



# Keeping it cool to take the heat: tropical lizards have greater thermal tolerance in less disturbed habitats

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## Abstract

Global climate change has profound effects on species, especially those in habitats already altered by humans. Tropical ectotherms are predicted to be at high risk from global temperature increases, particularly those adapted to cooler temperatures at higher altitudes. We investigated how one such species, the water anole (*Anolis aquaticus*), is affected by temperature stress similar to that of a warming climate across a gradient of human-altered habitats at high elevation sites. We conducted a field survey on thermal traits and measured lizard critical thermal maxima across the sites. From the field survey, we found that (1) lizards from the least disturbed site and (2) operative temperature models of lizards placed in the least disturbed site had lower temperatures than those from sites with histories of human disturbance. Individuals from the least disturbed site also demonstrated greater tolerance to high temperatures than those from the more disturbed sites, in both their critical thermal maxima and the time spent at high temperatures prior to reaching critical thermal maxima. Our results demonstrate within-species variability in responses to high temperatures, depending on habitat type, and provide insight into how tropical reptiles may fare in a warming world.

**Keywords** *Anolis* · Anthropogenic effects · Costa Rica · CT<sub>max</sub> · Microhabitat · Primary forest · Secondary forest · Thermoconformer

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## Introduction

Global average temperatures are climbing at a rapid rate (IPCC 2018), creating diverse impacts on the physiologies of individual species (e.g., Huey et al. 2009; Kearney et al. 2009; Kingsolver et al. 2013; Domenici and Seebacher 2020). On a fundamental level, it is uncertain how species in tropical regions will respond to a warming climate (Tewksbury et al. 2008). Because there is limited seasonal temperature variability in tropical regions relative to that of temperate regions, many tropical species, especially tropical ectotherms, have evolved to function optimally in narrow temperature ranges and are deemed thermal specialists (Janzen 1967; Feder and Lynch 1982; van Berkum 1988; Ghalambor et al. 2006; Deutsch et al. 2008; Polato et al. 2018). These thermal specialists may have limited capability to acclimate to even small changes in temperature (e.g., Wright et al. 2009; Clusella-Trullas and Chown 2014). Forest-dwelling tropical ectotherms may be even more vulnerable to increased environmental temperatures, as these species tend to experience constant shade under the forest

canopy, which may further narrow their optimal temperature ranges (Huey et al. 2009).

Human land use and corresponding microhabitat availability play a major role in how climate warming affects natural ecosystems (Oliver and Morecroft 2014; Algar et al. 2018; Schulte to Bühne et al. 2021). Forest cover is an effective temperature buffer, preventing heat from penetrating into habitats inhabited by cool-adapted organisms (Caissie 2006; Senior et al. 2018), which evolved in environments with relatively low ambient temperatures. Deforestation, therefore, has immediate detrimental effects on cool-adapted ecosystems by reducing shade and increasing ground temperatures (Dale 1997). The interactive effects of land use and climate change are predicted to be more severe in warmer and wetter biomes such as tropical forests (Mantyka-Pringle et al. 2014). Generalizations regarding tropical ectotherms' responses to climate warming may misrepresent their vulnerability when not considering these interactive effects, which represent one of the greatest threats to tropical biodiversity (Brodie et al. 2012; Greenwood et al. 2016). The role of fine-scale environmental conditions can even be seen within noncritical temperature ranges—in response to only subtle changes in temperature and moisture, populations of tropical amphibians and reptiles can shrink, demonstrating that multiple factors exacerbate tropical ectotherms' responses to climate change (Whitfield et al. 2007; Rohr and Palmer 2013). Tropical ectotherms may be at an enhanced risk of population declines if they live in human-impacted environments, as the potential role of microhabitat in mitigating the impacts of climate warming could be offset by broad-scale anthropogenic changes to habitat.

The water anole, *Anolis aquaticus*, is a tropical semi-aquatic lizard found near streams on lowland and premontane wet forests of southwestern Costa Rica and Panama (Savage 2002). *Anolis aquaticus* is small and brightly colored and uses boulders and rock crevices as refugia (Boyer and Swierk 2017; Putman et al. 2018), often diving into the water and remaining there for extended periods to escape threats (Swierk 2019; Boccia et al. 2021). This species is considered to be a thermoconformer (Savage 2002): its body temperature changes with the external temperature largely without additional thermoregulation (e.g., basking). Notably, *A. aquaticus* is a particularly cool-adapted species for the tropics, with field body temperatures averaging 20.8 °C over 4 years of study (Swierk, unpubl. data).

To evaluate how anthropogenic land use may affect populations of cool-adapted tropical forest ectotherms as temperature changes over time, we investigated the thermal ecology and thermal tolerances of *A. aquaticus* from sites along a gradient of human disturbance. We predicted that the availability of thermally suitable microhabitats along this disturbance gradient would vary, and that more disturbed sites would have higher ambient temperatures and, relatedly,

higher lizard operative environmental and body temperatures. We then examined whether lizards from warmer (potentially more disturbed) sites would experience either enhanced or reduced tolerances to higher temperatures. Individuals from warmer sites may better tolerate higher temperatures when exposed to short-term temperature stress, as they may already be acclimated to higher temperatures (e.g., Yang et al. 2008; Campbell-Staton et al. 2020). Alternatively, warmer sites could negatively affect lizard thermal tolerance due to their need to seek thermal refuge for larger portions of the day, a lack of thermally appropriate microhabitats, and/or chronic thermal stress (e.g., Sunday et al. 2014; Gunderson and Leal 2016; Kubisch et al. 2016; Ortega et al. 2016). Together, our predictions address the larger question of how tropical ectotherms will fare with projected temperature increases in a warming world.

## Methods

### Study sites

We conducted this study in 2016 and 2018 at Las Cruces Biological Station (LCBS), Coto Brus, Puntarenas Province, Costa Rica. LCBS is a wet forest at 1200 m a.s.l. consisting of a mosaic of primary and secondary forest at multiple stages of regrowth. Our study used three streamside sites within LCBS that represent a continuum of human disturbance: a primary forest ("PR"; Rio Gamboa, 0% secondary forest in a 200-m buffer of the collection site), an intermediate site ("IN"; Rio Java, 46% secondary forest), and a disturbed site ("DI"; Rio Cusingo, 87% secondary forest, consisting mostly of abandoned pasture land) (GIS Department, Las Cruces Biological Station, Organization for Tropical Studies; unpubl. data). The three sites were each separated from each other by 700 to 800 m and are otherwise similar in physical characteristics: tree- and boulder-lined small streams (averaging ~2.5 m in width and less than 2 m in depth) with steep banks and occasional small islands of vegetation.

We quantified differences in ecologically relevant temperatures for water anoles at sites along this disturbance gradient. We constructed operative temperature models (OTMs) containing iButtons (DS1921G-F5; Maxim/Dallas Semiconductor, Dallas, TX). Each cylindrical OTMs (6 × 2 cm; L × D) was made of copper pipe and painted brown to resemble *A. aquaticus* dorsal coloration to approximate realistic light reflectance and absorbance (Dzialowski 2005). Each site was monitored using eight OTMs for three nonconsecutive 3-day periods in July 2018 (i.e., the same month the thermal studies, described below, were conducted). At the start of each 3-day period, we secured the 8 OTMs on known lizard perches at four different levels of exposure: Low, Mid-Low,

Mid-High, and High, which corresponded, respectively, to > 75%, 50–75%, 25–50%, and < 25% cover (i.e., the coverage of overhanging rock, tree root complex, low vegetation over the perch as estimated by a human observer). This was to ensure that we recorded temperatures of the four varying levels of exposure equally during each 3-day period. The iButtons inside the OTMs recorded temperature data every 15 min during the 3-day period. At the end of 3 days, the OTMs were removed, data downloaded, and then were reinstalled several days later at different lizard perches at the four levels of exposure to commence another 3-day measuring period. In total, 24 unique 3-day OTM temperature datasets (totaling 2312 temperature measurements) were collected per site.

To determine whether sites along the disturbance gradient differed in ecologically relevant microhabitat exposure for *A. aquaticus*, we classified exposure (Low, Mid-Low, Mid-High, High; > 75%, 50–75%, 25–50%, and < 25% cover, respectively) at 60 random points at the 3 sites. We used a random number generator to create a list of random azimuths, distances, and heights from a central point at each site. Random points for assessing microhabitat were selected within the space known to be used by this species: we used an existing *A. aquaticus* habitat locality dataset (Swierk, unpubl. data), including more than 600 observations of microhabitat use at these same study sites from the previous 3 years, to limit the random number generator to heights and distances from the stream edge that were within actual bounds of known *A. aquaticus* use. In the event that the random coordinates directed to an impossible perch site (e.g., mid-air), we used the surface directly below or above the point (whichever was closer) as our random point.

### Field survey

In July 2016 and 2018, we measured the body surface temperatures ( $T_b$ ) of subadult and adult *A. aquaticus* in the field at the three sites along the disturbance gradient.  $T_b$  was measured using an infrared thermometer (IRT) (EnnoLogic Dual Laser Infrared Thermometer et650D, Eugene, OR). *Anolis aquaticus* typically remain motionless when approached slowly; we, therefore, were able to take IRT measurements immediately prior to capture from a distance of < 30 cm, with the beam pointed at the center of the lizard's side, aligned with the lizard's body axis (Hare et al. 2007). In some cases, it was necessary to use a lasso to capture (but not otherwise handle) lizards immediately prior to temperature measurement. Sex, snout-vent length (SVL; mm), mass (g), time of day, and exposure level of perch (Low, Mid-Low, Mid-High, High, defined as above) were recorded following temperature measurement. Each lizard was given two dots of nail polish on the dorsal base of its tail as a unique identifying marker, as temperature data were

collected on some lizards again in the following weeks. Each lizard was then released at its site of capture.

### Estimating critical thermal maximum

In 2018, we captured 61 subadult and adult *A. aquaticus* along the disturbance gradient of 3 sites (primary forest (PR), 19; intermediate (IN), 26; disturbed (DI), 16) and transported them to a temperature-controlled room (21 °C) at the LCBS laboratory. Each lizard was kept in an individual terrarium (230 × 155 × 170 mm; L × W × H) covered on the outside with brown paper to prevent undue stress from seeing nearby conspecifics. Terraria contained a hide box and petri dish of water, and each terrarium was misted several times daily with water. Lizards were not fed while in the laboratory. Lizards remained in terraria overnight, and trials were scheduled so that each had a 24-h acclimation period prior to start time.

To begin a trial, we recorded a lizard's initial  $T_b$  prior to handling using the IRT and then placed it into a muslin drawstring bag. We then placed the bag in an incubator (Benchmark MyTemp™ Digital Mini Incubator, model H2200-H, Edison, NJ) set at 40 °C, which allowed lizards' body temperature to increase at an approximate rate of 0.5 °C per min. Every 90 s, we conducted a righting response test and recorded  $T_b$ . The righting response test consisted of placing a lizard on its dorsum on a flat surface in the incubator; lizards will turn right side up when they are not thermally stressed. We used established protocols to stimulate the lizard to right itself by probing its upper hindlimbs and base of its tail with blunt forceps (Muñoz et al. 2014). If the lizard did not right after probing within 15 s, its  $T_b$  was recorded as its critical thermal maximum ( $CT_{max}$ ), and the time spent within the 40 °C incubator prior to failure to right was its  $Time_{max}$ . All 61 lizards successfully completed  $CT_{max}$  trials, though three trials were discarded due to heating rate irregularities in the incubator. Following trials, lizards were given identifying markings as above and released at their sites of capture within 48 h of initial capture.

Control trials were performed to ensure that loss of righting reflex was not due to a confounding factor (e.g., handling stress). In control trials ( $n = 20$ ), individuals were kept in muslin bags in the incubator at 21 °C (ambient temperature) and were administered righting tests every 90 s for 30 min. No individuals failed to right themselves during control trials.

### Infrared thermometer (IRT) validation

An infrared thermometer (IRT) is an accurate and reliable tool for measuring  $T_b$  of small reptiles and amphibians (Hare et al. 2007; Rowley and Alford 2007). IRTs can be superior to other methods of temperature measurement (e.g., cloacal

thermometers) in small ectotherms, because they are non-invasive and do not require handling and restraint, which can artificially elevate  $T_b$  or alter behavior. We validated that the IRT provided an accurate method of measuring  $T_b$  in *A. aquaticus* over the range of temperatures they were exposed to in both the laboratory and field. In 2016, we collected a control set of lizards ( $n=52$ ) from the three study sites, transported them to the laboratory, and warmed them in a 30 °C incubator for 10 min. We measured  $T_b$  for each lizard before and after the warming period (total  $n=104$ ) with both the IRT and a Digisense digital thermometer (Cole-Parmer; Vernon Hills, IL) inserted into the cloaca. A linear regression of the IRT and cloacal temperatures demonstrated a high level of agreement and low error between the two measurements ( $R^2=0.95$ ,  $F_{1,102}=1856$ ,  $P<0.001$ ; mean deviation=0.62).

## Statistical methods

OTM temperatures were compared across sites using a linear mixed model, with temperature as the response, site and exposure level and their interaction as factors, and time of day and OTM ID as random effects. Exposure levels at the random control points were compared across sites using an ordered logistic regression (*polr* command in the *MASS* package; Venables and Ripley 2002). Following this, we ran a Chi-square analysis to determine *post hoc* whether there were equal numbers of control points across all sites falling into each of the four exposure level categories.

To test how anole body temperatures differed among sites, we performed a linear mixed model using the package *lmerTest* (Kuznetsova et al. 2017). Body temperature was the response variable, site and year were factors, time of day was a covariate, and lizard ID was the random effect. We next ran an ordered logistic regression to determine how perch exposure level (Low (0) to High (3)) varied among sites, with exposure level as the response variable and site and year as factors; in this model, only the first observation of each lizard was used in analysis, as lizards were frequently observed on the same perch over a season. Sex, SVL, and body condition (the residuals of a regression of the cube root of mass and SVL; Stamps et al. 1994) were initially included in these models but did not significantly improve fit, as determined by likelihood ratio tests using full and reduced models, and they were removed according to standard model selection procedures (Burnham and Anderson 2002; Crawley 2012).

We used a linear model to test how  $CT_{max}$  was influenced by site, with  $CT_{max}$  as the response and site as the predictor. We then used two analyses to examine how  $Time_{max}$  was influenced by site: a linear model to test the effect of site on  $Time_{max}$ , and also a survival analysis with non-constant hazard and Weibull errors (*survreg* function in the *survival* package; Therneau 2015) to examine how the time-to-event

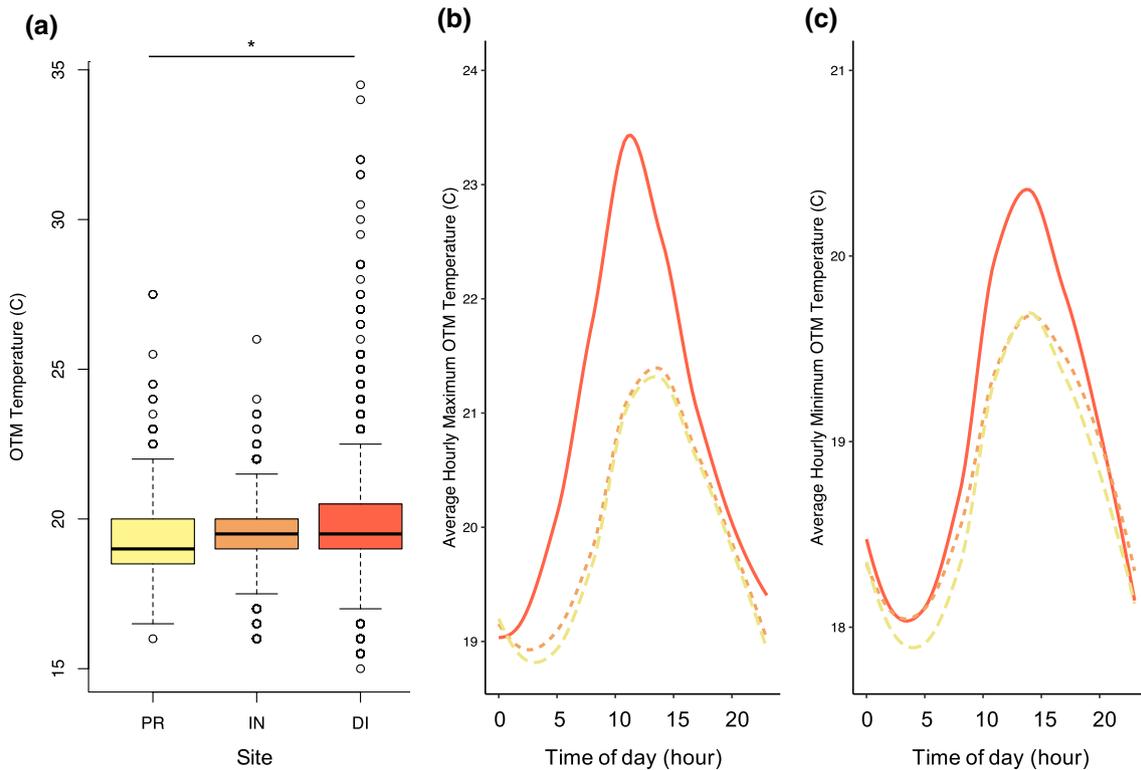
(in our case, time until a lizard failed to right itself) was affected by site.  $Time_{max}$  was square-root transformed to better meet model assumptions prior to analysis. The *SurvReg-CensCov* package (Hubeaux and Rufibach 2014) was used to calculate hazard ratios following the survival analysis. We used the *predict* function to estimate the predicted mean time to lizards' failure to right. Our initial linear models included sex, SVL, and body condition as additional predictors, but we removed these variables from our final models as they did not significantly improve model fit, as determined by likelihood ratio tests using full and reduced models (Crawley 2012).

P values of each factor and covariate were obtained by likelihood ratio tests of the full model against a reduced model, using the package *car* (Fox and Weisberg 2019) to compute test statistics for generalized linear models. Following each linear model, the *emmeans* package (Lenth 2020) was used to calculate contrasts of the estimated marginal means.

## Results

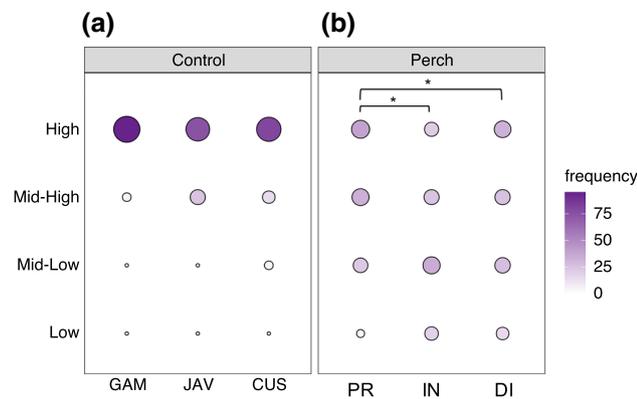
OTM temperatures varied by site ( $\chi^2_2=263.4$ ,  $P<0.001$ ) and exposure ( $\chi^2_1=282.8$ ,  $P<0.001$ ), such that the primary (PR) site maintained the lowest temperatures (average of 19.2 °C  $\pm$  0.139) (PR vs. DI:  $P<0.001$ ; PR vs. IN:  $P=0.003$ ), followed by the intermediate (IN) site (19.4 °C  $\pm$  0.140) (IN vs. DI:  $P<0.001$ ), then the disturbed (DI) site (19.8 °C  $\pm$  0.139) (Fig. 1). The interaction of site and exposure was significant ( $\chi^2_6=31.883$ ,  $P<0.001$ ), such that the DI site had notably higher temperatures at its "High" exposure perches. Over all sites, OTMs placed at "High" exposure perches were significantly higher in temperature (19.8 °C  $\pm$  0.151) than those at "Low" (19.4 °C  $\pm$  0.150), "Mid-low" (19.3 °C  $\pm$  0.151), and "Mid-high" (19.4 °C  $\pm$  0.150) exposure perches (all  $P<0.001$ ), but there were no differences in the OTM temperatures at any other combination of exposure levels (all  $P>0.7$ ). Exposure levels at randomly selected control points did not vary by site (LR=3.592,  $P=0.166$ ; Fig. 2a). At all sites, the control point exposure levels were disproportionately represented ( $\chi^2_2=69.100$ ,  $P<0.001$ ), with most control points ranked as "High" exposure.

A total of 460 lizard body temperatures and 221 perch exposure levels were recorded in 2016 and 2018 (see Fig. 3). Site significantly affected lizard body temperature ( $\chi^2_2=12.029$ ,  $P=0.002$ ) (Fig. 4; year:  $\chi^2_1=4.053$ ,  $P=0.044$ ; time of day:  $\chi^2_1=24.273$ ,  $P<0.001$ ). Body temperatures at the primary site (PR) were an average of 0.35 °C ( $\pm$  0.15) lower than those at the intermediate site (IN) ( $P=0.047$ ) and 0.58 °C ( $\pm$  0.17) lower than those at the disturbed sites (DI) ( $P=0.004$ ), though the difference between IN and DI body temperatures was not

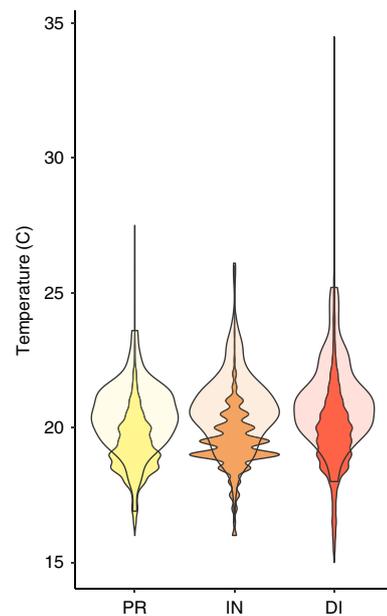


**Fig. 1** **a** Boxplot representation of temperatures (°C) recorded by operative thermal models (OTMs) at the three study sites (PR=primary; IN=intermediate; DI=disturbed) along a disturbance gradient (least to most disturbed). Asterisk represents significant differences

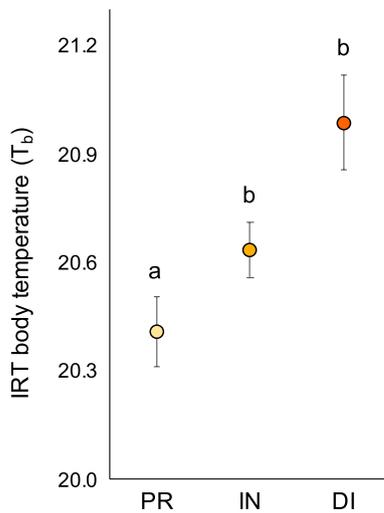
( $P < 0.05$ ) among all three sites. **b** Hourly averages of maximum and **c** minimum temperatures recorded by OTMs at the three sites (PR, dashed line; IN, dotted line; DI, solid line)



**Fig. 2** Exposure levels (Low, Mid-Low, Mid-High, and High; cover = > 75%, 50–75%, 25–50%, and < 25%, respectively) of **a** randomly selected control points and **b** perch sites of lizards at each of the three study sites (PR=primary; IN=intermediate; DI=disturbed) along a disturbance gradient (least to most disturbed). For each site, total observations were scaled to 100 so that circles represent relative frequencies of points with various exposure levels at a given site. Darker shades and larger circles represent greater relative frequencies of observations at that exposure level. Asterisks represent significant differences ( $P < 0.05$ ) in average exposure level between sites



**Fig. 3** Violin plot representation of temperatures (°C) recorded by operative thermal models (OTMs) at each site (PR=primary; IN=intermediate; DI=disturbed) (darker shades of color) overlaid with the field-measured body temperatures of *Anolis aquaticus* (lighter shades of color) at each site



**Fig. 4** Mean body temperature ( $T_b$ ) measurements recorded using an infrared thermometer (IRT) of *Anolis aquaticus* at the three study sites (PR=primary; IN=intermediate; DI=disturbed) along a disturbance gradient (least to most disturbed). Lower case letters represent significant differences between groups. Error bars represent  $\pm 1$  standard error

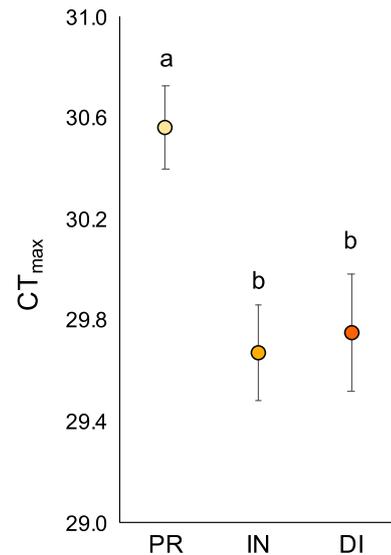
significant ( $P=0.357$ ). Site likewise influenced the level of perch exposure (LR = 18.304,  $P < 0.001$ ) (year: LR = 5.604,  $P=0.018$ ; Fig. 2b): lizards at the primary site (PR) on average had significantly higher levels of exposure than those at IN ( $P=0.001$ ) and DI ( $P=0.015$ ).

The effect of site on  $CT_{max}$  was significant ( $F_{2,55}=4.912$ ,  $P=0.011$ ): lizards from the primary site (PR) had an average  $CT_{max}$  of 0.89 °C ( $\pm 0.30$ ) higher than those from IN ( $P=0.016$ ) and 0.81 °C ( $\pm 0.34$ ) higher than those from DI ( $P=0.052$ ); lizards from IN and DI did not differ in  $CT_{max}$  ( $P=0.964$ ) (Fig. 5). The effect of site on  $Time_{max}$  was significant ( $F_{2,55}=9.103$ ,  $P < 0.001$ ) and demonstrated a similar pattern: lizards from PR had a  $Time_{max}$  that was 5.56 min ( $\pm 1.32$ ) longer than those from IN ( $P < 0.001$ ) and 4.18 min ( $\pm 1.50$ ) longer than those from DI ( $P=0.026$ ), though lizards from IN and DI did not differ ( $P=0.487$ ).

The survival analysis likewise demonstrates a significant effect of site on  $Time_{max}$  ( $\chi^2_2=9.47$ ,  $P=0.009$ ; Fig. 6): the primary site (PR) had a longer  $Time_{max}$  than the intermediate site (IN) (hazard ratio = 2.467,  $z=-2.86$ ,  $P=0.004$ ) and disturbed site (DI) (hazard ratio = 2.164,  $z=-2.17$ ,  $P=0.030$ ), but IN and DI did not differ (hazard ratio = 0.876,  $z=-0.07$ ,  $P=0.687$ ).

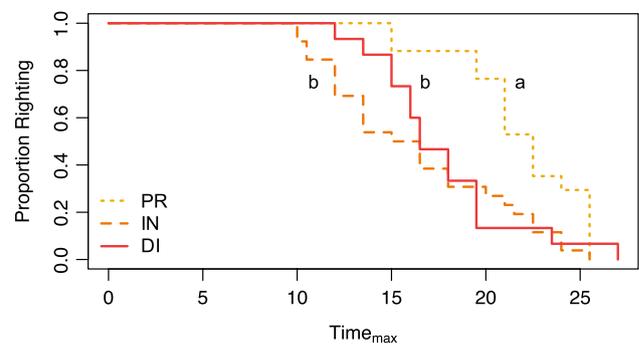
## Discussion

Cool-adapted tropical ectotherms may be at risk from increasing environmental temperatures associated with global climate change, and this threat may be exacerbated



**Fig. 5** Mean critical thermal maxima ( $CT_{max}$ ) of *A. aquaticus* from three study sites (PR=primary; IN=intermediate; DI=disturbed) along a disturbance gradient (least to most disturbed). Lower case letters represent significant differences between groups. Error bars represent  $\pm 1$  standard error

by land use change such as deforestation. We examined if *A. aquaticus* from sites over a disturbance (history of deforestation) gradient experienced varied thermal environments, and how individuals from these sites differentially responded to increased temperatures. Over this gradient, operative thermal models of *A. aquaticus* recorded the highest temperatures and the greatest variance at the most disturbed site, and the lowest temperatures at the least disturbed site. Similarly, field measurements of *A. aquaticus* body temperatures varied over this gradient, with those from the least disturbed site having lower body temperatures than those at the more disturbed sites. Individuals from the least disturbed site also



**Fig. 6** Survival curves from the survival analysis with non-constant hazard and Weibull errors demonstrating the proportion of *A. aquaticus* from each of the three study sites (PR=primary; IN=intermediate; DI=disturbed) that passed the righting test over time. Lower case letters represent significant differences between groups

demonstrated greater tolerance to high temperatures than those from the more disturbed sites, in both the maximum temperature tolerated and the amount of time spent at high temperatures. These parameters are both ecologically relevant: the maximum temperature tolerated (as reflected in the  $CT_{max}$  analysis) can help predict species' persistence as global climate changes alter maximum environmental temperatures, and the amount of time individual lizards endured higher temperatures (Time<sub>max</sub> analyses) can inform how the durations of periodic warming episodes may impact cool-adapted species.

Contrary to the idea that *A. aquaticus* from the warmer, more disturbed sites may have acclimated to higher temperatures, our results instead suggest that some aspect of these disturbed habitats appear to reduce their thermal tolerance; perhaps elevated mean temperatures resulted in chronic stress or required lizards to remain in thermal refugia longer each day (e.g., Gunderson and Leal 2016; Kubisch et al. 2016; Ortega et al. 2016). In support of this, we note that lizards at the primary site were more likely to use microhabitats (Fig. 2b) that were more closely in proportion to their availability in the environment (Fig. 2a): high exposure microhabitats were most common, and lizards at the primary site were most likely to select high exposure microhabitats. However, lizards at the disturbed sites sought out microhabitats that less closely matched their abundance in the environment, as they preferentially used microhabitats with lower levels of exposure despite the fact these microhabitats were less abundant. Across all sites, OTM temperatures increased with microhabitat exposure and, notably, a significant site\*exposure interaction on temperature indicates that the highest exposure microhabitats at the DI site were relatively warmer than those at the other sites. These patterns suggest that the level of site disturbance and overall temperature play a role in lizards' selection of microhabitats (see Beever et al. 2017; Sun et al. 2021), with lizards from cooler, less disturbed sites using thermally distinct microhabitats from their counterparts at warmer, disturbed sites.

Patterns demonstrating the relationship of habitat temperatures or disturbance in relation to ectotherm thermal tolerances have so far been equivocal, often highlighting the multiple and interacting factors at play. Interspecifically, higher levels of exposure and ambient temperatures have been found to correspond to greater thermal tolerances in lizards (e.g., Bruschi 2016). Intraspecifically, we found the opposite pattern: *A. aquaticus* individuals from sites with greater ambient temperatures had lower thermal tolerances. Our results complement an intrapopulation study by Logan et al. (2021), demonstrating that male brown anoles (*Anolis sagrei*), which occupy cooler microhabitats, have greater heat tolerances than females, and a study demonstrating that Australian skinks from warmer habitats have lower optimal sprinting temperatures (Muñoz et al. 2016). In contrast,

McMillan et al. (2011) identified that western fence lizards (*Sceloporus occidentalis*) from cooler populations were more physiologically impaired by high temperatures. Yet, several studies lack evidence of any relationships between thermal tolerance and ambient temperature in herpetofauna (e.g., Rivera-Ordóñez 2019; Gvodzík and Castilla 2001).

If local adaptation to higher temperatures is physiologically possible in *A. aquaticus*, as it appears to be in other tropical lizards (e.g., Gilbert and Miles 2017, Llewellyn et al. 2018; Leal et al. 2012; Campbell-Staton et al. 2020; Kanamori et al. 2021), there may have been insufficient time to permit adaptation to arise, even though dispersal among our sites is expected to be low given this species' natural history. Adaptation to cool temperatures has been estimated to occur over 35 generations in *Anolis cristellatus* (Leal et al. 2012), and perhaps even more quickly. The generation time of *Anolis aquaticus* is relatively long for a small anole, at 6 to 8 months (Márquez and Márquez 2009); whether or not this explains a lack of adaptation to these conditions is unknown.

As environmental temperature and level of site disturbance were correlated, the factor (e.g., habitat degradation, higher temperatures) causing variation in thermal tolerance in *A. aquaticus* among sites is difficult to disentangle within the context of our study. Even while acknowledging this, we note that regardless of the source, if chronic stressors like habitat degradation or thermal challenges exist, they may act to reduce an individual's tolerance to future stressful conditions (e.g., Rich and Romero 2005; Meester et al. 2018). Alternatively, short-term phenotypic plasticity in lizards in response to higher temperatures (heat hardening) can have multiple negative phenotypic side effects (e.g., Gilbert and Miles 2019). Likewise, behavioral shifts in response to elevated temperatures carry negative physiological consequences in lizards that can seriously impact fitness (e.g., Theisinger et al. 2017).

Whether the effects of altered thermal environments are detrimental to a species depends not only on its tolerance to high temperatures but also on whether the temperatures experienced in its habitat are near or already exceed its thermal limits (see Williams et al. 2008). In the Neotropics, temperatures have been rapidly increasing (Donat et al. 2013), have already increased between 0.7° and 1 °C since the 1970's (Magrin et al. 2014), and are predicted to climb over 3 °C in the next 80 years (Aguilar et al. 2009), with extreme predictions exceeding an increase of 6 °C in Central America (Magrin et al. 2014). Although the range of  $CT_{max}$  values and OTM-recorded temperatures currently overlap partially only at our most disturbed (DI) site, modest predictions of future temperature increase in the Neotropics would push *A. aquaticus* populations near or exceeding their  $CT_{max}$  at all our sites. Our assessment of available temperatures experienced by the lizards was based on stationary OTMs

placed in various microhabitats (Dzialowski 2005). OTMs were placed where *A. aquaticus* were previously sighted, recording the temperature ranges experienced by lizards at those locations. However, free-ranging lizards move throughout their environment, and even thermoconformers exhibit temperature preferences, as also suggested by our comparison of microhabitat temperatures of lizard-selected perches with temperatures recorded by OTMs (Fig. 3). That said, because thermoconforming ectotherms like *A. aquaticus* tend to have such low body temperatures and low  $CT_{max}$  compared to many other lizard species, even relatively small changes in microhabitat temperatures could greatly reduce performance and may be detrimental to survival (Kearney et al. 2009).

Tropical premontane forests tend to represent some of the cooler areas within a tropical landscape. If future climate predictions prove to be correct, then *A. aquaticus* and similarly cool-adapted ectotherms may have limited options for retreat via species migration upslope as ambient temperatures rise in their current premontane habitats over the next century (Logan et al. 2013). As Janzen (1967) identified early on, tropical montane and premontane species are often thermally limited in their abilities to disperse or migrate, a concept that has received strong support by more recent models (e.g., Buckley et al. 2013). Tropical premontane and montane species migrating to cooler zones have physical upper limits of available habitat (Colwell et al. 2008; La Sorte and Jetz 2010; Freeman et al. 2018), earning a dramatic nickname for their upward elevational migrations: the “escalator to extinction” (Marris 2007). Identifying the exacerbating effects of land use change in tropical forests may therefore provide a local-scale strategy to combat this “escalator to extinction”.

The association of lizard thermal tolerance and human land use history suggests that this small Neotropical lizard may already be experiencing detrimental effects of temperature stress, as *A. aquaticus* from warmer and more disturbed sites may fare more poorly during periodic high temperatures episodes that are becoming more frequent by the decade (Donat et al. 2013). Climate change in tropical premontane habitats in Central America is predicted to be particularly amplified (Enquist 2002; Karmalkar et al. 2008), with the premontane “life zone” expected to transform into lower altitudinal life zones over time (Jiménez et al. 2011). While warm-adapted ectotherms in this region are expected to have a distinct advantage in habitats that are affected by both climate change and deforestation (Sartorius et al. 1999; Frishkoff et al. 2015), cool-adapted ectotherms may not have the capacity to adapt to even small changes in temperature. These effects may be worsened by habitat loss and fragmentation. Further studies examining how tropical herpetofauna respond to temperature stressors today can provide insight

on the link between climate change and diversity in years to come (Nowakowski et al. 2018; Taylor et al. 2021).

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**Availability of data and materials** Data to accompany this paper are deposited in the Open Repository at Binghamton (ORB) and are freely accessible.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed. Use of animals was reviewed and approved by UCLA ARC (2016–051–03C) and Yale University (IACUC approval #2016–20,103).

## References

- Aguilar MY, Pacheco TR, Tobar JM, Quinonez JC (2009) Vulnerability and adaptation to climate change of rural inhabitants in the central coastal plain of El Salvador. *Climate Res* 40:187–198. <https://doi.org/10.3354/cr00805>
- Algar AC, Morley K, Boyd DS (2018) Remote sensing restores predictability of ectotherm body temperature in the world’s forests. *Glob Ecol Biogeogr* 27:1412–1425. <https://doi.org/10.1111/geb.12811>
- Beever EA, Hall LE, Varner J et al (2017) Behavioral flexibility as a mechanism for coping with climate change. *Front Ecol Environ* 15:299–308. <https://doi.org/10.1002/fee.1502>
- Boccia CK, Swierk L, Ayala-Varela FP, Boccia J, Borges IL, Estupiñán CA, Martin AM, Martínez-Grimaldo R, Ovalle S, Senthivasan S, Toyama KS, del Rosario CM, García A, Glor R, Mahler DL (2021) Repeated evolution of underwater rebreathing in diving *Anolis* lizards. *Curr Biol* 31:1–8. <https://doi.org/10.1016/j.cub.2021.04.040>
- Boyer JFF, Swierk L (2017) Rapid body color brightening is associated with exposure to a stressor in an *Anolis* lizard. *Can J Zool* 219:213–219. <https://doi.org/10.1139/cjz-2016-0200>

- Brodie J, Post E, Laurance WF (2012) Climate change and tropical biodiversity: a new focus. *Trends Ecol Evol* 27:145–150. <https://doi.org/10.1016/j.tree.2011.09.008>
- Brusch GA IV, Taylor EN, Whitfield SM (2016) Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia* 180:325–334. <https://doi.org/10.1007/s00442-015-3467-3>
- Buckley LB, Tewksbury JJ, Deutsch CA (2013) Can terrestrial ectotherms escape the heat of climate change by moving? *Proc R Soc B* 280:20131149. <https://doi.org/10.1098/rspb.2013.1149>
- Bühne HST, Tobias JA, Durant SM, Pettorelli N (2021) Improving predictions of climate change–land use change interactions. *Trends Ecol Evol* 36:29–38. <https://doi.org/10.1016/j.tree.2020.08.019>
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodal Inference: a practical information-theoretic approach*, 2nd edn. Springer, New York
- Caissie D (2006) The thermal regime of rivers: a review. *Freshw Biol* 51:1389–1406. <https://doi.org/10.1111/j.1365-2427.2006.01597.x>
- Campbell-Staton SC, Winchell KM, Rochette NC, Fredette J, Maayan I, Schweizer RM, Catchen J (2020) Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat Ecol Evol* 4:652–658
- Clusella-Trullas A, Chown SL (2014) Lizard thermal trait variation at multiple scales: a review. *J Comp Physiol B* 184:5–21
- Colwell RK, Brehm G, Cardelús CL et al (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261. <https://doi.org/10.1126/science.1162547>
- Crawley MJ (2012) *The R Book*, 2nd edn. John Wiley & Sons Inc, Chichester
- Dale VH (1997) The relationship between land-use change and climate change. *Ecol Appl* 7:753–769
- De ML, Stoks R, Brans KI (2018) Genetic adaptation as a biological buffer against climate change: Potential and limitations. *Integr Zool* 13:372–391. <https://doi.org/10.1111/1749-4877.12298>
- Deutsch CA, Tewksbury JJ, Huey RB et al (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci* 105:6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Domenici P, Seebacher F (2020) The impacts of climate change on the biomechanics of animals. *Conserv Physiol* 8:1–7. <https://doi.org/10.1093/conphys/coz102>
- Donat MG, Alexander LV, Yang H et al (2013) Updated analyses of temperature and precipitation extreme indices since the beginning of the twentieth century: the HadEX2 dataset. *J Geophys Res Atmos* 118:2098–2118. <https://doi.org/10.1002/jgrd.50150>
- Dzialowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *J Therm Biol* 30:317–334. <https://doi.org/10.1016/j.jtherbio.2005.01.005>
- Enquist CAF (2002) Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *J Biogeogr* 29:519–534. <https://doi.org/10.1046/j.1365-2699.2002.00695.x>
- Feder ME, Lynch JF (1982) Effects of latitude, season, elevation, and microhabitat on field body temperatures of Neotropical and temperate zone salamanders. *Ecology* 63:1657–1664
- Fox J, Weisberg S (2019) *An R companion to applied regression*, 3rd edn. Sage, Thousand Oaks
- Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc Natl Acad Sci* 115:11982–11987. <https://doi.org/10.1073/pnas.1804224115>
- Frishkoff LO, Hadly EA, Daily GC (2015) Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. *Glob Change Biol* 21:3901–3916. <https://doi.org/10.1111/gcb.13016>
- Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G (2006) Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integr Comp Biol* 46:5–17. <https://doi.org/10.1093/icb/iej003>
- Gilbert AL, Miles DB (2017) Natural selection on thermal preference, critical thermal maxima and locomotor performance. *Proc R Soc B* 284:20170536
- Gilbert AL, Miles DB (2019) Antagonistic responses of exposure to sublethal temperatures: adaptive phenotypic plasticity coincides with a reduction in organismal performance. *Am Nat* 194:344–355
- Greenwood O, Mossman HL, Suggitt AJ, Curtis RJ, Maclean IMD (2016) Using in situ management to conserve biodiversity under climate change. *J Appl Ecol* 53:885–894. <https://doi.org/10.1111/1365-2664.12602>
- Gunderson AR, Leal M (2016) A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecol Lett* 19:111–120
- Gvozdík L, Castilla AM (2001) A comparative study of preferred body temperatures and critical thermal tolerance limits among populations of *Zootoca vivipara* (Squamata: Lacertidae) along an altitudinal gradient. *J Herpetol* 35:486–492
- Hare JR, Whitworth E, Cree A (2007) Correct orientation of a handheld infrared thermometer is important for accurate measurement of body temperatures in small lizards and tuatara. *Herpetol Rev* 38:311–315
- Hubeaux S, Rufibach K (2014) *SurvRegCensCov*: weibull regression for a right-censored endpoint with a censored covariate. *Arxiv Preprint arXiv*. <https://doi.org/10.48550/arXiv.1402.0432>
- Huey RB, Deutsch CA, Tewksbury JJ et al (2009) Why tropical forest lizards are vulnerable to climate warming. *Proc R Soc B* 276:1939–1948. <https://doi.org/10.1098/rspb.2008.1957>
- IPCC (2018) *Global Warming of 1.5°C*. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. Cambridge University Press, Cambridge, UK and New York, NY, USA. <https://doi.org/10.1017/9781009157940>
- Janzen DH (1967) Why mountain passes are higher in the tropics. *Am Nat* 101:233–249
- Jiménez M, Chain A, Locatelli B (2011) Efectos del cambio climático en la distribución de zonas de vida en Centroamérica. *Recursos Naturales y Ambiente* 59–60:32–40
- Kanamori S, Cádiz A, Díaz LM, Ishii Y, Nakayama T, Kawata M (2021) Detection of genes positively selected in Cuban *Anolis* lizards that naturally inhabit hot and open areas and currently thrive in urban areas. *Ecol Evol* 11:1719–1728
- Karmalkar AV, Bradley RS, Diaz HF (2008) Climate change scenario for Costa Rican montane forests. *Geophys Res Lett* 35:1–5. <https://doi.org/10.1029/2008GL033940>
- Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc Natl Acad Sci USA* 106:3835–3840. <https://doi.org/10.1073/pnas.0808913106>
- Kingsolver JG, Diamond SE, Buckley LB (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct Ecol* 27:1415–1423. <https://doi.org/10.1111/1365-2435.12145>
- Kubisch EL, Corbalán V, Ibarquengoytia NR, Sinervo B (2016) Local extinction risk of three species of lizard from Patagonia as a result of global warming. *Can J Zool* 94:49–59
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. *J Stat Softw* 82:1–26

- La Sorte FA, Jetz W (2010) Projected range contractions of montane biodiversity under global warming. *Proc R Soc B: Biol Sci* 277:3401–3410. <https://doi.org/10.1098/rspb.2010.0612>
- Leal M, Gunderson AR (2012) Rapid change in the thermal tolerance of a tropical lizard. *Am Nat* 180:815–822
- Lenth RV (2020) emmeans: Estimated Marginal Means, aka Least-Squares means. R package version 1.4.7. <https://CRAN.R-project.org>. Accessed Jan 2021
- Llewelyn J, Macdonald SL, Moritz C et al (2018) Adjusting to climate: acclimation, adaptation and developmental plasticity in physiological traits of a tropical rainforest lizard. *Integrative Zool* 13:411–427. <https://doi.org/10.1111/1749-4877.12309>
- Logan ML, Huynh RK, Precious RA, Calsbeek RG (2013) The impact of climate change measured at relevant spatial scales: new hope for tropical lizards. *Glob Change Biol* 19:3093–3102. <https://doi.org/10.1111/gcb.12253>
- Logan ML, Neel LK, Nicholson DJ, Stokes AJ, Miller CL, Chung AK, Curlis JD, Keegan KM, Rosso AA, Maayan I, Folfas E, Williams CE, Casement B, Gallegos Koyner MA, Padilla Perez DJ, Falvey CH, Alexander SM, Charles KL, Graham ZA, McMillan WO, Losos JB, Cox CL (2021) Sex-specific microhabitat use is associated with sex-biased thermal physiology in *Anolis* lizards. *J Exp Biol*. <https://doi.org/10.1242/jeb.235697>
- Magrin GO, Marengo JA, Boulanger J-P et al (2014) Central and South America. In: Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 1499–1566
- Mantyka-Pringle CS, Martin TG, Moffatt DB, Linke S, Rhodes JR (2014) Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. *J Appl Ecol* 51:572–581. <https://doi.org/10.1111/1365-2664.12236>
- Márquez CM, Márquez LD (2009) Reproductive biology in the wild and in captivity of *Anolis aquaticus* (Sauria: Polychrotidae) in Costa Rica. *Boletín Técnico Serie Zoológica* 8:50–73
- Marris E (2007) The escalator effect. *Nat Clim Change* 1:94–96. <https://doi.org/10.1038/climate.2007.70>
- McMillan DM, Irschick DJ, Rees BB (2011) Geographic variation in the effects of heat exposure on maximum sprint speed and Hsp70 expression in the western fence lizard *Sceloporus occidentalis*. *Physiol Biochem Zool* 84:573–582
- Muñoz MM, Stimola MA, Algar AC, Conover A, Rodriguez AJ, Landestoy MA, Bakken GS, Losos J (2014) Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proc R Soc B* 281:20132433
- Muñoz MM, Langham GM, Brandley MC, Rosauer DF, Williams SE, Moritz C (2016) Basking behavior predicts the evolution of heat tolerance in Australian rainforest lizards. *Evolution* 70:2537–2549. <https://doi.org/10.1111/evo.13064>
- Nowakowski AJ, Watling JI, Thompson ME, Bruschi GA IV, Catenazzi A, Whitfield SM, Kurz DJ, Suárez-Mayorga A, Aponte-Gutiérrez A, Donnelly MA, Todd BD (2018) Thermal biology mediates responses of amphibians and reptiles to habitat modification. *Ecol Lett* 21:345–355. <https://doi.org/10.1111/ele.12901>
- Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wires Clim Change* 5:317–335. <https://doi.org/10.1002/wcc.271>
- Ortega Z, Mencía A, Pérez-Mellado V (2016) Behavioral buffering of global warming in a cold-adapted lizard. *Ecol Evol* 6:4582–4590
- Polato NR, Gill BA, Shah AA, Gray MM, Casner KL, Barthelet A, Messer PW, Simmons MP, Guayasamin JM, Encalada AC, Kondratieff BC, Flecker AS, Thomas SA, Ghalambor CK, Poff NL, Funk WC, Zamudio KR (2018) Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proc Natl Acad Sci* 115:12471–12476. <https://doi.org/10.1073/pnas.1809326115>
- Putman BJ, Azure KR, Swierk L (2018) Dewlap size in male water anoles associates with consistent inter-individual variation in boldness. *Current Zoology* 65:189–195. <https://doi.org/10.1093/cz/zoy041>
- Rich EL, Romero LM (2005) Exposure to chronic stress downregulates corticosterone responses to acute stressors. *Am Physiol Regul Integr Comp Physiol* 288:1628–1636. <https://doi.org/10.1152/ajpregu.00484.2004>
- Rivera-Ordóñez JM, Nowakowski AJ, Manansala A, Thompson ME, Todd BD (2019) Thermal niche variation among individuals of the poison frog, *Oophaga pumilio*, in forest and converted habitats. *Biotropica* 51:747–756
- Rohr JR, Palmer BD (2013) Climate change, multiple stressors, and the decline of ectotherms. *Conserv Biol* 27:741–751. <https://doi.org/10.1111/cobi.12086>
- Rowley JLL, Alford RA (2007) Non-contact infrared thermometers can accurately measure amphibian body temperatures. *Herpetology* 38:308–311
- Sartorius SS, Vitt LJ, Colli GR (1999) Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biol Cons* 90:91–101. [https://doi.org/10.1016/S0006-3207\(99\)00019-1](https://doi.org/10.1016/S0006-3207(99)00019-1)
- Savage JM (2002) The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas. University of Chicago Press, Chicago
- Senior RA, Hill JK, Benedick S, Edwards DP (2018) Tropical forests are thermally buffered despite intensive selective logging. *Glob Change Biol* 24:1267–1278. <https://doi.org/10.1111/gcb.13914>
- Stamps JA, Krishnan VV, Andrews RM (1994) Analyses of sexual size dimorphism using null growth-based models. *Copeia* 1994:598–613
- Sun BJ, Ma L, Wang Y, Mi CR, Buckley LB, Levy O, Lu HL, Du WG (2021) Latitudinal embryonic thermal tolerance and plasticity shape the vulnerability of oviparous species to climate change. *Ecol Monogr* 91:e01468
- Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci* 111:5610–5615
- Swierk L (2019) *Anolis aquaticus* (*Norops aquaticus*) (Water Anole) underwater breathing. *Herpetol Rev* 50:134–135
- Taylor EN, Diele-Viegas LM, Gangloff EJ, Hall JM, Halpern B, Massey MD, Rödder D, Rollinson N, Spears S, Sun B, Telemeco RS (2021) The thermal ecology and physiology of reptiles and amphibians: a user's guide. *J Exp Zool A* 335:13–44. <https://doi.org/10.1002/jez.2396>
- Tewksbury JJ, Huey RB, Deutsch CA (2008) Ecology: putting the heat on tropical animals. *Science* 320:1296–1297. <https://doi.org/10.1126/science.1159328>
- Theisinger O, Berg W, Dausmann KH (2017) Compensation of thermal constraints along a natural environmental gradient in a Malagasy iguanid lizard (*Oplurus quadrimaculatus*). *J Therm Biol* 68:21–26
- Therneau T (2015) A package for survival analysis in S. version 2.: <https://CRAN.R-project.org/package=survival>. Accessed Jan 2021
- van Berkum FH (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am Nat* 132:327–343. <https://doi.org/10.1086/284856>
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

- Whitfield SM, Bell KE, Philippi T, Sasa M, Bolaños F, Chaves G, Savage JM, Donnelly MA (2007) Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc Natl Acad Sci USA* 104:8352–8356. <https://doi.org/10.1073/pnas.0611256104>
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* 6:e325
- Wright SJ, Muller-Landau HC, Schipper J (2009) The future of tropical species on a warmer planet. *Conserv Biol* 23:1418–1426. <https://doi.org/10.1111/j.1523-1739.2009.01337.x>
- Yang J, Sun Y-Y, An H, Ji X (2008) Northern grass lizards (*Takydromus septentrionalis*) from different populations do not differ in thermal preference and thermal tolerance when acclimated under identical thermal conditions. *J Comp Physiol B* 178:343–349

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