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Thermal tolerances of different life stages, sexes, and species of widow spiders (Araneae: Theridiidae)

Cody L. Barnes[1,2], **Nicholas W. Blay**[1,3], and **Shawn M. Wilder**[1]: [1]Department of Integrative Biology, Oklahoma State University, Stillwater, Oklahoma 74078, USA; E-mail: cody.l.barnes@okstate.edu; [2]Present Address: Department of Biology, Utah State University, Logan, UT 84321, USA; [3]Present Address: Department of Biology, Wartburg College, Waverly, IA 50677, USA

Abstract. Temperature strongly shapes the physiology and distributions of ectotherms. Environmental extremes and the range of temperatures encountered can limit persistence. Further, thermal tolerance limits are thought to be one of the factors limiting the distributions of invasive species. The critical thermal maximum (CT_{Max}) and critical thermal minimum (CT_{Min}) are metrics frequently applied for defining upper and lower thermal tolerances, respectively. Temperatures contained within the boundaries of the CT_{Max} and CT_{Min} comprise the thermal tolerance range. In this study, we tested whether thermal tolerances differed between two native (*Latrodectus hesperus* Chamberlin & Ivie, 1935 and *L. mactans* (Fabricius, 1775)) and one invasive (*L. geometricus* CL Koch, 1841) widow species (*Latrodectus* Walckenaer, 1805). We separately tested if thermal tolerances differed by life stage and sex. Using species distribution modelling, we also tested if thermal extremes or temperature range most accurately correspond with current species occurrences in the United States. We hypothesized that *Latrodectus geometricus* would have lower thermal tolerance range and that minimum temperatures would most influence their present distributions since they presumably originated from a more equatorial climate. We found that CT_{Min} did not vary by developmental stage, but was highest in males. We found that the CT_{Min} and CT_{Max} of *L. geometricus* (3.2, 51.5 °C) and *L. mactans* (1.9, 52.4 °C) were higher than *L. hesperus* (-1.9, 49.6 °C). Males also had the narrowest thermal tolerance range in the three species examined. Lastly, we found that the highest performing distribution model was the one correlating minimum temperature with *L. geometricus* occurrences.

Keywords: CT_{Min}, CT_{Max} *Latrodectus*, development, invasive species

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Over a lifetime, temperature may strongly shape the behavior and physiology of ectotherms (Huey & Pianka 1977; Angilletta et al. 2002a). Thermal tolerance also influences species distributions across space. That is, many species may experience contractions in distributions as temperatures exceed their thermal limits or, alternatively, thermal adaptations in other species may enable broadening of distributions (Bates et al. 2013). Constructing frameworks that pair physiology with abiotic limiting factors to predict abundances and distributions of native and invasive animals will be particularly important for understanding the consequences of climate change and other anthropogenic influences (Pintó-Marijuan & Munné-Bosch 2013; Rius et al. 2014; Lehmann et al. 2020).

The critical thermal maximum (CT_{Max}), critical thermal minimum (CT_{Min}), and thermal tolerance range are metrics frequently used for defining thermal physiology of animals. CT_{Max} originally referred to the upper temperature at which escape locomotory function is lost, while CT_{Min} was defined as the lower temperature at loss of locomotion (Cowles & Bogert 1944; Hazell & Bale 2011). These parameters have also been more recently characterized by the loss of righting response or the onset of spasms (Lutterschmidt & Hutchison 1997a). Temperatures within the upper and lower boundaries (i.e., CT_{Min} to CT_{Max}) encompass the thermal tolerance range. A growing focus on global climate change has spurred interest in physiological thermal limits, CT_{Max} in particular.

Thermal tolerance range is greatest in early developmental stages for some ectotherms (Bowler & Terblanche 2008) but is greatest in adults of other species (Xu & Ji 2006). The thermal tolerance range of species also generally increases with absolute latitude (Gutiérrez-Pesquera et al. 2016; Payne & Smith 2017). The upper thermal limit, CT_{Max}, has been found to differ both between life stages (Tolbert 1979; Floyd 1983; Barnes et al. 2019) and among many different species (Kellerman et al. 2012; Verble-Pearson et al. 2015). However, variation in CT_{Min} can be higher than that of CT_{Max}, likely due in part to absolute minimum environmental temperatures being more variable than absolute maximum temperatures (Gaston & Chown 1999). Further, lower thermal tolerance has been proposed to more strongly shape latitudinal range boundaries of organisms than upper thermal tolerances (Sunday et al. 2012). Lastly, thermal tolerance should positively correlate with the geographic range of species distribution, since the greater climatic variability at high latitudes would function as the main selection factor (climate variability hypothesis; Bozinovic et al. 2011).

Several different physiological and behavioral strategies enable survival at low temperatures. Organisms can be classified as those capable of surviving the formation of internal ice (i.e., freeze tolerant species) and those that maintain body fluids in the liquid state (i.e., freeze-avoiding species), with most arthropods in the latter group (Sinclair et al. 2003). The CT_{Min} is positively related to body size in several ectotherms (Doughty 1994; Di Santo & Lobel 2017; Wu et al. 2017), yet some studies of arthropods have not found a relationship (Gaston & Chown 1999; Hu & Appel 2004) or instead found a negative relationship (Fordyce & Shapiro 2003; Kaspari et al. 2015). The thermal limits of less than 1% of arachnid species are represented in the literature so far (Lutterschmidt & Hutchison 1997b; Schmalhofer 1999; Table 1). Characterization of lower thermal limits in arachnids will

Table 1.—Summary of previously published thermal tolerance limits (CT_{Min} and CT_{Max}) and tolerance range (TolRange) across representative families, genera, and species of arachnids.

Family	Genus	Species	Description	CT_{Min}	CT_{Max}	TolRange	Source
Toxopidae	*Myro*	*kerguelenensis*	Pickard-Cambridge, 1876	-6.5	35.3	41.8	Jumbam et al. 2008
Linyphiidae	*Prinerigone*	*vagans*	(Audouin, 1826)	-7.5	35.6	43.1	Jumbam et al. 2008
Lycosidae	*Pardosa*	*glacilalis*	(Thorell, 1872)	-5.7	46.6	52.3	Anthony et al. 2019
	Pardosa	*moesta*	Banks, 1892	-4.5	44.7	49.2	Anthony et al. 2019
	Rabidosa	*rabida*	Walckenaer, 1837	0.0	42.9	42.9	Stork 2012
Salticidae	*Habronattus*	*clypeatus*	(Banks, 1895)	11.6	55.0	43.4	Brandt et al. 2020
	Habronattus	*conjunctus*	(Banks, 1898)	12.1	52.5	40.4	Brandt et al. 2020
	Habronattus	*geronimoi*	Griswold, 1987	6.0	54.0	48.0	Brandt et al. 2020
	Habronattus	*hallani*	(Richman, 1973)	9.5	53.1	43.6	Brandt et al. 2020
	Habronattus	*pugillis*	Griswold, 1987	9.3	53.1	43.8	Brandt et al. 2020
	Habronattus	*virgulatus*	Griswold, 1987	9.2	54.4	45.2	Brandt et al. 2020
Sicariidae	*Loxosceles*	*laeta*	(Nicolet, 1849)	-4.1	48.4	52.5	Alfaro et al. 2013
	Sicarius	*thomisoides*	Walckenaer, 1847	6.6	44.2	37.6	Taucare-Rios et al. 2018
Scytodidae	*Scytodes*	*globula*	Nicolet, 1849	-3.6	45.0	48.6	Alfaro et al. 2013
Theraphosidae	*Aphonopelma*	*hentzi*	(Girard, 1852)	5.7	42.6	36.9	Punzo 1991
	Grammostola	*vachoni*	Schiapelli & Gerschman, 1961	5.3	46.1	41.4	Schwerdt et al. 2020
Theridiidae	*Latrodectus*	*geometricus*	CL Koch, 1841	3.2	51.5	48.3	This Study
	Latrodectus	*hesperus*	Chamberlin & Ivie, 1935	-1.9	49.6	51.5	This Study
	Latrodectus	*mactans*	(Fabricius, 1775)	1.9	52.4	50.5	This Study
Thomisidae	*Misumenops*	*asperatus*	(Hentz, 1847)	-1.4	45.1	46.5	Schmalhofer 1999
	Misumenoides	*formosipes*	(Walckenaer, 1837)	2.2	48.2	46.0	Schmalhofer 1999

likely be an important first step towards identifying whether cuticular waxes, cryoprotectants, metabolic arrest, or other strategies enable freeze tolerance or if arachnids are primarily freeze-avoiding.

Web-building widow spiders of the genus *Latrodectus* (Walckenaer, 1805) are distributed on all continents except Antarctica (Garb et al. 2004). Within the central United States, the distributions of three widow spiders overlap. The southern black widow (*Latrodectus mactans* (Fabricius, 1775)) is distributed throughout the southern and central United States, while the western black widow (*Latrodectus hesperus* Chamberlin & Ivie, 1935) is distributed across much of the western United States. Human-mediated transport has been attributed with the cosmopolitan global distribution of the brown widow (*Latrodectus geometricus* CL Koch, 1841), including recent invasion into the southern United States (Garb et al. 2004). In a previous ecological niche modelling study, *L. geometricus* were projected to have a low probability of occurrence across most of the United States (Taucare-Ríos et al. 2016). *Latrodectus geometricus* were thought to be originally distributed either within Africa or South America; the species seems most genetically similar to other *Latrodectus* in Africa, but the initial species description was from Colombia (Vincent et al. 2009).

Further range expansion in the United States by *L. geometricus* has the potential to pose conservation and management concerns. Establishment of *L. geometricus* could result in declines or loss of native widows. Within the United States, Vetter et al. (2012) have suggested that the invasion of *L. geometricus* is closely linked with the urban interface but rarely observed in agricultural locations. Another *Latrodectus,* the red katipo (*L. katipo* Powell, 1871), is listed as endangered due to the impacts of interbreeding and displacement by an invasive congener (Vink et al. 2011). From a species management perspective, the venom of *L. mactans*, *L. hesperus*, and *L. geometricus* are all potentially severe enough to warrant a visit to a hospital (McCrone 1964; Müller 1993), but *L. geometricus* are generally considered less toxic (Vetter et al. 2012). CT_{Max} was not previously found to differ between *L. mactans* and *L. geometricus*, but decreased with each progressive developmental stage (Barnes et al. 2019). However, CT_{Min} and thermal tolerance range have not yet been determined in widow spiders. A more comprehensive understanding of the thermal ecology of widows could provide novel insight into the persistence of both native and invasive species.

The purpose of this study was to determine if CT_{Min} and thermal tolerance range differed between two native widow species (*L. mactans* and *L. hesperus*) and an invasive congener (*L. geometricus*). Further, we tested whether CT_{Min} and thermal tolerance range varied among widow life stages and between sexes. Selection could have favored expression of traits in juveniles and males that allow them to tolerate a wider range of temperatures given that they are more mobile and likely to relocate webs throughout the thermal landscape (Lubin et al. 1993). When comparing species, we hypothesized that *L. geometricus* should have a higher CT_{Min} and reduced thermal tolerance range because of their more equatorial native distribution. To experimentally test these predictions, we measured CT_{Min} of widows in the laboratory, and compared them using separate statistical models for life stages and sexes. For species distributions, we predicted that low extreme temperatures should predict the United States of America distribution of *L. mactans*, *L. hesperus*, and *L. geometricus* more effectively than either high extreme temperatures or the range of temperatures. We also predicted that the species native to the United States, *L. mactans* and *L. hesperus*, would have greater niche breadth in this region than the invasive species, *L. geometricus,* which has a more equatorial native distribution. To test this, we developed ecological niche models to evaluate relationships between environmental variables (i.e., temperature, humidity, and human influence) and *Latrodectus* distributions in the USA. That is, we paired laboratory assays of thermal physiology with ecological niche models assembled using corresponding environmental variables and species occurrence records.

METHODS

Species collection and acclimation.—Individuals of each species were collected in areas where we knew that they could easily be located. *Latrodectus mactans* were collected from local residences in Payne County, Oklahoma from September through November 2018. *Latrodectus hesperus* were collected from Coconino County, Arizona in October 2018. *Latrodectus geometricus* were collected from residential areas in Los Angeles and Orange Counties, California in December 2018. Thermal tolerance experiments were not conducted on these field-collected spiders but, rather, their offspring that were raised in standardized controlled conditions in the laboratory. Wild caught females of each species were brought back to the laboratory at Oklahoma State University (Stillwater, OK) and maintained to produce offspring to be used in experiments. Cohorts of each species were raised from the eggs produced in the laboratory. Spiders were individually separated from clutches approximately two weeks after hatching. Widows were maintained on a diet of vinegar flies (*Drosophila melanogaster*) and crickets (*Acheta domesticus*) in a common garden design at a constant 25 ± 1 °C and14L:10D light regime, which were identical to conditions in Barnes et al. (2019). Widows were acclimatized to these conditions from hatching to the time in which experimental trials were conducted. For this experiment, widows were haphazardly pulled from multiple clutches of continuously maintained laboratory cultures of each species, but the clutches were not recorded. We separated widows into three age classes with five individual spiders per age class. The sample sizes per treatment are less than some other studies (range: $n = 5–25$), but our results had relatively low standard error and most P-values were either well below (< 0.01) or well above (> 0.25) our $P = 0.05$ threshold. Spiderlings were approximately 1–2 months old, while juveniles were 2–3 months old. Mature males were identified by darkened palps (3–9 months old), while mature females were identified by sclerotized epigynum (6–9 months old). Color pattern varies substantially, even within cohorts and across molts for any individual spider, and is not consistently different between males and females prior to maturity (Kaston 1970). Prior to their use in trials, we matched different widow species by mass, using an analytical balance with resolution of 0.01 mg for each development stage to ensure distinct classes and assess allometric scaling of thermal tolerance.

CT_{Min} laboratory trials.—Laboratory trials of CT_{Min} were conducted by placing each spider in a 6 cm by 2 cm glass vial, which was then attached up-right to a wire test tube rack and partially submerged (approximately $3/4^{ths}$ of the test tube, or about 4 cm) into an ice chest (Excursion 28.4 liter, The Coleman Company). The ice chest was filled with 210 g/L brine to depress the freezing point. One vial was left empty and designated as a control chamber to confirm that vial temperatures were comparable to water temperatures. The assignment of spiders' vials and the control vial within the test tube rack was randomized for each trial. The temperatures of the water and within the control vial were determined using a pair of K-type thermocouples and measured with a 4-channel thermocouple data logger (UX120–014M, Onset Computer Corporation). The sensors were verified via submergence in an ice bath prior to trials. Spiders were acclimated to the chambers and start temperature (room temperature; 24.5 ± 0.2 °C) for a minimum of 5 minutes. Then, the water bath was cooled at a constant rate, using the brine solution frozen into 8 mL cubes using a cryogenic freezer. Cubes were added to the cooler every 150s and circulated with a small aquarium pump, until the lower thermal limits were determined for all trial spiders. All spiders recovered from freezing within one hour of trial completion (i.e., climbing and resuming web construction).

The lower thermal stress response (CT_{Min}) is defined as the lower limit to functional performance. For this experiment, CT_{Min} was documented as the temperature at which each spider was unable to respond (moving away, waiving first pair of limbs, or grasping) to light prodding with a soft–tipped paint brush (Schmalhofer 1999). The top of each test-tube remained open throughout the duration of the trial so that the apparatus could remain in the water while each spider was checked for loss of responsiveness. No spasms were noted during the CT_{Min} trials. To assess these behaviors, the same observer (CLB) determined onset of each response in real time.

CT_{Max} laboratory trials and thermal tolerance range.—Following the CT_{Min} trials, we estimated the thermal tolerance range as the difference between the CT_{Min} from this experiment and the CT_{Max} from a previous study of spiders from the same populations of *L. geometricus* and *L. mactans* (Barnes et al. 2019). We replicated the CT_{Max} protocol for *L. hesperus* across the three age classes, to allow us to estimate thermal tolerance range for that species. *Latrodectus hesperus* selected for the CT_{Max} trials were not previously run in the CT_{Min} trials. Five different spiderlings, juveniles, males, and females were each run for the CT_{Min} and CT_{Max} trials. Thus, we had a final replication size totaling twenty spiders for each species. This was the same number used in the previous study of CT_{Max} (Barnes et al. 2019).

Ecological niche modelling concurrent to the laboratory assays.—Next, we developed ecological niche models to evaluate relationships between environmental temperature and *Latrodectus* distributions in the continental United States of America. Occurrence data sets for *L. geometricus, L. mactans,* and *L. hesperus* were obtained from the Global Biodiversity Information Facility (GBIF; online at http://gbif.org/). The accuracy of occurrences in GBIF are ensured through screening of several commonly used standards such as the Darwin Core Standard, Ecological Metadata Language standard, and the Biological Collection Access Service standardization protocols. These data represent presence of individuals and do not imply the existence of breeding populations. The presence of individuals may also not be even across the entire range. For example, in desert habitats in the southwestern USA, occurrences of brown widows are primarily associated with urban areas.

From a total of 6,490 occurrence records downloaded, we filtered records lacking spatial data and outside of the lower 48 states. Duplicates were screened using ENMTools v. 1.3 (Warren et al. 2008, 2010). This led to the final numbers of 1,008 *L. geometricus*, 547 *L. mactans*, and 1,506 *L. hesperus* records. We downloaded the fine-scale bioclimatic variables from the WorldClim database (online at http://worldclim.org/), at 30-seconds spatial resolution (about 900 m at the equator). More specifically, the environmental variables we used were Bio5 (Max Temperature of Warmest Month), Bio6 (Min Temperature of Coldest Month), and Bio7 (Temperature Annual Range) to further evaluate our predictions of *Latrodectus* CT_{Max}, CT_{Min}, and tolerance range, respectively. We developed an alternative model for evaluating humidity using the WorldClim variable Water Vapor Pressure and another alternative model using the Human Influence Index (Wildlife Conservation Society and the Center for International Earth Science Information Network 2005). The precedence for the humidity alternative model is that, from comparison of coastal and desert parks in southern California, it has been proposed that brown widow distribution expansion could be limited in areas with low humidity (Lewis 2013). An alternative model using the Human Influence Index was developed to evaluate distributions with anthropogenic disturbance, as North American widows are characterized as being synanthropic (Vetter et al. 2012; Schraft et al. 2021). Using Pearson correlation analysis, we did not find strong ($r>0.5$), significant ($P<0.05$) relationships between the BioClim variables. We extracted Bio5 and Bio6 layer values to points for each species occurrence, then calculated the difference from the physiological thermal tolerance limits (i.e., CT_{Min} and CT_{Max}) for determining the thermal safety margin. The thermal safety margin is an indication of a species' vulnerability to climate warming or cooling (Sunday et al. 2014). This layer extraction process also enabled visualization of the range of minimum and maximum environmental temperatures experienced across the occurrences.

We constructed species distributions models (SDM) using MaxEnt version 3.4.1 software (online at http://biodiversityinformatics.amnh.org/open_source/maxent/). The SDM applied 80% of the occurrence data to develop the models and the remaining 20% were used for testing. A 10% training presence was used to threshold the SDM and final models were converted to the binary output (i.e., absent or present). We applied the clamping option to avoid environmental extrapolations outside the range of the training data (Owens et al. 2013). We tested the accuracy of models using the ROC (Receiver Operating Characteristic) curve analysis (area under curve, or AUC index). The area under the receiver-operator index (AUC) refers to the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point (Jiménez-Valverde 2012). Finally, we projected the model outputs using ArcMap 10.6.1 software (ESRI, Redlands, CA, USA).

We assessed the niche breadth and overlap of the environmental variables associated with the combination model integrating physiological tolerances of widows (Bio5, 6, and 7) using ENMTools 1.3 (Warren et al. 2010). Niche breadth was calculated using Levins' inverse concentration metric, ranging from 0 (single grid geographic cell has a non-zero suitability) to 1 (all cells are equally suitable). Niche overlap of widows was compared using the Schroener's D and Hellinger's I indices. The indices range from 0 (no overlap) to 1 (entire overlap) (Warren et al. 2008, 2010). We ran 100 randomly generated pseudoreplicate models to compare the indices for the true observed niche overlap with the null distribution of the 100 replicates (Warren et al. 2008; Taucare-Ríos & Piel 2021). We rejected the null hypothesis of niche conservatism if the true niche overlap value was smaller than the null distribution ($P < 0.05$).

Statistics.—We used ANCOVA to test if rate of temperature change over time differed between the chamber and ambient water temperatures (i.e., homogeneity of regression slopes). We found that the rate of cooling for the chambers (-0.92 ± $3.27\text{x}10^{-3}$ °C min^{-1}) did not differ from the rate at which the water was cooled (-0.92 ± 3.28×10^{-3} °C min^{-1}; $F_{1,18901}= 0.87$, $P=0.66$). That is, the temperatures experienced by spiders closely followed the environmental change. We also used ANCOVA to test if the cooling rates differed between trials and we found statistically significant but small differences in ramping rate by trials (range: 0.89 to 1.19 °C min^{-1}; $F_{11,18893}= 149367.9$, $P<0.0001$). This rate is at the upper end of the typical ramping protocol, which could cause higher susceptibility to shock (Lutterschmidt & Hutchison 1997a, b). However, our ramping rates are within the range of other studies; the studies listed in Table 1 used ramping rates of -0.2 °C min^{-1} to -3 °C min^{-1}.

We tested if mass differed by development stage and species using ANOVA. We used pooled linear regression to test for a relationship between mass and CT_{Min}. Mass was log transformed to meet the assumption of normal distribution. ANOVA was used to test if CT_{Min} differed between species and sizes of widows. A separate ANOVA was used to test if CT_{Min} differed between mature male and female widows. We did not combine models for development stage, species, and sexes because development of external characters that reliably indicate sex in widows (i.e., male palps and female sclerotized epigyna) are not present in spiderlings and young juveniles.

The CT_{Max} heating rate for the *L. hesperus* trials in this study (1.65 ± 0.01 °C min^{-1}) was similar to that of our previous study for *L. geometricus* and *L. mactans* (1.57 ± 0.04 °C min^{-1}). The heating rates were at the upper end of those used in comparable studies and likely greater than those naturally-occurring, which could result in overestimation of CT_{Max} (Terblanche et al. 2007, 2011). We also tested for differences in thermal tolerance range using ANOVA for the three spider age classes. Lastly, we tested if CT_{Min}, CT_{Max}, thermal tolerance range, and safety margins differed across the three species, after collectively pooling life stages and sexes, using ANOVA. Tukey post hoc tests were applied when significant effects were discovered. Statistical analyses were conducted using the JMP 12 software package (SAS Institute, Cary, NC, USA).

RESULTS

Mass significantly differed by developmental stage ($F_{2,51} = 11.69$, $P< 0.0001$), but not by species ($F_{2,51} = 2.21$, $P = 0.12$) in the linear regressions. Juveniles were larger than spiderlings and adults were largest. Spiders within a given developmental stage did not differ with respect to mass, which confirms that our size matching was effective. Further, mass was negatively related to CT_{Min} in *L. mactans* ($R^2 = 0.27$, $F_{1,\ 18} = 6.58$, $P =$

Table 2.—ANOVA table summarizing the effects of developmental stage, species, and the interaction of development stage and species on widow thermal tolerance. **Boldface text** indicates significant values.

Variable	d.f.	F	*P*
CT_{Min}			
Development Stage	2, 51	0.51	0.60
Species	2, 51	5.96	**0.0047**
Development Stage x Species	4, 51	0.91	0.46
CT_{Max}			
Development Stage	2, 50	10.90	**<0.0001**
Species	2, 50	14.71	**0.0001**
Development Stage x Species	4, 50	2.67	**0.04**
Tolerance Range			
Development Stage	2, 50	14.20	0.36
Species	2, 50	1.05	0.79
Development Stage x Species	4, 50	0.68	0.61

Table 3.—ANOVA table summarizing the effects of sex, species, and the interaction of sex and species on widow thermal tolerance. **Boldface text** indicates significant values.

Variable	d.f.	F	*P*
CT_{Min}			
Sex	1, 24	21.26	**0.0001**
Species	2, 24	6.15	**0.0070**
Sex x Species	2, 24	3.27	**0.05**
CT_{Max}			
Sex	1, 24	0.39	0.64
Species	2, 24	6.25	**0.007**
Sex x Species	2, 24	0.18	0.83
Tolerance Range			
Sex	1, 24	10.99	**0.0029**
Species	2, 24	2.22	0.13
Sex x Species	2, 24	1.38	0.27

0.02) and *L. hesperus* ($R^2 = 0.47$, $F_{1,\ 18} = 15.86$, $P = 0.0009$) (i.e., larger spiders tolerated lower temperatures), but not in *L. geometricus* ($R^2 = 0.03$, $F_{1,\ 18} = 0.65$, $P = 0.43$).

We ran separate analyses for developmental stage and sex since both could not be included in the same model (i.e., we could not identify the sex of juveniles and spiderlings) (Tables 2, 3, Figs. 1, 2). In the model for developmental stage, there was a significant effect of species on CT_{Min} ($F_{2,51} = 5.96$, $P = 0.0047$), but not the categorical variable developmental stage ($F_{2,51} = 0.51$, $P = 0.60$) nor the interaction of developmental stage and species ($F_{4,51} = 0.91$, $P = 0.46$). *Latrodectus hesperus* had lower CT_{Min} than *L. mactans* and *L. geometricus* (Table 2; Fig. 1). The model analyzing the effect of sex on CT_{Min} also reported a significant effect of species ($F_{2,\ 24} = 6.15$, $P = 0.007$; Table 3). Based on the posthoc test for the main effect of sex, *L. hesperus* had significantly lower CT_{Min} than *L. geometricus*. The CT_{Min} of *L. mactans* was intermediate to and did not statistically differ from the other two species. There was also a significant difference in CT_{Min} between male and female widows (Table 3; Fig. 2). The CT_{Min} of female widows was lower than male widows ($F_{1,\ 24} = 21.26$, $P = 0.0001$). Similar to Barnes et al. (2019), we found that CT_{Max} for *L. hesperus* decreased with developmental stage ($F_{2,\ 50} = 10.90$, $P = 0.0001$; Table 2; Fig. 1). We also did not find a difference in CT_{Max} between males and females ($F_{1,\ 24} = 0.39$, $P = 0.54$; Table 3; Fig. 2).

For thermal tolerance range, we did not find a significant difference in range with developmental stage ($F_{2,\ 50} = 0.23$, $P = 0.79$), species ($F_{2,\ 50} = 1.05$, $P = 0.36$), or the interaction of developmental stage and species ($F_{4,\ 50} = 0.68$, $P = 0.61$; Table 2; Fig. 1). The thermal tolerance range was greater in female widows than males ($F_{1,\ 50} = 10.99$, $P = 0.0029$), but we did not

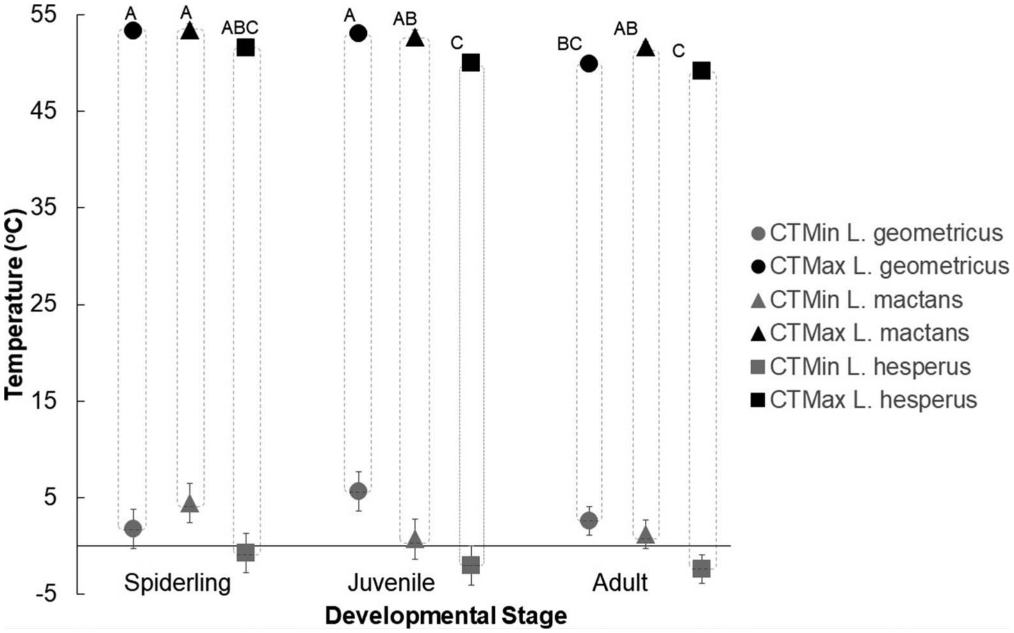

Figure 1.—Critical thermal minima (gray), critical thermal maxima (black), and thermal tolerance ranges (dashed region) of *L. geometricus* (circles), *L. mactans* (triangles), and *L. hesperus* (squares) by life stages (each point represents means in °C ± 1 SE). Within each age class, different letters denote means that are significantly different from one another in post hoc analyses for critical thermal maxima.

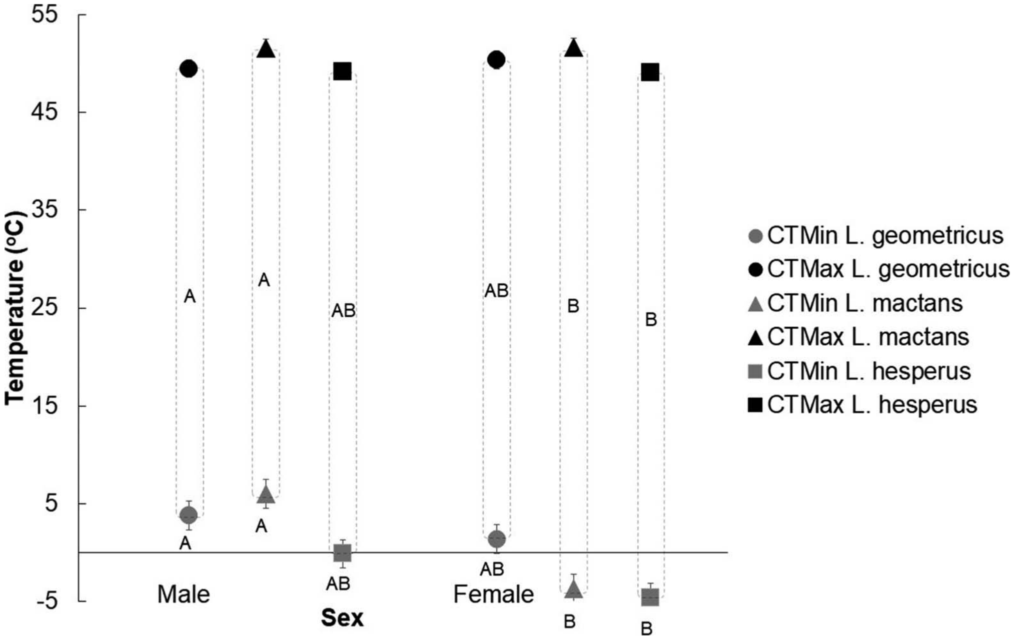

Figure 2.—Critical thermal minima (gray), critical thermal maxima (black), and thermal tolerance ranges (dashed region) of *L. geometricus* (circles), *L. mactans* (triangles), and *L. hesperus* (squares) by sexes (each point represents means in °C ± 1 SE). Within each sex, different letters denote means that are significantly different from one another in post hoc analyses. There are separate sets of letters for critical thermal minima and thermal tolerance ranges.

find an effect of species ($F_{2,\ 50} = 2.22$, $P = 0.13$) or the interaction of sex and species ($F_{2,\ 50} = 1.38$, $P = 0.27$; Table 3; Fig. 2).

We found that the present distributions of *Latrodectus* are strongly correlated with environmental temperature, humidity, and human influence (Figs. 3, 4). Model performances were generally greatest in describing the distribution of *L. geometricus* (Tables 4, 5). Although the highest AUC scores were produced in the models combining all environmental variables, the minimum temperature was the most descriptive single variable and contributed greatest to the combined models (Table 4). The lower thermal safety margins differed between *L. geometricus* (3.5 ± 0.1 °C), *L. hesperus* (-1.5 ± 0.1 °C), and *L. mactans* (2.2 ± 0.1 °C) ($F_{2,\ 3058} = 322.68$, $P < 0.0001$). The maximum temperature models most greatly overpredicted the species distributions (Fig. 3) and had low AUC (Table 4). The upper thermal safety margins differed between *L. geometricus* (21.2 ± 0.1 °C), *L. hesperus* (19.9 ± 0.2 °C), and *L. mactans* (18.6 ± 0.2 °C) ($F_{2,\ 3058} = 120.56$, $P < 0.0001$). The alternative models for humidity and anthropogenic impacts did not perform better than the best thermal variable models for each widow species (Table 5).

The niche breadth of *Latrodectus hesperus* (0.707) was higher than that of *L. mactans* (0.382) and *L. geometricus* (0.093). The invasive species, *L. geometricus*, differed in climatic niche, with relatively low overlap, in comparisons with the natives *L. mactans* ($D = 0.44$, $I = 0.76$) and *L. hesperus* ($D = 0.33$, $I = 0.62$). The niche overlap comparison was higher between the two native species, *L. mactans* and *L. hesperus* ($D = 0.51$, $I = 0.82$). The niche overlap values were significantly smaller than the null distributions for the comparisons of *L. geometricus* and *L. mactans* ($D_{H0} = 0.93 \pm 0.002$ vs. $D_{H1} = 0.44$ and $I_{H0} = 0.99 \pm 0.001$ vs. $I_{H1} = 0.76$; t-test, df = 99, $P < 0.05$), *L. geometricus* and *L. hesperus* ($D_{H0} = 0.94 \pm 0.001$ vs. $D_{H1} = 0.33$ and $I_{H0} = 0.99 \pm 0.001$ vs. $I_{H1} = 0.62$; t-test, df = 99, $P < 0.05$), and lastly *L. mactans* and *L. hesperus* ($D_{H0} = 0.95 \pm 0.001$ vs. $D_{H1} = 0.51$ and $I_{H0} = 0.99 \pm 0.001$ vs. $I_{H1} = 0.82$; t-test, df = 99, $P < 0.05$). These results indicate niche divergence, as opposed to conservatism, between the three widow species.

DISCUSSION

Our results suggest that the primary factors driving the lower thermal limits for these three spiders of the genus *Latrodectus* are differences in species and sexes. Females exhibited lower CT_{Min} and we found that *L. hesperus* displayed the lowest CT_{Min} of the three species examined (Tables 2, 3; Figs. 2, 3). This is in contrast to the upper thermal limits, which appear to be more strongly influenced by developmental stage (Barnes et al. 2019). Further, we found that the thermal tolerance range was greater in female widows compared to the males.

Measures of air temperatures exceeding the upper thermal limits do not regularly occur in the United States (Fig. 5), but the measures of temperatures of conductive surfaces at scales which arachnids occur have not yet been well studied (Barnes et al. 2019). The translation of coarse-scale air temperature measurements to microclimate-based measurements will be an important area for future study (Alford et al. 2018; Montejo-Kovacevich et al. 2020). As stated previously, Vetter et al. (2012) found that the invasive *L. geometricus* were much more prevalent in urban habitats and seemed to be relatively rare in rural and natural areas. This was also supported by high support for the human influence index model (Table 5; Fig. 4). Their affinity for urban habitats, or at least areas of high

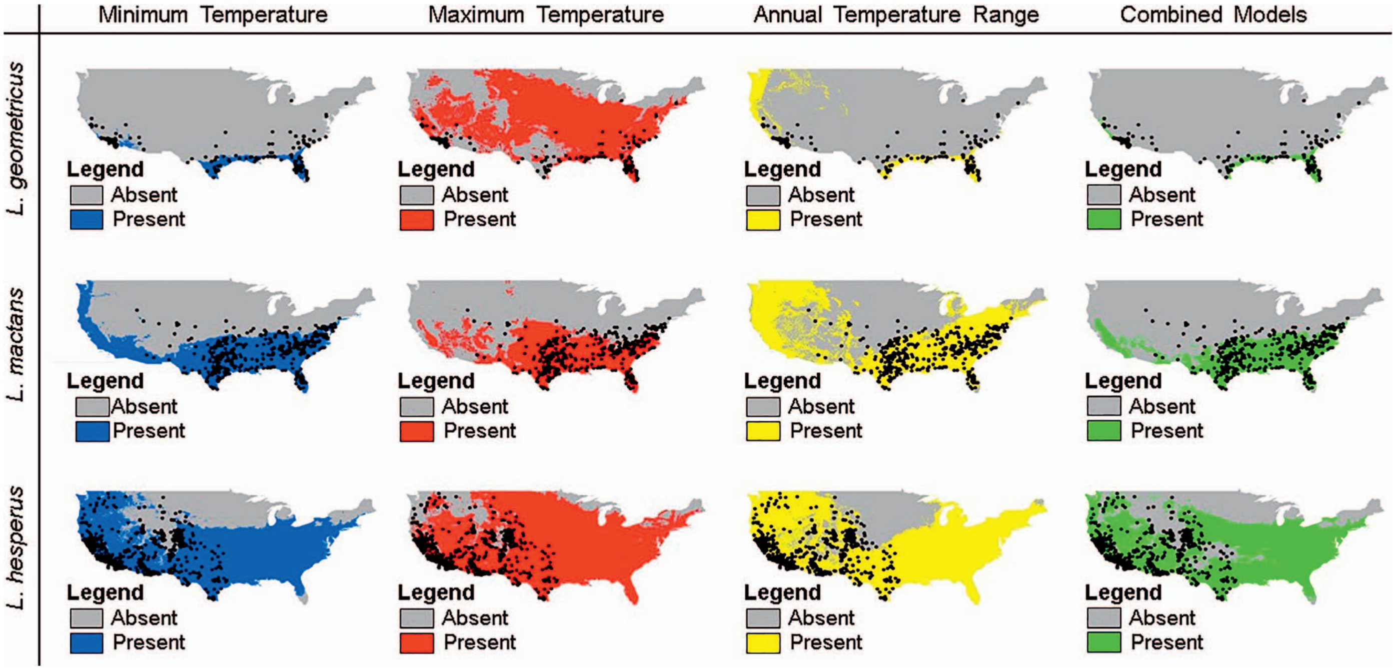

Figure 3.—Niche distribution models for widow species evaluating predictions of $1km^2$-resolution environmental data pertinent to the thermal limits (minimum and maximum temperature), tolerance ranges (annual temperature range), and integrating thermal limits and range (combined models). Models represent the areas where species are predicted to be present (dark blue, red, yellow, and green) or absent (gray), based upon correlations of environmental data and known occurrences submitted to the Global Biodiversity Information Facility (black dots).

human disturbance, may help facilitate their spread as urban areas often act as "heat islands," which exhibit warmer temperatures compared to rural areas due to human activity. An increase in thermal refugia, such as through urban heat island effects in winter, could mediate range expansion by the peridomestic *L. geometricus* during near-freezing temperatures.

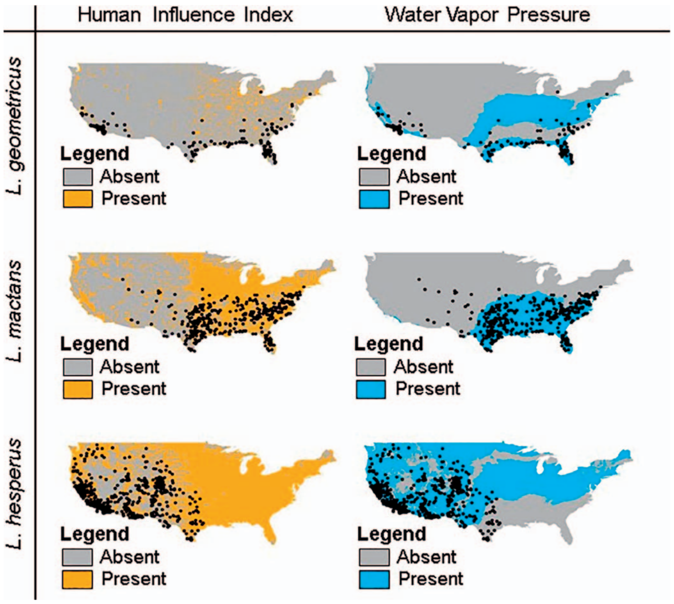

Figure 4.—Alternative niche distribution models for widow species evaluating predictions of anthropogenic impacts (human influence index) and humidity (water vapor pressure) at $1km^2$-resolution. The model represents the areas where species are predicted to be present (orange and light blue) or absent (gray), based upon correlations of the environmental data and known occurrences submitted to the Global Biodiversity Information Facility (black dots).

Further, rapid physiological acclimation to colder environments (McCann et al. 2014) and altered behavioral thermoregulation may also facilitate geographic expansion as evidenced in *Drosophila subobscura* (Huey & Pascual 2009). Whether or not these *Latrodectus* species can acclimate to tolerate lower temperatures and if acclimation ability differs among species remains unknown. Phenotypic plasticity in thermal tolerances may also provide a marginally effective buffer against environmental extremes (Gunderson et al. 2017), but this has not yet been studied in *Latrodectus*. Thermal plasticity may also occur over relatively short time frames (Cavalheri et al. 2019; Tarusikirwa et al. 2020). In addition to examining acclimation potential and phenotypic plasticity, another logical next step would be to investigate whether *L. geometricus* exhibit differences in thermal tolerance (e.g., CT_{Min} and CT_{Max}) within different parts of their range. This would illuminate how latitudinal clines shape thermal

Table 4.—Summary of AUC indices for environmental variables modelling distributions of *Latrodectus*. The separate models tested included Bio5 (Max Temperature of Warmest Month), Bio6 (Min Temperature of Coldest Month), Bio7 (Temperature Annual Range), and a model combining Bio5, Bio6, and Bio7.

Species	Bio5	Bio6	Bio7	Combined Models
L. geometricus	0.744	0.970	0.959	0.962
L. mactans	0.801	0.842	0.752	0.871
L. hesperus	0.662	0.746	0.719	0.774

Table 5.—Summary of AUC indices for alternative environmental variables modelling distributions of *Latrodectus*. The separate models tested included Human Influence Index (HII) and Water Vapor Pressure (WVP).

Species	HII	WVP
L. geometricus	0.943	0.879
L. mactans	0.787	0.867
L. hesperus	0.746	0.705

adaptability and provide insight into the amount of rapid evolutionary change (or lack thereof) occurring within the shifting distribution of *L. geometricus*.

Female widows were able to better tolerate lower temperatures than males. This is expected based on body size differences, as males are much smaller than females. In the field, males may be more exposed to environmental conditions since they have to move from their juvenile web site to find females. However, there may not be selection for males to possess adaptations for cold environments, as mating occurs during the summer and this is usually the only time that adult males are present in the population. Given that the CT_{Max} did not differ between males and females, CT_{Min} appears to be the primary cause for greater thermal tolerance range in females.

These results are among only a handful of studies documenting CT_{Min} and thermal tolerance range in Araneae (Table 1). The earlier studies employed a wide range of thermal ramping rates. Standardization and reduction of ramping rates to those parallel to naturally-occurring rates experienced by organisms will further clarify patterns in thermal tolerance across taxa (i.e., CT_{Max} and CT_{Min}; Terblanche et al. 2007, 2011). Data from our adult female *Latrodectus* (CT_{Min}- *L. geometricus*, 1.41°C, *L. mactans*: -3.65°C, and *L. hesperus*: -4.65°C) align with the general trends described here and suggest that species closer to the poles have lower CT_{Mins} and CT_{Maxs} compared to species found more equatorially (CT_{Max}- *L. geometricus*, 50.4°C, *L. mactans*: 51.7°C, and *L. hesperus*: 49.1°C). Further, we found support for the climatic variation hypothesis in that *L. hesperus* was the species with the most northerly documented occurrences, widest niche breadth, and, albeit marginally, widest thermal tolerance range. This lends some additional credibility to the observation that across arthropod taxa collectively, the lower thermal limits decline and variation increases with latitude while geographic variation in upper thermal limits is low (Gaston & Chown 1999; Addo-Bediako et al. 2000; Brandt et al. 2020; Fieler et al. 2021). Additional studies will also be needed to examine whether, perhaps like CT_{Max} (van den Berg et al. 2015), the lower thermal limits vary across seasons. Further, the relatively high CT_{Min} of spider species studied to date (Table 1) support the prediction that freeze-avoidance might be the predominant strategy in arachnids.

The ecological niche is comprised of the environmental conditions, such as temperature, in which an organism may persist (Grinnell 1917, 1924). Presence-only and environmental data sets have been applied using numerous modelling approaches, such as MaxEnt, for predicting species distributions (Elith et al. 2006). Niche expansion is relatively common amongst arthropods, but trends in magnitude vary by species and there have been recommendations that ecological niche models can be more effective when paired with other methods or experiments (Hill et al. 2017). Previously, species distribution models using MaxEnt have evaluated the invasive distribution of *L. geometricus* in the Americas (Taucare-Ríos et al. 2016). Those authors found that the annual mean temperature most precisely predicted the distribution of *L. geometricus* in North America and that the invaded region was mostly occupied by stabilizing populations rather than colonizing, locally adapting, or sink populations. In this study, using thermal physiological ecology as the framework

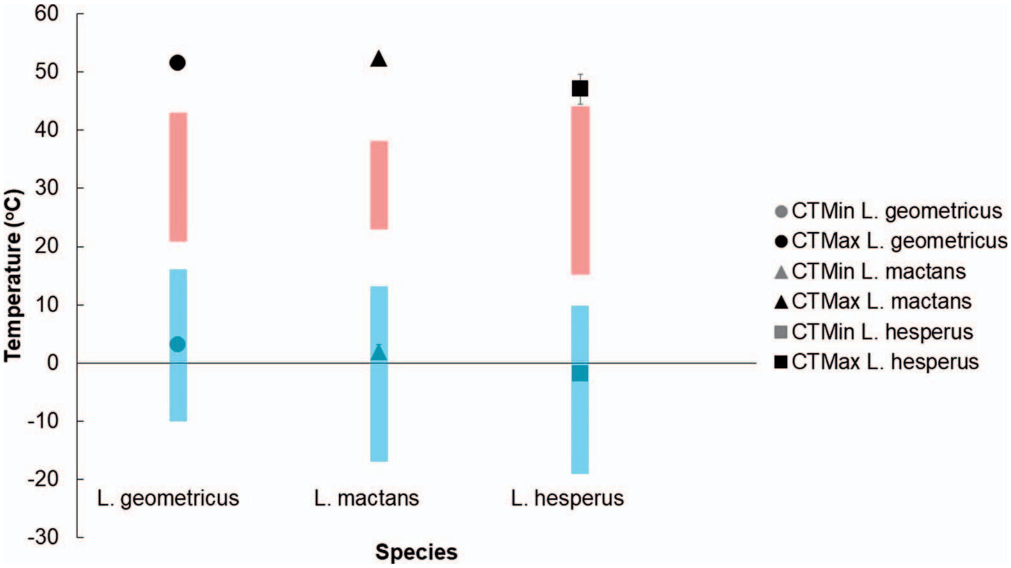

Figure 5.—Critical thermal minima (gray) and critical thermal maxima (black) of *L. geometricus* (circles), *L. mactans* (triangles), and *L. hesperus* (squares) (each point represents means in °C ± 1 SE). Red shaded area represents the range of maximum (Bio5 climate layer) and the blue shaded area represents the range of minimum temperatures (Bio6 climate layer) associated with occurrences submitted to the Global Biodiversity Information Facility.

for environmental variable selection, we found that the minimum temperature of the coldest month best predicted the species distributions of three *Latrodectus* widow spiders in the continental United States. Recalling the earlier modelling framework by Taucare-Ríos et al. (2016), we also tested annual mean temperature (Bio1) as both an independent variable and a variable combined with Bio5, Bio6, and Bio7. As an independent variable, Bio1 outcompeted Bio5. The Bio1 combined models' performance in predicting species distributions were not consistently better than those with just the other BioClim variables and analysis of variable contributions in MaxEnt suggested that the percent contribution by Bio1 was only about 10% (range: 5.7–16.3%). We propose that research pairing thermal physiological limits, environmental variables, and occurrence records could provide further mechanistic basis for model predictions of species distributions.

We have shown that within the United States, the invasive *L. geometricus* exhibits a higher CT_{Min} compared to native *L. hesperus* and no difference in CT_{Min} compared to the native *L. mactans*. These results suggest that *L. geometricus* tolerates similar temperature ranges as the native species and could expand if they use thermally-buffered habitats (e.g., urban interface) or if climate change alters temperatures. That is, anthropogenic climate change is causing many environments to warm on average and *L. geometricus* could extend its range northward as temperatures increasingly exceed their thermal minimum. This is additionally supported by our calculation that *L. geometricus* has relatively wide thermal safety margins, particularly when considering the CT_{Max} and range of maximum environmental temperatures (Fig. 5). The location data for documented occurrences in GBIF suggests that the core distribution area of *L. geometricus* is likely at present limited to the southern half of the United States, best supported by our distribution model for minimum temperature (Fig. 3), but our model for the Human Influence Index pinpoints urbanized areas further north as also containing suitable habitat (Fig. 4). Future research that would aid in our understanding of the ecological impacts of *L. geometricus* should investigate how thermal optima influence performance traits, particularly resource assimilation (Angilletta et al. 2002b) and how competition for resources influences the proliferation of *L. geometricus* as it continues to spread across the United States. Although it is evident that the full thermal profile is important in our understanding of the habitat and range an organism may occupy, our results suggest that CT_{Min} may disproportionately set the tolerance limits for survival in *Latrodectus*. Inclusion of CT_{Min}, rather than an exclusive focus on CT_{Max}, could be more informative and provide greater predictive power as we continue to grapple with predicting the impact of invasive species now, and into the future.

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