavior, and physiology to model the vulnerability of each of these species. Our projections suggest that forest-dwelling slender anoles will experience severely reduced locomotor performance, activity time, and energy budgets as the climate warms over the coming century. Conversely, the forest-edge-dwelling brown anoles may use behavioral compensation in the face of warming, maintaining population viability for many decades. Our results indicate that local habitat variation, through its effects on behavior and physiology, is a major determinant of vulnerability to climate change. When attempting to predict the impacts of climate change on a given population, broad-scale characteristics such as latitude may have limited predictive power.

KEYWORDS

Anolis, climate change, thermal niche, thermal performance curve, thermoregulatory behavior

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1 | INTRODUCTION

Several global- and regional-scale analyses have suggested that tropical ectotherms are more vulnerable to the effects of anthropogenic climate change than species at higher latitudes (Deutsch et al., 2008; Huey et al., 2009; Kearney et al., 2009; Sinervo et al., 2010; Sunday et al., 2010, 2014; Tewksbury et al., 2008; Urban et al., 2012). Tropical species are projected to experience greater restrictions in activity (Sinervo et al., 2010), physiological performance (Huey et al., 2009; Sunday et al., 2011, 2014), and energy budgets (Kearney et al., 2009), and greater declines in population growth rates (Deutsch et al., 2008) relative to temperate species. These predictions are based on the observation that the seasonally stable nature of tropical thermal environments has led to the evolution of narrow thermal niches, or thermal specialization (Deutsch et al., 2008; Huey et al., 2009; Kearney et al., 2009; Sinervo et al., 2010; Sunday et al., 2010, 2014; Tewksbury et al., 2008).

The prediction that tropical species may be more vulnerable to thermal change is reasonable, because, as with any niche specialist, thermal specialists should have limited capacity to maintain fitness when their environment shifts. Nevertheless, to encompass many species over vast geographic areas, global-scale studies often rely on coarse-scale climatic data (e.g., low-resolution temperature layers from WorldClim.org), simplistic measures of thermal physiology (e.g., critical thermal limits), and an assumption of thermoconformity (i.e., equating organismal body temperature with average air temperature). Moreover, global-scale analyses focus on macroecological variables and rarely consider the potential for in situ responses (e.g., plasticity and genetic adaptation). This approach, which has undoubtedly been useful in generating global-scale hypotheses, may mask substantial local variation in the vulnerability of populations (Fey et al., 2019; Gunderson & Leal, 2012, 2016; Logan et al., 2013, 2019; Potter et al., 2013; Sears et al., 2011).

The tropics contain a diverse array of terrestrial habitat types that can favor alternative behavioral strategies for maintaining optimal body temperatures (Gunderson & Leal, 2012; Kaspari et al., 2015; Logan et al., 2015). Many tropical species live in open or edge habitats that provide high levels of thermal heterogeneity (Gunderson & Leal, 2012; Logan et al., 2013). These habitats favor the behavioral strategy of thermoregulation, whereby individuals can shuttle between microclimates to maintain narrow body temperature distributions (Huey, 1974). Thermoregulators maintain stable internal body temperatures even as the ambient environment fluctuates (Hertz et al., 1993; Huey, 1974; Huey & Kingsolver, 1989; Huey & Slatkin, 1976). In contrast, there are also many tropical species that live under the shade of dense forest canopies. In these spatially homogeneous thermal environments, behavioral thermoregulation is costly because the large distances between sunny and shady microhabitat patches increase the energetic cost of behavioral shuttling (Huey et al., 2009). The thermal environments of closed-canopy tropical forests favor thermoconformity, whereby individuals allow their body temperatures to track ambient variation (Huey, 1974; Huey & Slatkin, 1976; Sears & Angilletta, 2015; Sears et al., 2016). For any

ectothermic species in any habitat, body temperature distributions ultimately depend on the interaction between thermoregulatory effort (i.e., where they fall on the continuum between perfect thermoconformity and perfect thermoregulation) and spatiotemporal variation in environmental temperature (Angilletta, 2009; Cox et al., 2018; Fey et al., 2019).

Local habitat structure, through its effects on behavior, should also affect the breadth of the thermal niche, and the populations with the broadest thermal niches should be the least vulnerable to climate change. Theory suggests that the breadth of a given population's thermal niche should correspond to that population's body temperature distribution, which is constrained by the environment (Gabriel & Lynch, 1992; Lynch & Gabriel, 1987). Populations that thermoregulate precisely should have narrow body temperature distributions and therefore narrow thermal niches. Indeed, many higher-latitude species are remarkably efficient at maintaining preferred body temperatures during activity (e.g., Agamid lizards from the southern tip of Africa [Logan et al., 2019] and Liolaemid lizards from the Andes of Argentina [Valdecantos et al., 2013]), suggesting that narrow thermal niches may be common in temperate and high elevation regions despite broad intra-annual variation in environmental temperature.

Although behavioral strategies interact with thermal landscapes to determine the thermal niches of populations, individuals also use behavior as their first line of defense when thermal environments change (Huey et al., 2003; Muñoz & Bodensteiner, 2019). Thus, the vulnerability of populations to climate change ultimately depends on the capacity to compensate for changes in temperature with behavioral adjustments, and this occurs in the context of the thermal niche (the same degree of behavioral thermoregulation has a greater compensatory effect on an organism with a narrow thermal niche; Buckley et al., 2013, 2015; Kearney et al., 2009). Without explicitly considering the interactions among thermoregulatory behavior, local thermal variation, and the breadth of the thermal niche, it is not possible to fully predict the vulnerability of ectotherm populations to climate change.

In this study, we evaluated the extent to which local habitat structure influences the predicted response to climate change in two species of tropical lizard. The brown anole (*Anolis sagrei*) lives in open and forest-edge habitat in The Bahamas (Losos et al., 2004) whereas the Panamanian slender anole (*Anolis apletophallus*; hereafter the "slender anole") occurs in closed-canopy tropical forest in Panama (Andrews & Sexton, 1981). First, we monitored field-active body temperatures in the context of the spatiotemporal structure of the thermal landscape to evaluate the thermoregulatory strategy employed by each population. Second, we examined the thermal performance breadth of each population by measuring both sprint speed and resting metabolic rate as a function of body temperature. Finally, we used these data to model the effects of rising environmental temperatures on locomotor performance, activity time, and energetics while explicitly considering the potential for behavioral buffering. We hypothesized that the physiological and behavioral phenotypes of each species would primarily be dictated by local

habitat structure and that the species with the broadest thermal performance breadth and the greatest capacity for behavioral thermoregulation would be the least vulnerable to climate change.

2 | METHODS

2.1 | Study system and experimental design

We sampled a population of adult (male SVL >35 mm; female SVL >30 mm) brown anoles on the island of Great Exuma in The Bahamas (23°31'60"N, - 75°49'60"W) and a population of adult (male and female SVL >38 mm) slender anoles from Soberanía National Park, Panama (9°6'59"N, - 79°41'47"W). Both species are generalist arthropod predators that perch at similar heights in their respective habitats (~0.5–1.5 m; Schoener, 1968; Scott et al., 1976). Both species maintain small territories (Sexton et al., 1963; Tokarz, 1998), store sperm (Calsbeek et al., 2007; Stapley, 2018), have short (<1 year) generation times (Andrews & Rand, 1974), and reach peak reproduction during northern hemisphere summers (~May–October; Andrews, 1979; Andrews & Rand, 1974; Logan et al., 2014). Nevertheless, they occur in very different structural environments. The brown anole lives in scrubby vegetation or along the edges of coppice forest (Figure S1), whereas the slender anole lives in the understory of lowland, closed-canopy forests (Figure S2).

2.2 | Environmental and field-active body temperatures

We used temperature data loggers to quantify variation in the local thermal environments available to lizards (Bakken, 1992; Bakken & Gates, 1975). We built these loggers in different ways for each species to account for the primary avenue of heat transfer in each habitat type. For brown anoles, which live in a habitat where heat transfer is dominated by solar radiation, we followed the method used by Logan et al. (2014, 2016, 2018). Brown anole data loggers were built from thin-walled, cylindrical copper piping, sized and painted to approximate the physical characteristics of an adult brown anole, and equipped with iButtons (Maxim Integrated) to record temperature. For slender anoles, which live in a habitat where heat transfer is dominated by convection, we coated iButtons in PlastiDip (PlastiDip International) for waterproofing, and then glued each to a small (10 cm) length of pine wood. To deploy data loggers (brown anole, $N = 24$; slender anole, $N = 34$), we haphazardly chose locations along linear transects meant to cover a large portion of each habitat type at our field sites. At each initially chosen location, we picked a random side of the transect (left or right), then walked a random distance from the transect (0–3 m in 1 m intervals) and placed the data logger at a random height in the vegetation (0.5–2 m in 0.5 m intervals) and orientation on the branch or tree trunk (facing upwards, facing downwards, or on the side of the branch). We programmed brown anole data loggers to record temperatures from April 17 to June 19,

2018 (every 60 min), whereas we programmed slender anole data loggers to record temperatures from July 11 to November 7, 2017 (every 100 min). Although these datasets were collected in different years, we verified that weather conditions were not anomalous at either location with respect to mean ambient conditions by examining historical weather station data (Bahamas: www.weatherunderground.com; Panama: Smithsonian Lutz Watershed Meteorological Station on Barro Colorado Island). Historical weather data are not available for the island of Great Exuma in The Bahamas, so we used data from a nearby island (New Providence). Mean annual temperatures differed by <1°C among years at each location, and as such, we treat our data logger measurements as capturing representative thermal profiles of the two different habitats. Hereafter, we refer to the temperatures recorded by these data loggers as “environmental temperatures” rather than “operative temperatures” because the latter require precise calibration with live animals. From 2018 onwards, we use data from a weather station we set up close to our field site on Great Exuma, The Bahamas (HOBO RX3000 Station, Onset Computer Co.) and the same weather station that we used to examine historical temperatures on Barro Colorado Island, Panama (Vaisala HMP60), to monitor monthly changes in ambient air temperatures at each of our field sites. We used general linear models to compare daily (0700–1800 h) and nightly (1800–0700 h) average environmental temperature (T_e), minimum T_e , and maximum T_e between sites.

At each site, as data loggers were recording environmental temperatures, we captured lizards by hand or slip noose and measured their field-active body temperatures (T_b) with an Omega HH147U type K thermocouple thermometer (brown anole, $N = 107$; slender anole, $N = 577$). We avoided pseudoreplication in The Bahamas by toe clipping individuals (two toes clipped per individual). If we captured an individual and found that it had been previously marked, it was immediately released, and no body temperature was recorded. In Panama, pseudoreplication was impossible as all captured individuals were subsequently transplanted to islands in the Panama Canal as part of a separate study. To compare thermoregulatory strategies, we fit general linear models with T_b as the dependent variable. The independent variables were mean environmental temperature (T_e) at the time of capture, species, body mass, and an interaction between T_e and species. Model comparisons were conducted with the MUMIN package in R version 3.6.2 (R Core Team 2020). We used Akaike's Information Criterion (AIC) scores to identify the best model (Akaike, 1987).

2.3 | Thermal sensitivity of locomotor performance

We measured lizard sprint speed following Logan et al. (2014, 2016, 2018) by sprinting lizards at five body temperatures that span their thermal tolerance range. Sprint speeds were measured on a group of brown anoles captured in 2011 for a previous study (Logan et al., 2014), and no other physiological trait was measured on these individuals. Similarly, sprint speed was measured in a subset of slender

anoles in 2018, and no other physiological trait was measured in those individuals. Because these species achieve different body temperature ranges in nature (see Section 3), we measured sprint speed at different sets of temperatures for each. We measured sprint speed at 15°, 22°, 28°, 35°, and 42°C in brown anoles ($N = 38$; data available only for males), and 15°, 20°, 25°, 30°, and 34°C in slender anoles ($N = 26$; males and females). Our sprint track consisted of a wooden dowel (diameter = 2.5 cm, length = 1 m) that was demarcated every 10 cm and placed at a 20° angle (to discourage hopping) in a rectangular plastic bin. We brought individuals to the desired temperature by placing them in an incubator prior to each set of trials. Typically, we left individuals in the incubator for 15–20 min to reach the target temperature for a given trial, although they were never left in the incubator for more than 5 min at the warmest trial temperature due to the risk of death from overheating. We confirmed that lizards were at the desired temperature by measuring cloacal body temperatures with an Omega HH147U type K thermocouple thermometer prior to each set of trials. We motivated lizards to run 3–4 times in quick succession at each trial temperature. We recorded each set of trials with a high-speed digital video camera (GoPro set to 120 frames per second), and videos were analyzed in the motion analysis program Kinovea (www.kinovea.org). We did not include trials in statistical analyses if they occurred more than 30 s after the lizard had been removed from the incubator due to the rapid rate at which the body temperature of small ectotherms can equilibrate to ambient conditions. We considered a lizard's sprint speed to be 0 m/s if the individual was unable to run 10 cm continuously, or if it was unable to remain on the vertical surface of the dowel without falling off. All individuals were given at least two hours' rest between trials, and no individual was sprinted at more than three temperatures per day. Lizards included in sprint speed trials were never kept in captivity for more than 72 h, and they were eventually released back to their original spot of capture.

The thermal performance curve (TPC) of each individual lizard was estimated by fitting the full set of asymmetric parabolic equations built into the program TableCurve 2D (Systat Software, Inc.) to the raw sprint data (Angilletta, 2006; Logan et al., 2013, 2014, 2016, 2018; Neel et al., 2020; Neel & McBrayer, 2018). The optimal model for each individual was selected using AIC (Akaike, 1987). From the best-fit TPC for each individual, we extracted several thermal performance traits: maximum sprint speed (P_{\max}), the thermal optimum (T_{opt}), and the performance breadth (the range of temperatures over which the individual can achieve at least 80% of maximum performance; T_{br} ; Huey & Stevenson, 1979). To accurately compare T_{opt} and T_{br} between populations, we first converted raw sprint speeds to relative sprint speeds by dividing each sprint speed value by each individual's P_{\max} . We analyzed relative instead of absolute sprint speed because the species were measured at different sets of temperatures and it is not clear how similar values of P_{\max} in different species translate into differences in fitness. To visualize the population-average TPC, we calculated each individual's mean relative sprint speed at each trial temperature and followed the same curve-fitting procedure as described above. To test for differences in thermal performance

traits between populations, we used general linear models with either " T_{opt} " or " T_{br} " as dependent variables and "species" and "body mass" (measured with a digital balance) as independent variables.

2.4 | Thermal sensitivity of resting metabolic rate

We quantified resting metabolic rates using PreSens (PreSens Precision Sensing) fiberoptic closed-system respirometry. We measured oxygen consumption (VO_2) at the ecologically relevant body temperatures of 25° and 35°C for brown anoles ($N = 32$; males and females), and 20° and 30°C for slender anoles ($N = 40$; males and females), randomizing the order of temperatures for batches of three to six individuals. In brown anoles, lizards that were assessed for RMR were also included in thermal tolerance trials (see below), but the trial order was randomized to eliminate potential order effects, and we never exposed individuals to both types of assay in the same day. In slender anoles, RMR was assessed for a subset of lizards caught in 2018, and these lizards were not exposed to any other physiological assay. No individual of either species was kept in captivity for more than 72 h during these experiments. All individuals of both species were given a minimum of 16 h in captivity prior to measurements to ensure that they were not in peak digestion, and all lizards were measured at times of the day during which they are typically active. We first placed lizards inside airtight jars (240 ml), then placed the jars inside of an incubator set to the desired trial temperature. We gave each lizard at least 1 h to acclimate to the incubator, and then measured O_2 every 2 s for 30 min thereafter. We calculated VO_2 (ml/g/h) as the mass-specific slope of O_2 depletion per unit time. To compare the thermal sensitivity of metabolic rates between populations, we calculated slopes and temperature coefficients (Q_{10}) for each individual. Q_{10} was calculated using the following standard formula:

$$Q_{10} = \frac{R_2}{R_1}^{\frac{10^\circ \text{C}}{(T_2 - T_1)}} \quad (1)$$

where R_1 is the VO_2 (ml/g/h) at the lower trial temperature (T_1 ; °C) and R_2 is the VO_2 (ml/g/h) at the upper trial temperature (T_2 ; °C). We used a general linear model to compare mean Q_{10} and slope values among populations. Neither the thermal sensitivity (Q_{10}) nor total oxygen consumption differed between the sexes for either species, so we pooled the sexes for climate change projections (see below).

2.5 | Thermal preference

We used laboratory thermal gradients to quantify each species' preferred temperatures (Bauwens et al., 1995; Bennett & Johnalder, 1984). Gradients were built from rectangular plastic bins (0.9 m long \times 0.4 m wide \times 0.3 m deep), with 250 W infrared heat bulbs suspended over one end of each bin. The temperature range in the gradients differed between species based on their respective field-active body temperature distributions and critical thermal limits (see Section

3). Thermal gradient temperatures spanned from 20° to 45°C for brown anoles ($N = 63$; males and females) and 22° to 38°C for slender anoles ($N = 55$; males and females). To record body temperatures, we inserted a type T thermocouple into each individual's cloaca and fixed it in place with a small piece of medical tape (Neel & McBrayer, 2018). We placed individuals of both species in the gradient for 1 h prior to the start of each trial to acclimate them to the unfamiliar conditions. We then measured internal body temperatures every 30 s, continuously, for 1 h thereafter. The individuals of both species that were assessed for T_{pref} were not assessed for any other physiological trait, nor were they kept in captivity for more than 72 h before being released to their original spot of capture. We decomposed the body temperature data for each individual into several different thermoregulatory traits, including the mean, minimum, maximum, standard deviation, and interquartile range (middle 50%) of temperatures selected in the gradient. To test for differences between populations, we used general linear models with each thermoregulatory trait as the dependent variable and "body mass" and "species" as independent variables.

2.6 | Thermal tolerance

We measured two proxies for upper and lower thermal tolerance limits. To measure critical thermal minima (CT_{min}), we cooled lizards (brown anoles, $N = 807$; slender anoles, $N = 813$; males and females of both species) in an incubator set to 2°C. We allowed each lizard to cool to body temperatures below the point at which they lost their righting response (established with pilot trials) and then removed the animal from the incubator and allowed it to heat back up toward room temperature. As the lizard warmed back up, we checked for a righting response every 5–10 s by gently flipping it onto its back and observing whether it could regain an upright position. We scored CT_{min} as the body temperature (measured with an Omega HH147U type K thermocouple thermometer) at which the individual regained its righting response. If a lizard failed to right itself, we gave that individual a minimum break of 30 min at room temperature before placing the lizard back in the incubator and conducting a second trial. If the lizard failed to achieve its righting response for a second time, we did not include it in the final dataset.

We also quantified the voluntary thermal maximum (VT_{max}) for each individual (brown anoles, $N = 812$; slender anole, $N = 843$; males and females of both species). VT_{max} is the upper body temperature where an animal displays fleeing behavior, and it may manifest in nature as the seeking of cooler microhabitats or thermal refugia when body temperatures reach a critical upper set point (Camacho & Rusch, 2017; Weese, 1917). To measure VT_{max} , we placed lizards that had been maintained at room temperature (22°C) inside small plastic containers within an incubator set to 50°C. We continuously observed lizards until they exhibited obvious fleeing behavior, which occurs abruptly at a threshold temperature and is easily distinguishable from normal exploratory movement around the container. Lizards typically took ~3–7 min to reach VT_{max} . Once an individual exhibited escape or fleeing behavior, we removed it from the incubator

and recorded its body temperature with an Omega HH147U type K thermocouple thermometer. This body temperature was scored as the individual's VT_{max} . Brown anoles that were assayed for CT_{min} and VT_{max} were also assayed for RMR (see above). Slender anoles that were assayed for these two traits, on the other hand, were not subjected to any other physiological or behavioral experiment. We randomized the order of exposure to different physiological assays in both species to eliminate potential order effects, and all lizards were given a minimum of 90 minutes rest between experiments. After no more than 72 h, lizards were either released back to their spot of capture or transplanted to experimental islands as part of a separate, ongoing experimental evolution study (e.g., Cox et al., 2020). We compared thermal tolerance limits between populations using general linear models with either CT_{min} or VT_{max} as dependent variables and "body mass" and "species" as independent variables.

2.7 | Projecting the impact of climate warming

We projected the effects of future climate warming on activity time, locomotor performance, and resting metabolic expenditure for each species. To do this, we first used our field-based measurements of thermoregulatory behavior to convert future environmental temperatures to future body temperatures of lizards in each habitat. As a result, all projections explicitly include the effects of behavioral buffering. We modeled thermoregulatory behavior by fitting a linear model (regression) relating field-active body temperature to mean environmental temperature (estimated as the average environmental temperature logged within 30 min of each body temperature measurement) for each species. The slope of this relationship can vary between zero and one, with a slope of zero defining perfect thermoregulation (if it overlaps with mean T_{pref}) and a slope of one defining perfect thermoconformity (Hertz et al., 1993). We retained the slope and y-intercept from these functions to predict lizard body temperatures under a range of environmental temperatures assuming that behavioral responses to warming remain consistent through the end of the century. Our projections are based on a warming scenario of a 3°C increase by the year 2100, which aligns with the IPCC's warming predictions for Central America and the Caribbean if there are no changes in global policies that limit CO₂ emissions (IPCC, 2018). We assume a uniform increase in temperature each year (+0.0365°C/year).

To project future activity levels, we assumed that lizards were active if predicted mean body temperature for the population was below the average VT_{max} for that population. We projected changes in activity time relative to present day (thus, activity time was set at 100% in the year 2019). To project changes in locomotor performance, we integrated our thermoregulatory model that predicts future body temperatures for each species with our polynomial functions that describe the relationship between body temperature and sprint performance. Again, as with activity time, we projected changes in sprint performance relative to present day. Thus, we set sprint performance for each species in 2019 to 100%. To project

changes in resting metabolic expenditure, we used standard indirect calorimetry methods (Lighton, 2008) to convert oxygen consumed (VO_2) to annual energy expenditure (kcal). We used our linear function describing the relationship between body temperature and oxygen consumption to predict energetic requirements under future climate conditions. We converted projected oxygen consumption at the annual (daytime) average environmental temperature to resting metabolic energy expenditure, assuming that both species remain active during an average of 12 hours per day over the year. We used measures of resting metabolic rates to make inferences about energy expenditure during activity because both species are sit-and-wait predators, and as such they spend large amounts of time being sedentary, even during activity hours. For example, Talbot (1979) reported that slender anoles spend over 80% of their day sitting still and scanning their environment for food. Our projections assume evolutionary stasis in thermoregulatory behavior and thermal tolerance, as well as limited potential for physiological plasticity.

3 | RESULTS

3.1 | Thermal heterogeneity and thermoregulatory strategy

Mean environmental temperature between 0700 and 1800 h and the daily maximal environmental temperature in edge habitat in The Bahamas exceeded those in forest habitat in Panama (ANOVA:

mean: $F_{1,58} = 551.90, p < 0.0001$; maximum: $F_{1,58} = 306.08, p < 0.0001$; Figure 1). By contrast, the daily minimal environmental temperature in Panama exceeded that in The Bahamas (ANOVA: minimum: $F_{1,58} = 836.73, p < 0.0001$). Average daily environmental temperature was $29.4 \pm 0.1^\circ\text{C}$ for brown anoles in The Bahamas and $25.9 \pm 0.1^\circ\text{C}$ for slender anoles in Panama. The range of average daily environmental temperatures spanned 21.0° to 40.7°C in brown anole habitat in The Bahamas and 22.9° to 29.6°C in slender anole habitat in Panama. Mean nighttime environmental temperature (between 1800 and 0700 h) was also higher in The Bahamas than in Panama but means differed much less than daytime environmental temperatures (ANOVA: average T_e : $F_{1,58} = 127.61, p < 0.0001$; maximum T_e : $F_{1,58} = 94.06, p < 0.0001$). Minimum nighttime environmental temperature was lower in The Bahamas than in Panama (ANOVA: minimum T_e : $F_{1,58} = 541.269, p < 0.0001$). The average nighttime minimum and maximum environmental temperatures spanned 19.7 – 29.6°C in The Bahamas and 22.3 – 26.6°C in Panama.

Field-active body temperatures (T_b) were higher in brown anoles ($\bar{x} = 31.86 \pm 0.20^\circ\text{C}$) than slender anoles ($\bar{x} = 28.15 \pm 0.04^\circ\text{C}$; ANCOVA: $F_{2,674} = 442.4, p < 0.0001$). Mass did not affect brown anole body temperatures (ANCOVA: $F_{2,85} = 1.25, p = 0.60$), but did affect slender anole body temperatures, with heavier lizards having slightly lower field-active body temperatures ($F_{2,495} = 230.8, p < 0.0001$). Environmental temperatures describe much of the variation in field-active body temperatures in Panama ($R^2 = 0.48, F_{2,495} = 230.8, p < 0.0001$), but not in The Bahamas ($R^2 = 0.03,$

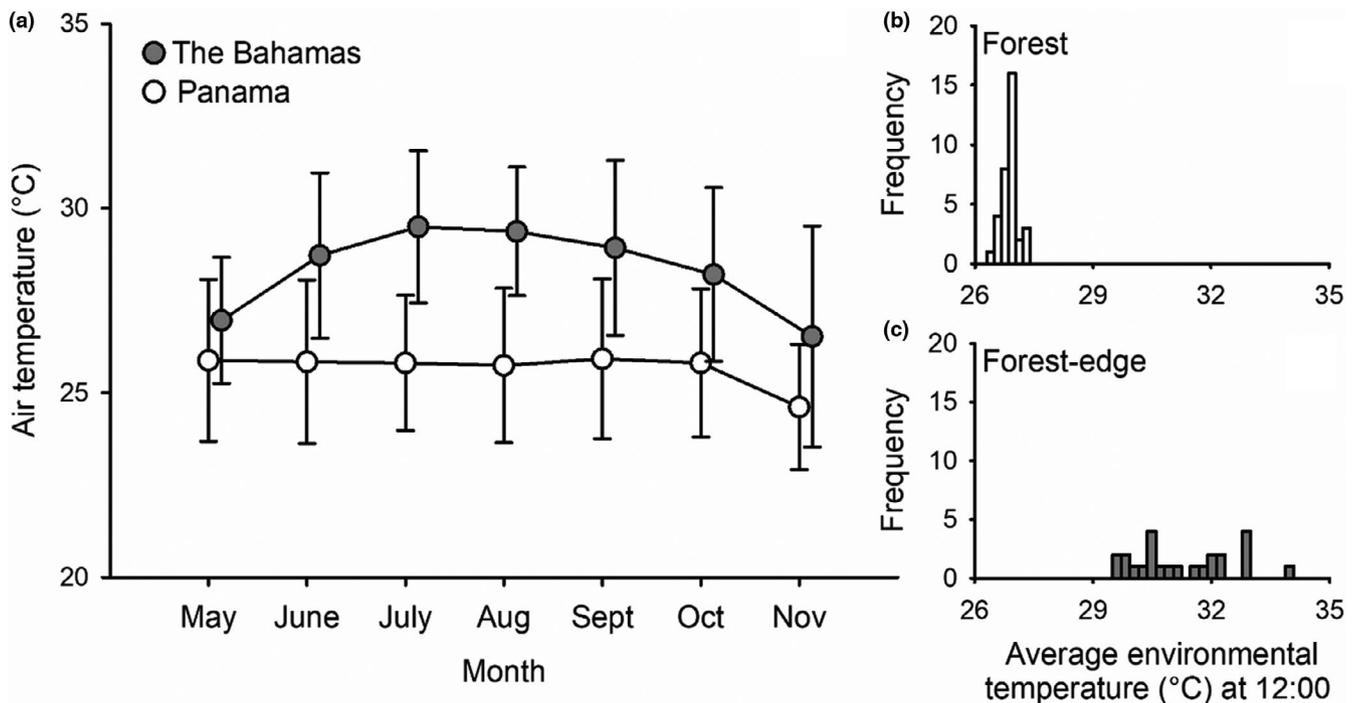


FIGURE 1 Variation in thermal environments among sites. (a) Monthly average ambient air temperature from local weather stations in Great Exuma, The Bahamas (closed circles) and Barro Colorado Island, Panama (open circles). Means \pm 1 SD are shown. (b) Frequency distributions of the average midday (1200) environmental temperatures available to lizards in Soberania National Park, Panama and (c) Great Exuma, The Bahamas, as measured via data loggers distributed randomly in the habitat of each species

$F_{2,85} = 1.25$, $p = 0.28$), and the slopes of the linear regressions between mean environmental temperature and mean field-active body temperature differed between species (ANCOVA: $F_{3,680} = 732.1$, $p < 0.0001$, Figure 2). The body temperatures of slender anoles in Panama closely tracked environmental temperatures ($M = 0.77$), whereas body temperatures of brown anoles in The Bahamas were relatively independent of environmental temperatures ($M = 0.23$).

3.2 | Thermal physiology

In a thermal gradient, brown anoles selected warmer mean (brown: $\bar{x} = 31.11 \pm 0.6^\circ\text{C}$; slender: $\bar{x} = 27.05 \pm 0.3^\circ\text{C}$; ANCOVA: $F_{2,112} = 34.34$, $p < 0.0001$), minimum (brown: $\bar{x} = 28.60 \pm 0.6^\circ\text{C}$; slender: $\bar{x} = 25.49 \pm 0.3^\circ\text{C}$; $F_{2,112} = 19.69$, $p < 0.0001$), and maximum (brown: $\bar{x} = 33.36 \pm 0.6^\circ\text{C}$; slender: $\bar{x} = 29.30 \pm 0.3^\circ\text{C}$; $F_{2,112} = 31.59$, $p < 0.0001$) temperatures, compared to slender anoles. The standard deviation of body temperatures chosen in a thermal gradient did not differ between species ($F_{2,112} = 0.68$, $p = 0.4$). The interquartile range of body temperatures chosen was $30.22^\circ - 32.09^\circ\text{C}$ for brown anoles and $26.16^\circ - 27.86^\circ\text{C}$ for slender anoles. Mass did not affect the mean (ANCOVA: $F_{2,112} = 34.34$, $p = 0.34$) or range (ANCOVA: $F_{2,112} = 1.883$, $p = 0.45$) of preferred temperatures selected in the thermal gradient.

The thermal optimum (T_{opt}) for sprint performance was higher in brown anoles ($\bar{x} = 32.23 \pm 0.76^\circ\text{C}$) than in slender anoles ($\bar{x} = 27.85 \pm 0.51^\circ\text{C}$; ANCOVA: $F_{2,58} = 10.58$, $p = 0.0001$; Figure 3). Thermal performance breadth (T_{br}) was nearly twofold larger in brown anoles ($T_{\text{br}} = 12.99 \pm 0.98$), compared to slender anoles ($T_{\text{br}} = 6.94 \pm 0.53$; ANCOVA: $F_{2,58} = 12.05$, $p < 0.0001$, Figure 3). Mass did not affect T_{opt} or T_{br} in either species (T_{opt} : ANCOVA: $F_{2,58} = 10.58$, $p = 0.72$; T_{br} : ANCOVA: $F_{2,58} = 12.05$, $p = 0.92$). The critical thermal minimum (CT_{min}) was lower in slender

anoles ($\bar{x} = 13.74 \pm 0.08^\circ\text{C}$) than brown anoles ($\bar{x} = 15.00 \pm 0.09^\circ\text{C}$; ANCOVA: $F_{3,1521} = 60.1$, $p = 0.0001$). Mass affected CT_{min} , with smaller individuals having lower CT_{min} in both species (ANCOVA: $F_{3,1521} = 60.1$, $p < 0.0001$). Maximum voluntary temperatures (VT_{max}) were higher in brown anoles ($\bar{x} = 35.78 \pm 0.08^\circ\text{C}$) than in slender anoles ($\bar{x} = 29.62 \pm 0.06^\circ\text{C}$; ANCOVA: $F_{3,1552} = 1225$, $p < 0.0001$). Mass did not affect VT_{max} in either species (ANCOVA: $F_{3,1552} = 1225$, $p = 0.062$). There was no interaction between body mass and species for either CT_{min} (ANCOVA: $F_{3,1521} = 60.1$, $p = 0.67$) or VT_{max} (ANCOVA: $F_{3,1552} = 1225$, $p = 0.32$). The thermal sensitivity of resting metabolic rate was greater in slender anoles than in brown anoles (ANCOVA: $F_{1,70} = 19.22$, $p < 0.0001$, Figure 4). The slope of the relationship between oxygen consumption (VO_2 ; ml/g/h) and body temperature was greater for slender anoles ($\bar{x} = 0.076 \pm 0.009$) than for brown anoles ($\bar{x} = 0.030 \pm 0.004$). Temperature coefficients (Q_{10}) for resting metabolic rates were also higher in slender anoles ($Q_{10} = 5.81 \pm 0.60$) compared to brown anoles ($Q_{10} = 2.88 \pm 0.67$; ANOVA: $F_{1,71} = 10.61$, $p = 0.0017$).

3.3 | Projected effects of climate warming

We projected larger declines in performance across all metrics in slender anoles compared to brown anoles (Figure 5). Annual activity levels were unaffected in both species until about the year 2045, at which point projected body temperatures for slender anoles began to rise above the species' maximum voluntary temperature (VT_{max}) for an increasing portion of the day, and their activity time begins to decline precipitously (Figure 5A). Similarly, after several decades of steady increases in environmental temperature, we project a sharp decline in locomotor performance in slender anoles, while brown anoles remained relatively unaffected (Figure 5B). Our model suggests a 32.1% decrease in relative locomotor performance for the slender anole by the year 2100, while brown anoles should experience a mere 2.7%

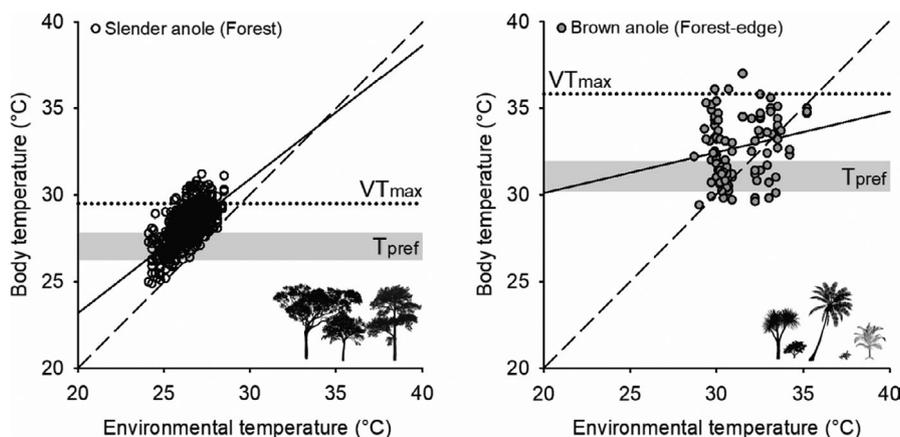


FIGURE 2 Body temperatures of slender anoles in Panama (left) and brown anoles in The Bahamas (right) as a function of mean environmental temperature (averaged across all data loggers) during the time the lizard was captured. Dashed lines represent a slope of one (perfect thermoconformity). Horizontal gray rectangles show the middle 50% of preferred temperatures selected in a thermal gradient (T_{pref}). The mean voluntary thermal maximum (VT_{max}) for each species is shown with dotted horizontal lines in each panel

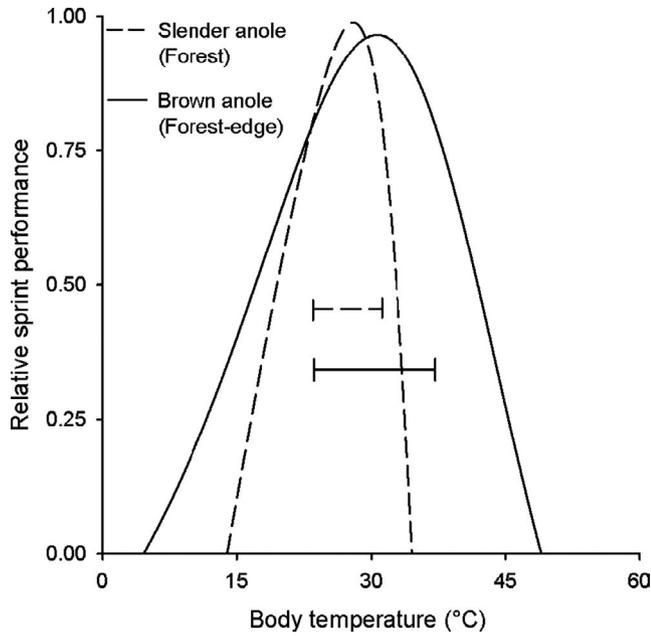


FIGURE 3 Thermal sensitivity of sprint performance in Panamanian slender anoles (dashed line) and Bahamian brown anoles (solid line). The 80% thermal performance breadths for the slender anole (dashed bracket) and brown anole (solid bracket) are also shown

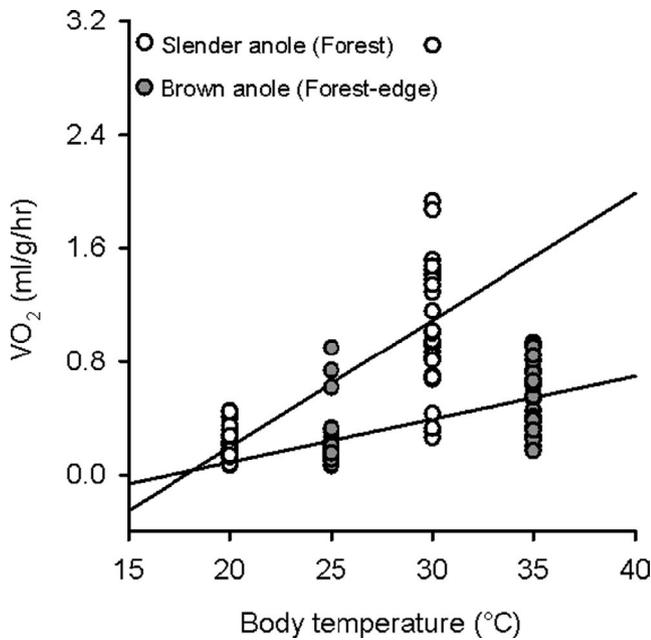


FIGURE 4 Thermal sensitivity of resting metabolic rate in Panamanian slender anoles (open circles) and Bahamian brown anoles (closed circles)

decrease in locomotor performance. Our models suggest that resting metabolic expenditure (kJ/year) will increase steadily in slender anoles while remained relatively unchanged in brown anoles through the year 2100 (Figure 5C). Whereas annual resting metabolic expenditure is predicted to increase by 18.9 kJ in slender anoles over the next century, it is predicted to increase by only 1.8 kJ in brown anoles.

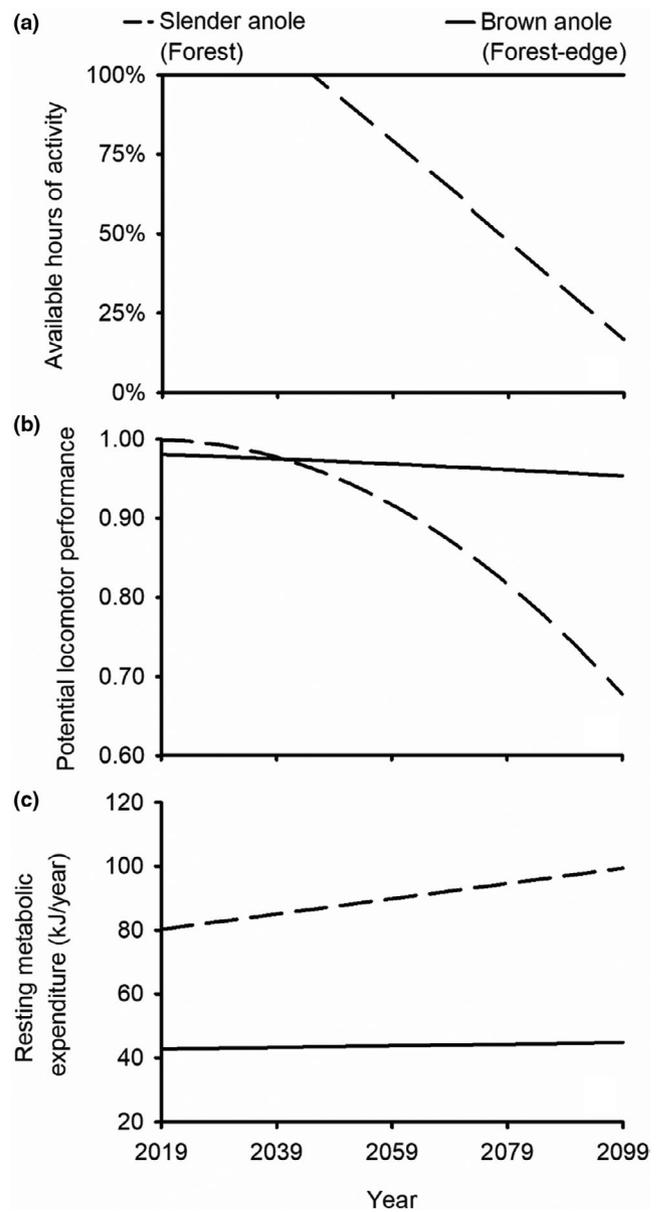


FIGURE 5 Projected changes in (a) potential activity time (assuming that lizards become inactive when predicted body temperatures exceed voluntary thermal maxima), (b) relative locomotor performance, and (c) annual energy expenditure. The projections in (a) and (b) are all relative to present day, assuming that activity and locomotor performance are currently maximized. We assumed a uniform 3°C increase in average (daytime) environmental temperature through the end of the century (+0.0365°C/year for 80 years)

4 | DISCUSSION

We integrated detailed measurements of local thermal environments, behavior, and physiology to test whether two closely related species of tropical ectotherm are likely to respond to climate change in the same way. Congruent with our hypotheses, we found that slender anoles from lowland tropical forest in Panama live in a spatially homogenous thermal environment. On average, slender anole habitat provides only 25% of the range of midday environmental

temperatures compared to brown anole habitat (Figure 1). As a result, slender anoles thermoconform, experiencing the full temporal range of temperatures in their habitat during activity. Despite their lack of thermoregulation, the low temporal variation in temperature experienced by slender anoles in Panama (Figure 1 and Figure S3) has led to a narrow thermal niche in that species. By contrast, the forest-edge-dwelling brown anole lives in a spatially heterogeneous environment (Figure 1 and Figure S4). As a result, they actively thermoregulate and maintain a narrow range of body temperatures relative to the wide range of temperatures available during activity (Figure 2). Compared to slender anoles, brown anoles had a much broader thermal niche (possibly due to the greater variation in nocturnal temperature distributions in The Bahamas). By explicitly modeling behavioral thermoregulation in the context of each population's current thermal niche, we showed that slender anoles may experience significant declines in activity and performance, while brown anoles may only be minimally impacted by future climate warming (Figure 5a–c).

Our study populations differed in thermal physiology. Brown anoles had higher thermal optima, broader performance breadths, higher thermal preferences, and higher voluntary thermal maxima, relative to slender anoles. Generally, differences in thermal physiology between populations matched differences in body temperature distributions, but the thermal physiology of our study species did not always follow our a priori predictions. For example, the slender anole had a lower CT_{min} than the brown anole despite living in a much more temporally stable thermal environment. Nighttime temperatures under the forest canopy in Soberanía National Park rarely drop below 21°C, yet this species has a CT_{min} of less than 14°C. It is unclear why this would be the case because slender anoles must only very rarely, if ever, experience temperatures this cold in lowland Panama. It seems that the abnormally low CT_{min} of this species may be linked (via pleiotropy, genetic linkage, or physical constraint) to some other physiological function that is not directly related to environmental temperature but nevertheless permits them to maintain the righting response at extremely low body temperatures (Hochachka & Somero, 2002). Regardless, the CT_{min} of slender anoles is so far outside their thermal performance breadth that it had little impact on our climate change projections for that species. Also note that body size affected some thermal traits, including field-active body temperatures in slender anoles and CT_{min} in both species, but the main effect of “species” was still significant, implying that thermal traits have adapted to local environments independent of the effects of body size.

The thermal sensitivity of resting metabolic rate was higher in slender anoles than in brown anoles. Because brown anoles experience far more thermal variation between nighttime lows and daytime highs, selection may favor a reduced thermal sensitivity of metabolic rate to help reduce the energetic burden of large temperature swings (Buckley et al., 2012; Dillon et al., 2010; Logan et al., 2019). The higher thermal sensitivity of metabolism in the slender anole, in combination with its thermoconforming behavioral strategy, has large implications for their energetic demands under

climate warming. We predict that slender anole energetic demands will increase steadily over the coming century, and this increase may lead to population declines if less energy becomes available for reproduction.

Our climate-impact models, which explicitly include the effects of behavior, suggest that slender anoles will experience substantial declines in locomotor performance and activity time. These predictions occur not only because slender anoles are thermal specialists, but also because they do not have the capacity to buffer themselves against changing conditions using thermoregulatory behavior. Interestingly, a recent analysis of 40 years' worth of slender anole abundance data demonstrated that a population on Barro Colorado Island, Panama, has been declining steadily for many years and that this decline was associated with historical climate patterns (Stapley et al., 2015). Our results suggest that population declines are likely to continue. By contrast, our projections suggest that brown anoles will experience almost no change in locomotor performance, activity time, and energetic expenditure, even when mean environmental temperatures exceed their tolerance limits. This insensitivity to global warming occurs because brown anoles actively thermoregulate, seeking out cooler microsites when the broader habitat becomes too warm.

Previous global analyses have suggested that tropical species are especially vulnerable to rapid climate change (Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2009, 2012; Sinervo et al., 2010; Sunday et al., 2010, 2014; Tewksbury et al., 2008). Our climate-impact projections that incorporated empirical measures of thermoregulatory behavior and thermal physiology generated contrasting predictions for how two low-latitude congeners will respond to climate warming (Figure 5a–c). Some of these differences were dramatic. For example, we predict that the activity time of brown anoles will be virtually unaffected by warming through the end of the century. In sharp contrast, as temperatures continue to rise, the proportion of the day where slender anoles could be active (i.e., when predicted $T_b < VT_{max}$) should begin to decrease rapidly after the year 2045. By the year 2100, if average environmental temperature has increased by 3°C, potential activity time for slender anoles is projected to decrease by more than 83% relative to present day (Figure 5A), and the slender anole would likely experience local extirpation in Soberanía National Park. Restricted windows for activity have been linked to lizard extinctions in previous studies (Sinervo et al., 2010) and may represent a critical determinant of population viability. Taken together, our fine-scale ecological, physiological, and behavioral data support the results of prior studies that suggested tropical forest ectotherms are particularly vulnerable to anthropogenic climate change (Huey et al., 2009, 2012).

Although we studied different species, an important role of habitat structure in determining behavioral strategy and physiology has also been found among populations within individual species. For example, Huey (1974) found that a population of Puerto Rican crested anoles (*Anolis cristatellus*) living in open habitat in a public park actively thermoregulated while an adjacent population living in closed-canopy forest thermoconformed. Gunderson and

Leal (2012) found a similar pattern in the same species by comparing populations living in xeric and mesic forest habitat. Neel and McBrayer (2018) discovered different patterns of thermoregulation and thermal physiology in populations of the Florida scrub lizard (*Sceloporus woodi*) occupying managed and unmanaged habitat. These patterns of intraspecific variation suggest that local habitat variation can give rise to divergent behavioral strategies, and by extension, extinction probabilities, on short temporal and fine geographic scales.

It is important to note that our analysis ignores potential avenues of in situ adaptation such as acclimation (plasticity) and genetic adaptation. A number of recent studies have suggested that thermal physiology may have the capacity to both acclimate and evolve rapidly under changing environmental conditions (Gilbert & Miles, 2017; Leal & Gunderson, 2012; Logan et al., 2014), and these processes have the potential to significantly alter climate-impact predictions (but see Logan et al., 2018, Martins et al. 2018, and Logan et al., 2019 which found low heritability of the thermal niche). Slender anoles are forced to experience the diel variation in their thermal environments during activity. Thus, in the event of climate warming, heat-intolerant individuals should be rapidly removed by selection and baseline thermal physiology could evolve relatively quickly (Lynch & Walsh, 1998). Indeed, we measured mean VT_{max} and T_b values for slender anoles that were about 1 and 0.5°C higher, respectively, than the values for these traits measured 50 years ago by Ballinger et al., (1970), although the experimental procedure for VT_{max} differed slightly between these two studies and cannot be ruled out as the source of the difference in that trait. Regardless, this pattern suggests that thermal tolerance may have already evolved (or changed via plasticity) as a result of recent climate warming. Because our climate-impact projections do not include the potentially mitigating effects of plasticity and genetic adaptation, they should be seen as likely overestimating the vulnerability of the slender anole. Additionally, tropical forests may buffer changes in temperature to some extent, reducing the magnitude of change experienced by slender anoles relative to brown anoles (De Frenne et al., 2019). Our analyses also ignore other variables that are likely to change as a result of climate change, including precipitation, cloud cover, wind dynamics, and the frequency of extreme weather events (Bonebrake & Deutsch, 2012; Bonebrake & Mastrandrea, 2010; Campbell-Staton et al., 2017; Clusella-Trullas et al., 2011; Grant et al., 2017; Logan & Cox, 2020). Finally, although we used an integrative, data-rich approach, our study consisted of a comparison of only two species, and as such, our results should be interpreted with caution. Next-generation climate-impact models should not only include estimates of local thermal environments, physiology, and behavior, but should also consider how these factors interact to constrain or facilitate in situ adaptation to multi-modal environmental change across a diverse range of species.

We found that a tropical forest lizard may be substantially more vulnerable to climate change than a closely related species living in forest-edge habitat. This pattern is likely driven by the way in which habitat structure constrains thermoregulatory buffering of suboptimal environmental temperatures (Neel & McBrayer, 2018). Tropical

lowland forests are thermally homogenous in space, and forest lizards are forced to thermoconform in these environments. Despite the thermoconforming behavior of slender anoles, the temporal stability of the thermal environment experienced by this species has resulted in a narrow thermal niche. Our projections suggest that the combination of the slender anole's narrow thermal niche with their thermoconforming behavior may reduce population sizes over the next several decades. By contrast, the edge-dwelling brown anole can shuttle between microclimates to maintain body temperatures that deviate from mean environmental temperatures. Because the brown anole has a broader thermal niche and is able to use behavior to compensate for changes in the thermal environment, they should experience minimal, if any, declines in population size. Contrary to previous studies that treat tropical organisms as uniformly vulnerable, our study suggests that local habitat structure is probably the primary factor driving variation in vulnerability. Indeed, it is likely that many temperate species are at risk under climate change, while many tropical species are not and that data on local thermal environments are necessary for accurate climate-impact forecasts.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sn02v6x3q> (Neel et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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