Introduction: Many studies have arisen at similar conclusions regarding the range of responses species can use to combat changing environments in response to anthropogenic climate change. Species can use different forms of plasticity, such as behavioral or physiological shifts, to buffer themselves from changing environments on short-term scales. However, these mechanisms are not expected to contribute strongly to long-term persistence (*1*, *2*). To persist over longer timescales, species can respond in one of three ways: track their current thermal environments in latitude (a shift in geographic range), remain in altered thermal environments through genetic adaptation to novel conditions, or fail to accommodate these changes and go extinct (*1*–*3*). Despite the limited range of potential responses species can use to cope with rapidly changing environments, evolutionary adaptation is woefully understudied relative to other response options (but see *6*). An evolutionary response to climate change depends on both the strength of natural selection exerted by altered thermal environments and the phenotypic variation within and among populations. Current climate models have assumed population-level responses to climate change will be similar, using either a limited number of population estimates throughout their ranges, or an overreliance on historical data presuming no adaptive changes in phenotypic traits over time (*1*, *2*). These oversimplifications do not consider that many populations inhabit unique environments throughout a species range. If populations diverge in phenotypic traits throughout a species range, then predictions about species-level responses are likely imprecise. A more realistic approach of understanding how adaptation can buffer species from climate change requires assessing how spatial and temporal changes in temperature influence the fitness of populations distributed over environmental gradients in nature. If populations throughout a species range are predicted to respond similarly to climate change, then these two phenomena must be supported: (1) a common association between the population's preferred range of body temperatures and thermal environment (i.e., thermal constraints on activity are similar among populations, see *7*); and (2) performance depreciation due to warmer body temperatures should similarly reduce population fitness via diminished reproductive output, a higher rate of mortality, or energetic imbalance. If populations inhabiting different thermal environments differ in their phenotypic traits, then these two trends cannot be assumed, and populations are likely to experience idiosyncratic ecological and evolutionary shifts in response to climate change. If this scenario occurs, then rapid species-level adaptation can occur (*4*). Here, I describe a project to investigate spatiotemporal fluctuations in natural selection acting on thermal traits using tree lizards (*Urosaurus ornatus*) as a model. If selection is consistent throughout the range of *U. ornatus* inhabiting different thermal environments, then populations in the northern edge of the species' range should be capable of exploiting altered thermal niches at higher latitudes, buffering them from extinction. If selection is heterogeneous throughout their range and populations are locally adapted, then it will require stronger evolutionary responses for populations to persist in environments altered by climate change.

Methods: I will sample *U. ornatus* populations from Organ Pipe National Monument (ORPI) in southwestern Arizona, from the Appleton-Whittell Research Ranch (AWRR) in southeastern Arizona, and from the Dead Horse Canyon (DHCA) in southeastern Utah. These three sites span a large portion of the distribution of *U. ornatus*, and represent increasingly warmer environments (ORPI > AWRR > DHCA). To characterize the operative thermal environment, I have constructed operative thermal models (OTM)s which mimic the heating profile of adult *U. ornatus*. 100 OTMs will be deployed throughout each site at microhabitats used by lizards. Thermochron iButtons sensitive to 0.5°C will measure temperature every 30 minutes throughout the study. I will sample individuals in May 2018, September 2018, March

2019, and May 2019. These points correspond to the initiation of breeding, the period following the first reproductive cycle, the period after winter hibernation, and the start of the following breeding season. At each time point, I will capture >200 individuals and measure: thermal preference(T_{pref}), and the thermal sensitivity of performance (thermal performance curve; TPC) using sprint speed: a measure of performance capable of predicting survival in lizards (*4*).

T_{pref} is the body temperature selected when freed from ecological constraints, and is measured by placing lizards into a thermal gradient and measuring body temperature throughout the trial. To monitor lizard body temperature whilst in the gradient, I affix Type T thermocouples to the cloacal surface of each lizard that are attached to an OMEGA™ TC-08 data logger which records body temperatures every 10 seconds for 90 minutes. Thermal performance curves describe how traits integral to the fitness of an organism (such as sprint speed) vary as a function of body temperature. To estimate TPCs, I will conduct sprint speed trials at different body temperatures throughout the tolerance range of *U. ornatus* (12 – 43°C). Lizards will be warmed or cooled to seven different body temperatures which characterize the body temperatures they experience in the field, and those at which performance can be optimized. I will hold individuals at the target temperature for 30 minutes prior to estimating performance. To estimate sprint speed, I will motivate lizards to run down a 1m racetrack lined with 10cm splits. These trials will be recorded with a 240-fps camera suspended over the top of the track. Every individual will perform two trials per temperature, and be allotted 2 hours of rest between trials at different temperatures. To quantify natural selection, I will use the multiple regression approach established by Lande and Arnold (*8*). I will use survival as the estimate of fitness, and quantify selection gradients using logistic regression (*9*). I will assign every lizard a unique toe-clip identification and release them after all measures are concluded, and estimate their survival by performing recapture surveys during each subsequent sampling period. I will quantify whether T_{pref}, performance, or TPCs predict survival across these populations of *U. ornatus*, and if these patterns of selection are spatially (across populations) and temporally (across all four sampling periods) conserved. In addition, I will combine data on T_{pref} and the operative thermal environment to model how climate change will influence activity rates. I will also extrapolate changes in temperature and use TPCs to estimate how warmer environments and will affect performance traits, which are predictors of reproductive success and survival in *U. ornatus.*

Significance: Species with limited capacities for dispersal are unlikely to buffer themselves from deleterious thermal environments by tracking current conditions (*10, 11*). Plasticity may provide a short-term response to changing thermal environments, but is unlikely to facilitate long-term species persistence (*12*). It is therefore necessary to understand how selection acts on thermal traits across multiple spatiotemporal timescales and identify potential environmental drivers of trait variation to establish an understanding of adaptation to changing environments (*4*). There is a paucity of data regarding the fitness consequences of thermal trait variation, and how selection targets thermal traits. Measuring the magnitude of selection acting on T_{pref} and TPCs is a fundamental requirement for assessing adaptation to novel environmental conditions, and this project will be followed with estimating how these traits are inherited across multiple generations to estimate the evolutionary potential in these traits. Performance traits predict fitness in lizards (*13*, *14*), and quantifying the thermal sensitivity of these traits and their responses to selection provides the means to predict the potential for physiological adaptation to temperature. This project is the first to synthesize ecological, behavioral, and physiological data in an effort to quantify the selective pressures imposed by climate change throughout the range of a broadly-distributed and vulnerable species.

<u>References</u>

1. L. B. Buckley, J. C. Ehrenberger, M. J. Angilletta, Thermoregulatory behavior limits local adaptation of thermal niches and confers sensitivity to climate change. *Funct. Ecol.* **29**, 1038–1047 (2015).
2. B. Sinervo *et al.*, Erosion of lizard diversity by climate change and altered thermal niches. *Science (80-.).* **328**, 894–899 (2010).
3. C. A. Deutsch *et al.*, Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 6668–6672 (2008).
4. M. L. Logan, R. M. Cox, R. Calsbeek, Natural selection on thermal performance in a novel thermal environment. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 14165–14169 (2014).
5. A. R. Gunderson, M. Leal, A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecol. Lett.* **19**, 111–120 (2016).
6. I. Keller, O. Seehausen, Thermal adaptation and ecological speciation. *Mol. Ecol.* **21**, 782–799 (2012).
7. R. B. Huey, R. D. Stevenson, Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Am. Zool.* **19**, 357–366 (1979).
8. R. Lande, S. J. J. Arnold, The measurement of selection on correlated characters. *Evolution (N. Y).* **37**, 1210–1226 (1983).
9. F. J. Janzen, H. S. Stern, Logistic regression for empirical studies of multivariate selection. *Evolution (N. Y).* **52**, 1564–1571 (1998).
10. G. A. Villaverde, N. Zucker, Sperm Storage Resulting in Viable Offspring in the Tree Lizard Urosaurus Ornatus (Sauria: Phrynosomatidae). *Southwest. Nat.* **43**, 92–95 (1998).
11. M. Massot, J. Clobert, R. Ferriere, Climate warming, dispersal inhibition and extinction risk. *Glob. Chang. Biol.* **14**, 461–469 (2008).
12. A. R. Gunderson, J. H. Stillman, Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B Biol. Sci.* **282**, 1–8 (2015).
13. J. F. Husak, S. F. Fox, M. B. Lovern, R. A. Van Den Bussche, Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution*. **60**, 2122–2130 (2006).
14. D. B. Miles, The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evol. Ecol. Res.* **6**, 63–75 (2004).