

University of Nevada, Reno

**Implications of Global Climate Change on the Lizard  
*Sauromalus ater* in the Mojave**

A thesis in partial fulfillment of the  
requirements for the degree of Master of Science in  
Biology

by

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## Abstract

Recently, scientists have predicted that many ectotherm populations are at a high risk for extinction. Extinction hypotheses for lizards are based upon the concept that thermoregulatory behavior by lizards may be constrained due to decreased activity periods as caused by warmer air temperatures. To determine risks of extinction or extirpation, a series of population-specific processes must be understood including the ability to adjust physiology (incl, acclimation and acclimatization), to migrate to new locations, to adjust activity, or evolve new thermal biologies. Chuckwalla populations in the Mojave and Sonoran Deserts are likely to be facing extinction threats due to warming, but thermal models and recent research suggest that ectotherms may not be constrained by activity time, yet may face the largest threats by other factors caused by the predicted climate change.

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## Introduction

Recent literature addresses threats posed by climate change upon populations of ectothermic animals, specifically lizards (Deutsch et al., 2008, Huey et al. 2009, Sinervo et al. 2010, Huey et al. 2010, Kingsolver et al. 2013). Predictions are that this kind of threat can stem from warming interacting with thermoregulatory behavior in ways that would reduce the amount of time for activity to acquire food, mates, etc (Huey et al. 2009). These predictions are generally based upon body-temperature-specific physiological processes (Huey and Stevenson 1979, Huey and Slatkin 1976, Sinervo et al. 2010, Huey et al. 2010). For example, Sinervo et al. (2010) predicted that lizard species would have a high probability of extinction, when they are forced into a smaller number of hours at which it is possible for the lizards to attain optimal body temperatures (Huey et al. 2010).

Sinervo's approach has been to state a hypothesis and subsequently collect data "to prove" the hypothesis (Sinervo et al 2010). A more appropriate scientific approach would be to state alternative or null hypotheses and collect data on those hypotheses (Popper 1959). For example, instead of hypothesizing that lizard populations will go extinct, one could hypothesize how lizard populations might evade extinction. These could serve as alternative hypotheses to a hypothesis predicting lizard extinction. Example alternative hypotheses may include: (a) individuals' ability to adjust their "acceptable (or optimal) body temperature ( $T_b$ ) range" in different thermal environments. This hypothesis posits that physiology might be flexible in the face of changing thermal environments. (b) Individuals could change their activity to times (daily or seasonally) to thermoregulate

normally to optimal body temperatures, but at different times of the day or year. (c) Populations could move to a new location where climates are similar to those in which the individuals evolved. This would mitigate climate changes as individuals move to new climates that are similar to their native climates (e.g., populations might move to higher elevations to avoid warmer temperatures). (d) Populations could evolve to become well suited to new environmental conditions under climate change. In light of this alternative approach, this paper will focus on the role played by thermoregulation on activity patterns of lizard individuals and populations found in the Mojave and Sonoran Deserts of western North America. For some temperate ectotherm populations, the degree to which climate warming will affect populations depends on options for behavioral and physiological compensation (Forister 2010, Kingsolver et al. 2013).

Here, we will specifically address the first two alternative hypotheses regarding flexibility in thermoregulation, and the effect of thermoregulation on activity patterns of a species of lizard found in the Mojave and Sonoran Deserts. We focused on two populations of the herbivorous common chuckwalla (*Sauromalus ater*) located at high and low elevations to encompass the considerable differences in thermal environments afforded by elevation. The lower population is located at Amboy Crater, San Bernardino County, California (~240m), and the higher elevation is found at the southern end of the Granite Mountains, San Bernardino County, California (~1000m). These populations were studied in the cool spring season, and in the hot summer season.

## Approach

The approach in this thesis is to present the hypothesis by Sinervo et al. (2010) in relation to alternative hypotheses, and to collect data on some of the alternative hypotheses.

*Extinction hypothesis (Sinervo et al. 2010):* lizard extinctions will occur due to an improper match between physiology and thermal environments reducing the activity time available to lizards to attain adequate fitness (in this hypothesis, Sinervo et al. assume that physiology is inflexible).

*Alternate Hypothesis 1:* Individuals may adjust their preferred body temperature; thus, physiology may be flexible. Seasonal adjustment of preferred body temperatures for some lizard species has been widely reported (Christian and Tracy 1983, Christian et al. 1999, Christian et al. 2006). What is less certain are the affects of seasonal climactic changes and body temperature on physiological performance of lizards in relation to body temperature and the environments associated with those body temperatures. Considering a temperate ectotherm example, we hypothesize that Chuckwalla lizards can physiologically adjust to perform in different local climates and different seasons to provide a capacity of these lizards to be physiologically flexible in ways that would allow them adjust as the climate shifts. To evaluate this potential, we assessed preferred body temperatures of Chuckwalla populations found at very different elevations at the coolest time of lizard activity, and at the warmest time of lizard activity. We placed lizards in a laboratory thermal gradient in which lizards had the ability to select a body position that yielded their desired thermal preference (DeWitt 1967, Porter et al. 1973). We also

measured body temperatures of lizards in the field with temperature-sensitive-data-loggers and tracking-transmitters for extended periods of time throughout the entire activity season. Body temperatures of lizards in the field were compared with operative temperatures recorded from numerous copper models operative temperature models placed at both elevations. Additionally, locomotory performance in relation to body temperature was measured in a sprint-track at which lizards were coerced to reach maximum speeds (Huey and Hertz 1982). Sprint performance was repeated in each season for lizards at each elevation. Lastly, gaping temperature (the point at which a lizard exhibited distress due to heat) was assessed for lizards at each elevation early and late in the activity season. At hand then is the notion that physiological flexibility of chuckwallas to acclimate to thermal environments in different seasons or elevations could indicate potential thermal flexibility that could be advantageous for population persistence in the face of climate change.

*Alternate Hypothesis 2:* Individuals might behaviorally change their activity times (daily or seasonally) to mitigate climate change; thus, behavior might be flexible.

To determine physiological activity, we observed thermoregulatory behavior for both high and low elevation populations in spring and summer seasons. The thermal environments of high and low elevations spanned the varying climactic conditions expected under any climate change scenario. By comparing to previous studies of thermoregulation of chuckwallas, we can analyze any long-term patterns in activity times and behavior (Zimmerman and Tracy 1989).

*Alternate Hypothesis 3:* Populations might move to new locations where climate change is mitigated (e.g., higher elevations). This hypothesis is not addressed in this thesis.

*Alternate Hypothesis 4:* Populations might evolve to become well suited to new climate. This hypothesis is not addressed in this thesis.

## Materials and Methods

### *Laboratory preferred body temperatures*

In the laboratory, we assessed the preferred (selected) body temperatures of lizards in a thermal gradient (Figure 1). Lizards were placed in a laboratory thermal gradient in which the substratum temperatures ranging 25 to 45 °C. Thus, lizards could select positions in the gradient that resulted in different body temperatures, and preferred body temperatures would be those consistently selected. The gradient was fabricated from a galvanized sheep watering tank approximately 2 m in length and 0.5 m wide. The tank was divided down the middle along the long axis with a wooden wall to create two “lanes” resulting in two identical gradients in the tank. Two identical boards, the length of the dividing wood (ca. 10 cm width), were affixed to the bottom edge on each side of the wood creating a lip to provide a hiding spot for the lizards. The bottom of the gradient was a sheet of aluminum (approximately 4 mm thick) that conducted heat efficiently along the length of the gradient. The sheet was covered with sand to diffuse heat distribution of the floor of the gradient. The gradient apparatus was elevated above the laboratory floor, and the warm end of the gradient was heated with six 75 watt and two 100 watt ceramic heaters. At the cool end of the gradient, 4 mm copper tubing was wound back and forth across the bottom of the gradient and secured (using epoxy) to the underside of the gradient, and this cooling tube was insulated from the laboratory environment using insulation styrofoam. Circulating through the copper tubing was a coolant (a mixture of ethylene glycol and water) circulated with a refrigerated circulator.

Lizards that were to be placed in the gradient were equipped with a temperature sensitive data logger (iButton, Thermochron DS1921G, with a sensitivity range between  $-40^{\circ}\text{C}$  to  $85^{\circ}\text{C}$ , and an accuracy  $\pm 1^{\circ}\text{C}$ , resolution  $0.5^{\circ}\text{C}$ ). These data loggers were placed against the lizard's chest in a vest fabricated with orthopedic and gaffer tape. This arrangement was shown previously to register temperatures that are essentially identical to cloacal body temperature of the lizard. Vests were also previously shown not to prevent normal movement by the lizard. After the lizard was equipped with its vest, it was placed in the gradient for a minimum of two days, a time long enough for lizards to settle down (stop moving around constantly within the gradient) and move to positions in the gradient that are relatively consistent over time, and relatively consistent among individuals. Gradients were monitored via video surveillance to avoid human disturbance. Means of body temperatures taken every ten minutes in the gradient were taken and preferred (selected) body temperature of each individual lizard was calculated from the temperature data during which time the lizard was visibly thermoregulating (defined as oscillating body temperatures over a small range of temperatures). Preferred body temperatures of 10 to 15 males and a similar number of female lizards were assessed in Spring and in Summer from the Granite Mountain and Amboy sites.





Figure 1: Two laboratory-controlled temperature gradients separated by a wood median equipped with thermal data loggers.

#### *Distress temperature assessment*

Twenty-one lizards from Amboy and sixteen lizards from Granite Mountains were separately placed in a constant temperature cabinet where the body temperatures of lizards were elevated slowly until the lizards opened their mouth in a gape indicating stress to high body temperatures. Cloacal temperatures were taken at the “gaping” point for each individual.

#### *Performance temperature assessment*

To assess temperature-dependent locomotory performance, we measured the sprint rate of lizards in relationship to body temperature, using a lizard race track. Lizards were

warmed in a constant temperature cabinet to six selected temperature ranges (25°C-27.99°C, 28°C-30.99°C, 31°C-33.99°C, 34°C-37.99°C, 38°C-41.99°C, >42 (±2 °C) in a random order, all ranges between 25 °C and 45 °C. Target temperature ranges were recorded and measured cloacally with a thermocouple (Schultheis rapid-reading thermometer) inserted approximately 4 cm in the cloaca for each individual. Upon reaching target body-temperature ranges, lizards were placed on a video monitored sprint track and sprinted three times within each temperature range.

The racetrack was built using three 2.5 cm by 30 cm boards assembled to create a tri-folding portable racetrack with 30 cm sidewalls (Figure 2). The track walls were approximately 1.8 m in length that was sanded and painted throughout. At each 0.25 m interval along the length of the track, the track was labeled and sectioned off using bright yellow duct tape. A dark pillowcase was secured at the end of the track to which lizards ran (perhaps this dark place seemed like a protective retreat. Three Logitech Quickcam Pro 9000 webcams were fastened to the sidewalls of the track, each capturing the sprint track from a different angle. Sprint times were determined using Debut Video Capture (NCH Software, 2012) and reviewed in high-definition slow-motion using Prism Video File Format Converter (NCH Software, 2012). The fastest sprint time at each temperature for each individual was recorded to the nearest 0.001 second.

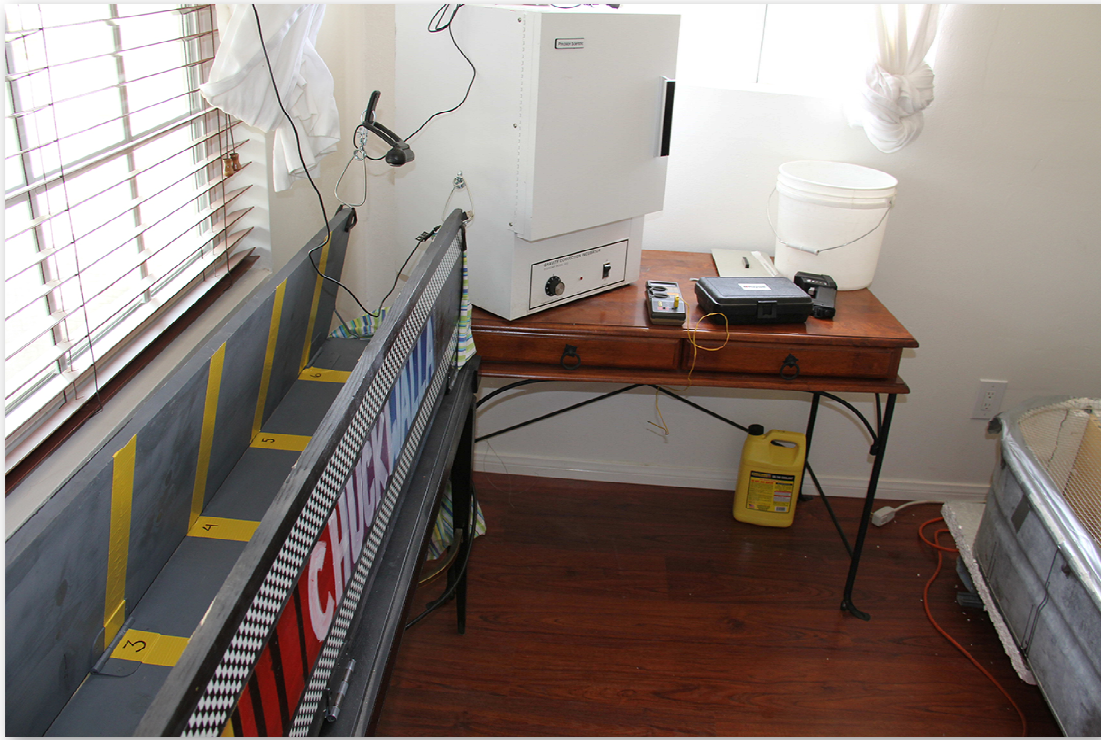


Figure 2. Measured and marked sprint track with several video cameras.  
Sprint track placed in a controlled ambient thermal environment.

*Body temperatures in the field*

To assess patterns of activity and patterns of thermoregulation by lizards in the field, we tracked lizards using radio telemetry by affixing radio BD-2 transmitters (Holohil Systems Ltd.) to lizards. These lizards were also equipped with temperature-sensitive data loggers (iButton Thermochron DS1921G (range  $-40^{\circ}\text{C}$  to  $85^{\circ}\text{C}$ , accuracy  $\pm 1^{\circ}\text{C}$ , resolution  $0.5^{\circ}\text{C}$ )). To outfit lizards with such devices, previously-proven affective vests were tailor-made on each individual (Wakeling 2012). The chuckwalla was sprayed with skin-protecting adhesive spray, and a layer of orthotic cloth tape was wrapped once around the lizard under the armpits. The transmitter was then attached to the tape on the backside of the lizard; inset between the scapula and the spine ridge. Below the sternum and between the costal regions of the ribs, the iButton was affixed to the anterior side of the lizard so that only a single layer of cloth tape separated the temperature logger and the lizard's skin. A layer of gaffer's tape was then cut to fit each lizard to constrain the orthopaetic tape as the first protective layer. Thin gaffer's tape straps were fabricated over the shoulders, converging at the chest and back. A secondary protective sheath of gaffer's tape was placed over the cephalic chest area, and a final protective gaffer's tape layer was applied entirely over the previous layers. Tape was carefully cut using blunt-nosed scissors providing liberal movement space under the arms and around the neck to avoid chaffing. Insecure ends and extra pieces of the vest were eliminated to minimize bulk and discomfort. These lizards were then returned to the field to participate in the experiments to assess activity and thermoregulation in the field. GPS coordinates were marked and lizards were returned within 100 m of their original collection locations. Lizards were tracked every 2-3 days to ensure that the vest had not inhibited chuckwalla

activity, and the vest had remained intact. Vests and iButtons were replaced every two weeks on each individual and new GPS coordinates were recorded at each lizard locality. IButtons were downloaded electronically using the software, Thermodata (version 3.0). The lizards used in this field-thermoregulation experiment were captured a second time and, taken to the lab at Twentynine Palms where aspects of their physiological performance were assessed within 3-4 days.

### *Operative temperatures in the field*

To provide a reference for data indicating thermoregulation by lizards in the field, we used physical operative temperature ( $T_e$ ) models in the field to assess the range of potential body temperatures available to lizards in their natural environments. We fabricated  $T_e$  models from sheet copper ( $\pm 0.013$ cm Copper K&S precision metals #6000 foil series). We formed the models into a very generalized shape of a lizard, and then we painted the models with a double-coat of **Valspar Exterior (color:6000-6B)** paint, which was determined (using a Beckman DK-2A spectrophotometer) to have approximately the same integrated absorptance of solar radiation as does a living chuckwalla (approx. 89% (Porter 1967)). We measured the spectral reflectivity of chuckwallas using a Beckman DK-2A spectrophotometer. We then integrated the data from the spectrophotometer on clear-day solar radiation (McCullough and Porter 1971) to obtain the integrated absorptance of chuckwallas. Then, we tested our painted  $T_e$  models against real chuckwallas by tethering lizards in direct sun on a clear day next to several versions of  $T_e$  models. Several shapes of  $T_e$  models were used before we got good concordance between the temperatures of the  $T_e$  models and an actual lizard. iButton

positions within the  $T_e$  models were also tested leading us to locate the iButton distal from the model center.

To predict accurately thermal availability using the models, several microhabitats were chosen at each site. Calibrated  $T_e$  models were placed in the field in positions and postures typical of positions and postures of actual lizards. This included placing some models in rock crevices as well as in surface positions in the sun and shade. Crevice temperatures were measured by placing iButtons into cloth pouches, lowering them deep into the crevices. Thirty copper models, and five crevice models, were randomly placed at each of the Amboy and Granite Mountain sites. Heavy-duty double-stick tape was used to affix models to rock surfaces. Five iButtons at each site were affixed to wooden dowels (0.3 m and 1.0 m above the ground) and protected from wind by cardboard cones to record ambient air temperature at each site. Temperature data were logged every 15 minutes, and all iButtons were replaced every two weeks (without altering the position of copper models). iButtons were downloaded to a laptop computer using a logger device and Thermodata (version 3.0) software.

#### Mojave Region Climate Assessment

To determine rates of climate change in the San Bernadino County, CA region, eight climate stations were selected to be compared monthly over the years of 1975-2012.

Selected NOAA regional stations included: Barstow, Baker, Mojave, Needles, Mitchell Caverns, Barstow/Daggett, Twentynine Palms, Death Valley. Data were collected using the dataset collection search link at <http://www.ncdc.noaa.gov/cdo-web/search?datasetid=GHCNDMS>. Warmest mean temperature values were recorded

monthly for each regional station and compared against all other selected stations.

Precipitation analysis for the San Bernardino county, CA region was generated through a data selecting tool at

[http://www.cefa.dri.edu/Westmap/Westmap\\_home.php?page=timeplot.php](http://www.cefa.dri.edu/Westmap/Westmap_home.php?page=timeplot.php). This

precipitation analysis tool generates a line graph data set of average yearly rainfall over a 12-month period in the San Bernardino County region for a succession of years, starting in 1930.

## Results

### *Population Sampling Locations*

Lizard populations were strategically selected from two locations representing a high elevation at the Granite Mountain site (~1000m) and low elevation at the Amboy Crater site (~240m) (Figure 3).

Both sites were well populated by chuckwallas, and provide suitable chuckwalla habitat with plenty of suitable rocky outcroppings for shelter; granite rocks at the Granite Mountain site, and lava rocks at the Amboy Crater site. Our sample year, 2012, was a drought year, resulting in less than normal vegetation at both sites, but extremely scarce vegetation at the Amboy site (Figure 4).

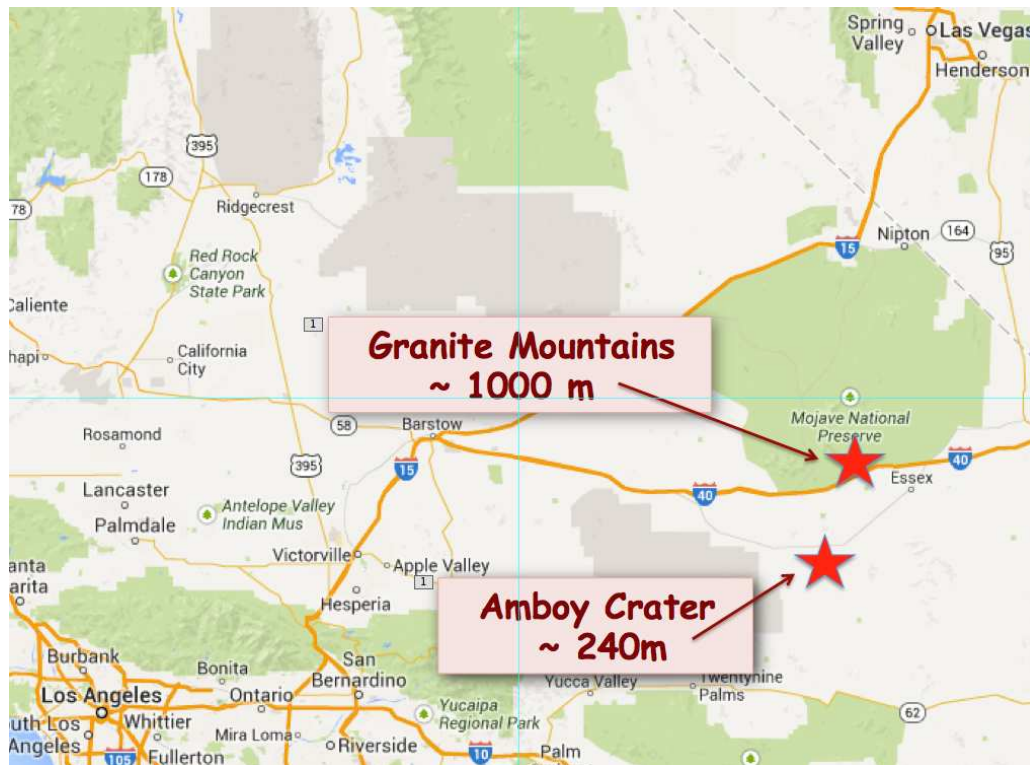


Figure 3. Granite Mountain (~1000m) and Amboy crater (~240m)  
Chuckwalla population sites.



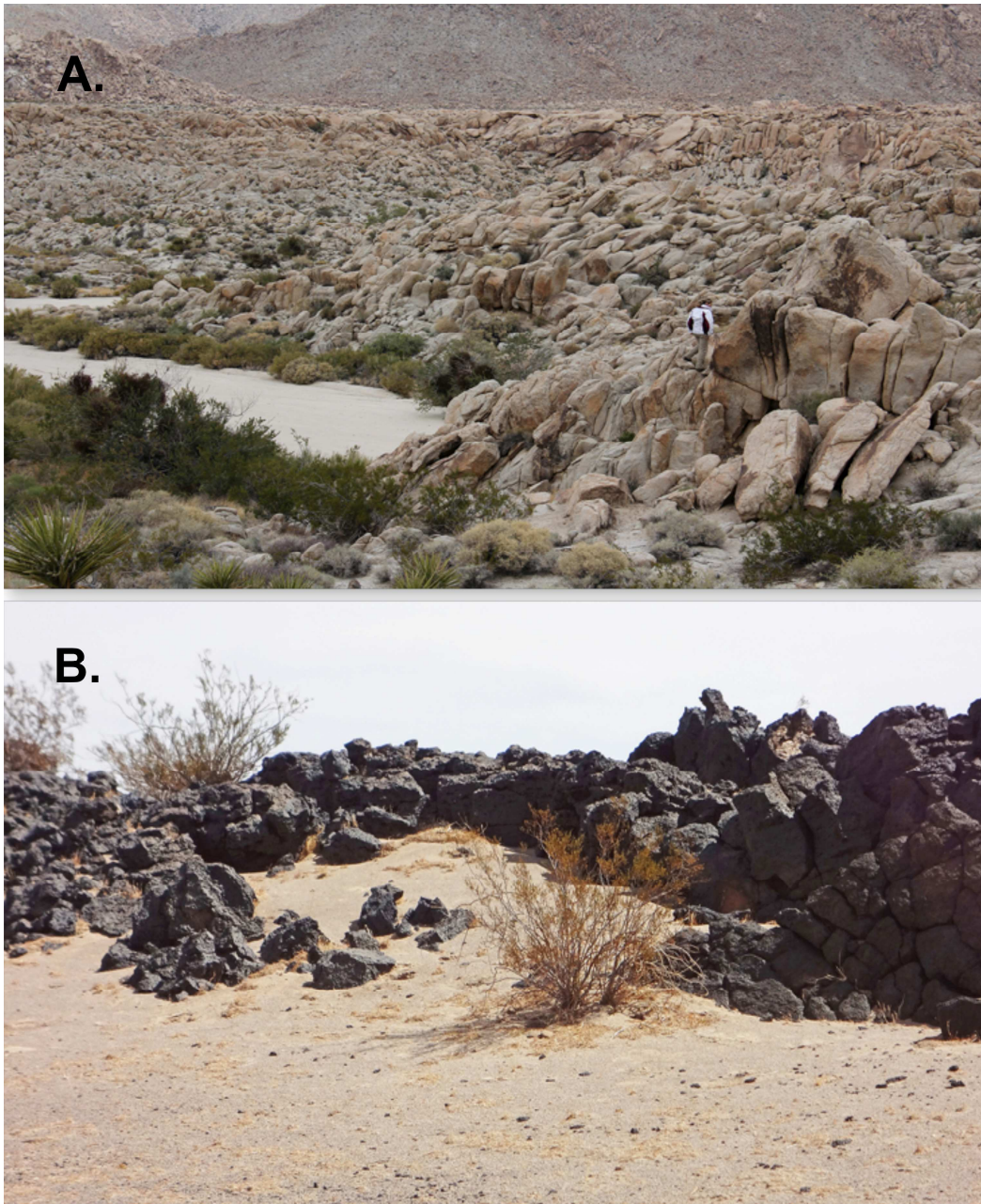


Figure 4. Granite Mountain site (A) and Amboy Crater site (B).

*Laboratory preferred body temperatures*

Body temperatures selected by lizards in the lab controlled thermal gradient were individually graphed and analyzed using Excel. Individual graphs displayed oscillating peaks during the daytime periods when the lizard was thermoregulating, and a characteristic flat line at the single temperature when the lizard slept. Graphs for each lizard were scanned for times of the characteristic “shuttling” temperatures, and those were averaged for eighteen individuals and the resulting total means were plotted against preferred temperature means of the same population of lizards in a prior study in 1976 (Figure 5).

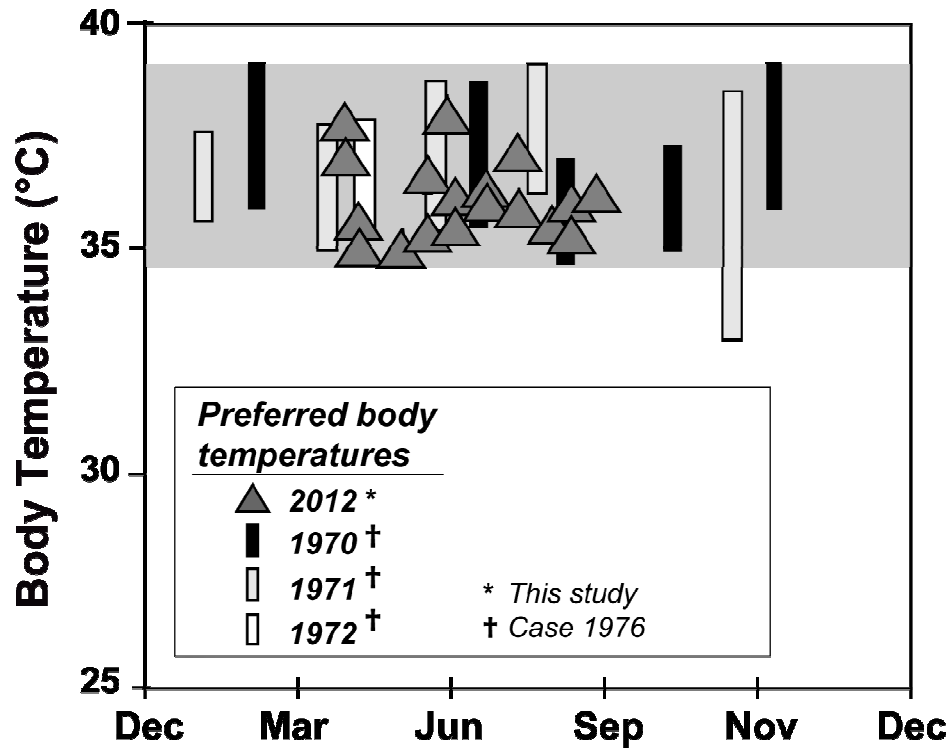


Figure 5: Preferred body temperatures of 18 chuckwallas in the spring-summer of 2012 plotted as grey triangles against preferred body temperatures of chuckwallas in 1970, 1971, and 1972 (plotted as white, grey, and black vertical bands) for corresponding months. The horizontal grey band represents the preferred temperature range.

*Heat stress temperatures*

The body temperatures at which lizards became stressed was determined for twenty-one lizards from Amboy and sixteen lizards from Granite Mountains. The Amboy stress temperatures were the same throughout the activity season ( $F_{1,20} = 0.99$ ,  $p = 0.33$ ), but the stress temperatures for lizards at Granite Mountains were lower in the early spring, and then they converged to be the same as those for Amboy in summer ( $F_{1,14} = 7.66$ ,  $p = 0.015$ ). Thus, the Granite mountain indicates an acclimation of stress temperatures from a cooler maximum stress range in the spring to a warmer range, eventually equivalent to that of the Amboy lizards, in the summer. The preferred body temperatures for the Granite Mountain lizards showed no significant trend with season.

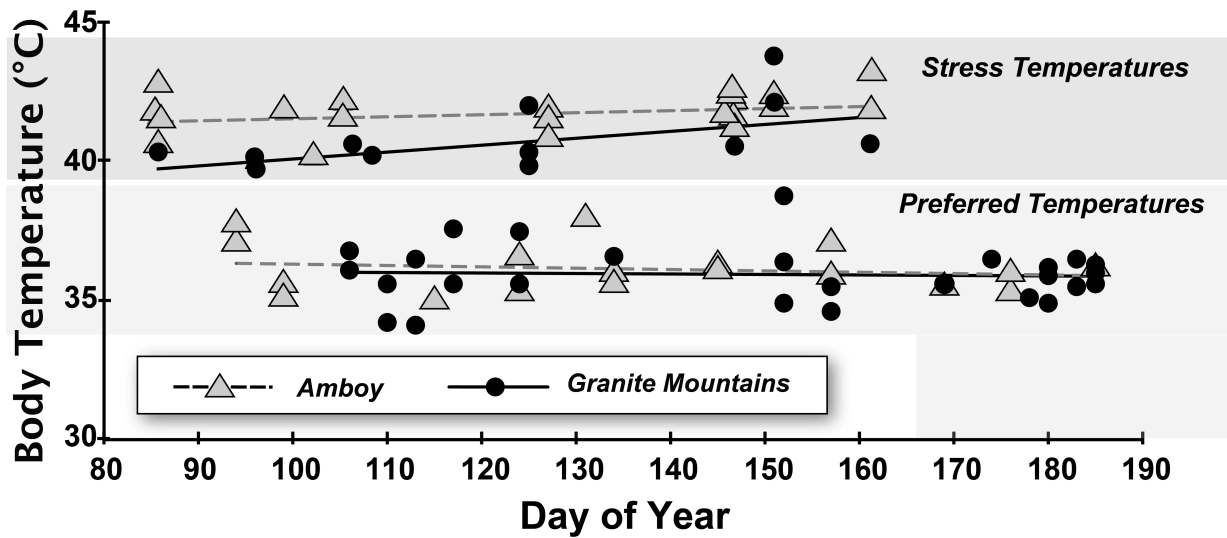


Figure 6. Stress temperatures (darker grey above) and preferred temperatures (lighter grey below) plotted against day of year. Amboy population is represented by light grey triangles and dashed lines, Granite population is represented by black circle and solid lines.

#### *Performance temperature assessment*

Lizards from both Granite Mountain site and Amboy crater site were sprinted individually and measured for the body temperature that produced the best sprint performance. Data points represent the percent of maximum three replicate sprints at a particular body temperature. In spring, the Granite Mountain lizards reached maximum sprint performances in the range 33.6C to 39.0 °C, but in summer, the same lizards had

acclimated to perform better at higher body temperatures (36.8C to 42.0 °C). On the other hand, the body temperatures for maximum sprint performance at Amboy did not change with season (Spring = 36.0C to 42.4 °C, and Summer = 36.0C-42.0 °C). Analysis of Variance indicates that this pattern is significant ( $F_{1,33} = 16.2, p = 0.05$ )

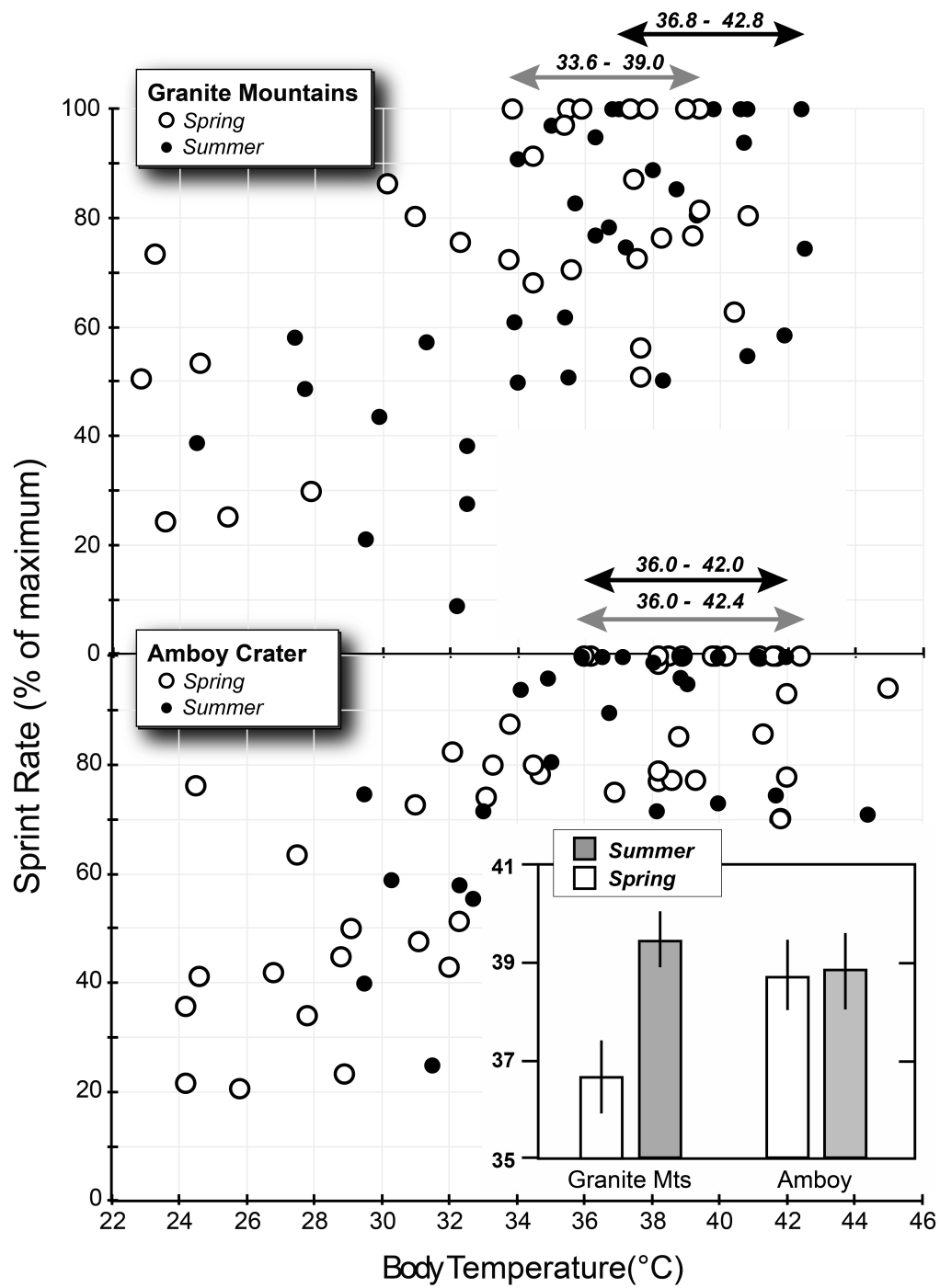


Figure 7: Sprint Rate (% of maximum performance) as a function of body temperature.

### *Activity and field body temperatures*

Body temperatures of lizards were logged every fifteen minutes to determine while animals were in the field. We inferred that an animal was actively thermoregulating the same as we did for lizards in the thermal gradient. Specifically, In the example trace of a lizard for two days in Figure 8, it is easy to see that the lizard became active after the sun came up, and maintained a body temperature between 34 and 39 °C by shuttling between cooling environments and warming environments (Figure 8). When you combine the information from that graph with the information in Figure 9, you can see that the temperatures achieved by the lizard were not possible by remaining in a crevice. Thus, the lizard can be inferred to be active on the above ground (out of a crevice) to achieve the body temperatures. During times at which the lizard is inactive, the oscillation ceases and body temperatures drop steadily until the next day. The plateau at which the lizard is thermoregulating also expresses the overall time period that the lizard is active on the rock surface and not inside the crevices for a particular day. From the figure below, we can see that the lizard was on the surface for 8 hours on April 30<sup>th</sup> and only 7 hours on May 1<sup>st</sup>.

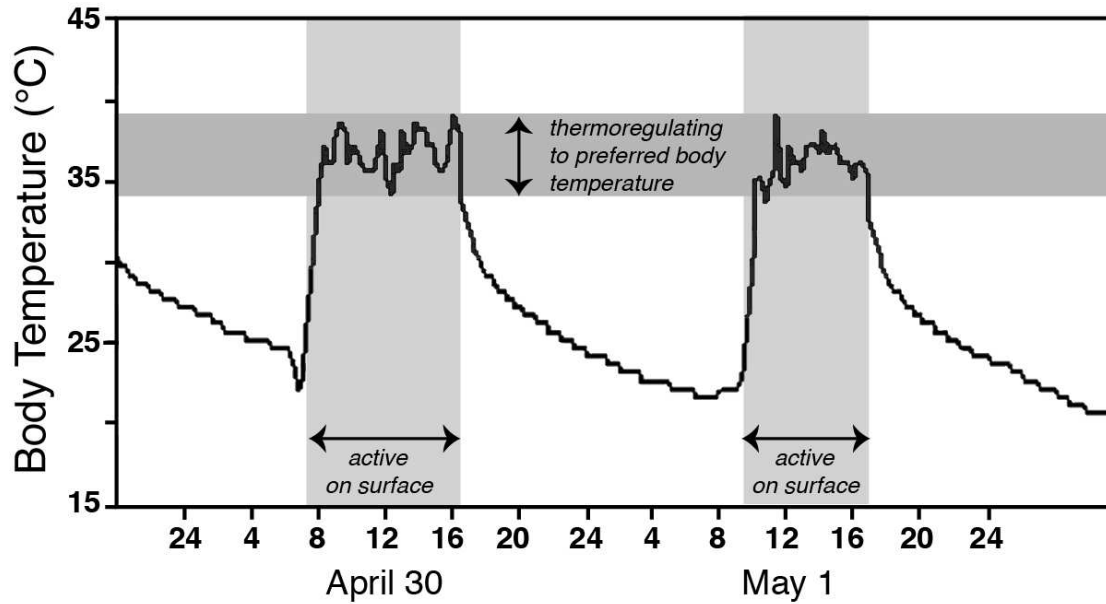


Figure 8. The actual thermal breadth that can be obtained for the particular individual in the sun (light grey) and thermal breadth found within the shade (dark grey). The black line represents the individual field temperatures of the vested lizard.



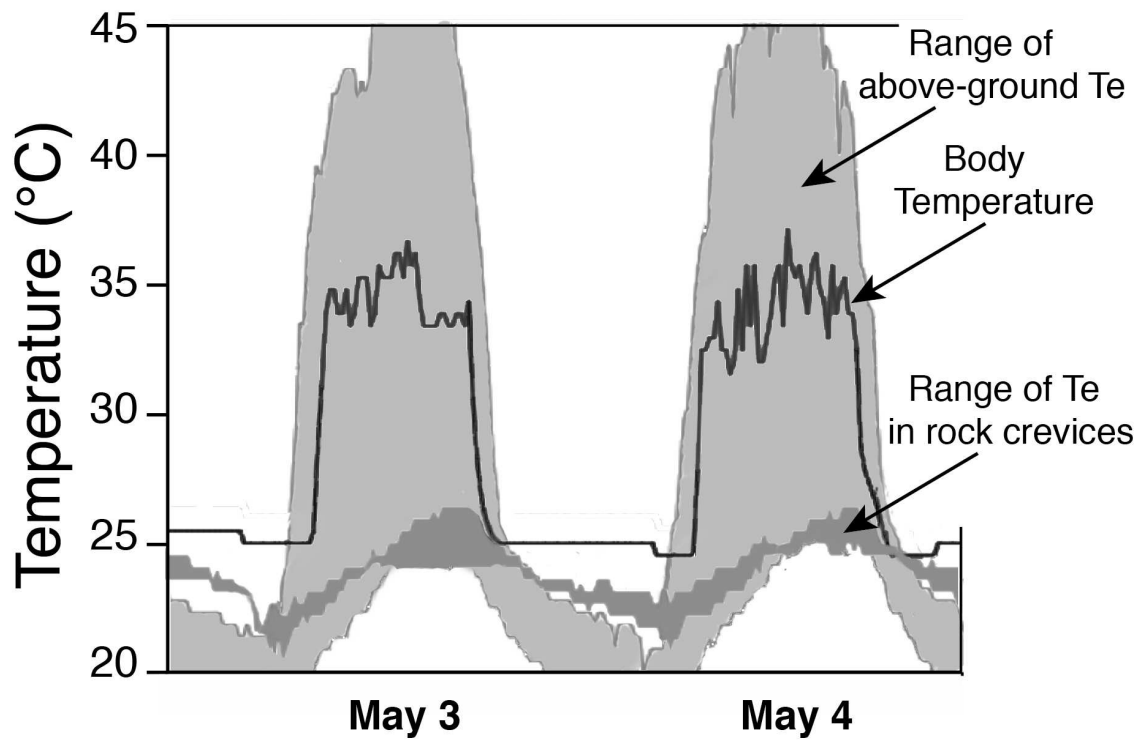


Figure 9. Daily temperature ranges in °C (light grey) plotted with daily in-crevice temperature ranges in °C (dark grey). Individual chuckwalla is displayed as a solid line.

Traces were made for every lizard at both sites throughout the time that they had data loggers. Three slices in time are presented below (Figure 10) with each lizard represented with a different color. Thus, if the same color is found in each panel, that indicates that the lizard was tracked throughout all three time periods. Shorter traces usually indicate the shorter lengths of data strings caused by a failure of the data logger or the fact that we retired lizards as the season progressed due to problems (actual or potential) with the vests.

In the Granite Mountain traces, it is clear that essentially all the lizards were active and maintaining a preferred body temperature in April. In late May, some lizards did not thermoregulate all of the time in which being above ground would have yielded preferred body temperatures, and by mid June, most lizards remained in crevices or did not exhibit the above ground thermoregulatory behavior that was so clear in April. Some lizards in mid June reached body temperatures that our laboratory data indicates would have caused heat stress, but usually this occurred fleetingly.

A similar analysis for lizards at Amboy showed a very different pattern. Specifically, individuals do not appear to be active consistently for long periods of time during the day at any time of year. Additionally, there were times during the year when individuals appeared to be able to attain their preferred body temperatures while remaining in their crevices, and lizards occasionally allowed their body temperatures to reach heights that would cause heat stress. However, the overall difference between Amboy and Granite Mountains lizards is that the Granite Mountain lizards actively thermoregulated above ground, and the Amboy lizards rarely participated in above-ground activity.

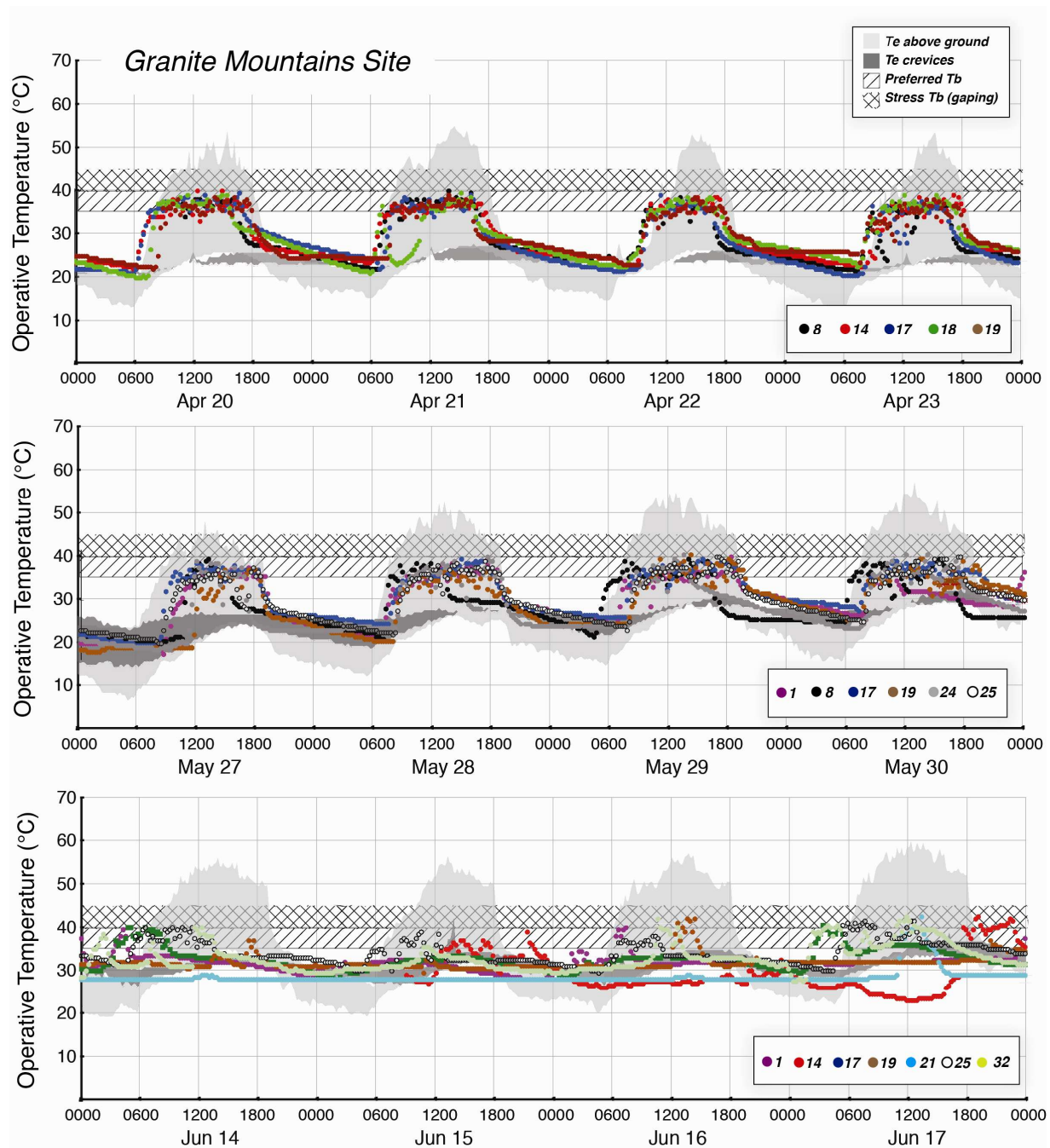


Figure 10. Colored dots represent body temperatures of an individual lizard through time. The range of operative temperatures is depicted in the light gray areas, and the range of crevice temperatures is indicated with the dark gray area. The lower hatched rectangle indicates the preferred body temperatures as assessed in the lab. The upper hatched rectangles indicate the range of temperatures in which animals showed heat stress in the lab.

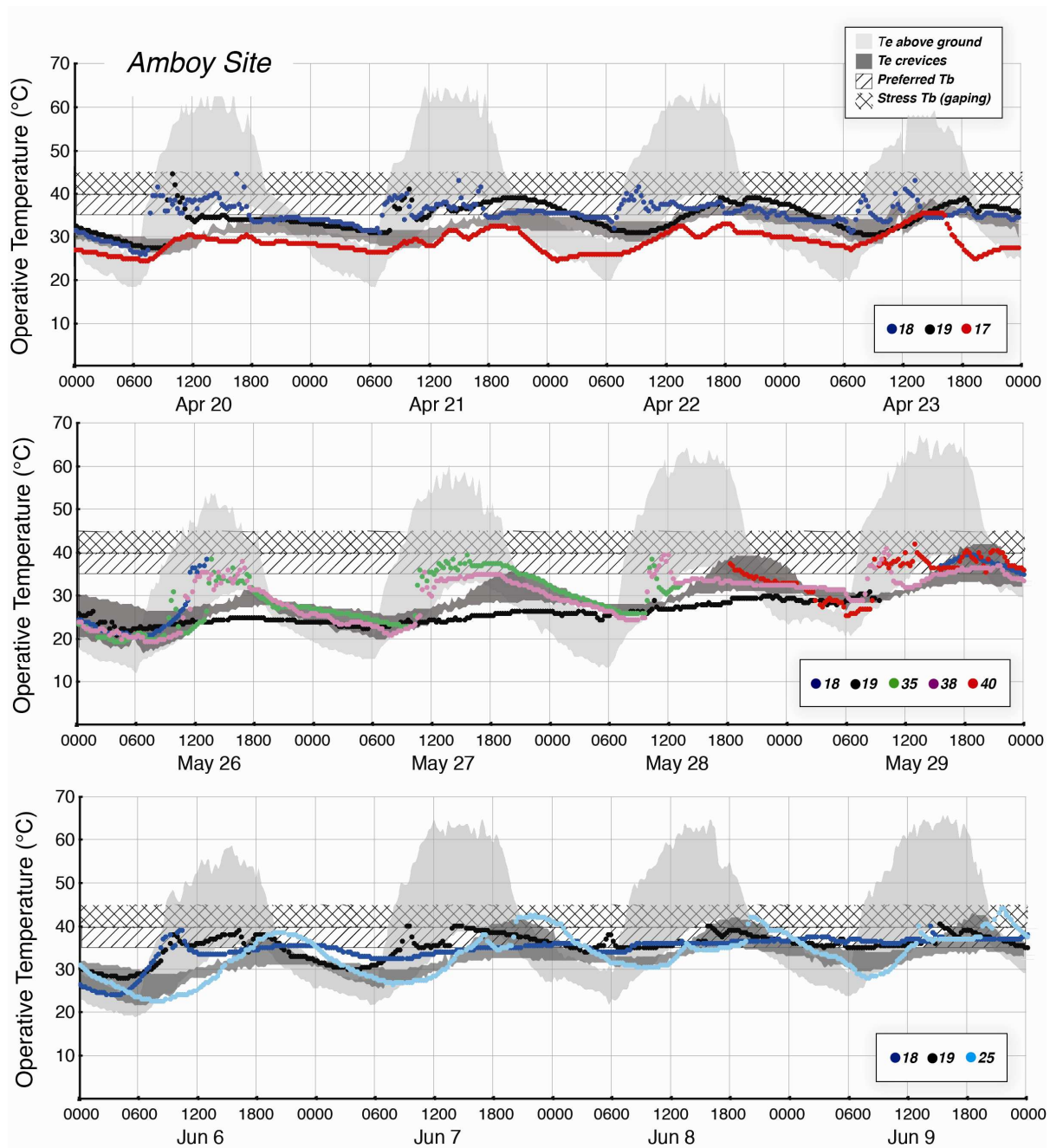


Figure 11. Colored dots represent body temperatures of an individual lizard through time. The range of operative temperatures is depicted in the light gray areas, and the range of crevice temperatures is indicated with the dark gray area. The lower hatched rectangle indicates the preferred body temperatures as assessed in the lab. The upper hatched rectangles indicate the range of temperatures in which animals showed heat stress in the lab.

We analyzed all body temperature traces for all lizards to add up the number of hours that each lizard was found to be within its preferred body temperature range. At the Granite Mountain site, lizards were active at their preferred body temperature anywhere from zero hours up to as many hours as the operative temperatures (above ground) were at preferred body temperatures (Fig 12 A).

By the end of April at the Amboy site, lizards achieved preferred body temperatures anywhere from zero to 24 hours during the day. Thus, they frequently came to preferred body temperatures for more hours than achievable by being in places that would yield body temperatures the same as attained by operative temperature models. Furthermore, the number of hours that operative temperature models came to temperatures within the preferred body temperature range was less than half as many hours as that at the Granite Mountain site.

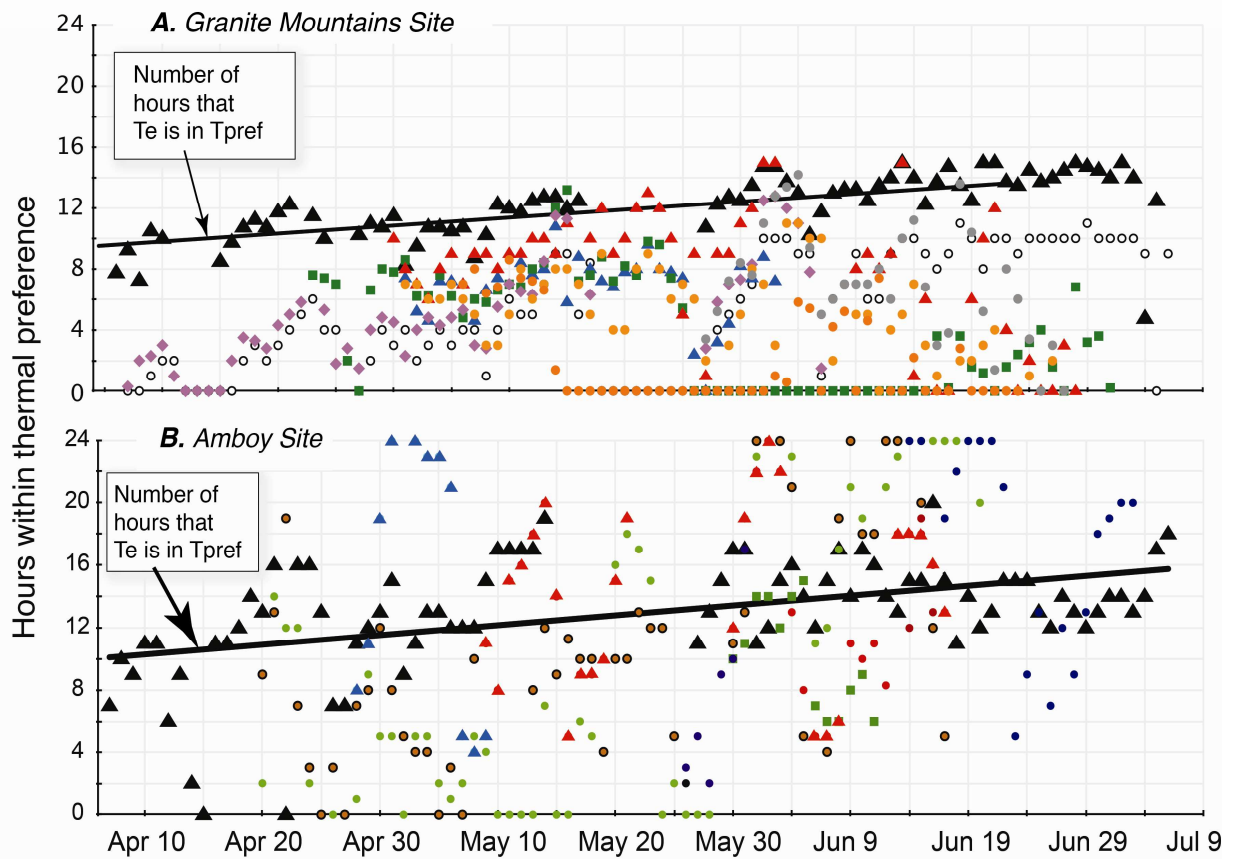


Figure 12. Hours per day that individual lizards were active within their preferred body temperature range. Black triangles are the hours at which Operative temperatures were within the preferred temperature range.

Surveying all the traces of body temperatures in the field can allow us to infer the percent of all monitored lizards that were active above ground (Figure 13). One hundred percent of animals in the Granite Mountains were active on all days until late May or early June. Thereafter, the percent of lizards active went down with time although more than 60% were still active as June became July. At Amboy, only a small minority of monitored lizards (ca. 15%) were active in the early part of the season, and by early June, no lizards were active above ground.

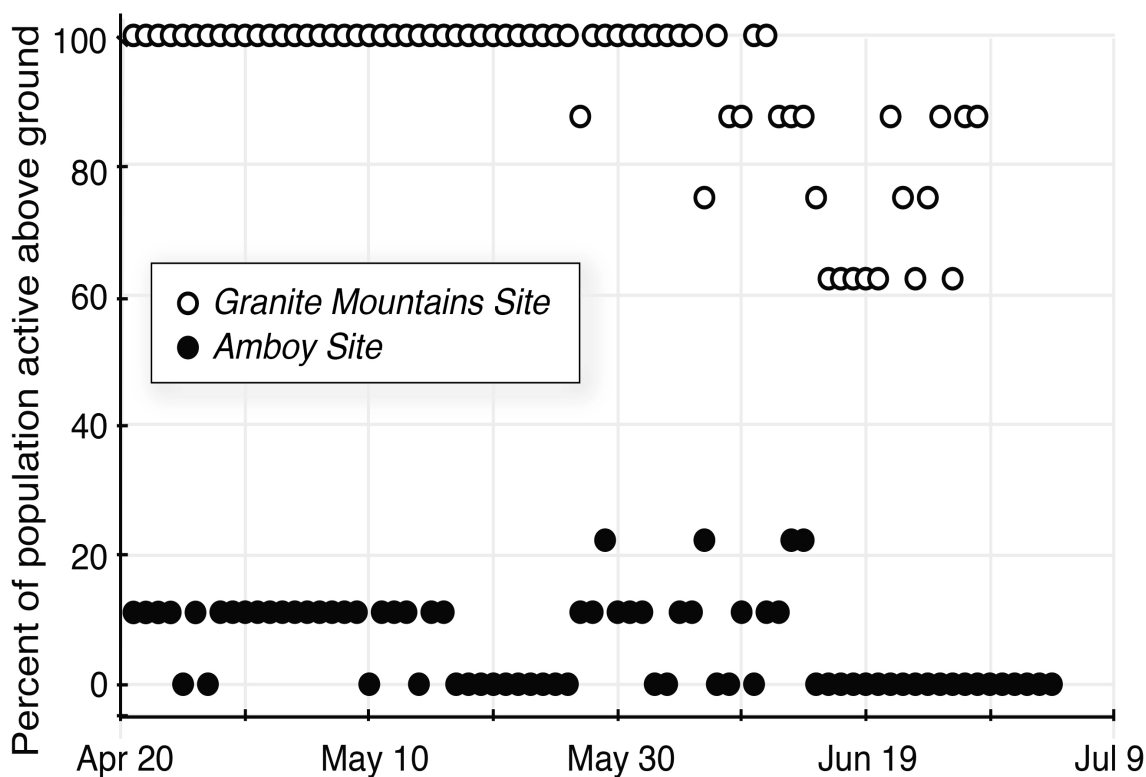


Figure 13. Percent of Granite (empty circle) and Amboy (black circle) population above ground during the activity season in 2012.

When the hours for (a) in each day, (b) the average number of hours in which the operative temperature is within the thermal preference, and (c) the average number of hours in which lizards are active and with body temperatures that are within the thermal preference, there are some remarkable results (Figure 14). Specifically, never to the lizards, regardless of site or season, remain active during all the time in which they could attain preferred body temperatures. In Spring, lizards from Granite Mountains were active about 75% of the time in which they could attain preferred body temperatures, but in summer, the lizards were active only about 10% of the time in which they could attain preferred body temperature. At Amboy, lizards were always much less active. In Spring, they were active about 30% of the time during which they could attain preferred body temperature, and in Summer, they were essentially not active at all.



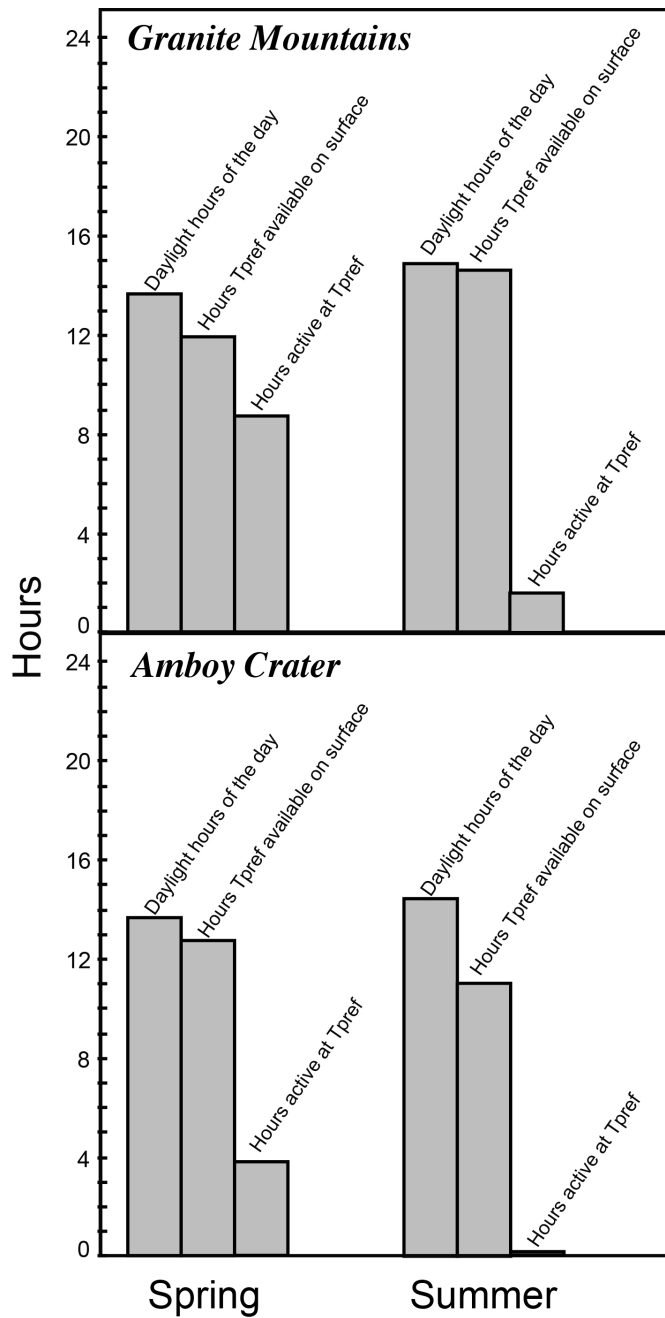


Figure 14. Granite Mountain (left) and Amboy Crater (right) population sample statistics for daylight hours per day, hours of Tpref available on the surface, and actual hours active on surface for spring and summer seasons.

*Climate change assessment*

Figure 15 illustrates the average temperature change monthly for the Mojave and Sierra regions between 1970 and 2010. Temperatures were recorded and displayed using Excel. Fitted curves reveal that the climate change trend over the last 40 years has resulted in cooler winter temperatures contrasting with hotter temperatures in the summer with maximum temperatures peaking in mid summer. Spring and fall seasons have remained consistent and reflect little temperature fluctuations. Although temperatures yearly have increased overall, a monthly breakdown over the years reveals that not all seasons are heating up.

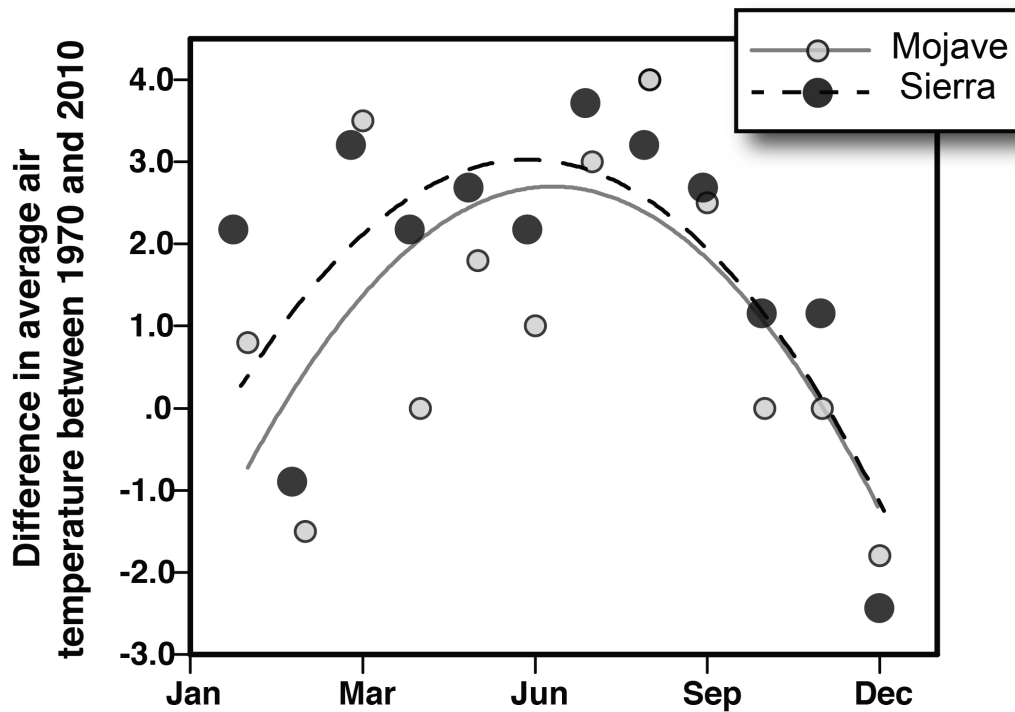


Figure 15. Light shaded dots for the Mojave data and dark shaded dots for the Sierra data mark the difference in average air temperature between 1970 and 2010. A dashed line shows the fitted curve for Sierra and a solid line is the fitted curve for the Mojave.

This figure addresses the occurrence of drought between 1970 and 2013 for San Bernardino County, CA in the Mojave region. Drought did not occur until approximately 1998 as shown by the grey dots each preceding year. After 1998, there were four recorded occurrences of drought every 3 to 5 years that is indicated by a precipitation of less than 5 cm.

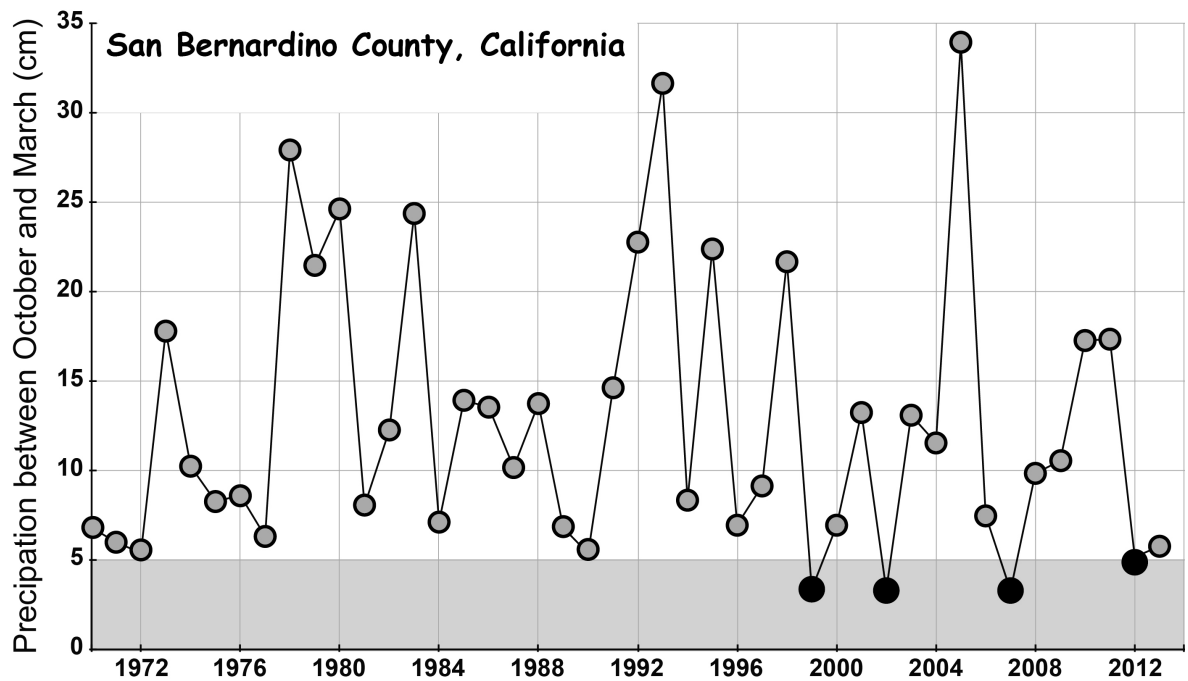


Figure 16. Precipitation between October and March from 1970 until 2013 in San Bernadino County, CA. Grey dots represent the precipitation if above 5cm, black dots represent the precipitation if below 5cm.

## Discussion

The recent literature has posited that more than a third of all the world's species of lizards will be negatively affected by global climate warming, and that 20% of the world's species of lizards will go extinct. However, this conclusion derives from analyses that do not consider the potential physiological and behavioral means by which lizard species could avoid extinction. Thus, the extinction hypothesis suggests that populations of lizards will go extinct due to improper matches between physiology and thermal environments reducing the activity time available to lizards to attain adequate fitness, but alternative hypotheses are pertinent. For example, Individuals might adjust their preferred body temperature as has shown to occur in several species of lizards, and this indicates flexibility in physiology that could defeat an extinction trajectory. Similarly, lizard Individuals might behaviorally change their activity times (daily or seasonally) in ways that could mitigate climate change, so behavioral flexibility could also defeat an extinction trajectory. Additionally, lizard populations might move to new locations where climate change is mitigated (e.g., higher elevations). Finally, lizards might evolve to become well suited to a novel climate.

In this thesis, the first two alternative hypotheses to the extinction hypothesis (see the introduction) were analyzed using data collected on chuckwallas from two populations (Granite Mountains, and Amboy Crater in California). The two populations differed in elevation as a means to collect data from a very hot site, and a site much cooler.

Additionally, we studied lizards from these two sites during two seasons of the year so as to assess individuals in a cooler and warmer season.

Lizards collected from both sites were placed in a thermal gradient to assess their preferred body temperature when all other the lizards are freed to respond only to differences in temperature in the gradient. The range of preferred body temperatures of chuckwallas was 34 – 39 °C regardless of study site or season. Furthermore, that range of body temperatures was essentially identical to the preferred body temperatures measured forty years previously in lizards from one of the same sites in this study (Case 1976).

In addition to preferred body temperatures, we assessed the body temperatures at which lizards were stressed thermally as indicated by the body temperature at which the lizards gaped. The range of body temperatures at which lizards from Amboy gaped was the same in spring and summer seasons (ca. 39 – 44°C), but the gaping temperatures for lizards from Granite Mountains were lower (ca. 39-41°C) in spring, but the gaping temperatures trended upwards as the season progressed until the gaping temperatures were similar to those of lizards from Amboy. This pattern suggest that chuckwallas have the ability to acclimate to different thermal environments, and this flexibility likely could help mitigate the effects of climate change.

We assessed the body-temperature-dependent sprint performance in the same lizards whose preferred body temperatures were assessed. Lizards at the Amboy site sprinted at maximum speed when their body temperatures were 36 – 42°C regardless of the season in which the lizards were assessed. However, for lizards from the Granite Mountain Site, maximal sprint performance in springtime was much lower than that measured in lizards

from Amboy (33.6 – 39°C), but roughly the same in summer as the range seen in Amboy lizards (36.8 – 42.8°C). Thus, it appears that lizards from Granite Mountains have the ability to acclimate in the face of different ambient thermal environments, and that this thermal flexibility may be useful to lizards confronted by global climate change.

The lower-elevation Amboy Crater population performed and functioned at a high body temperature range regardless of season, but the more flexible pattern of physiological performance seen in the Granite Mountain chuckwallas may reflect adaptations to thermal environments that can be relatively very cool in winter and warm without being extremely hot in summer, but this speculation should be a subject of future research.

Bearing on the original questions about threats to climate warming, our findings indicate profoundly interesting patterns. Specifically, even though we found that both populations of chuckwallas have an inflexible preferred temperature range, these lizards nevertheless can survive and perform in warmer thermal conditions. Although the preferred temperature range for individuals remained constant at approximately 36.5°C (Figure 3 & 4) and even remaining constant over a span of 40 years (Case 1976), chuckwallas performed best on the sprint track at 36°C to 42°C (Figure 5). Thus, if chuckwallas were forced into situations that would cause them to come to body temperatures higher than their preferred body temperature, they would perform very well at those higher body temperatures. Moreover, the activity times (daily and seasonally) showed by chuckwallas at both sites, and regardless of season were always less than activity times that would yield preferred body temperatures. That suggests there is no constraint on activity due to

high ambient temperatures, and this further suggests that the extinction hypothesis is not supported.

So why don't the chuckwallas exploit all available activity time? And why would an increase in temperature be thought to negatively impact populations? Rising temperatures would likely provide chuckwalla populations with more available thermal preference time, shouldn't that be good for population survival? The first thing we must understand is activity time. Activity time for chuckwallas is the period in which the lizard can acquire and expend energy through forage, digestion, defending territory, and mating (Tracy 1982, Grant and Porter 1992). The more activity time, the more time to digest food and create energy (Tracy 1982, Grant and Porter 1992). In our results (figure 12) it is clear that both populations have more available thermal preference time as the environment heats up from spring approaching summer, yet both populations are found to be active significantly less time in the summer than the spring. It is clear from the sample field data that activity time is not the limiting factor.

Other processes could cause the actual hours of activity to be less than the number of available hours in the preferred temperature range. Limiting activity may limit water and energy loss for individuals. Retaining water and energy in times of drought and paucity of food is crucial for these lizards. Much less activity time was observed for the Amboy population and this is also where drought was visible. There was no vegetation or signs of water observed in this region in the summer season and as a result, there was also no activity. In addition, decreased activity time would also decrease exposure to predators.

Actually, it may be naïve to imagine that activity time constrained by a thermal environment could ever be very important for this herbivorous reptile. Food consumed by chuckwallas requires about six days in transit through the digestive track, so foraging time may not be the rate-limiting process in energy acquisition. Furthermore, in laboratory settings, chuckwallas can become satiated in less than 20 minutes (Tracy pers. comm.). This again suggest that time for foraging may be a resource that would be difficult to be constrained by warming ambient temperatures.

Populations are generally found to be less active in the summer when food is limited than in spring when food is more abundant. We observed that in a drought year (2012) chuckwallas were less active than reported in previously researched years (Case 1976, Zimmerman and Tracy 1989). Our investigation of climate change over the last 40 years has shown some shortened activity seasons due to ambient temperatures, and increase in the frequency of drought. Droughts cause chuckwallas reduce reproduction, activity, and abandon social relations as a means to minimize energy and water loss (Nagy, 1973; Smits, 1985). If frequencies of drought were to increase with climate change, the resultant paucity of food resources becomes the more pertinent challenge to survival. Growth and reproduction of chuckwallas is supported by energy resources in the form of succulent vegetation, particularly flowers of desert annuals (Case 1976). Food availability is not only dependent on the ability of vegetation to adapt to and flourish in changing climate, but the timing in which the vegetation should be available. Because climate change will shorten spring and fall seasons, the timing of forage could be crucial, and that timing also may increase the risk of population extinction for herbivorous ectotherms.



Because drought does occur in the desert southwestern US, chuckwallas have responded with adaptations in the form of physiological mechanisms to survive the paucity and unpredictability of food resources. Chuckwallas found at lower elevations tend to have more stored fat to evade problems following a poor resource year by improving their chances of survival (Case 1976, Tracy 1999). More research to measure survival rates of chuckwallas in repetitive drought years is very important.

Our examination of the hypotheses posed by Sinervo and Huey regarding extinctions caused by increasing thermal constraints due to climate change shows that risks from the temperature-mediated activity constraint focuses attention away from the more likely important risk due to climate change. We found that the direct increase in air temperature caused by climate change likely will have little important effect on the chuckwallas' ability to survive. The indirect affects of climate change, and particularly change that increases the frequency of droughts, however, will put populations at risk of malnourishment caused by a dearth of food resources.

## Literature Cited

Bakken, George S. "Measurement and Application of Operative and Standard Operative Temperatures in Ecology." *American Zoologist*. 32(2):194-216.

Barrows, C. "Sensitivity to climate-change for two reptiles at the Mojave-Sonoran Desert interface." *Journal of Arid Environments*. 75(7): 629-635.

Case, T.J. 1976. "Body Size Differences Between Populations of the Chuckwalla, *Sauromalus Obesus*." *Ecology* 57(2):313-323.

Case, T.J. 1976. Seasonal Aspects of Thermoregulatory Behavior in the Chuckawalla, *Sauromalus obesus* (Reptilia, Lacertilia, Iguanidae). *J. Herpetology* 10:85-95.

Christian, K.A., C.R. Tracy, and W.P. Porter. 1983. Seasonal shifts in body temperature and use of microhabitats by the Galapagos land iguana. *Ecology* 64(3): 463-468.

Christian, Keith A., Tracy, Christopher R., and Tracy, C. Richard. "Evaluating Thermoregulation in Reptiles: An Appropriate Null Model." *The American Naturalist*, Vol. 168: 421-430.

- Christian, K.A., G. Bedford, B. Green, A. Griffiths, K. Newgrain, and T. Schultz. 1999. Physiological ecology of a tropical dragon, *Lophognathus temporalis*. *Australian Journal of Ecology*, 24:171-181.
- Deutsch C. A., Tewksbury J. J., Huey R. B., Sheldon K. S., Ghalambor C. K., Haak D. C., Martin P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude." *PNAS*, Vol. 105(18): 6668-6672.
- DeWitt, C.B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. *Physiological Zoology*. 40: 49-66.
- Forister, M.L., A. C. McCall, N. J. Sanders, J. A. Fordyce, J. H. Thorne, J. O'Brien, D. P. Waetjen, and A.M. Shapiro. 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *PNAS* 107: 2088-2092.
- Fuller, A., Dawson, T., Helmuth, B., Hetem, R., Mitchell, D., and Maloney, S. 2010. Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology*. 83(5): 713-720.
- Grant, Bruce W., and Warren P. Porter. "Modeling global macroclimatic constraints on ectotherm energy budgets." *American Zoologist* 32.2 (1992): 154-178.

Huey, R., Deutsch, C., Tewksbury, J., Vitt, L., Hertz, P., Perez, H., and Garland, T. 2009. Why tropical lizards are vulnerable to climate change. *The Royal Society*. 276: 1939-1948.

Huey, R.B., Losos, J.B., and Moritz, C. 2010. Are lizards toast? *Science* 328: 832-833

Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51:363–384.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* 19:357–366.

Kearney, M., Shine, R., Porter, W., and Wake, D. 2009. The Potential for Behavioral Thermoregulation to Buffer "Cold-Blooded" Animals against Climate Warming. *National Academy of Sciences*.106: 3835-3840.

Kingsolver, J., Diamond, S., and Buckley, L. 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional ecology* 27(2013): 1415-1423.

Munson, S., Muldavin, E., Belnap, J., Peters, D., Anderson, J. 2013. Regional signatures of plant response to drought and elevated temperature across a desert ecosystem. *Ecology*. 94(9): 2030-2041.

Popper, Karl. The Logic of scientific discovery. London: Hutchinson & Co., 1959.

Porter, W.P., Mitchell, J.W., Beckman, W.A., & DeWitt, C.B. 1973. Behavioral implications of mechanistic ecology. *Oecologia (Berlin)* 13:1-54.

Sinervo, B., et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science*. 328: 894-899.

Tewsbury, Joshua J., Huey, Raymond P., Deutsch, Curtis A. “Putting the Heat on Tropical Animals.” *Science*. 320:1296-1297.

Tracy, C.R. (1976). A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecol. Monogr.*, 46, 293–326.

Tracy, C.R. (1982). Biophysical modelling in reptilian physiology and ecology. In: *Physiology C: Physiological Ecology* (eds Gans, C & Pough, FH). Academic Press, London. 275–321.

Tracy, C.R. & Christian, K.A. (1986). Ecological relations among space, time, and thermal niche axes. *Ecology*, 67, 609–615.

Tracy, C.R. 1992. Ecological responses of animals to climate. *In: Global Warming and Biological Diversity*, R.L. Peters and T.E. Lovejoy (Eds.), Yale University Press, New Haven, CT. 171-179.

Tracy, C.R. 1999. Differences in body size among Chuckwalla (*Sauromalus obesus*) populations. *Ecology*. 80(1):259-271.

Trullas, Susana, Blackburn, Tim M., Chown, Steven L. "Climatic Predictors of Temperature Performance Curve Parameters in Ectotherms Imply Complex Responses to Climate Change". *The American Naturalist*. 177:(6)738-751.

Zimmerman, L.C. and C.R. Tracy. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. *Physiological Zoology* 62: 374-409.