

Critical thermal tolerance of invasion: Comparative niche breadth of two invasive lizards

Allison R. Litmer^{a,b,*}, Christopher M. Murray^{a,c}

^a Department of Biology, Tennessee Technological University Pennebaker Hall, #207 1100 N. Dixie Avenue, 38505, Cookeville, TN, USA

^b Department of Biology, University of Arkansas, SCEN 601, 650 West Dickson Street, Fayetteville, AR, 72701, USA

^c Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA, 70402, USA

ARTICLE INFO

Keywords:

Biogeography
Physiology
Evolution
Lizard
Introduced
Climate

ABSTRACT

Understanding the evolution of thermal tolerance in ectotherms is particularly important given the current period of rapid change in the environment and thermal climate. Specifically, introduced species have the potential to evolve different thermal tolerances than native populations due to rapid evolution and novel selection pressures. Our study examined critical thermal tolerance in two introduced lizard species, the European wall lizard (*Podarcis muralis*) in Ohio and Kentucky, and the Mediterranean gecko (*Hemidactylus turcicus*) from Texas through Alabama. We tested the hypotheses that critical thermal maximum, minimum, and breadth varies among introduced populations of *P. muralis* and *H. turcicus*, and that critical thermal tolerance broadens when moving away from the introduction site, because dispersal across novel environments may remove dispersers with narrow thermal tolerances. We found that among *P. muralis* populations, CT_{min} and thermal breadth were significantly different. Specifically, when moving away from the introduction site, lizards exhibited increased cold tolerance and broader thermal breadth. Variability in thermal parameters were also lowest at the site closest to the introduction point in *P. muralis*. In contrast, *H. turcicus* had no significant differences in critical thermal minimum, maximum, or breadth among sites, or with respect to distance from introduction point. However, we did find little variability in thermal maximum, compared to greater variability in overall tolerance and critical thermal minimums. Thus, this study shows that selection on thermal tolerance and dispersal characteristics occur in novel climatic environments. Understanding how thermal tolerance changes over time can aid in predicting establishment and movement of introduced species, with applications for native species during a time of global climatic change.

1. Introduction

Changes in environmental conditions can influence the physiological capacity for survival of an organism (Huey and Bennett, 1990). Alterations in physiological processes, morphology, and behavior occur that can increase fitness with the associated variability in the environment. The relationship between the niche of a species and geographic distribution is complex, and the breadth of the niche, ability of the organism to disperse, and availability of suitable habitat are important contributing factors (Pulliam, 2000; Knouft et al., 2006). Currently, environmental change is occurring on a global scale; therefore, understanding drivers of evolutionary processes in response to novel and changing environments is increasingly important, specifically with respect to thermal variation.

Life history characteristics, acclimatization, and geographic location play an important role in the sensitivity of organisms to the thermal environment (Buckley and Huey, 2016). Performing within the ecological and physiological fundamental niche is beneficial for survival, and should be reflected in the evolution of thermal sensitivity in response to temperatures experienced by the organism (Huey and Bennett, 1987). However, because organisms have multiple mechanisms for coping with the thermal environment, thermal tolerance is often considered to be phylogenetically conserved (Huey and Bennett, 1990). In contrast, selection may favor evolution of physiological processes linked to temperature in populations where organisms cannot use behavior to buffer climatic changes, which may be observed among select parts of a species distribution (Huey and Kingsolver, 1989). The various mechanisms influencing thermal tolerance, and the wide-range of environmental

* Corresponding author. Department of Biology, University of Arkansas, SCEN 601, 650 West Dickson Street, Fayetteville, AR, 72701, USA.

E-mail addresses: arlitmer@uark.edu (A.R. Litmer), cmurray@selu.edu (C.M. Murray).

<https://doi.org/10.1016/j.jtherbio.2019.102432>

Received 4 December 2018; Received in revised form 9 September 2019; Accepted 4 October 2019

Available online 5 October 2019

0306-4565/© 2019 Elsevier Ltd. All rights reserved.

parameters experienced by a species throughout its distribution, make organismal response to thermal change of interest.

Geographic distribution often correlates with the range of temperatures a species can withstand. Narrow physiological tolerances are often observed in low-latitude organisms, compared to relatively broad tolerances of higher-latitude organisms in related species (often in ectotherms) (Pianka, 1970; Van Berkum, 1988). As hypothesized by Janzen (1967), and later tested by Ghalambor et al. (2006), the range in climatic variation experienced influences the evolution of physiological traits (Weeks and Espinoza, 2013). When applying Janzen's explanation for distribution via physiological tolerances, evidence suggests that niche breadth correlates with climatic variation experienced by a lineage (Ghalambor et al., 2006). Patterson (1984) and Logan et al. (2014) also noted that intraspecific ability to acclimatize during thermal changes differed based on the geographic origin of the individual tested. Therefore, when individuals disperse to novel locations, the thermal regime experienced may play a key role in the evolution of traits. The physiological tolerance of dispersers, and suitable habitat, provides a link between physiological niche breadth of individuals in the core population and peripheral populations (Pulliam, 2000). As a result of dispersal, newly colonized populations tend to have traits more representative of generalists, compared to the core, or mainland population, which are more specialized in niche (Patterson, 1984; Stevens et al., 2012). Because physiological processes evolve, we can predict that individual success is constrained by physiological parameters.

Ectotherms, such as lizards, are often used in studies addressing the influence of dispersal and thermal conditions on physiology due to their sensitivity to temperature and behavioral response to environmental conditions (e.g., Hertz and Huey, 1981; Leal and Gunderson, 2012; Logan et al., 2014; Pontes-da-Silva et al., 2018). Although it is often suggested that thermal physiology has low evolvability (Van Damme et al., 1990; Clusella-Trullas and Chown, 2013), an evolutionary model ran by Buckley and Huey (2016) suggested that when the distribution of temperatures varies by geographic location, the thermal breadth of an organism also varies. In addition, genetic constraints vary across the distribution of a species, which can alter behavioral responses and geographic variation in thermal tolerance. Often, genetic variation will increase, or decrease, with respect to the core of the distribution (Eckert et al., 2008), which may be reflected in evolution of thermal tolerance, independent of the environment. The genetic composition of introduced species are often unique due to presence of founders' effect, resulting in variable evolutionary changes. Therefore, introduced species offer unique systems to study comparative physiology and dispersal requirements in response to novel environments over short time periods. For invaders, niche requirements immediately determine if an initial population increase or decrease occurs upon introduction (Holt et al., 2005). However, sufficient genetic variation paired with successful establishment may allow dispersal through novel environments, promoting further establishment. Understanding the thermal tolerance of invading species could aid in forecasting movement of the invasion front, future establishment, and influence on native species. Additionally, nocturnal versus diurnal introduced species may rely on different variables for persistence. If allelic diversity is variable throughout a species' distribution, the resulting fundamental niche may be constrained in response.

In the current study, we assessed critical thermal tolerance as a proxy of fundamental niche breadth in two introduced lizard species [European Wall Lizard (*Podarcis muralis*) and Mediterranean Gecko (*Hemidactylus turcicus*)] with respect to distance from the introduction site. The two species studied here are of particular interest because they differ in activity time and life history strategy, yet have successfully established multiple introduced populations. Therefore, comparisons of physiological response to invasion with a particular focus on thermal tolerance can be made between *P. muralis* and *H. turcicus*. Additionally, comparisons between thermal physiology of nocturnal and diurnal lizards is of interest, because while many nocturnal species are considered

thermoconformers, evidence suggests they may behaviorally thermo-regulate (Kearney and Predavec, 2000). We hypothesized that critical thermal maximum, minimum, and breadth would vary based on geographic location with respect to the introduction site due to increased disperser characteristics. Additionally, we hypothesized that the breadth of critical thermal tolerance would broaden when moving away from the introduction site in *P. muralis* and *H. turcicus* because dispersal across novel environments may remove dispersers with narrow thermal tolerance. We surveyed sites in Ohio and Kentucky for *P. muralis*, and along a longitudinal transect when sampling for *H. turcicus* in an attempt to minimize the influence of latitude across the wide range, which has been shown to influence thermal variation. Our study objectives were to (1) determine the critical thermal tolerance across the geographic range of a wide-ranging and narrow-ranging introduced lizard species; (2) compare variation in thermal tolerance among sites across the introduced populations; and (3) determine if thermal tolerances vary, and breadth increases, as distance to the introduction site increases across a longitudinal gradient.

2. Materials and methods

2.1. Focal species

2.1.1. *Podarcis muralis*

Podarcis muralis is a small lacertid lizard native to central and southern Europe with multiple established introduced populations in North America and Europe (Michaelides et al., 2015). After a single introduction event in 1952, *P. muralis* established a population in Cincinnati, OH, and have expanded to northern Kentucky and Indiana (Strijbosch et al., 1980; Brown et al., 1995; Gherghel et al., 2009). *Podarcis muralis* actively forage during the day, and are successful at inhabiting urban areas with rock walls and abandoned buildings, which gives them a competitive edge in the urbanized introduction site in Cincinnati, OH (Gherghel et al., 2009). In Cincinnati, *P. muralis* have the ability to supercool and survive freezing events of temperatures as low as -4.75°C (Claussen et al. 1990). In Europe (source population), the average optimal body temperature of *P. muralis* is $35.45^{\circ}\text{C} \pm 0.31$ SE, average critical thermal maximum is $44.21^{\circ}\text{C} \pm 0.13$ SE (body temperature), and median preferred body temperature is 34.15°C (Bauwens et al., 1995). Native populations of *P. muralis* exhibit thermoregulatory behaviors, where an inverse correlation exists between the number of lizards basking in full sun, and air and substrate temperature (Braña, 1991). Additionally, during cold conditions, native *P. muralis* body temperatures have been found to exceed the substrate temperature, and during warm conditions the body temperature is typically lower than the substrate temperature (Braña, 1991), indicating their ability to thermo-regulate. Slight differences in mean body temperatures have also been detected where high altitude populations of *P. muralis* have lower average body temperatures than lowland populations (Braña, 1991). To our knowledge, dispersal rate has not been clearly assessed in Cincinnati, however, it has been documented that *P. muralis* inhabit talus slopes on railways (which are abundant in Cincinnati), aiding in dispersal (Heeden and Hedeem, 1999; Gherghel et al., 2009). Genetic analysis suggests the initial colonization of *P. muralis* in Cincinnati underwent a bottleneck resulting in loss of genetic variation, with a high degree of distinction among geographically close populations (Lescano, 2010). The genetic structure of this introduced population suggests low gene flow among peripheral populations, despite the high population densities, allowing for the prediction that variation occurs within the physiology of *P. muralis* among populations as a result.

2.1.2. *Hemidactylus turcicus*

The Mediterranean Gecko (*Hemidactylus turcicus*) is a small lizard native to Eurasia and Africa (Gomez-Zlatar et al., 2006), and was introduced into Key West, Florida around 1910 (Fowler, 1915), and again in New Orleans, Louisiana before 1950 (Etheridge, 1952).

Additional introduction sites exist throughout the United States, but were excluded from this study. *Hemidactylus turcicus* has proved to be a highly successful invader in a wide-range of locations and climates, and is nocturnal, inhabiting urban areas with rock walls and implementing a wait-ambush foraging tactic in its introduced range (Selcer, 1987; Hitchcock and McBrayer, 2006). Evidence suggests that *H. turcicus* are thermoconformers, active at temperatures below their preferred and optimum temperatures, and experiencing body temperature fluctuation in correspondence to seasonal temperature changes (Hitchcock and McBrayer, 2006). Mean body temperature of *H. turcicus* in their introduced range in the United States has been found to range from 27.8 °C (Angilletta et al., 1999) to 28.5 °C (Hitchcock and McBrayer, 2006). Lack of thermoregulation is hypothesized to be a result of constraints from the available thermal environment at night. Ecological niche modeling of climatic variables has found that the minimum temperatures experienced by *H. turcicus* has a high degree of similarity as native ranges in the Mediterranean, suggesting that thermal minimum may be a limiting factor for this species (Rödger and Lötters, 2009). In an urban environment, *H. turcicus* have an estimated dispersal rate of 20 m per year (Stabler et al., 2011). The genetic structure of *H. turcicus* in southeast United States indicates decreased heterozygosity in peripheral populations when moving away from the New Orleans introduction site (Schwaner et al., 2008), with distinct populations separated by a few meters to several hundred kilometers. The large distribution of *H. turcicus* in southeastern United States, the increased ability to successfully establish, and potentially low gene flow among peripheral populations make this species an ideal model to assess thermal tolerance among the introduction sites and invasion front.

2.2. Lizard surveys

In May 2018 we collected *P. muralis* during daytime hours in Cincinnati, OH from Tusculum View Apartments (2.58 km from core upon introduction, $n = 6$ lizards, $\bar{x} = 48$ mm snout-vent length), Alms Park (3.34 km from core, $n = 6$, $\bar{x} = 66$ mm snout-vent length), Ault Park (4.47 km from core, $n = 15$, $\bar{x} = 66$ mm snout-vent length), and in Fort Thomas, KY from Inverness Place Apartments (3.88 km from core, $n = 15$, $\bar{x} = 54$ mm snout-vent length). While the Fort Thomas, KY site was not the farthest from the introduction site, it is separated by the Ohio River, which may be an influencing factor for lizard dispersal (Fig. 1A). In July 2017 and June 2018 we collected *H. turcicus* beginning approximately 2 h after sunset in New Orleans, LA (core population on introduction) ($n = 5$ lizards, $\bar{x} = 47$ mm snout-vent length), Hammond, LA (72.42 km from core, $n = 14$, $\bar{x} = 48$ mm snout-vent length), Mobile, AL (209.22 km from core, $n = 18$, $\bar{x} = 48$ mm snout-vent length), Auburn, AL (521.91 km from core, $n = 16$, lizards not viable for analyses; see results), Port Arthur, TX (368.54 km from core, $n = 15$, $\bar{x} = 52$ mm snout-vent length), and Austin, TX (738.69 km from core, $n = 7$, $\bar{x} = 47$ mm snout-vent length) (Fig. 1B). We captured all lizards by hand or noose, consisting of a fishing pole with a dental floss noose at the end, and recorded data on sex, mass and snout-vent length (SVL).

2.3. Critical thermal tolerance

We placed individual lizards in perforated plastic Tupperware containers (12 cm width x 15 cm length x 6.5 cm height), which were placed inside a larger plastic container (39 cm width x 55 cm length x 15.5 cm height) filled with ~1.5 cm of water at a starting temperature of 27 °C, immersing the lizard's body and tail (Brusch IV et al., 2015; Von May et al., 2019). The water temperature was gradually increased every 3 min by 0.5 °C by adding 15–40 mL of water at 100.0 °C heated by an electric kettle. Water additions did cause a gradual increase in the level of water in the large tub; therefore, small amounts of water were removed gradually to prevent drowning. We monitored water temperatures using a glass VWR Spirit Precision Thermometer, precise to the first decimal place. After each increase in temperature, lizards were

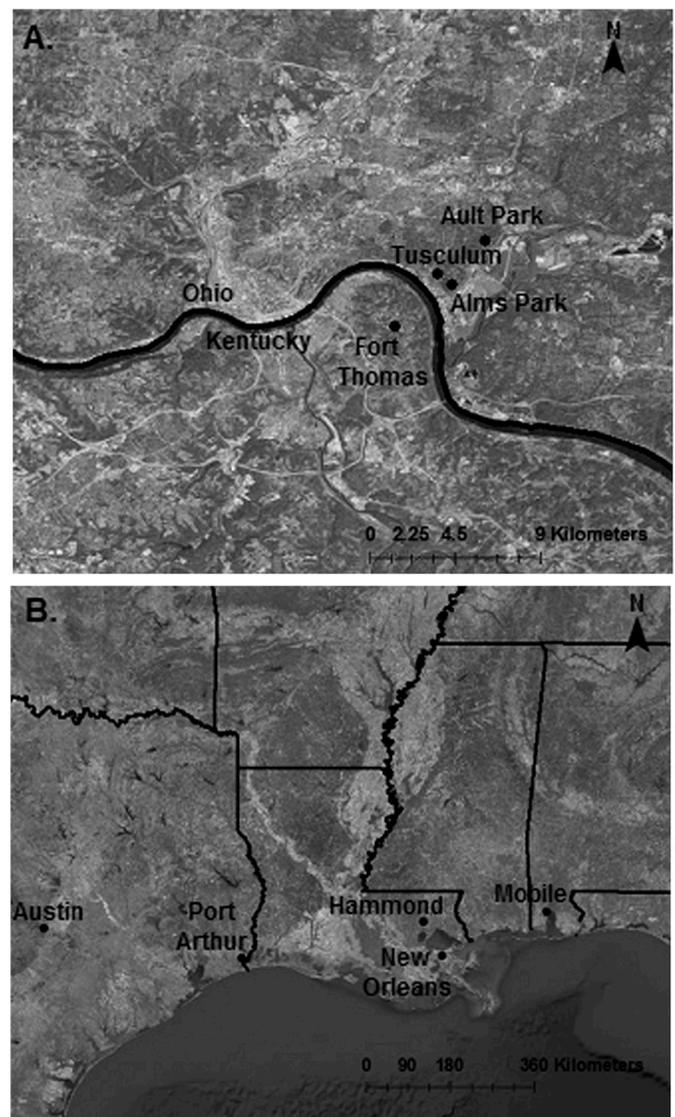


Fig. 1. Map of four sites surveyed for *Podarcis muralis* in Cincinnati, OH and Fort Thomas, KY, with Tusculum being the site closest to the introduction point (A), and map of five sites surveyed for *Hemidactylus turcicus* in Austin, TX, Port Arthur, TX, Hammond, LA, New Orleans, LA (introduction site), and Mobile, AL (B).

momentarily removed and placed on their back to determine if they could maintain normal righting reflex. Righting reflex assessment and water temperature changes were always assessed by ARL. When functional, lizards righted themselves immediately, so if the lizard failed to do so for more than 5 s (Von May et al., 2019), the water temperature was recorded as the individual lizard's critical thermal maximum (CT_{max}), as the individual is presumed functionally dead. We implemented the same method to determine critical thermal minimum (CT_{min}) of lizards; water temperature in the large container was gradually decreased every 3 min by 0.5 °C by adding ~15–40 mL of water from an ice bath (~0 °C). In between trials, the lizards were placed in a container held at room temperature to recover until active again. Prior to all thermal tolerance trials, righting reflex of lizards was assessed.

2.4. Data analysis

We determined the breadth of critical thermal tolerance within each lizard's fundamental niche using the formula:

We used ANCOVAs to test the effects of site on CT_{max} , CT_{min} , and breadth, with lizard SVL as a covariate, for *P. muralis* and *H. turcicus* (Cox et al., 2006; Beal et al., 2015). When the interaction of SVL and site were not significant, SVL was removed and an ANOVA was used. We verified the assumption of normality by conducting a test of equally distributed residuals after fitting the model, where the mean residuals were equal to zero and the variance was equal to one. A post-hoc Tukey HSD was performed to determine among site differences. To take into account the variation in thermal tolerance within sites we calculated the coefficient of variation for breadth, CT_{max} , and CT_{min} using the formula:

$$CV = (\text{standard deviation} / \bar{x}) * 100$$

Temperature data were not standardized for SVL when calculating CV because the ANCOVAs suggested that SVL did not have a significant interaction with the thermal parameters, and the values are more comparable when using raw data as opposed to a ratio (Beaupre and Dunham, 1995; Jasieński and Bazzaz, 1999). To determine if there was a significant linear trend in CT_{max} , CT_{min} , and breadth, with respect to the introduction site for both species, we used a linear model. All analyses were conducted with $\alpha = 0.05$, in R i386 3.4.1 (R Core Team, 2017).

3. Results

3.1. Thermal tolerances

When we assessed righting reflex prior to starting thermal trials, all lizards from Auburn lacked the ability to right themselves, therefore we were unable to include these specimens in our analysis. Water temperatures deemed as critical thermal maximum for *P. muralis* ranged from 29.5 °C to 35.5 °C, with an average of 32.2 °C, critical thermal minimum ranged from 8.5 °C to 25.3 °C with an average of 18.6 °C, and a thermal breadth ranged from 4.9 °C to 27.0 °C with an average of 13.6 °C (Table 1). Water temperatures deemed as critical thermal maximum for *H. turcicus* ranged from 28.0 °C to 34.5 °C, with an average of 32.0 °C, critical thermal minimum ranged from 12.0 °C to 26.0 °C, with an average of 20.0 °C, and thermal breadth ranged from 4 °C to 18.0 °C.

3.2. Site variation

SVL did not significantly affect any thermal parameters measured for either *P. muralis* or *H. turcicus*, and therefore ANOVAs were ran (SVL as the covariate was excluded). CT_{max} did not significantly vary among *P. muralis* sites, however, CT_{min} ($DF = 3, F = 5.659, p = 0.003$) and thermal breadth ($DF = 3, F = 5.12, p = 0.005$) were significant. Post-hoc Tukey HSD comparisons indicated that CT_{min} was significantly lower for *P. muralis* from the Ault population ($\bar{x} = 15.8$ °C, 4.47 km from core)

Table 1

Average critical thermal maximum and minimum temperatures, and thermal breadth, \pm SEM, across sites of European wall lizards (*Podarcis muralis*) and Mediterranean geckos (*Hemidactylus turcicus*).

Site	Average Temperature (°C)		
	CT_{max}	CT_{min}	Breadth
<i>Podarcis muralis</i>			
Tusculum	31.5 \pm 0.3	22.6 \pm 0.5	8.9 \pm 0.6
Alms Park	32.5 \pm 1.1	16.4 \pm 2.4	16.1 \pm 3.3
Ault Park	33.0 \pm 0.5	15.8 \pm 1.3	17.2 \pm 0.3
Fort Thomas	31.3 \pm 0.4	21.9 \pm 1.1	9.4 \pm 1.4
Overall Average	32.2 \pm 0.3	18.6 \pm 0.9	13.6 \pm 1.1
<i>Hemidactylus turcicus</i>			
New Orleans	30.2 \pm 1.1	18.9 \pm 1.3	11.3 \pm 2.0
Hammond	32.8 \pm 0.6	19.8 \pm 0.9	13.1 \pm 1.2
Mobile	31.7 \pm 0.5	20.9 \pm 1.2	10.7 \pm 1.0
Port Arthur	32.1 \pm 0.5	18.0 \pm 0.4	14.1 \pm 0.8
Austin	30.6 \pm 0.6	20.7 \pm 1.9	9.9 \pm 1.9
Overall Average	32.0 \pm 0.3	20.0 \pm 0.4	18.0 \pm 0.6

than lizards from Tusculum ($\bar{x} = 22.6$ °C, $p = 0.019$, 2.58 km from core) and Fort Thomas ($\bar{x} = 21.8$ °C, $p = 0.013$, 3.88 km from core) (Fig. 2A). In corroboration with the CT_{min} results, post-hoc Tukey HSD comparisons also revealed that thermal breadth was also significantly broader for *P. muralis* from the Ault population ($\bar{x} = 17.2$ °C) than lizards from Tusculum ($\bar{x} = 8.9$ °C, $p = 0.032$) and Fort Thomas ($\bar{x} = 9.4$ °C, $p = 0.014$) (Fig. 2B). The ANOVAs did not detect any significant effect of site on CT_{max} , CT_{min} , or thermal breadth for *H. turcicus*.

The coefficient of variation for *P. muralis* was lowest for all thermal parameters at Tusculum, the site closest to the introduction point (Table 2). The CV for CT_{max} and CT_{min} was highest at Alms (3.34 km from core), followed by Ault (4.47 km from core), and Fort Thomas (3.88 km from core). The CV for breadth in thermal tolerance was highest for Ault, the site farthest from the introduction point, followed by Alms, and Fort Thomas. The CV for *H. turcicus* was relatively similar for CT_{max} among sites, with Port Arthur (368.54 km from core) being the lowest and Austin (738.69 km from core) being the highest (Table 2). However, the CV for CT_{min} for *H. turcicus* was more variable among sites, with Port Arthur having the lowest Austin having the highest. The CV for breadth of thermal tolerance was lowest in Port Arthur, and greatest in Austin.

3.3. Thermal variation by distance

The linear model detected no significant trend between *P. muralis*

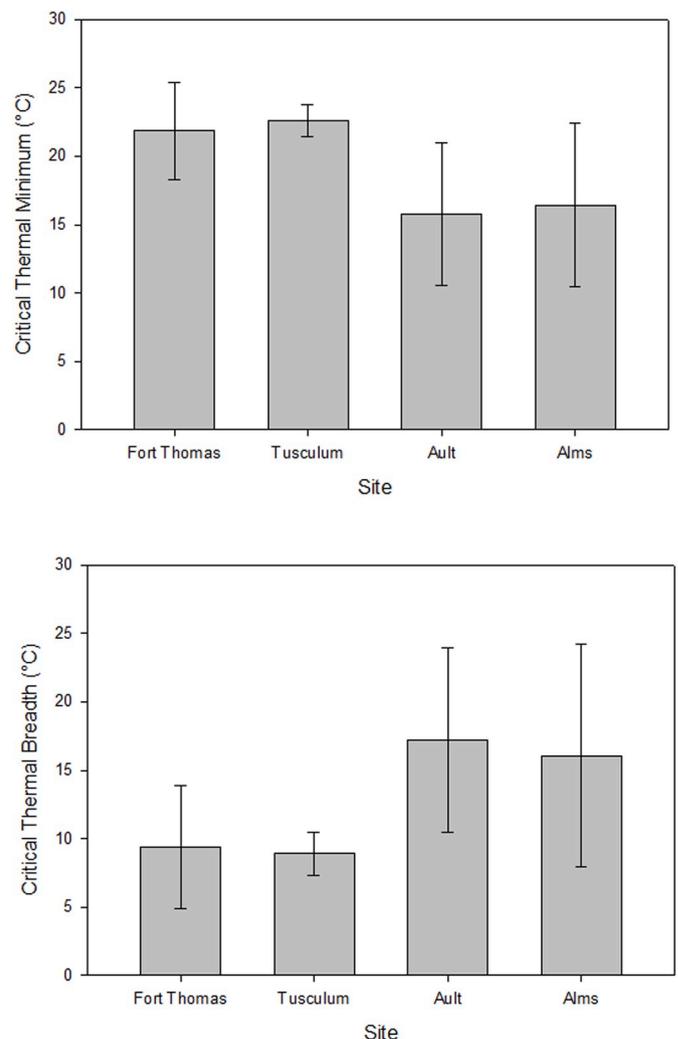


Fig. 2. Bar graphs showing critical thermal minimum (A) and critical thermal breadth (B) by site for *Podarcis muralis*.

Table 2

Coefficient of variation for critical thermal tolerance parameters across sites of European wall lizards (*Podarcis muralis*) and Mediterranean geckos (*Hemidactylus turcicus*).

Site	Coefficient of Variation		
	CT _{max}	CT _{min}	Breadth
<i>Podarcis muralis</i>			
Tusculum	2.5	5.3	17.4
Alms Park	8.4	36.4	50.8
Ault Park	5.8	24.1	68.5
Fort Thomas	3.8	16.2	47.7
<i>Hemidactylus turcicus</i>			
New Orleans	7.8	15.2	39.4
Hammond	6.6	17.7	35.1
Mobile	6.9	16.8	39.5
Port Arthur	6.3	8.1	22.2
Austin	8.8	24.5	51.1

CT_{max} and distance from the introduction point. However, CT_{min} significantly decreased as distance from the introduction site increased (DF = 35, $F = 5.548$, $R^2 = 0.134$, $p = 0.024$) (Fig. 3A), and a thermal breadth increased as distance from the introduction site for *P. muralis* (DF = 13, $F = 5.062$, $R^2 = 0.132$, $p = 0.031$) (Fig. 3B). Therefore, there was an overall trend in lower CT_{min} and broader thermal breadth among *P. muralis* lizards found farther from the introduction site. There were no

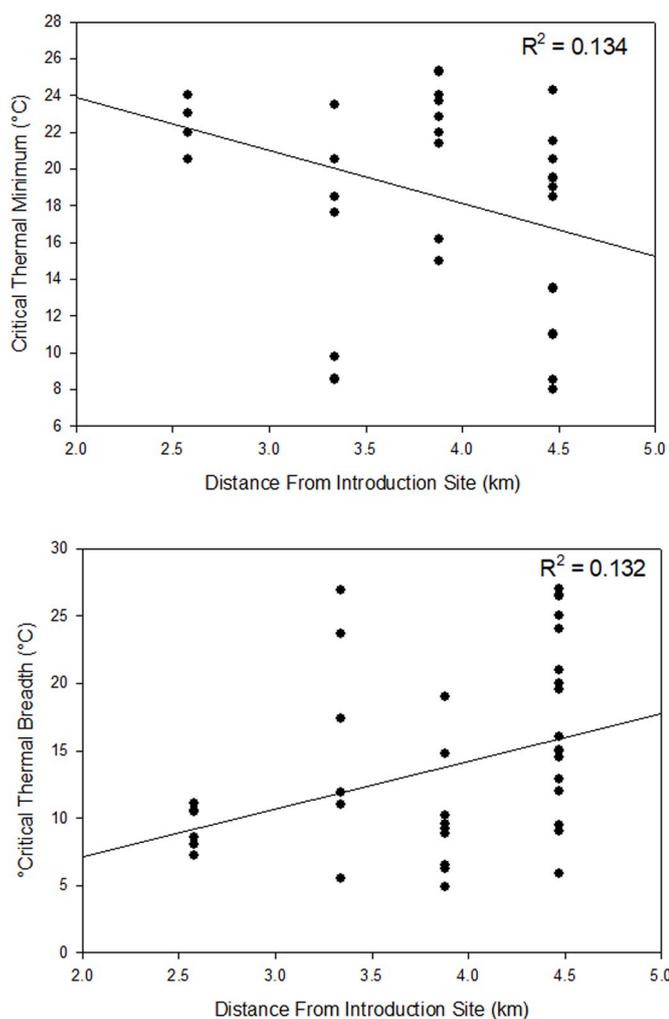


Fig. 3. Scatterplots showing negative linear correlation between critical thermal minimum, and positive correlation between critical thermal breadth, with distance from introduction site for *Podarcis muralis*.

significant trends in CT_{max}, CT_{min}, or thermal breadth and distance from the introduction point for *H. turcicus*.

4. Discussion

Based on the results of this study, we failed to falsify our hypothesis that critical thermal tolerances vary among populations, and that critical thermal breadth broadens when moving away from the core, among populations of the introduced European wall lizard. However, we were able to falsify the same hypotheses for the introduced Mediterranean gecko. We observed significant variation in thermal tolerance across the introduced distribution of *P. muralis* in Cincinnati, OH and a nearby population in Fort Thomas, KY. Specifically, the introduced population of *P. muralis* exhibited no significant variation in CT_{max}, but had a significantly different CT_{min} and critical thermal breadth based on site. Among our survey sites for *P. muralis*, Ault Park lizards (site farthest from the introduction site) had an increased ability to withstand colder temperatures than Tusculum (site closest to introduction point) and Fort Thomas, resulting in a significantly broader critical thermal breadth in the Ault Park population compared to Tusculum and Fort Thomas populations. We did not observe any significant differences in thermal tolerances among survey sites for *H. turcicus*. We did detect a pattern when looking at the variation of critical thermal tolerances among lizards surveyed. For *P. muralis*, variation in all thermal parameters assessed was lowest at Tusculum, the site closest to the introduction point. For CT_{max} and CT_{min}, variation was greatest at Alms Park, followed by Ault Park and Fort Thomas. Whereas, variation in critical thermal breadth was greatest at Ault Park, followed by Alms Park and Fort Thomas. For *H. turcicus*, there was not a high degree of variation in CT_{max} among sites, but there was variation in CT_{min} and critical thermal breadth where Port Arthur had the lowest variation and Austin had the highest. Among *P. muralis* populations, we detected a significant trend in increased distance from the introduction site, lower critical thermal minimums, and broader thermal tolerances. Thus, populations farther from the introduction site exhibited increased ability to withstand colder temperatures, resulting in a broader thermal fundamental niche. However, no linear trends were detected in thermal tolerance across the wide introduced range of *H. turcicus*.

The detection of variable thermal tolerance across a distribution that was observed in *P. muralis* suggests that selection in novel climatic environments on dispersers may influence the thermal niche of a species at a population level. Low variation in thermal tolerance at the introduction site for *P. muralis* supports the prediction that some peripheral populations throughout the distribution of an introduced species may have a wider range of characteristics, more representative of generalists, selected on through dispersal. Additionally, the linear trend in increased cold tolerance as distance from the introduction site increased for *P. muralis* suggests that some peripheral populations may have undergone selection leaving only suitable dispersers in novel environments than lineages of lizards that remained at or near the introduction site.

Extreme temperatures that result in individual mortality are more likely to drive selection on thermal tolerance than daily average temperatures (Buckley and Huey, 2016). Logan et al. (2014) found that when translocating a population of brown anoles (*Anolis sagrei*) to a warmer environment, mortality increased and selection occurred for a wider thermal performance breadth. It was also reported by Leal and Gunderson (2012), in the Puerto Rican crested anole (*Anolis cristatellus*), that an introduced population in Miami, FL had increased tolerance for colder temperatures than the source population, which resides in an area with warmer winters (Leal and Gunderson, 2012). Across the range of *P. muralis* in Cincinnati, it has been found that high mortality can occur overwinter, with no significant effect of substrate choice (Mackey, 2010). However, surviving lizards were found to typically reduce activity earlier than others (Mackey, 2010). Therefore, mortality among the remaining active lizards may drive selection for increased cold tolerance among those that could stay active and still survive. The

thermoregulatory behavior of reducing activity may buffer individual *P. muralis* that seek shelter earlier in the season from evolving lower critical thermal minimum, whereas, the increased activity time of others could provide time to move and disperse, potentially resulting in the increased cold tolerance among peripheral populations.

An additional factor to consider when making comparisons among thermal trials in a lab setting is the introduced stress, which could result in variable responses. It may be possible that the individuals that dispersed from the introduction site had the ability to respond less severely to stress, and therefore were able to withstand thermal trials longer. The CT_{max} for *P. muralis* populations assessed here were on average lower than those of a European population previously assessed using a different method with a more rapid change in temperature (Bauwens et al., 1995). Duration of thermal trial and (therefore starting temperature) have been shown to have an effect on critical thermal tolerance outcomes (Terblance et al., 2007), and designing shorter thermal trials may result in greater thermal maximums and lower thermal minimums. Therefore, the longevity of thermal trials should be taken into consideration when making direct comparisons among studies using different methodology. However, for the purposes of comparison among populations within this study, the same methodology was implemented allowing for direct comparisons.

The similarity in thermal tolerances between Alms Park and Ault Park, and Alms Park and Tusculum, despite Ault Park being closer to Tusculum than Alms Park is of interest. In Cincinnati, there is an abundance of railways that serve as potential habitat and means for dispersal for *P. muralis* (Heeden and Hedeem, 1999; Gherghel et al., 2009). There is a railway that runs alongside Tusculum, Alms Park and Ault Park, with Alms Park situated in the middle of the three sites. The location of these sites in relation to the railway could allow *P. muralis* to disperse readily from Alms Park to Tusculum and Ault Park, resulting in similarities between Alms Park and the surround two sites. Therefore, it may be hypothesized that the differences in Ault and Tusculum, but similarities in Alms and the surrounding sites, may be a result of increased dispersal rate when using the railway as opposed to dispersal through the urban landscape. Additionally, Fort Thomas is the farthest site from Ault Park, and separated by the Ohio River, which may explain the significant differences observed between the two sites.

When comparing the results from this study for *P. muralis* and *H. turcicus*, it appears that life history strategy has a dramatic influence on evolution of the thermal niche upon introduction as a result of temperatures experienced. A diurnal, thermoregulatory, active foraging life history strategy, as exhibited by *P. muralis*, may have different selective pressures than the nocturnal, thermoconforming, wait-ambush strategy, exhibited by *H. turcicus*. The introduced population of *P. muralis* tested here originated from a native population in Lake Garda, Italy (Deichsel and Gist, 2001), where temperatures drop as low as -2°C (World Weather Online, 2018), whereas, in Cincinnati temperatures drop as low as -31°C (National Weather Service, 2018). Lower extreme cold temperatures could be a driving force in the increased critical thermal minimum exhibited by *P. muralis* throughout its distribution in Cincinnati and northern Kentucky, especially due to the observed winter mortality (Mackey, 2010). The cost of foraging can be higher for active foragers (Nagy et al., 1984); therefore, the presence of novel temperatures in addition to high costs of active foraging could contribute strong selective pressures for survivorship in *P. muralis*. The lower variation in thermal breadth near the introduction site at Tusculum may be a result of a buffer from thermoregulatory behaviors (Huey and Kingsolver, 1993), whereas selection on disperser traits allowing for activity during colder temperatures may have resulted in the greater variability in thermal minimum at the site farthest from the introduction point.

In contrast, our data indicate that *Hemidactylus turcicus* may not experience extreme temperatures driving strong selection on thermal tolerance. Typically, high degrees of variation in thermal tolerance are observed along latitudinal gradients (Sunday et al., 2010). Along the longitudinal transect surveyed for *H. turcicus*, temperatures may not be

extreme enough to result in a change in thermal tolerance throughout the distribution. Additionally, the similarity in thermal tolerances among *H. turcicus* populations could be the result of proximity to the ocean, which has been found to act as a climatic buffer for other geckos (Weeks and Espinoza, 2013). As a nocturnal species, *H. turcicus* avoids extreme hot temperatures during the day, which was reflected in low variation in CT_{max} among populations. Additionally, some nocturnal species have been found to behaviorally thermoregulate by selecting sites or postures that allow them to avoid unfavorable hot or cold temperatures in their environment (Kearney and Predavec, 2000). Although *H. turcicus* has the ability to survive cold winters (Wessels et al., 2018), activities may be limited by cool temperatures experienced throughout the night (Hitchcock and McBrayer, 2006). Variation in cold temperatures daily and seasonally could contribute to selection for increased thermal minimum in *H. turcicus*, if those temperatures were extreme. However, temperatures in the introduced range of *H. turcicus* surveyed in this study do not differ dramatically from those in their native ranges. In parts of the Mediterranean, temperatures can drop as low as 0°C (Piccarreta et al., 2014), compared to the introduced locations in this study where low temperatures range from $3.3 - 6.1^{\circ}\text{C}$ (US Climate Data, 2018). Additionally, as a diurnal species, *P. muralis* may experience greater fluctuation in daily temperatures when active compared to *H. turcicus*, when active at night. Therefore, the lack of extreme temperatures and selective pressures, thermoregulatory behaviors, and proximity to the ocean, may allow *H. turcicus* to persist, without changes in thermal tolerances.

Thermal tolerance data can be a useful tool in predicting introduced species success and range expansion (Tepolt and Somero, 2014; Iacarella et al., 2015; Marras et al., 2015). Based on the results of this study, it appears that *P. muralis* is susceptible to cold temperatures, and may undergo rapid evolution in response to extreme cold events in novel environments, allowing for increased thermal tolerance. Additionally, it appears that maximum temperature is not a limiting factor for success and movement of *P. muralis*. Therefore, when predicting the invasion success and expansion of introduced *P. muralis* populations, the evolution of thermal tolerances should be considered, in regards to the ability of this species to adapt to colder temperatures rapidly and expand in thermal tolerance over generations. However, there is little interspecific competition in Cincinnati for *P. muralis* in the urban landscape surveyed, which may contribute to its success in this location (Lescano, 2010).

When predicting introduction success and movement of *H. turcicus*, thermal tolerance may not be a limiting factor when considering a longitudinal directionality. Based on the findings here, *H. turcicus* doesn't exhibit variance in thermal tolerance across a wide range of sites in the United States, potentially as a result of lack of extreme temperature change along this gradient. However, when considering movement upon a latitudinal gradient, thermal tolerance may be more variable, influencing establishment.

Currently, we are experiencing a time of accelerated atmospheric change. Impacts of thermal tolerance on species distribution and selection are crucial for understanding how survivorship of native organisms will be affected (Pörtner and Farrell, 2008), and predicting introduced species distributions (Ficetola et al., 2007; Kearney and Porter, 2009). The results of this study indicate that the survivorship and evolvability of an organism in response to a novel thermal environment may be dependent on life history characteristics and the breadth of the fundamental niche, at least for diurnal lizards. Extreme temperatures resulting in mortality and selection on fundamental niche may facilitate evolution in thermal tolerance for species in the future. However, life history and magnitude of temperature change appears to play key roles in facilitating successful invasion. Therefore, it is important to consider the phylogenetic constraints on life history, evolvability, behavior, and the thermal regime when studying species response to novel thermal regimes.

5. Conclusions

Variation in the thermal climate can influence the physiological tolerance throughout a species distribution. During a period of rapid climatic change, understanding the ability of thermal tolerance to evolve is important. Introduced species offer a unique opportunity for studying rapid evolution in novel environments, specifically in respect to physiological tolerance and dispersal. Typically, the fundamental niche, and thermal tolerances, are considered to be phylogenetically conserved throughout a lineage (Hoffmann et al., 2013). However, recent evidence suggests that when experiencing novel climatic regimes micro-selection may occur on such physiological process. The increased cold tolerance in *P. muralis* throughout the introduced ranges suggests that ectotherms may possess evolvability in thermal tolerance in response to climate change. However, this may not be applicable to all ectotherms and many factors may influence this, as suggested by the lack of variability in *H. turcicus*. Additional research is needed to expand the scope of this study to understand further how species respond to rapid change in the thermal climate.

Funding

This work was supported by Tennessee Technological University and the Center for the Management, Utilization, and Protection of Water Resources. Neither funding source played a role in study design, data collection, analysis, interpretation, writing of the report, or in the decision to submit the article for publication.

Declaration of competing interest

None.

Acknowledgements

We thank Hayden Mattingly for improvement and comments on a previous draft of this manuscript. We also thank the many people who helped with data collection and statistical analyses, including M. Schrum, A. Grajal-Puche, T. Coleman, C. Bravo, D. Walker, J. Bynum, M. Kearley, D. Kearley, C. Kearley, M. Kearley, and C. Crother. All work was performed in accordance with the regulations and recommendations of the Institutional Animal Care and Use Committee of Tennessee Technological University.

References

- Angilletta Jr., M.H., Montgomery, L.G., Werner, Y.L., 1999. Temperature preference in geckos: diel variation in juveniles and adults. *Herpetologica* 55, 212–222.
- Bauwens, D., Garland Jr., T., Castilla, A.M., Van Damme, R., 1995. Evolution of sprint speed in Lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* 49, 848–863.
- Beal, S.M., Lattanzio, M.S., Miles, D.B., 2015. Differences in the thermal physiology of adult Yarrow's spiny lizards (*Sceloporus jarrovi*) in relation to sex and body size. *Ecol. Evol.* 4, 4220–4229.
- Beaupre, S.J., Dunham, A.E., 1995. A comparison of ratio-based and covariance analyses of a nutritional data set. *Funct. Ecol.* 9, 876–880.
- Braña, F., 1991. Summer activity patterns and thermoregulation in the wall lizard, *Podarcismuralis*. *Herpetol. J.* 1, 544–549.
- Brown, R.M., Gist, D.H., Taylor, D.H., 1995. Home range ecology of an introduced population of the European wall lizard *Podarcis muralis* (Lacertilia: Lacertidae) in Cincinnati, Ohio. *Am. Midl. Nat.* 1995, 344–359.
- Brusch IV, G.A., Taylor, E.N., Whitfield, S.M., 2015. Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia* 180, 324–334.
- Buckley, L.B., Huey, R.B., 2016. How extreme temperatures impact organisms and the evolution of their thermal tolerance. *Integr. Comp. Biol.* 56, 98–109.
- Claussen, D.L., Townsley, M.D., Bausch, R.G., 1990. Supercooling and freeze-tolerance in the European wall lizard, *Podarcis muralis*, with a revisional history of the discovery of freeze-tolerance in vertebrates. *J. Comp. Physiol. B* 160 (2), 137–143.
- Clusella-Trullas, S., Chown, S.L., 2013. Lizard thermal trait variation at multiple scales: a review. *J. Comp. Physiol.* 184, 5–21.
- Cox, R.M., Zilberman, V., John-Alder, H.B., 2006. Environmental sensitivity of sexual size dimorphism: laboratory common garden removes effects of sex and castration on lizard growth. *Funct. Ecol.* 20, 880–880.
- Deichsel, G., Gist, D.H., 2001. On the origin of the common wall lizards *Podarcis muralis* (Reptilia:Lacertidae) in Cincinnati, Ohio. *Herpetol. Rev.* 32, 230–232.
- Eckert, C.G., Samis, K.E., Lougheed, S.C., 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.* 2008, 1170–1188.
- Etheridge, R.E., 1952. The warty gecko, *Hemidactylus turcicus* (Linnaeus), in New Orleans, Louisiana. *Copea* 1952, 47–48.
- Ficetola, G.F., Thuiller, W., Miaud, C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. *Divers. Distrib.* 13, 476–485.
- Fowler, H.W., 1915. Cold-blooded vertebrates from Florida, the west Indies, Costa Rica, and eastern Brazil. *Proc. Acad. Nat. Sci. Phila.* 67, 244–269.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G., 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Comp. Biol.* 42, 5–17.
- Gherghel, I., Strugariu, A., Sahlean, T.C., Zamfirescu, O., 2009. Anthropogenic impact or anthropogenic accommodation? Distribution range expansion of the common wall lizard (*Podarcis muralis*) by means of artificial habitats in the north-eastern limits of its distribution. *Acta Herpetol.* 4, 183–189.
- Gomez-Zlatar, P., Moulton, M.P., Franz, R., 2006. Microhabitat use by introduced *Hemidactylus turcicus* (Mediterranean Gecko) in north central Florida. *Southeast. Nat.* 5, 425–434.
- Heeden, S.E., Hedeon, D.L., 1999. Railway-aided dispersal of an introduced *Podarcis muralis* population. *Herpetol. Rev.* 30, 57.
- Hertz, P.E., Huey, R.B., 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards in Hispaniola. *Ecology* 62, 515–521.
- Hitchcock, M.A., McBrayer, L.D., 2006. Thermoregulation in nocturnal ectotherms: seasonal and intraspecific variation in the Mediterranean gecko (*Hemidactylus turcicus*). *J. Herpetology* 40, 185–195.
- Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S., 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct. Ecol.* 27, 934–949.
- Holt, R.D., Barfield, M., Gomulkiewicz, R., 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? Species invasions: insights into ecology, evolution, and biogeography, pp. 259–290.
- Huey, R.B., Bennett, A.F., 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41, 1098–1115.
- Huey, R.B., Bennett, A.F., 1990. Physiological adjustments to fluctuating thermal environments: an ecological and evolutionary perspective. *Stress Proteins Biol. Med.* 19, 37–59.
- Huey, R.B., Kingsolver, J.G., 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4, 131–135.
- Huey, R.B., Kingsolver, J.G., 1993. Evolution of resistance to high temperature in ectotherms. *Am. Nat.* 142, S21–S46.
- Iacarella, J.C., Dick, J.T.A., Alexander, M.E., Ricciardi, A., 2015. Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. *Ecol. Appl.* 25, 706–716.
- Janzen, D.H., 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101, 233–249.
- World Weather Online, 2018. Riva Del Garda Monthly Climate Averages.
- Jasienski, M. and Bazzaz, F. A. The fallacy of ratios and the testability of models in biology. *Oikos* 84:321–326.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Kearney, M., Predavec, M., 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* 81, 2984–2996.
- Knouft, J.H., Losos, J.B., Glor, R.E., Kolbe, J.J., 2006. Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis* *segregi* group. *Ecology* 87, s29–s38.
- Leal, M., Gunderson, A.R., 2012. Rapid change in the thermal tolerance of a tropical lizard. *Am. Nat.* 180, 815–822.
- Lescano, N.V., 2010. Population Bottlenecks and Range Expansion in *Podarcis muralis*, a Wall Lizard Introduced from Italy. University of Cincinnati. Unpublished Master's Thesis.
- Logan, M.L., Cox, R.M., Calsbeek, R., 2014. Natural selection on thermal performance in a novel thermal environment. *Proc. Natl. Acad. Sci.* 111, 14165–14169.
- Mackey, T.L., 2010. Habitat Selection and Overwintering Survival of the Introduced Wall Lizard, *Podarcis muralis*. University of Cincinnati. Unpublished Master's Thesis.
- Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., Butenschön Kay, S., Bitetto, D.M., Quattrocchi, G., Sinerchia, M., Domenici, P., 2015. Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conser. Physiol.* 3, 1–14.
- Michaelides, S.N., While, G.M., Zajac, N., Uller, T., 2015. Widespread primary, but geographically restricted secondary, human introductions of wall lizards, *Podarcis muralis*. *Mol. Ecol.* 24, 2702–2714.
- Nagy, K.A., Huey, R.B., Bennett, A.F., 1984. Field energetics and foraging mode of Kalahari Lacertid lizards. *Ecology* 65, 588–596.
- Patterson, J.W., 1984. Thermal acclimation in two subspecies of the tropical lizard *Mabuya striata*. *Physiol. Zool.* 57, 301–306.
- Pianka, E.R., 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51, 703–720.
- Piccarreta, M., Lazzari, M., Pasini, A., 2014. Trends in daily temperature extremes over the Basilicata region (southern Italy) from 1951 to 2010 in a Mediterranean climatic context. *Int. J. Climatol.* 35, 1964–1975.
- Pontes-da-Silva, E., Magnusson, W.E., Sivero, B., Caetano, G.H., Miles, D.B., Colli, G.R., Diele-Viegas, Fenker, J., Santos, J.C., Werneck, F.P., 2018. Extinction risks forced by

- climatic change and intraspecific variation in the thermal physiology of a tropical lizard. *J. Therm. Biol.* 2018, 50–60.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–691.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rödger, D., Lötters, S., 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob. Ecol. Biogeogr.* 18 (6), 674–687. <https://doi.org/10.1111/j.1466-8238.2009.00477.x>.
- Schwane, T., DeVries, A., Budge, D., Schwane, D., 2008. Genetic variation in founder populations of the Mediterranean gecko, *Hemidactylus turcicus*, across the southern United States. *Amphibia-Reptilia* 29, 438–442.
- Selcer, K.W., 1987. Seasonal variation in fatbody and liver mass of the introduced Mediterranean gecko, *Hemidactylus turcicus*, in Texas. *J. Herpetol.* 21, 956–962.
- Stabler, L.B., Johnson, W.L., Locey, K.J., Stone, P.A., 2011. A comparison of Mediterranean gecko (*Hemidactylus turcicus*) populations in two temperate zone urban habitats. *Urban Ecosyst.* 15, 653–666.
- Stevens, V.M., Trochet, A., Van Dyck, H., Clobert, J., Baguette, M., 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecol. Lett.* 15, 74–86.
- Strijbosch, H., Bonnemayer, J.J.A.M., Dietvorst, P.J.M., 1980. The northernmost population of *Podarcis muralis* (Lacertilia, Lacertidae). *Amphibia-Reptilia* 1, 161–172.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2010. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* 278, 1823–1830.
- Tepolt, C.K., Somero, G.N., 2014. Master of all trades: thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas*. *J. Exp. Biol.* 217, 1129–1138.
- Terblance, J.S., Deere, J.A., Clusella-Trullas, S., Janion, C., Chown, S.L., 2007. Critical thermal limits depend on methodological context. *Proc. R. Soc. B* 274, 2935–2942.
- US Climate Data, 2018. Your Weather Service.
- Van Berkum, F.H., 1988. Latitudinal patterns of the thermal sensitivity of spring speed in lizards. *Am. Nat.* 132 (3), 327–343.
- Van Damme, R., Bauwens, D., Verheyen, R.F., 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. *OIKOS* 57, 61–67.
- Von May, R., Caatenazzi, A., Santa-Cruz, R., Gutierrez, A.S., Moritz, C., Rabosky, D.L., 2019. Thermal physiological traits in tropical lowland amphibians: vulnerability to climate warming and cooling. *PLoS One* 14, e0219759.
- Weeks, D.M., Espinoza, R.E., 2013. Lizards on ice: comparative thermal tolerances of the world's southernmost gecko. *J. Therm. Biol.* 38, 225–232.
- Wessels, J.L., Carter, E.T., Hively, C.L., Hayter, L.E., Fitzpatrick, B.M., 2018. Population viability of nonnative Mediterranean house geckos (*Hemidactylus turcicus*) at an urban site near the northern invasion front. *J. Herpetol.* 52, 215–222.
- National Weather Service, 2018. Cincinnati Climate Records.
- Allison R. Litmer** is a graduate student pursuing a Ph. D. in Biology at the University of Arkansas. She has a Bachelor's of Science degree from Northern Kentucky University and a Master's of Science degree in Biology from Tennessee Technological University. Her graduate research examines the physiological ecology of *Sceloporus* lizards with an emphasis on modeling effects of climate change on lizard sustainability, physiology, and energy budgets.
- Christopher M. Murray Ph.D.** is an assistant professor at Southeastern Louisiana University, interested in physiological ecology, functional and diagnostic morphology and biogeographic and systematic philosophy.