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## The Influence of Temperature, Prey Availability, and Population of Origin on Ectotherm Energetics

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The Influence of Temperature, Prey Availability, and Population of Origin on Ectotherm  
Energetics

A dissertation submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy in Biology

by

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This dissertation is approved for recommendation to the Graduate Council.

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## Abstract

Climate change poses threats to organisms regarding direct and indirect effects of warming temperatures. Laboratory studies and predictive models are useful for understanding how temperature influences organisms, and the future of species' life history and persistence. This dissertation expands upon current approaches to thermal studies and climate models, while investigating effects of warming nighttime temperature and altered prey availability on individuals and populations. Lizards in the genus *Sceloporus* were used as model organisms, as they are broadly distributed with thermally sensitive physiologies. The *first dissertation chapter* conducted meta-analyses to examine temperature-induced changes in food consumption, activity, and life history. Prominent knowledge gaps were identified on indirect effects of warming temperatures, despite the abundance of climate change models on lizards. Mechanistic studies concerning energy budgets are important for assessing changes in fitness and life history. Rates of food consumption and digestion are the primary drivers determining the size of an individual's energy budget. Digestive processes are often among the most sensitive traits to temperature changes for many ectotherms and are therefore important for understanding the effects of climate change and local environment on fitness. Thermal sensitivity of physiological processes can vary locally, which many climate models fail to consider. The *second dissertation chapter* explored variation in thermal sensitivity of digestion, identifying distinct differences among populations of *Sceloporus* lizards. Additionally, many studies focus on stable temperature treatments, as opposed to daily temperature cycles experienced in nature. Daily temperature cycles, and patterns of temperature experienced, provide more realistic conditions for assessing the effects of temperature, which may improve our current understanding of organismal thermal biology. The *third dissertation chapter* compared data from stable and cycling treatments, finding differences

between methods, which varied among physiological processes. Additionally, processes differed between two daily temperature cycles consisting of different temperature patterns. Together, the first three dissertation chapters identified a need for data on combined direct and indirect effects of climate change, focused on a singular population, and under realistic projected daily temperature cycles. Therefore, the *fourth dissertation chapter* quantified changes in energy budgets due to warming nighttime temperature (direct effect) and prey availability (indirect effect) prairie lizards (*Sceloporus consobrinus*). Chapter four identified interdependent effects of warming nighttime temperature and prey on energetics, with the magnitude of change being a prominent factor dictating performance. The *fifth dissertation chapter* projected the energy budgets quantified in the fourth chapter, in context of reproductive output and population growth rates, among nine potential scenarios. Projections exemplified how warming nighttime temperatures interact with prey availability to reduce reproductive output, and subsequent population growth rates. The current dissertation identified the importance of using methods that replicate realistic conditions to examine mechanistic questions, while considering local variation. Studies on individual energetics and combined abiotic and biotic changes offer mechanistic data to inform population projections. Future studies should consider more taxonomic groups and temperature scenarios, as well as additional factors which may change in tandem with temperature in the future.

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## **Dissertation Introduction**

The influence of climate on organism function, life history, and persistence has been of interest to biologists for decades (Porter and Gates 1969; Congdon et al. 1982; Huey 1982; Dunham et al. 1989). For ectotherms in particular, temperature mediates major physiological processes relating to fitness and population dynamics (Porter and Gates 1969; Dunham et al. 1989; Dunham and Overall 1994). Bioenergetics are important considerations for research aiming to identify mechanistic processes influencing allocation to maintenance, growth, storage, and reproduction (Congdon et al. 1982; Dunham et al. 1989). Energy budgets of ectotherms can be heavily influenced by temperature, as digestive processes dictate the size of the budget. Digestion encompasses a suite of processes which are often among the most thermally sensitive traits in ectotherms (Huey 1982; Leal and Gunderson 2015). Therefore, digestive and energetic studies are necessary to unravel mechanistic questions about the influence of climate on organisms.

Individual processes influence population dynamics (Dunham et al. 1989; Dunham and Overall 1994), which is a primary focus when projecting effects of climate on persistence and distribution. Understanding how individual energy budgets change in response to environmental conditions allows for a mechanistic understanding of population changes over time. However, there is a lack of research integrating individual and population mechanisms. With the increased threat of global climate change, focus has heightened on understanding the influence of temperature on organisms (Parmesan 2006). While many studies have identified patterns and phenomena likely to occur with warming global temperatures, many fail to identify mechanisms and nuances associated with climate change (Hannah et al. 2014; Urban et al. 2016). Projections often assume that entire species and genera respond similarly to climate change. However, some

evidence suggests that local variation in thermally sensitive traits can be prominent, even in closely related organisms (e.g. Grant and Dunham 1990; Beaupre et al. 1993; Angilletta 2001).

Typical studies in thermal biology, primarily focus on how variation in stable temperatures effect performance (e.g. Huey and Stevenson 1979; Sanger et al. 2018, Plasman et al. 2019). However, many ectotherms experience daily and seasonal variation in temperature, which is not captured with stable temperature treatments. Some evidence suggests that growth rates, developmental rates, and gene expression can change when animals experience stable temperatures versus daily cycles (Meeuwig et al. 2004; Podrabsky and Somero 2004; Dhillon and Fox 2007; Kern et al. 2015; Kingsolver et al. 2015; Coulter et al. 2015). Physiological traits are critical for organismal performance, but few data are available on physiology to determine how traditional methods compare to daily temperature cycling approaches. Additionally, the focus of climate studies often falls upon mean daily temperatures as opposed to cycling regimes (e.g. Paaijmans et al. 2013; Verberk et al. 2016; Pontes-da-Silva et al. 2018). However, many ectotherms thermoregulate during the day and may still be able to maintain preferred temperatures under future climate conditions. At night, the thermal landscape becomes more homogenous (Huey and Slatkin 1976), making nighttime warming more of a concern for many animals. Studies are lacking on specific effects of nighttime warming (Speights et al. 2017), especially in tandem with additional environmental changes.

To understand life history and persistence of ectotherms, factors aside from temperature should be considered. Specifically, examining how co-occurring changes in the abiotic and biotic environment influence physiology would be beneficial for enhancing theory on drivers of population change and informing climate change studies and predictions (Davis et al. 1998; Beaupre 2002; Poloczanska et al. 2008; Williams and Middleton 2008; Huey and Kingsolver

2019). As energetics are critical for understanding life history and fitness, examining influential factors influencing digestion, such as temperature change in tandem with prey availability, would offer informative insight. Individual changes in energetics due to nighttime warming and prey availability could then be used to understand how energy allocation could change, and effects on populations.

The purpose of this dissertation was to examine the effects of temperature on ectotherms, and the specific interactions of nighttime warming temperature and prey availability on individual energetics and populations. Lizards in the genus *Sceloporus* were used as model organisms for experiments and models because they have known thermal sensitivity and are broadly distributed (e.g. Newman and Patterson 1909; Crenshaw 1955; Beaupre et al. 1993; Telemeco et al. 2014). In Chapter 1, I use a series of meta-analyses to identify patterns in food consumption and individual growth rate in response to temperature and find data gaps on indirect effects (duration of daily activity time) of climate change. In Chapter 2, I quantify the thermal sensitivity of digestion for an understudied population of *Sceloporus* lizards, *S. consobrinus* in Arkansas. The data on *S. consobrinus* were used to test a common assumption of climate studies regarding similarity in thermal sensitivity among closely related organisms by making comparisons to two populations of *S. undulatus*. In Chapter 3, experimental studies were conducted to determine if, and how, digestive processes differ when ectotherms experience stable and daily cycling temperature regimes, with a comparison between two patterns of daily cycling. In Chapter 4, the effects of nighttime warming and prey availability on digestion and energetics were examined with a series of experiments spanning nine possible scenarios. Lastly, Chapter 5 expands upon the findings in Chapter 4 by projecting the effects of nighttime warming

and prey availability on reproductive output and population growth over time for each of the nine scenarios quantified in the lab.

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# **Meta-analyses on the interactions of body temperature, food consumption, duration of daily activity, and growth rate in an ectotherm**

## **1.1 Abstract**

Warming temperatures are known to influence ectotherm life history and physiology. As climate change increases global temperatures, the consequences of direct and indirect effects of warming are becoming of high interest in biology. Warming temperatures could alter daily activity, change rates of food consumption, and influence allocation of energy altering life history. Lizards are a taxon of concern regarding climate change, with documented thermal sensitivity in performance and life history. The current study used a series of meta-analyses to examine how body temperature, food consumption, duration of daily activity, and growth rate interact to influence lizards. The results indicated warming temperature increased food consumption but decreased growth rate. Meanwhile, increasing food consumption increases lizard growth rate. However, mechanistic studies are needed to determine the factors dictating identified trends, as the current approach is correlational. Overall, few data were available for the parameters of interest, with zero studies quantifying the influence of daily activity on food consumption. Restrictions in daily activity are a primary consideration with climate change models for lizards, however, empirical data quantifying the effects are lacking. The current study identified fruitful areas for future research, specifically on the effects of daily activity on energetics, to understand indirect and direct effects of climate change.



## 1.2 Introduction

Climate change is predicted to influence species with regards to direct effects of warming temperatures on fitness (Vose et al. 2005; Adler et al. 2008). Researchers have already documented changes in species' distribution, abundance, and phenology likely due to anthropogenic climate change (Walther et al. 2002; Parmesan and Yohe 2003; Sinervo et al. 2010; Cohen et al. 2018). As a result, research centered on how temperature affects organismal survival and function has become of interest (Williams et al. 2009; Heino et al. 2009). Many studies focused on climate change emphasize singular, direct effects such as performance and survival at extreme temperatures (e.g. Deutsch et al. 2008; Childress and Letcher 2017; Pinksy et al. 2019), or use broad-scale correlations among climatic variables and species' traits (such as corresponding critical thermal tolerances and regional climate; e.g. Bonino et al. 2014; Lourenco de Moraes et al. 2019; Silva et al. 2019) to predict future scenarios for organisms. While such direct effects are concerning, indirect effects of climate change may be of similar importance. Indirect effects of warming temperatures can include variation in resource availability or reductions in time spent performing beneficial behaviors due to activity restrictions, which may pose a threat sooner than unavoidable prolonged exposure to critical temperatures. Indirect effects of climate change may be especially important for small-bodied ectotherms whose overall function and behavior vary in response to minute changes in the thermal landscape (Fucini et al. 2014; Twardochleb et al. 2020).

For many ectotherms, even slight temperature shifts for portions of the day or season can alter behavior and rates of physiological processes (Huey and Stevenson 1979; Stevenson 1985). Such changes can have subsequent effects on life history, including traits influential to overall

persistence and abundance (Adolph and Porter 1993; Brewster et al. 2020). For example, increases in temperature can restrict daily activity (Gunderson and Leal 2015), resulting in lower energy acquisition due to less foraging time (Huey et al. 2010). When an organism's energy budget is reduced, fewer resources are available for growth, reproduction, storage, and overall maintenance (Congdon et al. 1982; Dunham et al. 1989). Such energy reductions become particularly important when paired with higher metabolic demands and quicker digestive passage times, which typically correlate with warmer body temperatures (Beaupre et al. 1993; McConnachie and Alexander 2003). Higher metabolism can result in a need to consume more food to meet daily maintenance requirements, which may be problematic if activity time (or time available to forage) is constrained in future climate scenarios and prey availability is insufficient. Lower energy budgets (Bonnet et al. 2001), and subsequently smaller body size if growth is reduced (Pincheira-Donoso and Tregenza 2011), can decrease the number of offspring produced per reproductive event, or result in less frequent reproductive events for some organisms. Lower reproductive output can then lead to an overall decline in abundance (Brewster et al. 2018). Additionally, reduced activity of certain species could result in a decline of prey availability for predators (Smolinský and Gvoždík 2014), while simultaneously easing predation among other prey species (Sentis et al. 2012). Therefore, even slight changes in temperature can influence ectotherms through reduced daily activity time and possible decreases in food consumption, leading to profound impacts on populations and communities. Understanding such mechanisms and indirect effects of temperature change may be critical for implementing effective management strategies and understanding the influence of climate on complex systems.

Indirect effects of warming temperatures and underlying mechanisms, such as the one previously described, may not be explicit in studies and predictive models where data are

focused on direct effects of warming temperatures. Such deficiencies are especially pronounced in predictive models where correlational analyses are used to draw conclusions about underlying mechanisms. For example, using measurements of field-active body temperature, preferred temperature, and thermal tolerances of blunt-nosed leopard lizards (*Gambelia sila*) in conjunction with operative temperature models, Ivey et al. (2020) concluded that warming temperatures will restrict activity time for *G. sila* to the point of local extirpation. However, Ivey et al. (2020) do not consider data on the activity time required to meet energetic demands or physiological and behavioral mechanisms for thermoregulation, which could buffer the effects of rising temperatures. Such extreme conclusions based on correlations, without an understanding of how activity and thermoregulation influences lizard reproduction, energetics, or trophic interactions, are limited in applicability. Additionally, temperature already results in differing activity times among populations of lizards naturally within a species, without causing extirpation (e.g. Sears 2005; Horváthová et al. 2013), suggesting restrictions to a certain degree may not be dire. However, among populations with differing durations of daily activity, variation in life history traits is frequently observed (Sears 2005; Horváthová et al. 2013; Brewster et al. 2018), which could alter population dynamics.

Literature reviews that summarize and collate the expected effects of climate related variables (e.g. temperature) on ectotherm life history are needed. Such examination will highlight what is known empirically about interactions of temperature, life history, and energetics, and identify knowledge gaps. Empirical data are of interest because many climate predictions to date examine and draw conclusions with little empirical evidence to validate assumptions, which may pose limitations in model applicability and accuracy. Additionally, an

analysis of the available literature will enhance our understanding of the influence of climate on organism function and complex systems, and provide direction for future studies.

Lizards are a taxon of interest with regards to climate change, life history, and thermal biology, and are commonly used as model organisms (Huey et al. 1982). Lizard life histories, physiologies, and behaviors heavily influenced by temperature (Adolph and Porter 1993; Zera and Harshman 2001; Huey et al. 2010) making them vulnerable to changing climatic condition. Many current studies and predictive models examining climate change in lizards have focused on critical thermal tolerances, body temperature, and habitat suitability (Sinervo et al. 2010; Fordham et al. 2012; Herrando-Pérez et al. 2018; Pontes-da-Silva et al. 2018), with little focus on empirically quantifying life history or energetics. Although, some researchers in recent years have worked to create bioenergetic models and increase ease of coding complex modeling procedures which can incorporate physiological processes (Kearney and Porter 2020).

Examination of individual growth rate in relation to direct and indirect effects of climate change would allow for evaluation of a plastic trait often influenced by abiotic and biotic factors. While a single life history trait will not capture the entire picture, it offers a initial starting point for identifying important trends. As temperatures increase, indirect effects of climate change, such as reduced prey availability or ability to perform active behaviors during the day, will be more pronounced. Prey availability can influence growth rate and interact with temperature and activity (Olsson and Shine 2002). Duration of activity is often of interest with regards to lizards and climate change (Cosendey et al. 2022) because it is influenced by temperature (Arenas-Moreno et al. 2018) and can alter life history (Karasov and Anderson 1984; Niewiarowski 2001). Growth rate varies in response to both, energy acquisition and duration of daily activity, and has the potential to influence reproductive output as a result, relating to fitness and population-

level processes (Dunham et al. 1989; Adolph and Porter 1993; Adolph and Porter 1996). Growth rate can also be associated with life history traits in lizards, particularly age and size at maturity. For example, lizards with high growth rates mature faster and at a smaller size in comparison to slower growing lizard populations (Adolph and Porter 1996). Due to reaching maturity quicker, these lizards have more reproductive events per season comparatively, considering all other things are equal (Bauwens and Díaz-Uriarte 1997). Additionally, lizard populations with high mortality have been found to have high growth rates in some cases (Bradshaw 1971; Sears 2005), favoring early maturation.

The current study asks the question: how do body temperature, food consumption, duration of daily activity, and growth rate interact to influence lizards? The primary objective of this study was to conduct multiple literature reviews and meta-analyses to determine how growth rate and food consumption are influenced by changes in body temperature and duration of daily activity time. Secondly, this study aims to conduct an additional literature review and meta-analysis to examine how lizard growth rate is influenced by food consumption, as a potential indicator of how changes in energy acquisition may influence life history. I hypothesize that lizard food consumption will increase with warmer temperatures. The hypothesis is founded on potential for higher metabolic demands or greater energy use during activity at warm temperatures. I also hypothesize that duration of daily activity will positively correlate with growth rate and food consumption, as more activity time may allow increased foraging rates and allocation of energy to growth.

## **1.3 Methods**

### *1.3.1 Literature Search and Data Extraction*

Systematic literature searches were conducted and reported following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) method (Liberati et al. 2009; Nakagawa et al. 2017) (Figures 1 - 5). Five literature searches using two databases, *Web of Science* and *ScienceDirect*, were conducted. Separate searches were conducted for each question addressed for the purpose of clarity and ease of filtering papers for specific data. Two databases were searched to increase the likelihood of finding papers on topics of interest. The results of each search were exported to EndNote 20, which was used to find and remove duplicate results. Titles and abstracts were then reviewed to determine if the paper was on lizards and if the appropriate variables were measured. After meeting those criteria, papers were further scrutinized based on criteria outlined below. Data could be from, although not limited to, treatments in a lab, outdoor enclosures, or the field, and between populations and/or between years, within a species. In the instance where manipulation was applied to lizards, data were only included from control treatments with no manipulation. Review papers, opinion articles, book chapters, and papers where data were presented as outcomes of a predictive model as opposed to being collected empirically were excluded. For inclusion in the meta-analysis, papers needed to report at least two measurements of the dependent variable to be compared, and standard deviation, or standard error and sample sizes so standard deviation could be calculated. Natural history papers with only a single measurement were excluded. Growth rate could be measured using lizard mass or snout-vent length, as the two variables are often correlated. Knowing consumption influences growth rate, data were only included when food was not restricted or manipulated between measurements, unless the food manipulation was the same within a single effect, for growth rate studies. Body temperature had to be measured via inserting a thermometer or thermocouple into the cloaca as opposed to body surface, atmospheric, or ground temperature,

and if the temperature treatments were initially applied to eggs or mothers treatments had to continue after hatching.

#### Growth Rate and Body Temperature

A literature search was conducted on 2 November 2021 using *Web of Science* for the terms: lizard + growth + “body temperature\*” with any date range, generating a result of 154 papers (Figure 1). A search was conducted on 22 November 2021 using *ScienceDirect* for the terms: “body temperature” + lizard + “growth rate” solely in the category “research articles”, generating a result of 213 papers (Figure 1). Search terms differed because *ScienceDirect* yielded many unrelated results without more specific terms. Between the two searches 13 duplicates were detected and removed, yielding 354 unique papers. After searching abstracts and titles 140 papers were removed because they were not on lizards, 135 papers were removed because they did not measure both variables of interest or did not have at least two measurements to compare, and 20 papers were removed because they did not report empirical data, but instead were opinion pieces or review articles, leaving 59 papers to be further reviewed. After filtering papers, 41 were removed because they did not measure  $T_b$  and/or growth rate, four were removed because they did not have a treatment comparison, four were removed for missing data, and two were removed for being a review paper and a book chapter, leaving eight papers with extractable data (Table 1).

#### Growth rate and Duration of Daily Activity

A literature search was conducted on 4 September 2021 in *Web of Science* for the terms: lizard + activity + growth with any date range, generating a result of 326 papers (Figure 2). A literature search was conducted on 22 November 2021 in *ScienceDirect* for the terms: “daily activity” + growth + lizard solely in the category “research articles”, generating a result of 129

papers (Figure 2). A total of four duplicates were found between the two searches resulting in 451 unique papers. After reviewing titles and abstracts, 160 papers were removed because they were not on lizards, 225 papers were removed because they did not measure daily activity and/or growth rate, and eight papers were removed because they were review or opinion articles, leaving 58 papers to be further scrutinized. After filtering papers, 40 were removed because they did not measure daily activity and/or growth rate, five were removed because they did not have a treatment comparison, and two were removed for missing data, leaving 11 papers with extractable data (Table 1).

#### Body Temperature and Food Consumption

A literature search was conducted on 8 November 2021 in Web of Science for the terms: lizard + consumption + “body temperature\*” with any date range, generating a result of 121 papers (Figure 3). A literature search was conducted on 8 November 2021 in ScienceDirect for the terms: consumption + “body temperature” + lizard, with any date range, in the category “research articles”, generating a result of 625 papers (Figure 3). Six duplicates were found between the two searches resulting in 741 unique papers. After reviewing titles and abstracts, 380 papers were removed because they were not on lizards, 289 papers were removed because they did not measure body temperature and/or food consumption, 47 papers were removed because they were reviews or book chapters, five papers were removed because they were predictive models without the necessary empirical data, and two were removed for lacking a comparison, leaving 18 papers to be further scrutinized. After filtering papers, five were removed because they did not measure body temperature and/or food consumption, one was removed because it did not have a treatment comparison, one was removed for missing data, and one was removed for force-feeding lizards, leaving ten papers with extractable data (Table 1).



### Duration of Daily Activity and Food Consumption

A literature search was conducted on 8 August 2022 in Web of Science for the terms: lizard + consum\* + activity with any date range, generating a result of 247 papers, and in ScienceDirect for the terms: lizard + consumption + “daily activity” with any date range, in the category “research articles”, generating a result of 81 papers (Figure 4). Four duplicates were found between the two searches resulting in 324 unique papers. After reviewing titles and abstracts, 122 papers were removed because they were not on lizards, 183 papers were removed because they did not measure duration of daily activity and/or food consumption, 14 papers were removed because they were reviews, and one paper was removed because it was a predictive model without the necessary empirical data, leaving four papers to be further scrutinized. After filtering papers, two were removed because they did not measure duration of daily activity and/or food consumption, one was removed because it did not have a treatment comparison, and one was removed for missing data, leaving zero papers with extractable data. Therefore, an assessment of the influence of duration of daily activity on lizard food consumption was not possible (Table 1).

### Growth Rate and Food Consumption

A literature search was conducted on 10 August 2022 in Web of Science for the terms: lizard + consum\* + growth with any date range, generating a result of 133 papers, and in ScienceDirect for the terms: lizard + consumption + “growth rate” with any date range, in the category “research articles”, generating a result of 336 papers (Figure 5). Five duplicates were found between the two searches resulting in 464 unique papers. After reviewing titles and abstracts, 312 papers were removed because they were not on lizards, 98 papers were removed because they did not measure duration of daily activity and/or food consumption, 21 papers were

removed because they were reviews, 14 papers were removed because they were book chapters, six were removed for applying treatments of external factors not of interest, one was removed for feeding lizards an unnatural diet, and two papers were removed because they were predictive models without the necessary empirical data, leaving 10 papers to be further scrutinized. To be included in the meta-analysis, papers need to include two measurements of growth rate, each under different amounts of food consumption. After filtering papers, four were removed because they did not measure duration of growth rate and/or food consumption, two were removed for applying treatments of external variables not of interest, and one was removed for missing data, leaving three papers with extractable data (Table 1).

### *1.3.2 Effect Size Calculation*

For each study used in meta-analyses data were extracted on treatments, means, standard deviations (or standard errors), sample sizes, and genus. Variation was expected to exist in units of measurement among studies and sample sizes to be low, and therefore unbiased standardized mean differences (SMD) were calculated using Hedges'  $g$  (Borenstein et al. 2009) for effect sizes. Each effect size is a comparison of either growth rate or consumption, and Hedges'  $g$  allows comparisons with variation in units of measurements because means are standardized by pooled standard deviation. For activity comparisons, mean growth rate and mean consumption quantified under low duration of activity was subtracted from high duration of activity. Therefore, the SMD indicates the effect of increasing activity time on growth rate and consumption. Positive effect sizes indicate an increase in growth or consumption when activity is increased, and negative effect sizes indicate a decrease in growth or consumption when activity is increased. For body temperature comparisons, mean growth rate or mean consumption at the lower  $T_b$  was subtracted from the mean at the higher  $T_b$ . Therefore, the SMD indicates the effect

of increasing body temperature. Positive effect sizes indicate an increase in growth or consumption when  $T_b$  is increased, and negative effect sizes indicate a decrease in growth or consumption when  $T_b$  is increased. In instances where a single study presented results from multiple activity or  $T_b$  treatments Hedges  $g'$  was calculated for each possible pairwise comparison.

### *1.3.3 Statistical Analyses*

To account for multiple effect sizes calculated for the same study a random effect of study number divided by effect number was added to all models, where each study was assigned a unique number, which was repeatedly assigned to each effect within the study, and each effect was given a unique number for the entire dataset. To consider variation in lizard taxa and relatedness, phylogenetic relationship was included in all models as a random effect, except when analyzing the influence of food consumption on growth rate where all studies were on *Sceloporus jarrovi*. To take temperature and duration of activity treatment into consideration, the difference in activity or  $T_b$  for each effect was calculated and included in models as a quantitative moderator variable to determine how much heterogeneity may be explained by treatment level. All analyses were conducted using R v4.1.2 (R Core Team 2021) and package 'metafor' (Viechtbauer 2010). All meta-analyses were performed on Hedges'  $g$  using multi-level random effects and meta-regression models. For each meta-regression a pseudo  $R^2$  was calculated.

### *1.3.4 Publication Bias*

To test for presence of publication, bias funnel plots were used to explore the relationship between standard error and standardized mean difference (Hedges  $g$ ) from the multi-level models. A time-lag bias may also occur when there is a delay in publishing nonsignificant

compared to significant results. To test for a time-lag bias the meta-regressions were re-iterated with publication year included as a moderator. To assess publication bias in the meta-analyses, Rosenthal's fail-safe number was used, which estimates the number of statistically nonsignificant studies needed to change the conclusion of the meta-analysis (Rosenthal 1979).

## **1.4 Results**

### *1.4.1 Growth Rate and Body Temperature*

A total of eight papers were used resulting in 24 unique effect sizes from eight species of lizard. Most effect sizes (87.5%) indicated a negative response of growth rate with increased  $T_b$ . The average effect size (Hedges'  $g$ ) was -0.0291, suggesting a slight decrease in lizard growth rate with warmer  $T_b$ , although there was no significant effect ( $p = 0.9415$ , 95% CI: -0.8061 – 0.7479, SE = 0.3964, Figure 6). There was a high degree of heterogeneity present in the model ( $I^2 = 88.9072$ ), almost entirely due to between group heterogeneity. The test of moderators indicated that the treatment level (difference in body temperature) had a significant effect ( $p = 0.0078$ ,  $Q = 7.0858$ , 95% CI: -0.2717 - -0.0413) where effect size increased with increasing difference in  $T_b$ , although the pseudo  $R^2 = -0.1940$  (Figure 7). Lizard genus also influenced model outcome (estimate = 1.8889).

There was strong evidence for publication bias based on the funnel plot, where effects were not symmetrically distributed (Figure 8). However, there was no evidence of a time-lag bias within the dataset ( $p = 0.8262$ , 95% CI: -0.0220 - 0.0276, SE = 0.0126). The fail-safe number was high relative to the number of papers in the analysis (fail-safe  $N = 161$ ,  $p < 0.0001$ ), indicating the dataset may be robust and a high number of significant statistical comparisons would be required to change the outcome of the meta-analysis.

### *1.4.2 Growth Rate and Duration of Daily Activity*

A total of 11 papers were used resulting in 59 unique effect sizes from eight species of lizard. Most effect sizes (88.1%) indicated a positive response of increased activity on growth rate. The average effect size was 1.2095, suggesting an overall strong, positive increase in lizard growth rate with increased daily activity time. There was a general trend of increased growth rate with increasing duration of daily activity (estimate = 0.8848 SD), although it was not significant ( $p = 0.0554$ , 95% CI: -0.0196 – 1.7094, SE = 0.4411) (Figure 6). There was a high degree of heterogeneity present in the model ( $I^2 = 95.0479$ ). Most of the heterogeneity was due to within study heterogeneity (56.6797%), followed by among study heterogeneity (25.7978%). Phylogenetic relationship did have some effect on the model (estimate = 0.3008 SD). Magnitude of treatment (difference in activity times) did not explain heterogeneity in the model (pseudo  $R^2 = -0.0227$ ,  $p = 0.1832$ ,  $Q = 1.7718$ , CI: -0.0537 – 0.2812, SE = 0.0855), although there was a slight trend of increasing effect size with increasing difference in activity times (Figure 7).

There was strong evidence for publication bias based on the funnel plot, where effects were not symmetrically distributed (Figure 8). There was also evidence of a time-lag bias within the dataset ( $p < 0.0001$ , 95% CI: -0.0360 - -0.0148, SE = 0.0054). However, the fail-safe number was high (fail-safe N = 4,786,  $p < 0.0001$ ), indicating the dataset may be robust and a high number of significant papers would be required to change the outcome of the meta-analysis.

#### *1.4.3 Body Temperature and Food Consumption*

A total of ten papers were used resulting in 159 unique effect sizes from nine species of lizard. Most effect sizes (77.36%) indicated a positive response of food consumption with increased  $T_b$ . The average effect size was 0.9365, suggesting an overall increase in lizard food consumption with warmer  $T_b$ . There was a significant effect of lizard  $T_b$  on food consumption ( $p = 0.0063$ , 95% CI: 0.1887 – 1.1451, SE = 0.2440, Figure 6) with an average estimate of

increased food consumption by 0.6669 standard deviations as  $T_b$  increases. There was a high degree of heterogeneity present in the model ( $I^2 = 88.2663$ ), mostly due to within-study heterogeneity (69.1492%). The test of moderators indicated that the treatment level (difference in body temperature) had a significant effect ( $p < 0.0001$ ,  $Q = 64.8328$ , 95% CI: 0.1125 – 0.1848) where effect size increased with increasing difference in  $T_b$ , although the pseudo  $R^2 = 0.3558$ , Figure 7). Phylogenetic relationship had no effect on the model.

There was strong evidence for publication bias based on the funnel plot, where effects were not symmetrically distributed (Figure 8). However, there was no evidence of a time-lag bias within the dataset ( $p = 0.0751$ , 95% CI: -0.0011 - 0.0234, SE = 0.0063). The fail-safe number was high relative to the number of papers in the analysis (fail-safe N = 51,885,  $p < 0.0001$ ), indicating the dataset may be robust and a high number of nonsignificant papers would be required to change the outcome of the meta-analysis.

#### *1.4.4 Growth Rate and Food Consumption*

A total of three papers were used resulting in eight unique effect sizes from one species of lizard, all on hatchlings and juveniles. All effect sizes indicated a positive response of growth rate with increased food consumption. The average effect size was 1.3103, suggesting a strong effect of overall increases in lizard growth rate with higher food consumption. There was a significant effect of lizard food consumption on growth rate ( $p = 0.0006$ , 95% CI: 0.7441 – 2.7261, SE = 0.5056, Figure 6) with an average estimate of increased growth rate by 1.7351 standard deviations as food consumption increases. There was a high degree of heterogeneity present in the model ( $I^2 = 58.1136$ ), mostly due to between-study heterogeneity (58.1140%). The test of moderators indicated that the treatment level (difference in food consumption) had no effect (Figure 7).

There was evidence for publication bias based on the funnel plot, where effects were not symmetrically distributed (Figure 8). However, there was no evidence of a time-lag bias within the dataset ( $p = 0.0693$ , 95% CI: -0.2204 - 0.0084, SE = 0.0584). The fail-safe number was high relative to the number of papers in the analysis (fail-safe N = 110,  $p < 0.0001$ ), indicating the dataset may be robust and a high number of nonsignificant papers would be required to change the outcome of the meta-analysis.

## **1.5 Discussion**

As ectotherms with known physiological and behavioral dependence on the environment, lizards are a model organism for assessing the effects of climate change on organisms. The current review highlights the small number of empirical studies addressing the interactions of temperature, duration of daily activity time, food consumption, and growth rate in lizards. In light of climate change many predictive models and research studies on animals emphasize temperature effects. While many climate models are focused on lizards (e.g. Buckley et al. 2008, Sinervo et al. 2010, Pontes De-Silva et al. 2018), the focus is often placed on correlations among critical thermal tolerances and local climatic conditions (e.g. Brusch, et al. 2016, Herrando-Pérez et al. 2019), lacking mechanism. Alternatively, some lizard climate models do incorporate mechanism, but rely on previously published data from similar taxa due to data limitations of data for a single study system or efforts to be broadly applicable to a wide geographic or taxonomic range (e.g. Buckley et al. 2008, Sinervo et al. 2010). The current study was focused on empirically collected data on temperature-dependent physiological mechanisms, life history, and behavior, making comparisons within single species, which appears to be less-commonly quantified than anticipated by the author. The literature review found few papers on the variables of interest. Among the studies that were analyzed, the meta-analyses suggested that warming

temperatures increased food consumption but decreased growth rate, although increasing food consumption increased growth rate. There was also a slight, although nonsignificant, trend where increasing duration of daily activity increased growth rates, which aligns with previous predictions (Adolf and Porter 1996). Underlying mechanisms linking temperature, food limitation, and growth would clarify the trends identified, as increasing temperatures without sufficient food may result in decreased growth.

Specifically, the literature search found zero empirical studies quantifying how duration of daily activity influences food consumption. The lack of studies on daily activity was surprising, considering that many lizard climate change models make predictions regarding alterations in duration of daily activity (e.g. Buckley 2013; Kearney 2013; Pontes-da-Silva et al. 2018). In fact, a review paper examining the relationship of lizard performance and climate change identified hours of daily activity to be one of the most predicted factors for lizard climate studies (Cosendey et al. 2022). However, it appears that the common method for assessing duration of daily activity is extrapolated from methods described by Hertz et al. 1993 and Sinervo et al. 2010, using operative temperature models and thermal preferences as opposed to direct field observations (Cosendey et al. 2022), which was part of the search criteria for the meta-analyses. If the current study incorporated estimates of activity from operative temperature models the search results and studies included in the meta-analyses would have been higher, although predictions may not be congruent. Operative temperature data do not consider factors outside of temperature restrictions when estimating daily activity. Therefore, operative temperature models are limited in applicability to understanding activity in nature when other factors are prevalent. Lastly, a variety of papers that draw conclusions on how restriction in daily activity may influence lizards assume a cost to foraging time or energetic constraints (e.g. Lara-



Reséndiz et al. 2015, Ivey et al. 2020). Such assumptions may be true in resource-limited systems where animals require longer foraging times to consume enough food. Second, reduced activity may force animals to experience lower body temperatures, which can slow digestive processes and cause a reduction in consumption and energy acquisition (Brewster et al. 2020). Still, it was unexpected to find that direct quantification of food consumption and daily activity were not observed in the literature, representing a gap in the knowledge. Data on how long lizards need to be active to consume enough food to maintain energetic demands would be beneficial to enhancing our understanding of life history, behavior, and the influence of climate.

The results of the meta-analyses indicated that lizard growth rate tends to decrease at warmer temperatures, while increasing with greater food consumption. Confoundingly, lizard food consumption tended to increase with warming body temperatures. Explanations for the decrease in growth rate at higher temperatures are the limited number of lizard taxa represented, interspecies variation in thermal tolerance, and the current climates lizards were acclimated to. Most effects for the analysis examining growth and  $T_b$  were on the lizard genus *Takydromus*, which has a thermal optimum for growth between 26 - 28°C (Ji et al. 1993, Chen et al. 2003), corresponding to the lowest temperatures assessed in studies. Due to the curvilinear nature of thermal performance curves, if data are only collected at and above the thermal optimum, results will indicate a decrease in performance with rising temperatures without capturing an initial increase in performance. Among the other lizard taxa assessed for the influence of  $T_b$  on growth rate, four out of eight had positive effects of increasing growth rates with temperature (Buffenstein and Louw 1982, Lorenzon et al. 1999, Sun et al. 2011, Gadsen et al. 2018) and the remaining four had small effect sizes indicating nearly no difference in growth rates. Additionally, three of the four negative effects for growth rate in relation to  $T_b$  for lizards outside

the genus *Takydromus* were at relatively cool temperatures where performance was low and were found to have no significant effects in the initial study from which the data were extracted (Mathies and Andrews 1997). Lastly, if lizards currently exist in a relatively cool climate below their thermal optimum, warmer temperatures may offer benefits, in contrast to lizards in warmer climates where warming temperatures incur a greater risk. Such conflicting results showcase the importance of including a wide range of temperatures when assessing organismal performance to gain a more complete understanding. Additionally, individual, species, and genera can drastically vary in thermal optimum, which is an important consideration when making assessments and predictions, especially when broad assumptions are being made across taxa and locations.

The meta-analyses also found that increasing temperature resulted in greater food consumption, which is supported by ectotherm studies suggesting that digestive passage time decreases, and metabolic rate increases, with warming temperature, allowing the gut to empty quicker so more food can be consumed (Beaupre et al 1993, Plasman et al. 2019, Yengle et al. 2022). Ectotherm metabolic rate also increases with warming temperatures (Nespolo et al. 2003, Lear et al. 2020), which may contribute to a need to consume more food, although changes of a few degrees may be negligible. Such results suggest that if ectotherms are exposed to warmer body temperatures in the future, it may result in a need to consume more food to meet energetic demands associated with rapid clearing of the gut and increased metabolic rate.

Longer durations of daily activity were found to result in a slight increase in lizard growth rate, supported by comparative field studies and common garden experiments. A reciprocal transplant study found that lizards in Nebraska had slower growth rates when transplanted to New Jersey, where the estimated daily activity time was reduced by ~2 hours (Niewiarowski and Roosenburg 1993). Knowing growth rate increases with food consumption, it

could be hypothesized that increasing daily activity time could allow organisms to forage longer and subsequently consume more energy for allocation to growth (assuming temperatures are adequate for gut clearance and there is room in the gut for more food). While no studies comparing consumption and activity time directly within a species were identified here, a between species comparison suggested that lizards with longer durations of daily activity consume more food (Avery 1978). It is also possible that ectotherms with longer durations of activity are exposed to warmer temperatures throughout the day or increase basking, prolonging time spent at higher body temperatures. Because lizard growth is influenced by behavioral and environmental variables, it has been found to be plastic, with inter- and intraspecific variation (Smith and Ballinger 1994). For example, Lu et al. (2018) found that despite having similar atmospheric temperatures, toad-headed lizards (*Phrynocephalus vlangalii*) at a high elevation site were able to maintain warmer body temperatures and had greater prey availability, resulting in faster growth rates compared to a low elevation site. Grant and Dunham (1990) found that canyon lizards (*Sceloporus merriami*) at high and low elevation sites had slower growth rates than lizards at a moderate elevation, although driven by different mechanisms. Canyon lizards at the high elevation site had the greatest availability of food and longest durations of daily activity, however, cooler retreat temperatures paired with greater costs associated with long durations of activity, resulted in slow growth rates (Grant and Dunham 1990). In contrast, low elevation lizards maintained warmer body temperatures when retreating and for the later part of the day, had lower food availability, and were forced to remain inactive at midday, which also resulted in slow growth rates compared to lizards at a moderate elevation site (Grant and Dunham 1990). Therefore, duration of daily activity, food consumption, and body temperature have

interdependent and sometimes additive effects on lizards and are important factors to consider with regard to life history and organismal response to climate.

Growth rate and food consumption were variables of interest in the current study because they can influence life history variables (Adolph and Porter 1996), which can correspond to fitness (Li et al. 2017). When assessing how organisms interact with climate it is important to consider how direct effects, such as warming temperatures, influence energetics and behavior. The results of the meta-analysis exemplify the interdependence of growth rate and food consumption, as well as their response to temperature and daily activity. Greater food consumption can result in a greater uptake of energy for allocation to growth (Avery 1971). Increased food consumption and decreased passage times with warming temperatures can also result in greater energy assimilation (Harlow et al. 1976, Angilletta et al. 2002, Brewster et al. 2020). Increased growth rates can be especially important for hatchling lizards, as they do not incur reproductive costs yet and can allocate more net energy to growth. Rapid hatchling growth rates can allow organisms to reach reproductive maturity quicker, which has been suggested to increase fitness in certain conditions (Li et al. 2017). Higher food processing rates from greater food consumption can also be important for increasing reproductive output in adults (Brewster et al. 2021). Therefore, if lizards experience increases in food consumption as temperature warms, growth rate and reproductive output may change.

The current study identified correlations between increasing temperatures and greater food consumption and growth rate in lizards and increased food consumption correlating with increased growth rates. While the findings can't be extrapolated to direct mechanisms, they suggest that if lizards experience warmer body temperature due to climate change, they may change rates of food consumption, possibly altering life history traits. Such changes in life

history can have fitness consequences and influence population-level processes. However, the findings were limited because data quality and availability were lacking. Specifically, more empirical studies are needed on how duration of daily activity influences bioenergetics and life history. Hours of restriction in activity is a widely used variable for predicting lizard response to climate change, yet quantitative information in natural populations on what influences daily activity are not available. Future research should aim to increase our understanding of the factors influencing daily activity, and how daily activity influences energy budgets and life history. Additionally, as ectotherms approach and exceed their thermal optimum, they may experience detrimental effects, which were not captured in the meta-analyses. It is important consider how warming body temperatures can create a need to increase food consumption to maintain energetic demands. However, food limitations or behavioral adjustments to avoid warming body temperature may pose a challenge for maintaining current life history strategies and reproductive output. More empirical data are needed to assess how direct and indirect effects of climate influence ectotherms in order to enhance our ability to make predictions and conserve ecosystems.

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## 1.8 Tables

**Table 1.** Literature searches were conducted using *Web of Science* and *ScienceDirect* and screened for inclusion in meta-analyses. The table indicates papers that were included in each meta-analysis.

Title	Authors	Year	Species
<b>Growth Rate and Body Temperature</b>			
Effect of water constraint on growth rate, activity, and body temperature of yearling common lizard ( <i>Lacerta vivipara</i> )	Lorenzon, et al.	1999	<i>Zootoca vivipara</i>
Quantifying the cost of thermoregulation: thermal and energetic constraints on growth rates in hatchling lizards	Brewster et al.	2013	<i>Crotaphytus collaris</i>

Influence of body temperature on food assimilation and locomotor performance in white-striped grass lizards, <i>Takydromus wolteri</i> (Lacertidae)	Chen et al.	2003	<i>Takydromus wolteri</i>
Influence of pregnancy on the thermal biology of the lizard, <i>Sceloporus jarrovi</i> : why do pregnant females exhibit low body temperatures?	Matheis and Andrews	1997	<i>Sceloporus jarrovi</i>
The influence of thermal environment and food availability on testosterone and gonadal recrudescence in male Chinese skinks [ <i>Plestiodon (Eumeces) chinensis</i> ]	Sun et al.	2011	<i>Plestiodon chinensis</i>
Ecology of <i>Sceloporus gadsdeni</i> (Squamata: Phrynosomatidae) from the central Chihuahuan Desert, Mexico	Gadsden et al.	2018	<i>Sceloporus gadsdeni</i>
Temperature effects on bioenergetics of growth, assimilation efficiency and thyroid activity in juvenile varanid lizards	Buffenstein and Louw	1982	<i>Varanus niloticus</i>
Food intake, assimilation efficiency, and growth of juvenile lizards <i>Takydromus septentrionalis</i>	Ji et al.	1993	<i>Takydromus septentrionalis</i>

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#### Growth Rate and Duration of Daily Activity

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Growth plasticity and thermal opportunity in <i>Sceloporus</i> lizards	Sinervo and Adolph	1994	<i>Sceloporus occidentalis</i>
Testosterone inhibits growth in juvenile male eastern fence lizards ( <i>Sceloporus undulatus</i> ): implications for energy allocation and sexual size dimorphism	Cox et al.	2005	<i>Sceloporus undulatus</i>

Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation	Niewiarowski	2001	<i>Sceloporus undulatus</i>
Effect of water constraint on growth rate, activity, and body temperature of yearling common lizard ( <i>Lacerta vivipara</i> )	Lorenzon et al.	1999	<i>Zootoca vivipara</i>
Effects of maternal basking and food quantity during gestation provide evidence for the selective advantage of matrotrophy in a viviparous lizard	Itonaga et al.	2012	<i>Pseudemoia entrecasteauxii</i>
Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity	Sears	2005	<i>Sceloporus graciosus</i>
An experimental study of the effects of weed invasion on lizard phenotypes	Downes and Hoefer	2007	<i>Lampropholis delicata</i>
Early activity rates do not predict growth and future body size of juvenile eastern fence lizards, <i>Sceloporus undulatus</i>	Rosier and Langkilde	2013	<i>Sceloporus undulatus</i>
Annual life-history variation in the striped plateau lizard, <i>Sceloporus virgatus</i>	Smith	1996	<i>Sceloporus virgatus</i>
Reciprocal transplant reveals sources of variation in growth rates of the lizard <i>Sceloporus undulatus</i>	Niewiarowski and Roosenburg	1993	<i>Sceloporus undulatus</i>
Acclimation to Water Restriction Implies Different Paces for Behavioral and Physiological Responses in a Lizard Species	Rozen-Rechels et al.	2020	<i>Zootoca vivipara</i>

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### Body Temperature and Food Consumption

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Thermal dependence of appetite and digestive rate in the flat lizard, <i>Platysaurus intermedius wilhelmi</i>	Graham et al.	2001	<i>Platysaurus intermedius</i>
Integrating bioenergetics and conservation biology: thermal sensitivity of digestive performance in Eastern Collared Lizards ( <i>Crotaphytus collaris</i> ) may affect population persistence	Brewster et al.	2020	<i>Crotaphytus collaris</i>
Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, <i>Eumeces elegans</i>	Du et al.	2000	<i>Plestiodon elegans</i>
The effect of temperature on digestive and assimilation efficiency, gut passage time and appetite in an ambush foraging lizard, <i>Cordylus melanotus melanotus</i>	McConnachi and Alexander	2004	<i>Cordylus melanotus</i>
The thermal dependence of feeding behavior, food consumption and gut passage time in the lizard <i>Lacerta vivipara jacquin</i>	Van Damme et al.	1991	<i>Zootoca vivipara</i>
Thermal dependence of feeding performance and resting metabolic expenditure in different altitudinal populations of toad-headed lizards	Hu et al.	2019	<i>Phrynocephalus vlangalii</i>
Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, <i>Takydromus septentrionalis</i>	Xiang et al.	1996	<i>Takydromus septentrionalis</i>
Selected body temperature, thermal tolerance and food assimilation in a viviparous skink, <i>Sphenomorphus indicus</i>	Ji et al.	1997	<i>Sphenomorphus indicus</i>

Food intake, assimilation efficiency, and growth of juvenile lizards <i>Takydromus septentrionalis</i>	Xiang et al.	1993	<i>Takydromus septentrionalis</i>
Temperature effects on bioenergetics of growth, assimilation efficiency and thyroid activity in juvenile Varanid lizards	Buffenstein and Luow	1982	<i>Varanus niloticus</i>

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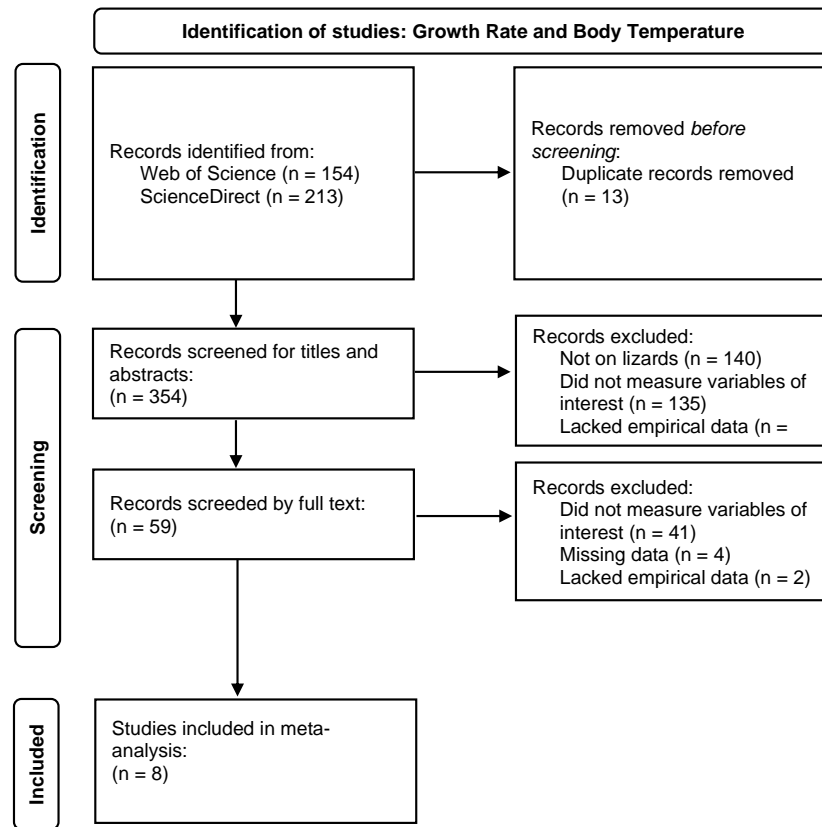
### Growth Rate and Food Consumption

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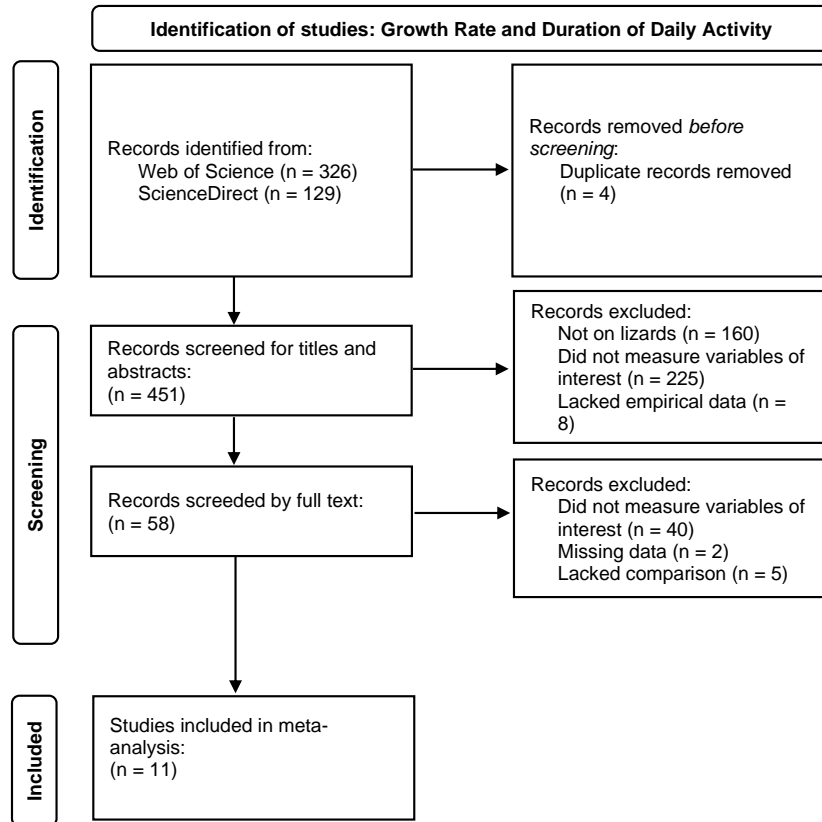
Effects of food restriction on growth, energy allocation, and sexual size dimorphism in Yarrow's Spiny Lizard, <i>Sceloporus jarrovii</i>	Cox et al.	2008	<i>Sceloporus jarrovii</i>
Nutritional modulation of IGF-1 in relation to growth and body condition in <i>Sceloporus</i> lizards	Duncan et al.	2015	<i>Sceloporus jarrovii</i>
Support for the thermal coadaptation hypothesis from the growth rates of <i>Sceloporus jarrovii</i> lizards	Patterson et al.	2017	<i>Sceloporus jarrovii</i>



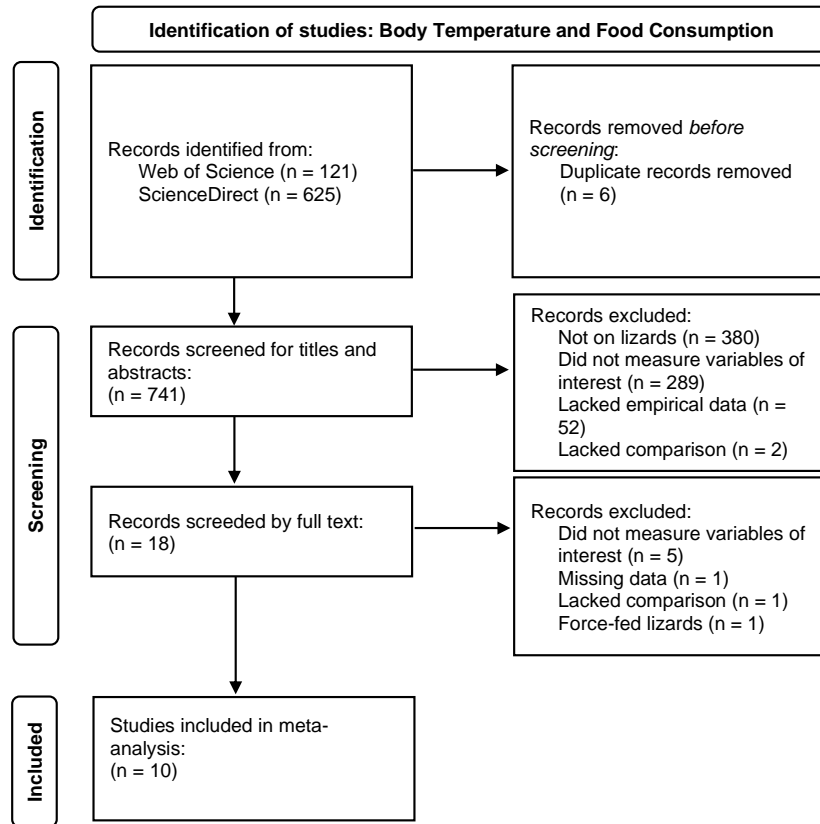
## 1.9 Figures



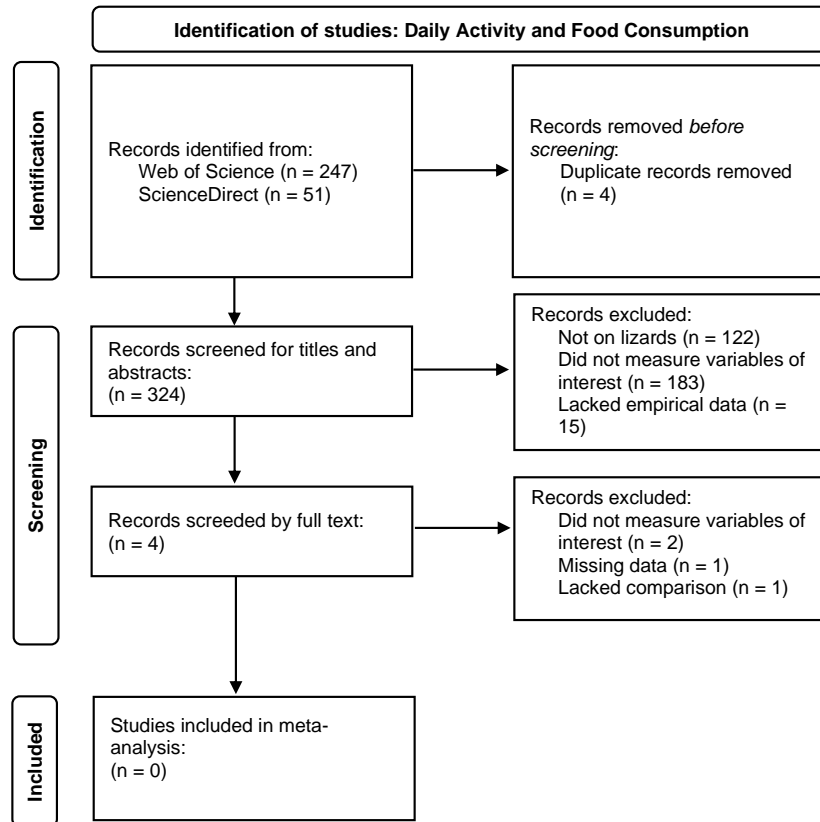
**Figure 1.** Papers were identified and screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach to assess the effect of body temperature on growth rate.



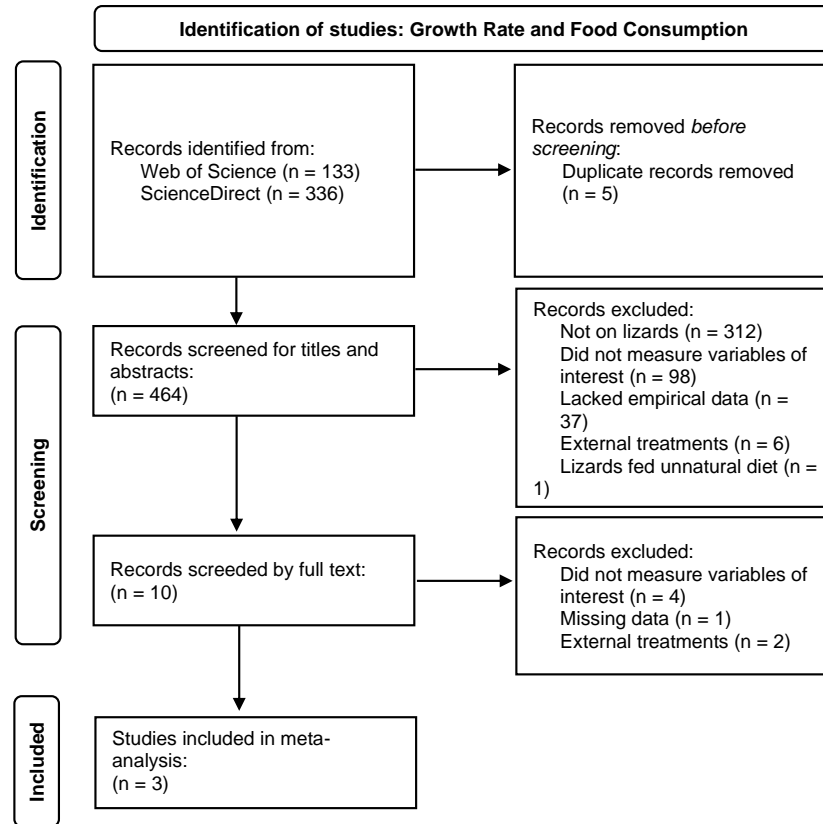
**Figure 2.** Papers were identified and screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach to assess the effect of duration of daily activity on growth rate.



**Figure 3.** Papers were identified and screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach to assess the effect of body temperature on food consumption.

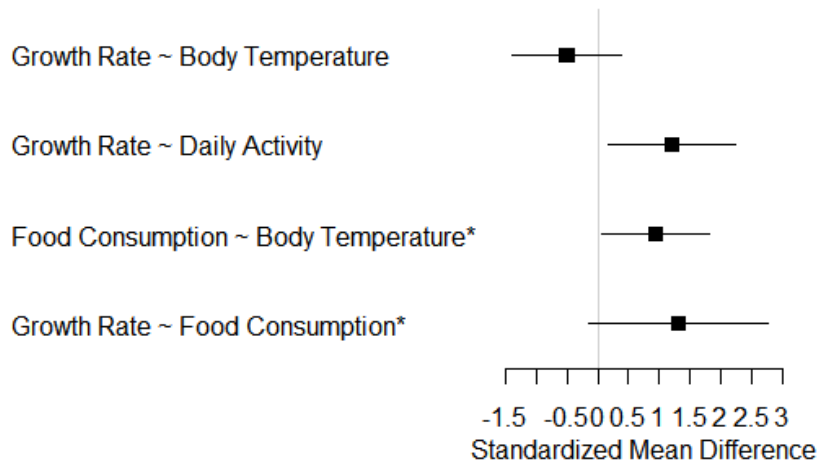


**Figure 4.** Papers were identified and screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach to assess the effect of duration of daily activity on food consumption.

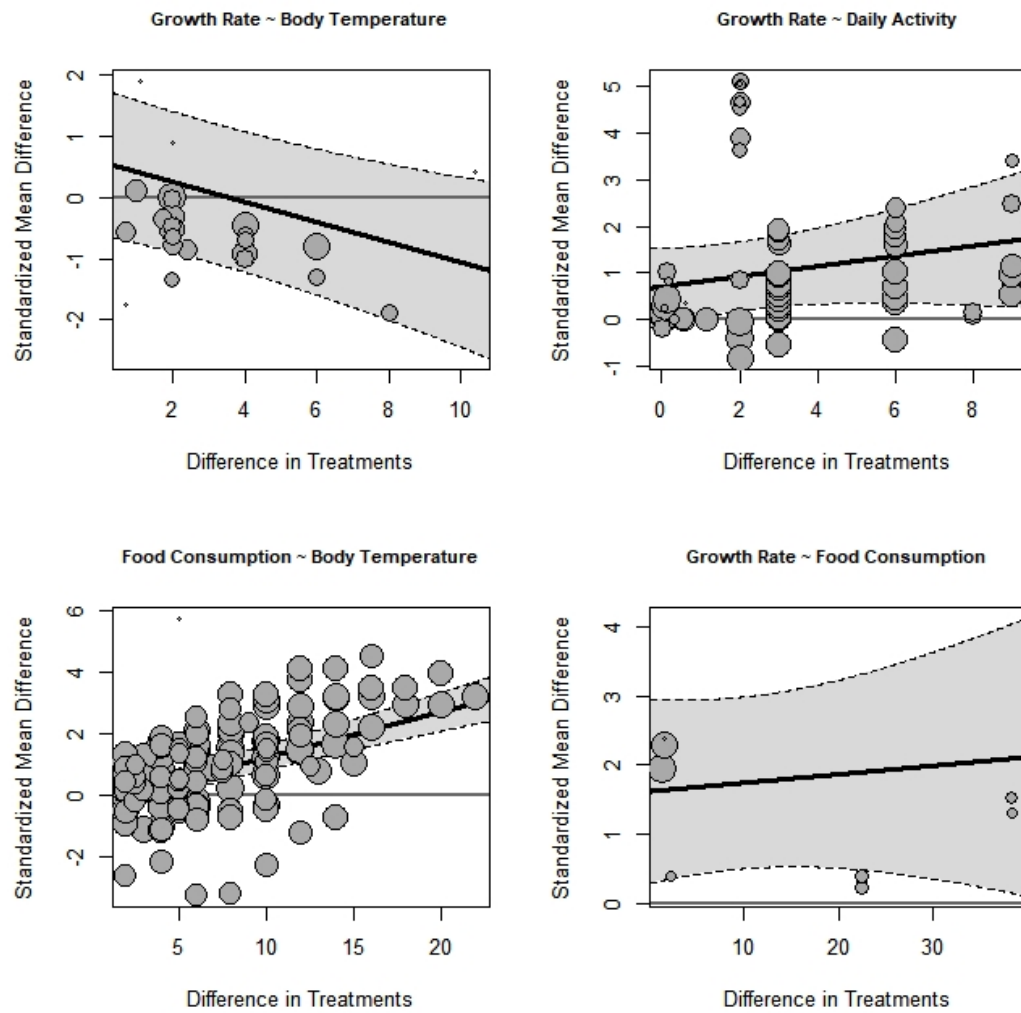


**Figure 5.** Papers were identified and screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach to assess the effect of food consumption on growth rate.

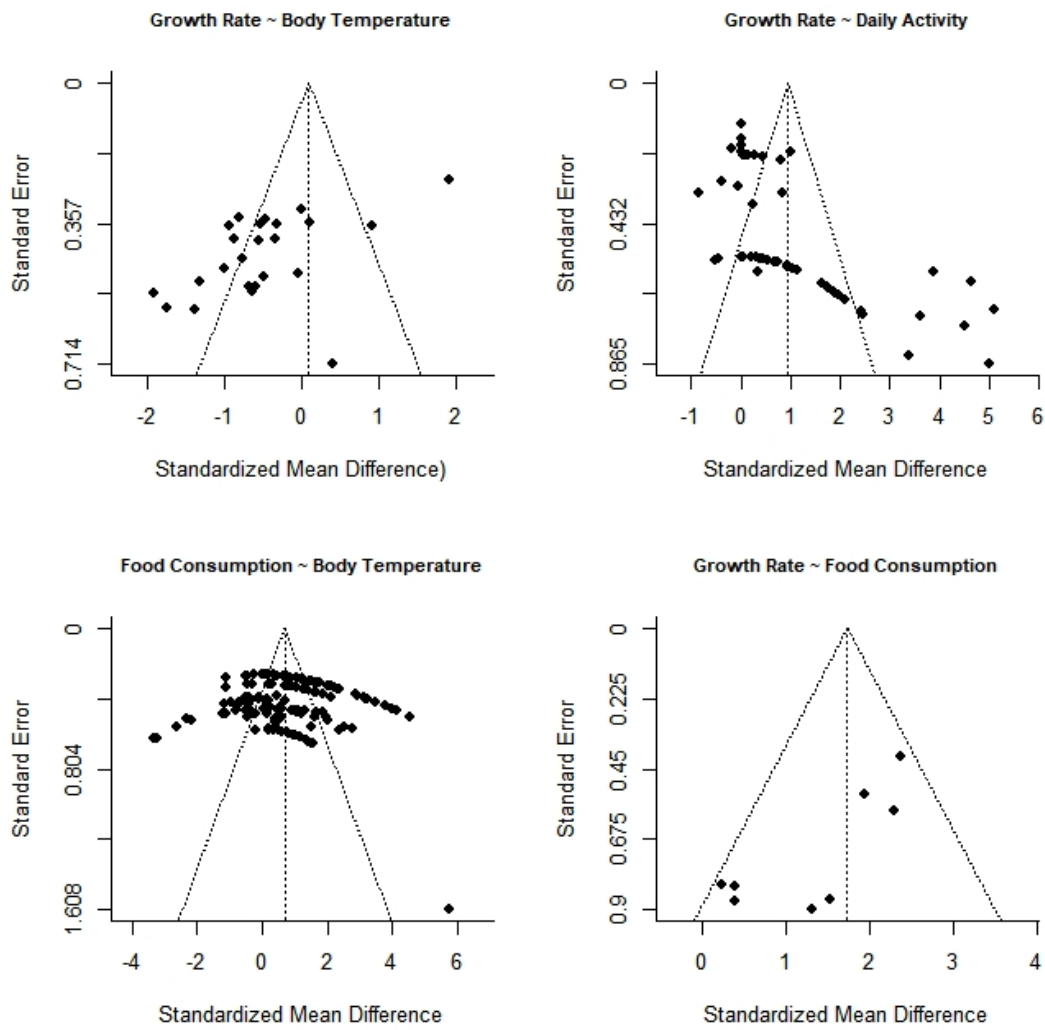
### Study



**Figure 6.** The results of the meta-analysis indicate that growth rate decreases with warming body temperatures while increasing with greater durations of daily activity and food consumption, and food consumption increased with warming body temperatures, in lizards. Standardized mean differences are represented on the y-axis, where negative values indicate a decrease in the dependent variable as the independent variable increases, and asterisks indicate significance.



**Figure 7.** Effect sizes increased as with greater differences in treatment level for analyses, except the influence of duration of daily activity on lizard growth rate.



**Figure 8.** Funnel plots for all meta-analyses lack symmetry, indicating presence of publication bias.



# **A geographic and taxonomic comparison of the thermal sensitivity of digestion in a model organism**

## **2.1 Abstract**

Individual variation in energetics, environment, and genetics can influence population-level processes. However, it is often assumed that locally measured thermal and bioenergetic responses apply among broadly related species, and throughout the intraspecific geographic range. Even closely related taxa may differ in thermal sensitivity of multiple functions, which may in turn influence population persistence, population vital rates, and the ability to respond to environmental changes. The objectives of this project were to quantify the thermal sensitivity of digestive physiology in an ectothermic species, and make comparisons among closely related, but geographically distinct, groups. *Sceloporus* lizards were used as a model organism, as they are known to exhibit thermally dependent physiologies and are geographically widespread. Digestive passage time, food consumption, fecal and urate production, metabolizable energy intake (MEI), and assimilated energy (AE) were compared for *Sceloporus consobrinus* in Arkansas and *S. undulatus* in South Carolina and New Jersey. Published data were acquired for NJ and SC lizards, while original data were collected for *S. consobrinus*. Comparisons of digestion among populations were made at 30°C, 33°C, or 36°C. Results suggest that digestive physiology differs among populations, with *S. consobrinus* being more efficient at warmer temperatures. In contrast, NJ and SC lizards had quicker passage times and lower fecal and urate production at 30°C in comparison to those in AR. The results of the current study exemplify how closely related organisms can differ in thermal sensitivity of performance. Such data are important for understanding how individual-level processes can vary in response to climate, with implications for improving future modeling approaches.

## 2.2 Introduction

Predictive models are a useful tool for understanding how and why biological systems change over time. Threats of climate change and habitat alterations are continuing to increase. Consequently, mechanistic models identifying causes of organismal change due to climate and habitat are increasingly important for conservation, management, and theory. Empirical studies often find that populations vary in response to environmental attributes (e.g. Niewiarowski et al. 1993; Qualls and Shine 1998; Kutcherov and Lopatina 2023). However, many modeling approaches and climate studies make the underlying assumption that related organisms respond similarly to climate (Sinervo et al. 2010; Buckley et al. 2010). Such assumptions can be problematic when untested because they may result in inaccurate predictions due to unjustified extrapolations of data.

Variation across geographic ranges in organism phenotype, even within a species, has been widely documented (Beaupre et al. 1993b; Porlier et al. 2012; Stelkens et al. 2012; Bonamour et al. 2019). Genetic differentiation across a species' range can influence phenotype, behavior, physiology, and morphology, among other things (Pauls et al. 2013). Differences in thermal tolerance among populations have even been linked to genetic differentiation within a species (Sørensen et al. 2001). Local adaptation and acclimatization are also important factors influencing population-level responses to climate and may become more pronounced in the future (Yannic et al. 2014; Fitzpatrick and Keller 2015). Differences in acclimatization and adaptive phenotypic plasticity may be even more drastic among populations in widespread species where environmental conditions vary greatly across a range (Jensen et al. 2018). Additionally, local environments pose unique challenges and trade-offs, producing different phenotypes and behaviors among populations.

Trade-offs influencing energy acquisition and allocation can influence individual life-history and fitness (Congdon et al. 1982; Dunham et al. 1989; Jordan and Snell 2002). Energetic trade-offs have the potential to vary across time and space, depending on community structure and environmental attributes (Turingan et al. 1995). For example, biotic interactions, such as predator-prey dynamics and competition, vary geographically and can alter activity times, behavior, foraging, and energy budgets (Dunham et al. 1989; Rydell et al. 1996; Terraube and Arroyo 2011; Vilella et al. 2020). In ectotherms, temperature plays a critical role in mediating physiological processes and the resulting life-history phenotype. Thermal performance curves (TPC) are often used to determine and predict how organisms' function at various temperatures (Huey and Slatkin 1976). Performance curves are curvilinear by nature, but the exact shape and magnitude can vary depending on the process of interest and individual being assessed (Angilletta 2006; Latimer et al. 2011). Energy available for allocation to survival, growth, maintenance, and reproduction is often linked to temperature in ectotherms (Congdon et al. 1982, Porter and Tracy 1983; Brewster et al. 2021). Therefore, if populations vary in thermal sensitivity of processes influencing energy budgets, such as food consumption and digestion, subsequent life history, persistence, and population-level dynamics could differ.

As temperature has been shown to influence bioenergetics differently among populations of ectotherms (Beaupre et al. 1993ab; Angilletta 2001; Niu et al. 2003), it is likely that subsequent reproductive output and survival also vary among populations due to temperature (Brewster et al. 2021). However, many studies modeling the influence of temperature, or other climatic attributes, on organisms focus on broad taxonomic levels, such as entire species or genera (e.g. Buckley et al. 2008; Kearney et al. 2010; Berriozabal-Islas et al. 2017). In such instances, data are combined or extrapolated from select populations or species to make one

comprehensive model. Many studies also fail to include bioenergetic mechanisms, because population-specific data are usually lacking and difficult to collect. However, population-specific bioenergetic data may prove informative for understanding the influence of climate on organisms, and enhance predictability.

Lizards have been considered a model organism in thermal biology for decades (e.g. Porter and Gates 1969, Tinkle and Ballinger 1972, Huey 1982, Grant and Dunham 1990). One particular group of interest is the genus *Sceloporus* (fence lizards) due to their broad distribution, thermal sensitivity, and variable life history (e.g. Newman and Patterson 1909; Crenshaw 1955; Telemeco et al. 2014). Multiple climate change models exist predicting *Sceloporus* lizard distribution and extinction, extrapolating data from select species and populations (e.g. Buckley 2008, Sinervo et al. 2010, Levy et al. 2015). However, life history and bioenergetic responses to temperature are known to differ among *Sceloporus* lizards, even within a relatively close geographic range (e.g. Tinkle and Ballinger 1972; Beaupre et al. 1993b; Angilletta 2001). Two populations with differing digestive responses to temperature are *S. undulatus* residing in South Carolina and *S. undulatus* residing in New Jersey (Angilletta 2001). South Carolina and New Jersey fence lizards are closely related but differ in life history phenotype and geographic location. South Carolina lizards mature quickly, have high reproductive rates, relatively small sizes at maturity, and high mortality (Tinkle and Ballinger 1972). In comparison, New Jersey fence lizards have delayed maturation, low reproductive rates, relatively large size at maturity, and low mortality (Haenel and John-Alder 2002). Much information on *Sceloporus* lizards originates from NJ and SC, along with a few other populations. However, one additional population of *Sceloporus* lizards of interest, and comparatively understudied, are prairie lizards (*S. consobrinus*). Prairie lizards are unique with regards to life history strategy in that they

mature relatively quickly in relation to their active season length (Adolph and Porter 1996) and have moderate reproductive output and survival (Tinkle and Ballinger 1972, Mosbey 2021). Additionally, *S. consobrinus* were historically diagnosed as being a subspecies of *S. undulatus* (Leaché et al. 2016). Currently, *S. consobrinus* are still closely related to, although distinct, from *S. undulatus*. Therefore, it is possible that variation in bioenergetics and temperature sensitivity influence the unique life history of *S. consobrinus*. However, bioenergetic data has yet to be collected for *S. consobrinus*.

The variation in life history and geographic location among the three aforementioned *Sceloporus* lizard populations make them an ideal study system for examining thermal sensitivity of energy budgets in closely related organisms. Determining differences among the populations may be important for understanding the effect of environment on energy budgets, with implications for climate change modeling. Additionally, if the populations appear to be physiologically similar in response to temperature, then it would provide support for models considering multiple populations of *Sceloporus* lizards. Alternatively, if the species appear to differ, it will clarify crucial differences previously ignored in models constructed on the genus *Sceloporus*.

The current study aims to quantify the influence of temperature on digestive physiology in *S. consobrinus* and make direct comparisons between species of *Sceloporus* lizards and among three populations. Specifically, fence lizards (*S. undulatus*) from New Jersey and South Carolina will be compared to prairie lizards (*S. consobrinus*) in Arkansas. Available data from Angilletta (2001b) on thermal sensitivity of bioenergetics for NJ and SC were acquired, whereas new data were collected for AR lizards. Digestive variables selected for comparison in response to temperature change were food consumption rate, digestive passage time, fecal and urate

production, metabolizable energy intake (MEI), and assimilated energy (AE). Comparisons were made among three temperature treatments (30°C, 33°C, and 36°C). Data were collected on *S. consobrinus* using feeding trials in the lab, where marked food items were tracked to estimate passage time, and food consumption and excrement were quantified. Analyses were conducted to compare digestive processes among temperatures for *S. consobrinus*, and to compare digestive process among populations within each temperature. *Sceloporus consobrinus* in AR have been selected for comparison to fence lizards because they represent an understudied group with a unique life history. I hypothesize that *S. consobrinus* will differ in thermal sensitivity of digestion, based on the differing life history strategy of rapid maturation within short active seasons, which could be a product of differing energy budgets.

## **2.3 Methods**

### *2.3.1 Study Animals*

Surveys were conducted in spring and summer of 2020 and 2021 in northwest Arkansas for adult *S. consobrinus*, by searching viable habitat. Forty-seven adult lizards (29 females and 18 males) were captured by hand or loop (consisting of a fishing pole with a loop on the end) and marked using numeric codes by clipping toes (Gifford et al. 2017). For each lizard, data collection included snout-vent length (SVL) using a clear ruler, mass using a Pesola spring scale, sex via presence (males) or absence (females) of post-anal scales, and body temperature using a fine wire thermocouple in the cloaca within the first two minutes of observing the lizard. Body temperature data were used to confirm if lab treatments (selected to mimic methods of Angilletta (2001b) represent typical temperatures experienced by lizards in nature. Males and females were as evenly distributed among treatments as possible to randomize any effect of sex. When brought to the lab, lizards were maintained in 10-gallon tanks with a natural sand substrate, heat lamps, a

hide box, and were misted with water three times a week. Lizards were fed crickets three times a week, supplemented with vitamin D every two weeks, and provided water ad-libitum.

### *2.3.2 Influence of Temperature on Digestion in *Sceloporus consobrinus**

To make direct comparisons of *S. consobrinus* in Arkansas and *S. undulatus* in South Carolina and New Jersey, methods were replicated from Angilletta (2001b) where digestive parameters were measured for *S. undulatus* from NJ and SC. Following Angilletta (2001b), the influence of temperature on food consumption, passage time, fecal production, urate production, MEI, and AE was quantified by exposing lizards to one of three temperature treatments; 30°C (n = 14), 33°C (n = 12), and 36°C (n = 11). Temperatures were maintained using an environmental chamber ( $\pm 0.5^\circ\text{C}$ ). During trials, lizards were maintained in plastic tanks (41.9 cm x 33 cm x 16.8 cm) lined with butcher paper, with a hide box, and provided water ad-libitum.

#### Feeding Trials

Feeding trials were conducted using Fluker's (Port Allen, LA) 2- and 3-week-old crickets (*Acheta domestica*) and began after all lizards had been acclimatized for a minimum of five days, had processed at least one meal, followed by a 3-day fasting period to clear the gut. At the onset of feeding trials, a single cricket was injected in the thoracic cavity with ~0.02 mL of a slurry containing water mixed with an ingestible, UV-fluorescent powder, which associated with the feces (Beaupre et al. 1993b). The UV-fluorescent powder does not influence edibility of crickets, and therefore the feeding trials could commence without force-feeding. The marked cricket was fed to lizards and the time of consumption was recorded. Lizard tanks were then monitored every 2 – 4 h for feces with the marker to estimate digestive passage time (Beaupre et al. 1993b). After the first mark was expelled, ~10 days were allotted to adequately quantify consumption and collect feces and urates. Next, a second mark was fed, and tanks were monitored again, to get a

second estimate of passage time. In between markers lizards were fed crickets weighed to the nearest 0.1 mg ad libitum every day. All feces and urates produced, beginning at the first appearance of the first marked cricket to the first appearance of the second marked cricket, were collected, separated, frozen, and freeze dried. Trials ended after the appearance of the second marked cricket in feces.

### *2.3.3 Statistical Analyses*

Analysis of Covariance was used to test differences in digestive physiology among temperatures and populations. Several variables (Trial Length, Lizard Mass, Consumption) were assessed as covariates for various subsequent analyses. Trial length did not influence any parameter at any temperature, nor was there an interaction between trial length and temperature for any analysis. For all ANCOVAs, post-hoc assessments were made to determine differences among treatments by plotting adjusted means with 95% confidence intervals (Day and Quinn 1989). Meaningful differences were deduced when a treatment mean was outside of the bounds of other treatments' confidence intervals. Residuals of analyses were tested for assumptions of parametric statistics. A type I error rate of 0.05 was adopted for all statistical procedures. All analyses were run in R (version 4.1.3, R Core Team 2022). Adjusted means were calculated using the package 'emmeans' (Length 2023).

### *2.3.4 Sceloporus consobrinus Data Analysis*

#### Food Consumption

To quantify food consumption (kJ), wet and dry masses (after being freeze-dried) were taken for ten crickets per trial and a conversion factor was determined. Using the relationship between wet and dry cricket mass, dry mass consumed by each lizard was determined. To determine the energy density of crickets, 30 freeze-dried crickets (10 per temperature treatment)



were homogenized and analyzed in triplicate using bomb calorimetry (Parr Semimicro Bomb Calorimeter). The three cricket energy densities were averaged and used to convert dry mass consumed into energy consumed (kJ). An ANCOVA was used to assess the effect of temperature on food consumption with lizard mass and trial length included as covariates along with interaction terms (mass\*temperature and trial length\*temperature) to test for heterogeneity of slopes.

#### Digestive Passage Time

Digestive passage time was calculated as the time from consumption of the marked cricket to the first appearance of the mark in feces. An ANCOVA was used to assess the effect of temperature on digestive passage time with trial length included as a covariate along with an interaction term (trial length\*temperature) to test for heterogeneity of slopes.

#### Fecal Production

To determine fecal production, samples from each individual lizard were homogenized and analyzed via bomb calorimetry. Energy densities were averaged among lizards within each treatment and used to determine fecal production. An ANCOVA was used to assess the effect of temperature on fecal production with trial length and food consumption included as covariates along with interaction terms (trial length\*temperature and food consumption\*temperature) to test for heterogeneity of slopes.

#### Urate Production

Uric acid samples from each individual lizard were freeze dried, homogenized and analyzed via bomb calorimetry. Energy densities were averaged for each treatment to determine urate production. An ANCOVA was used to assess the effect of temperature on urate production

with trial length and food consumption included as covariates along with interaction terms (trial length\*temperature and food consumption\*temperature) to test for heterogeneity of slopes.

#### Metabolizable Energy Intake

Metabolizable energy intake is a measure of the maximum potential energy to be allocated to growth, maintenance, storage, and reproduction, and was calculated using the formula:

$$MEI = C - F - U$$

where C is energy consumed (kJ), F is fecal production (kJ), and U is urate production (kJ). An ANCOVA was used to assess the effect of temperature on MEI with trial length and food consumption included as covariates along with interaction terms (trial length\*temperature and food consumption\*temperature) to test for heterogeneity of slopes.

#### Assimilated Energy

Assimilated energy represents digestible energy and was calculated using the formula:

$$AE = C - F$$

An ANCOVA was used to assess the effect of temperature on AE with trial length and food consumption included as covariates along with interaction terms (trial length\*temperature and food consumption\*temperature) to test for heterogeneity of slopes.

#### *2.3.5 Population Comparison Data Analysis*

To make direct comparisons among AR, NJ, and SC, the original dataset from Angilletta (2001b) was acquired. All methods for data collection in the current study were comparable to those used by Angilletta (2001). In brief, Angilletta (2001) conducting feeding trials using *S. undulatus* from SC and NJ over a range of stable temperatures, including 30°C (SC: n = 8, NJ: n = 3), 33°C (SC: n = 9, NJ: n = 15), and 36°C (SC: n = 5, NJ: n = 8). Digestive passage time was

also quantified using a marked cricket, and kilojoules consumed and excreted as urates and feces was determined via bomb calorimetry. Metabolizable energy intake and AE were calculated using the aforementioned formulas. Analyses of covariance with food consumption and lizard mass as covariates were run to determine the influence of temperature on digestion.

#### Food Consumption

A separate ANCOVA was performed for each temperature to compare food consumption among populations. Lizard mass and trial length were covariates, and interaction terms (mass\*population and trial length\*population) were used to test for slope heterogeneity.

#### Digestive Passage Time

A separate ANCOVA was performed for each temperature to compare digestive passage time among populations. Trial length was included as a covariate and the interaction term (trial length\*population) tested for heterogeneity of slopes.

#### Fecal Production

A separate ANCOVA was performed for each temperature to compare fecal production among populations. Trial length and food consumption were included as covariates and the interaction terms (trial length\*population and food consumption\*population) were used to test for heterogeneity of slopes.

#### Urate Production

A separate ANCOVA was performed for each temperature to compare fecal production among populations. Trial length and food consumption were included as covariates and the interaction terms (trial length\*population and food consumption\*population) were used to test for heterogeneity of slopes.

#### Metabolizable Energy Intake

A separate ANCOVA was performed for each temperature to compare MEI among populations. Trial length and food consumption were included as covariates and the interaction terms (trial length\*population and food consumption\*population) were used to test for heterogeneity of slopes.

#### Assimilated Energy

A separate ANCOVA was performed for each temperature to compare food consumption among populations. Trial length and food consumption included as covariates and the interaction terms (trial length\*population and food consumption\*population) were used to test for heterogeneity of slopes.

## **2.4 Results**

### *2.4.1 Influence of Temperature on Digestion in Sceloporus consobrinus*

The test of residuals differed slightly from normality in some instances, however all data followed a hump-shaped distribution and were deemed suitable for the robust procedures of ANCOVA (Blair 1981). Body temperatures of *S. consobrinus* from field sites in northwest Arkansas ranged from 22.9 – 36.7°C, with an average body temperature of 32.5°C (Table 1), supporting the relevance of temperature treatments.

#### Food Consumption

The energy density of crickets was  $20.5 \pm 1.4$  kJ/gram dry mass. Food consumption significantly differed among all temperatures, with a positive relationship between food consumption and temperature (ANCOVA  $p < 0.001$ ,  $F = 31.044$ , Figure 1A). Lizard mass (covariate) had no effect on food consumption and there was no interaction of mass and temperature on food consumption.

#### Digestive Passage Time

Passage time significantly decreased with warming temperatures (ANCOVA  $p < 0.001$ ,  $F = 18.41$ , Figure 1B), but did not significantly differ between 30°C and 33°C.

#### Fecal Production

Fecal production significantly differed among temperatures (ANCOVA  $p = 0.0254$ ,  $F = 4.146$ , Figure 1C), with all temperatures differing. Fecal production significantly increased with food consumption (covariate,  $p < 0.001$ ,  $F = 35.556$ , Figure 2) with no interaction between temperature and food consumption.

#### Urate Production

Urate production had a significant interaction between temperature and food consumption (ANCOVA  $p < 0.001$ ,  $F = 5.098$ , Figure 3). The interaction was a result of greater urate production in response to food consumption at 30°C in comparison to 33°C and 36°C. Therefore, 30°C was removed from the analysis. The ANCOVA indicated that urate production did not differ between 33°C and 36°C, but significantly increased with food consumption (covariate,  $p < 0.001$ ,  $F = 27.689$ , Figure 3), with no interaction between food consumption and temperature.

#### Metabolizable Energy Intake

There was a significant interaction between temperature and food consumption on MEI (ANCOVA  $p = 0.0159$ ,  $F = 4.747$ , Figure 4), preventing comparisons among all temperatures. The interaction was due to MEI increasing quicker with food consumption at 33°C and 36°C in comparison to 30°C, which resulted in the lowest MEI at 30°C. Therefore, 30°C was removed from the analysis and 33°C and 36°C were compared. Metabolizable energy intake was significantly higher at 36°C compared to 33°C (ANCOVA  $p < 0.001$ ,  $F = 2,068.701$ , Figure 1E), and MEI significantly increased with food consumption (covariate,  $p < 0.001$ ,  $F = 1,505.273$ ,

Figure 4). There was no interaction between food consumption and temperature treatment between the 33°C and 36°C trials on MEI.

#### Assimilated energy

Assimilated energy significantly increased with warming temperatures (ANCOVA  $p < 0.001$ ,  $F = 9,551.954$ , Figure 1F), with all temperatures significantly different. Assimilated energy also significantly increased with food consumption (covariate,  $p < 0.001$ ,  $F = 9,080.281$ , Figure 5), with no significant interaction between consumption and temperature.

#### *2.4.2 Population Comparison*

Again, the test of residuals differed slightly from normality in some instances, however all data followed a hump-shaped distribution and were deemed suitable for the robust procedures of ANCOVA.

#### Food Consumption

Food consumption did not vary among populations at 30°C, and there was no influence of mass or interaction between population and mass. At 33°C (ANCOVA  $p = 0.0115$ ,  $F = 5.537$ , Figure 6A) lizards from Arkansas consumed significantly less food than New Jersey and South Carolina lizards, with no effect of mass (covariate) and no interaction between mass and population. At 36°C, there was a significant interaction between lizard mass and population (ANCOVA  $p = 0.003$ ,  $F = 7.812$ , Figure 7). The heterogeneity of slopes was a result of relatively little change in food consumption in relation to lizard mass for AR lizards, which contributed to overall greater food consumption for AR. In contrast, NJ and SC had a positive relationship between food consumption and mass contributing to overall lower consumption rates. Therefore, the comparison of voluntary food consumption of NJ and SC to AR lizards was problematic, but

should not interfere with comparisons of other variables, especially those that use consumption in their calculation (AE, MEI).

#### Digestive Passage Time

Passage time estimates did not significantly differ among populations at any temperature (Figure 6B). There was an influence of mass on passage time at 36°C (mass\*temperature interaction:  $p = 0.0279$ ,  $F = 5.777$ , Figure 8), where large lizards tended to pass food slower for both the NJ and SC populations. There was no interaction between mass and population at any temperature.

#### Fecal Production

Fecal production did not differ among populations at 30°C, and there was no influence of food consumption or interaction between food consumption and population. At 33°C, all populations differed in fecal production (ANCOVA  $p < 0.001$ ,  $F = 17.345$ , Figure 6C), with Arkansas lizards excreting the least, followed by South Carolina and then New Jersey. Additionally, food consumption had a positive, significant, influence on fecal production (covariate,  $p < 0.001$ ,  $F = 26.321$ ), with no interaction between population and food consumption. At 36°C, Arkansas lizards produced significantly less feces than South Carolina and New Jersey (ANCOVA  $p < 0.001$ ,  $F = 11.769$ , Figure 6C). Food consumption had a positive, significant, influence on energy excreted as feces at 36°C (covariate,  $p < 0.001$ ,  $F = 56.139$ ), and there was no interaction of consumption and population.

#### Urate Production

Urate production significantly differed among populations at 30°C (ANCOVA  $p < 0.001$ ,  $F = 12.614$ , Figure 6D) and 33°C (ANCOVA  $p < 0.001$ ,  $F = 20.538$ , Figure 6D), but not at 36°C. Food consumption influenced urate production at all temperatures (covariate, 30°C:  $p < 0.001$ ,  $F =$

= 88.926, 33°C:  $p < 0.001$ ,  $F = 67.013$ , 36°C:  $p < 0.001$ ,  $F = 52.163$ ), with no interaction between population and food consumption. At 30°C Arkansas had significantly greater urate production than South Carolina. At 33°C, AR lizards had significantly lower urate production than NJ, with SC not differing from AR or NJ.

#### Metabolizable Energy Intake

Metabolizable energy intake significantly differed among populations at 30°C (ANCOVA: 30°C:  $p < 0.001$ ,  $F = 90.812$ , Figure 6E) and 33°C (ANCOVA  $p < 0.001$ ,  $F = 264.034$ , Figure 6E), being higher at 33°C than 30°C for all populations. At 30°C, there were no clear differences in confidence intervals among populations. At 33°C, Arkansas lizards had significantly higher MEI than South Carolina and New Jersey. Metabolizable energy increased with food consumption at 30°C (covariate,  $p < 0.001$ ,  $F = 1,172.267$ ) and 33°C (covariate,  $p < 0.001$ ,  $F = 1,776.879$ ) and had no interaction between population and food consumption at either temperature. At 36°C, there was an interaction between food consumed and population (ANCOVA  $p = 0.0232$ ,  $F = 4.732$ , Figure 9). The heterogeneous slopes were due to Arkansas lizards increasing MEI more rapidly with food consumption, which contributed to an overall higher MEI in AR, than NJ and SC at 36°C. Therefore, direct comparisons of AR to SC and NJ could not be made for MEI at 36°C.

#### Assimilated Energy

Assimilated energy was significantly different among populations at 30°C (ANCOVA  $p < 0.0001$ ,  $F = 281.330$ , Figure 6F) and 33°C (ANCOVA  $p < 0.001$ ,  $F = 803.350$ , Figure 6F). Assimilated energy significantly increased with food consumption for all populations at 30°C (covariate,  $p < 0.001$ ,  $F = 4,133.7$ , Figure 8) and 33°C (covariate,  $p < 0.001$ ,  $F = 5,205.604$ , Figure 6), with no interaction between food consumption and population at either temperature.



At 30°C, there were no defined differences in confidence intervals among populations in AE, similar to MEI. At 33°C, AE was significantly higher in Arkansas and South Carolina lizards compared to New Jersey. At 36°C, there was a significant interaction between population and food consumed on AE (ANCOVA  $p = 0.02$ ,  $F = 4.971$ , Figure 10). Again, AR lizards increased AE more rapidly with food consumption contributing to an overall higher AE at 36°C in comparison to NJ and SC.

## 2.5 Discussion

Closely related organisms can differ in response to environmental conditions. The current study found significant variation in digestive physiology due to temperature among two species spanning three populations of closely related lizards. Importantly, rates of food consumption were maximized at different temperatures and species differed in efficiency and values (kJ) of MEI, AE, fecal production, and urate production among temperatures. Additionally, the relationship of food consumption with MEI and AE differed between species at the warmest temperature considered. Digestive physiology and resulting energy budgets are important considerations for understanding life history, persistence, and fitness (Grant and Dunham 1990; Brewster et al. 2021). Therefore, the results of the current study provide evidence for possible temperature-dependent mechanisms underpinning variability among populations in response to climate. Additionally, findings indicated that various functions associated with food acquisition and digestion respond differently, and nonlinearly, with respect to temperature.

Populations varied in response to temperature increases. Initially, all populations increased food consumption, MEI, and AE, while decreasing passage time, with warming temperatures when comparing 30°C to 33°C. At 33°C, *S. undulatus* reached their highest rates of food consumption. At the warmest temperature, 36°C, South Carolina lizards declined in rates of

food consumption and NJ lizards plateaued. In contrast, *S. consobrinus* (AR) continued to increase food consumption at 36°C, resulting in the highest rates of food consumption observed. Additionally, *S. consobrinus* had the highest MEI and AE, and quickest passage time, observed among all treatments and populations at 36°C. The difference between species at 36°C suggests that *S. consobrinus* are more efficient in multiple processes at warm temperatures. Greater efficiency at warm temperatures for *S. consobrinus* was also exhibited by the higher rate of increase in MEI and AE with consumption at 36°C, in comparison to *S. undulatus*.

With regards to excretion, urate and fecal production in *S. undulatus* consistently increased with temperature. In comparison, *S. consobrinus* decreased fecal production as temperature increased, with the lowest fecal production at 36°C. Urate production in *S. consobrinus* also did not significantly differ between 33°C and 36°C. Therefore, the greatest variation among species in excretion occurred at warmer temperatures due to the efficiency of *S. consobrinus*. Arkansas lizards were able to maintain relatively stable rates of consumption irrespective of body size at 36°C when compared to SC and NJ, which also contributes to greater efficiency on average.

Metabolizable and assimilated energy can be representative of individual energy budgets, which in-part dictate fitness. Lower energy budgets can result in subsequently lower growth rates, smaller body size, reduced reproduction, or even death if maintenance costs are unmet (Brewster et al. 2021). Both MEI and AE are influenced by energy consumed through food and excreted as waste. For all three lizard populations assessed, the driving factor determining energy budgets was food consumption. Urate production is associated with catabolism during metabolic processes (Beaupre et al. 1993b). Therefore, urates could be associated with metabolic rate in relation to temperature. For *S. undulatus* and *S. consobrinus*, metabolic rate tends to plateau as

temperatures warm (Hughes et al. 1982; Angilletta 2001b). A plateau at warm temperatures is relatively comparable to the trend of urate production identified in *S. undulatus* (the rate of increase appears to become more gradual as temperatures warm), but not *S. consobrinus*. Therefore, *S. consobrinus* were able to maintain low levels of urate excretion even at warm temperatures despite a higher food consumption and stable metabolic rate. Low urate production and high food consumption both contributed to the overall higher MEI at 36°C of *S. consobrinus*.

In comparison to the populations studied here, digestive processes quantified in *S. merriami* differ in that processes measured were least efficient at 34°C, when compared to 31°C and 36°C (Beaupre et al. 1993b; Beaupre and Dunham 1995). However, *S. merriami* does experience a metabolic plateau at warm temperatures (Beaupre et al. 1993a). *Sceloporus occidentalis* exhibit a similar response in digestion to temperature when comparing unadjusted means as the SC population of *S. undulatus* (see Angilletta 2001b for unadjusted mean comparisons), with a peak near 33°C, followed by a decline (Hardwood 1979). Sprint speed and endurance in *Sceloporus* also plateau, similar to metabolism, at warm temperatures (Crowley 1985; Angilletta et al. 2002). Metabolic plateaus near and within the range of active body temperatures have been observed to some extent in other lizard species, such as legless lizards (*Anniella pulchra*; Fusari 1984), Agamids (*Ctenophorus nuchalis*; Frappell and Daniels 1991), and collared lizards (*Crotaphytus collaris*; Dawson and Templeton 1963). While traits other than digestion in *Sceloporus* tend to have varying levels of thermal sensitivity, digestive processes are often most sensitive (Angilletta 2006). Theories as to why various physiological processes have different thermal performance curves have been proposed historically (Huey 1982). One hypothesis for varying thermal performance is that energetic demands increase with higher metabolic rate and quicker sprint speed. In contrast, increasing digestive performance could offer

a great benefit, especially if metabolic demand does not proportionally increase. However, more data on metabolism and energetics on a wider range of taxa are needed to investigate this proposed hypothesis.

Thermal sensitivity of digestion can influence seasonal energy budgets, with subsequent repercussions for energy available for growth, reproduction, storage, and maintenance (Congdon et al. 1982; Grant and Porter 1992). Life history theory predicts that growth rate and body size have important consequences (Sears and Angilletta 2004). All three populations of *Sceloporus* lizards studied here maintain body temperatures  $\sim 33^{\circ}\text{C}$  in the field (Angilletta 2001; Bangs 2016; Table 1). Angilletta (2001b) predicted that daily and seasonal activity times were longer for SC lizards than NJ lizards. Activity predictions for *S. consobrinus* in Nebraska and Oklahoma (formerly *S. undulatus*) are  $\sim 2000$  hours per year, which is likely comparable to AR lizards (where data are unavailable), as seasonal cues may be similar. Seasonal activity for NE and OK prairie lizards falls in between those predicted for SC (2632 hrs) and NJ (1864 hrs) (Adolph and Porter 1996). Considering the maximum MEI (unadjusted for consumption) at  $33^{\circ}\text{C}$  and hours of activity (without subtracting energetic costs), seasonal energy budgets are predicted to be 508.9 kJ for SC, 264.1 kJ for NJ, and 141.7 kJ for AR. So, when adjusting for rates of food consumption, AR lizards are most efficient with the highest MEI at  $33^{\circ}\text{C}$  relative to the other populations. However, when considering the actual MEI measured, in conjunction with time available to acquire energy, AR lizards will have lower total energy budgets. The seasonal energy budgets calculated here attempt to follow the protocol described by Angilletta 2001b, however, I was unable to replicate the values reported in the manuscript.

The predicted differences in energy budgets could result in a variation in growth and reproductive rates, influencing population-level processes (Dunham et al. 1989). *Sceloporus*

lizards are ideal model organisms for thermal biology and life history because they are wide-ranging, thermally sensitive, and exhibit a variety of life history strategies (e.g. Adolph and Porter 1996). The SC population of *S. undulatus* are characterized by high growth rates, high reproductive output, relatively small body sizes, and quick maturation (Tinkle and Ballinger 1972). The NJ population of *S. undulatus* is characterized by slow growth rates, larger body size, delayed maturation, and relatively low reproductive output (Haenel and John-Alder 2002; Mosbey 2019). The AR population of *S. consobrinus* is characterized by high growth rates, moderate reproductive output, moderate body size, and quick maturation (Mosbey 2019). The NJ lizards tended to have lower rates of food consumption, MEI, and AE in response to warming temperatures compared to SC and AR. One possible explanation could be that NJ typically experiences cooler temperatures, and therefore lizards could be locally adapted to have lower sensitivity to warm temperatures. Ectotherms in cold environments also tend to invest in larger offspring to increase chances of survival (Angilletta et al. 2004). Body size has been documented to correlate with clutch and egg size in lizards (Abell 1999). Therefore, delaying maturation to reach larger body sizes in colder environments could increase fitness. New Jersey lizards may be least likely to experience hot temperatures of the populations considered, and potentially incur lower costs seasonally due to slower growth and lower metabolic demands, which may explain the identified patterns in thermal sensitivity. In contrast, SC lizards experience longer seasons and warmer temperatures (Adolph and Porter 1993; Angilletta 2001b) and are likely to reproduce more frequently within a season. Such factors could contribute to increased thermal sensitivity of bioenergetics as a mechanism to increase reproductive output seasonally and take advantage of a warmer environment. However, the current study did not examine evolutionary or genetic factors, which should be quantified to test the proposed hypotheses.

Adolph and Porter (1996) proposed a mechanism of short activity seasons resulting in delayed maturity and relatively “slow” life histories. Most populations of *Sceloporus* lizards follow the identified trend, except for *S. consobrinus* (represented as NE and KS populations of *S. undulatus* in Adolph in Porter 1993). In NE, *S. consobrinus* lizards were found to have relatively high growth rates compared to *S. undulatus* in NJ (Niewiarowski and Roosenburg 1993) and SC (Tinkle and Ballinger 1972). Therefore, despite the shorter active season and lower net energy budget of *S. consobrinus* compared to NJ and SC, it appears they may allocate a greater proportion of energy to growth. As a result, *S. consobrinus* reaches relatively large body sizes and matures by the second year of life (Ballinger et al. 1981; Adolph and Porter 1996; Mosbey 2019). As indicated by the current study, *S. consobrinus* are also more efficient at increasing consumption rates and metabolizable energy at relatively high temperatures. Therefore, efficient digestive physiology could also promote rapid energy acquisition when spending any time at warmer body temperatures throughout the day. This could allow *S. consobrinus* to increase energy budgets more effectively than other *Sceloporus* lizards.

The findings of the current study exemplify how closely related species, and populations within a species, can differ in thermal sensitivity. Many modeling approaches with regards to climate change consider broad taxonomic and geographic levels (e.g. Sinervo et al. 2010; Buckley et al. 2015). However, unaccounted for variation in physiological traits could result in inaccurate or inapplicable model predictions (Kearney 2013). As shown here, energy budgets are sensitive to temperature in ectotherms, and can differ among populations. Considering population-specific energy budgets may be important for understanding how life history varies in response to climate. Additionally, examining bioenergetics can identify potential mechanisms underlying organismal responses and observed phenomena. Many models, including

bioenergetic approaches, assume modeled organisms respond similarly to climate. However, one example of how this assumption can alter predictions is the model produced by Sinervo et al (2010) predicting that 20% of lizard species will be extinct within 70 years. When the model was reconstructed by Kearney (2013) to consider life history and bioenergetic variation, predictions drastically changed, finding that extinctions were unlikely among most modeled species. The findings here also indicate that thermal sensitivity of ectotherms is nonlinear, and therefore challenging to extrapolate. Not only do thermal performance curves among the populations differ in optimization for some processes, but the overall shape varies. *Sceloporus consobrinus* have increased efficiency in digestive physiology at warm temperatures comparably, and the relationship of physiological variables differed based on temperature and species. Therefore, a model focused on the genus *Sceloporus* may predict that lizards will decline or plateau in performance if extrapolating data from SC or NJ. However, it is possible that if climate change increases body temperatures AR lizards may benefit by increasing energy budgets and surviving at temperatures where performance is highly efficient. Although, an increase in performance could be constrained by other factors, including genetic constraints on body size limiting reproductive output. Additionally, other variables may be ill-suited for warmer temperatures, hindering performance.

In conclusion, closely related taxa can vary in unpredictable ways in response to climate. Future studies quantifying and predicting organismal response to temperature should consider relevant and fine scales to capture important variation. Such studies could enhance our ability to understand the consequences of climate change while advancing the paradigm of organismal variation in response to climate. Quick maturation, moderate body size, short seasonal activity, and moderate reproductive output are relatively uncommon life history traits to co-occur within a

population of *Sceloporus* lizards, based on the data available. As Adolph and Porter (1996) discuss, prairie lizards (*S. consobrinus*) represent an exception to the rule and a prime example of why generalized theories can be flawed. The results of the current study suggest a potential mechanism of increasing efficiency of consuming food and metabolizable energy irrespective of body size, paired with high allocation to growth rate early in life (Niewiarowski and Roosenburg 1993), yet a relatively short activity season for reproduction, producing the unique life history of *S. consobrinus*. Processes occurring at individual scales influence population-level dynamics (Dunham et al. 1989). Future studies examining species that are considered “special cases” (Dunham and Beaupre 1998) would improve our understanding of identified phenomena and potentially identify underlying mechanisms. While this study was not able to make population-level predictions, studies connecting individual-level processes with population dynamics are needed. Broad phenomena have been identified linking organismal responses to climate, yet more information on how finer scales vary and the resulting implications would greatly increase the body of knowledge while improving our ability to model populations.

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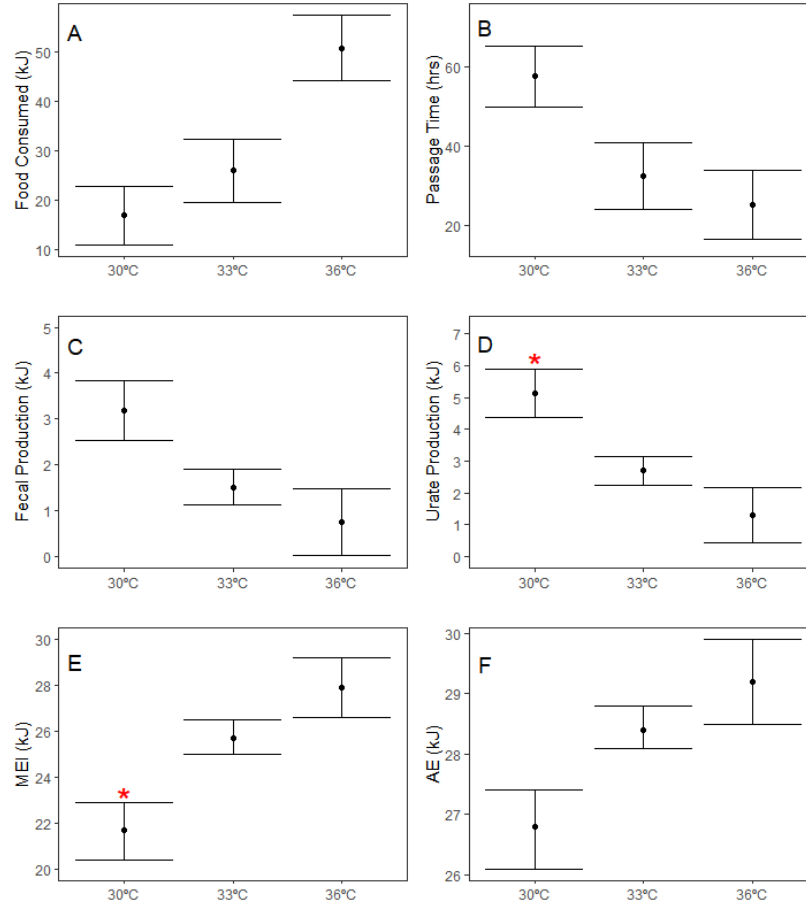
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## 2.8 Tables

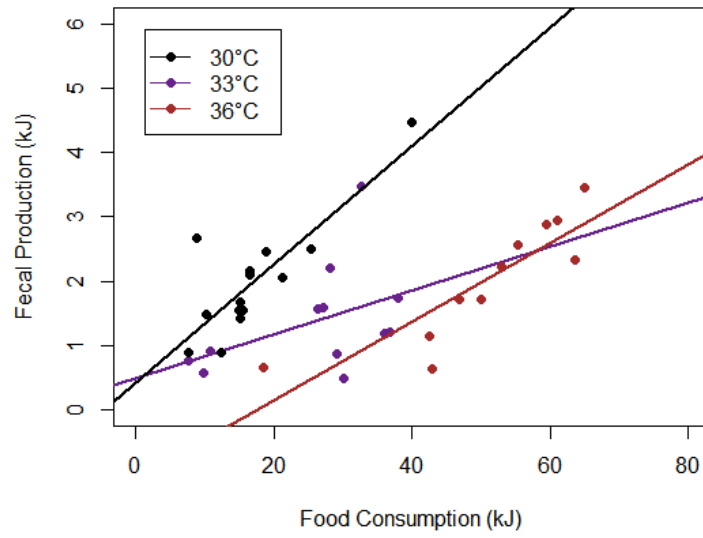
**Table 1.** Body temperature measurements of *Sceloporus consobrinus* in Arkansas were collected in 2020 and 2021 by inserting a thermocouple into the cloaca of active lizards. Body temperature measurements of *Sceloporus undulatus* in New Jersey and South Carolina are those reported by Angilletta (2001).

Species	Location	Average Body Temperature (°C)
<i>Sceloporus consobrinus</i>	Arkansas	$32.5 \pm 2.0$
<i>Sceloporus undulatus</i>	New Jersey	$34.0 \pm 0.3$
<i>Sceloporus undulatus</i>	South Carolina	$33.1 \pm 0.4$

## 2.9 Figures

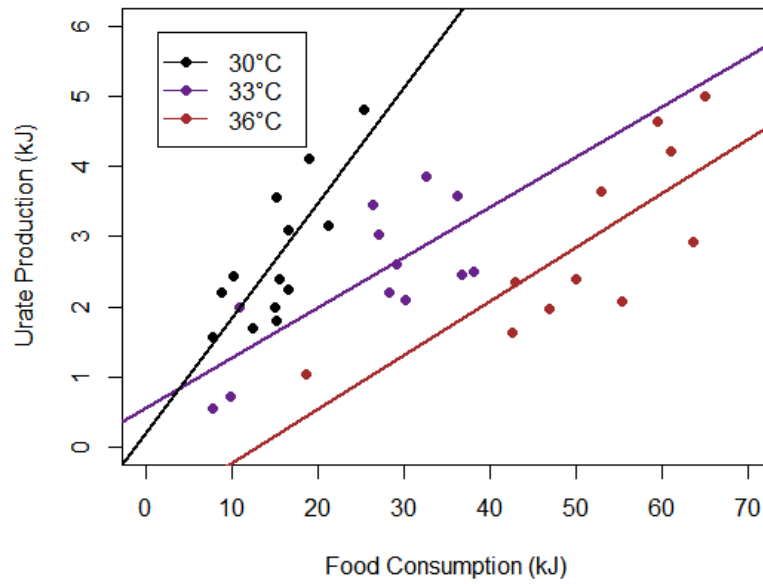


**Figure 1.** When assessing the influence of temperature on digestive physiology in *Sceloporus consobrinus*, passage time decreased while everything else increased as temperatures warmed. At 30°C, MEI and urate production did not have homogeneous covariate slopes with other temperatures, as indicated by asterisks, and these means should be interpreted with caution. The plot depicts adjusted means from ANCOVAs and 95% confidence intervals derived from adjusted means.

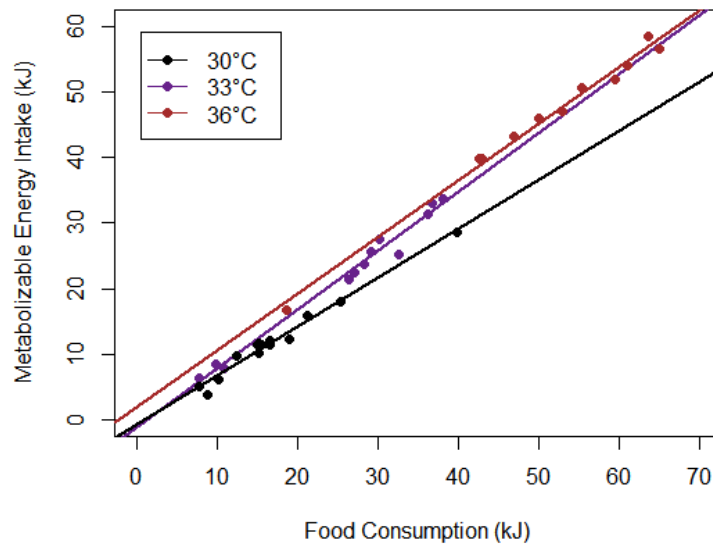


**Figure 2.** Fecal production increased with food consumption in *Sceloporus consobrinus* at all temperatures.

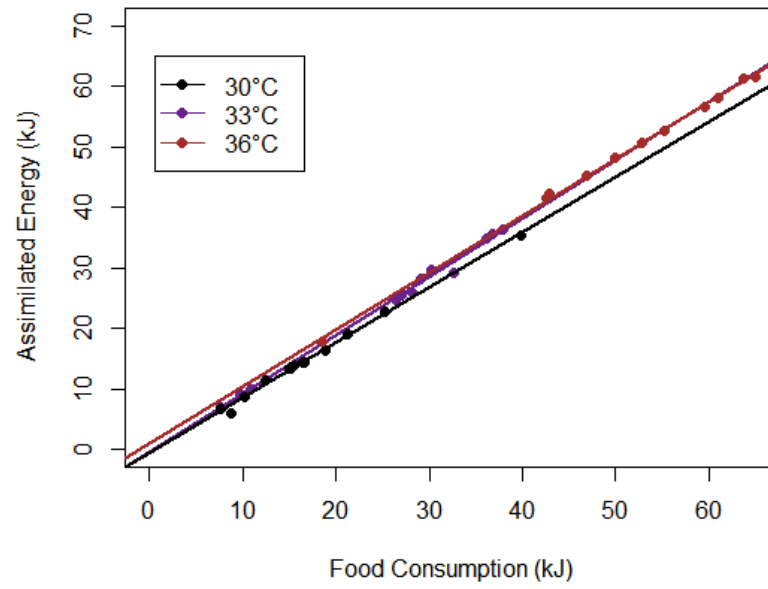




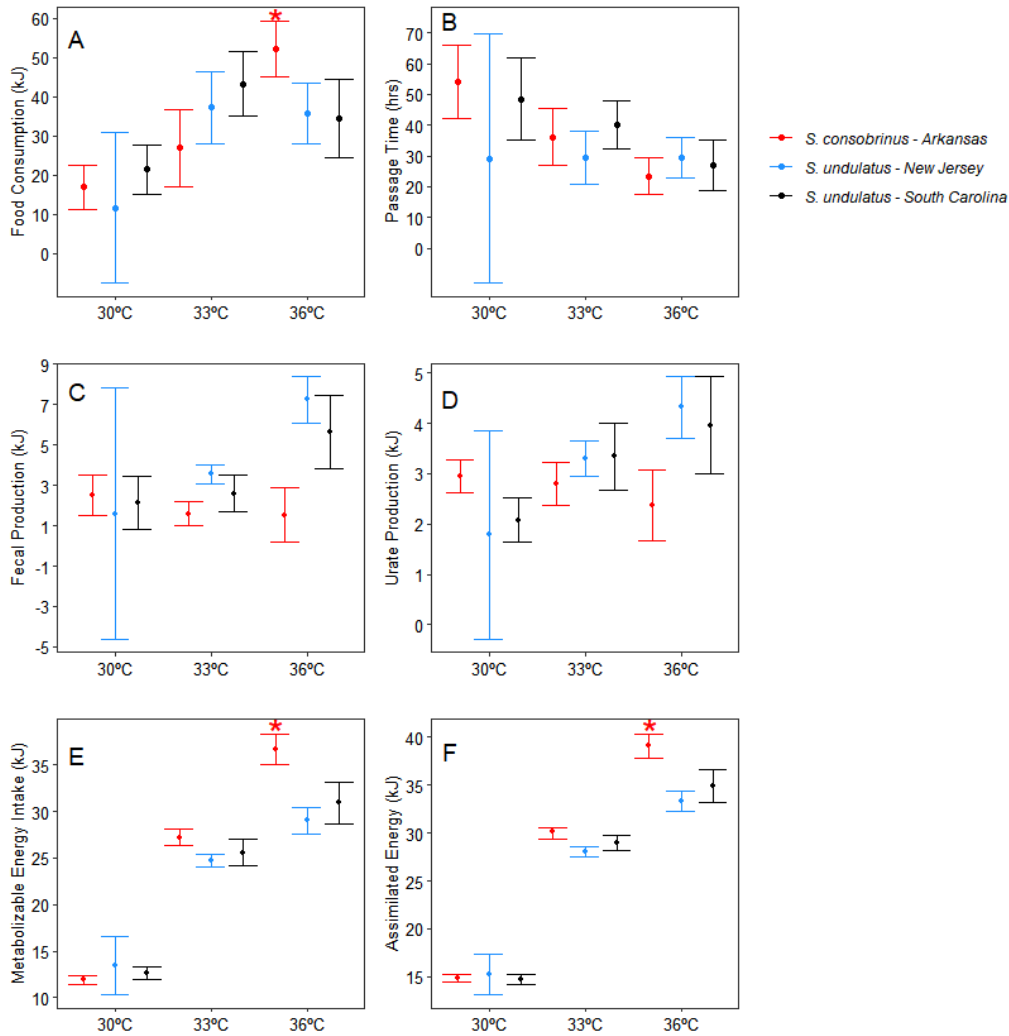
**Figure 3.** Urate production increased at a quicker rate in relation to food consumption at 30°C than 33°C and 36°C for *Sceloporus consobrinus*.



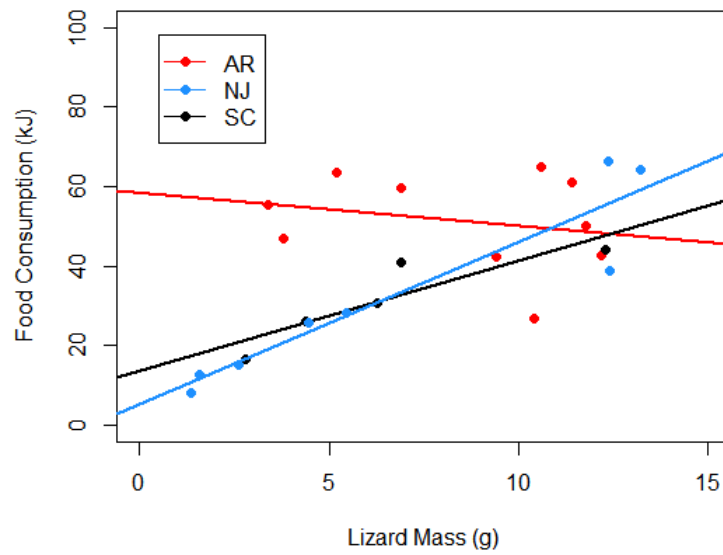
**Figure 4.** Metabolizable energy intake increased at a slower rate in relation to food consumption at 30°C than 33°C and 36°C for *Sceloporus consobrinus*.



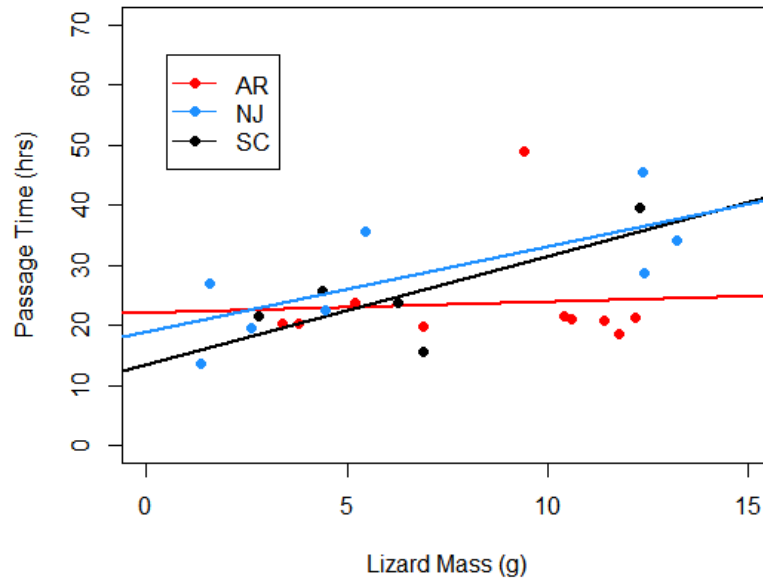
**Figure 5.** Assimilated energy increased with food consumption at at all temperatures for *Sceloporus consobrinus*.



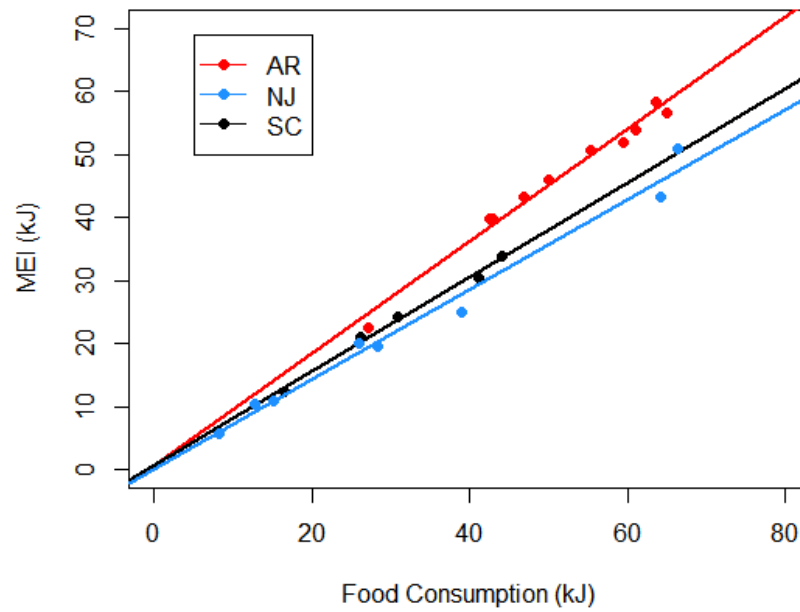
**Figure 6.** Prairie lizards (*Sceloporus consobrinus*) decreased passage time while increasing food consumption, MEI and AE, with no change in urate and fecal production, as temperatures increased. *Sceloporus undulatus* in NJ and SC followed the same trend as *S. consobrinus*, except for reducing food consumption and being less efficient with regards to fecal and urate production at 36°C. Slopes were heterogeneous for food consumption, MEI, and AE when comparing *S. consobrinus* to *S. undulatus* at 36°C, as indicated by asterisks. The plots show adjusted means from ANCOVAs and 95% confidence intervals derived from adjusted means.



**Figure 7.** Food consumption increased with lizard mass for *Sceloporus undulatus* (NJ and SC) while food consumption did not change in relation to body mass in *Sceloporus consobrinus* (AR), at 36°C.



**Figure 8.** Passage time increased with lizard mass for *Sceloporus undulatus* (NJ and SC), but not for *Sceloporus consobrinus* (AR), at 36°C.



**Figure 9.** Metabolizable energy intake increased slower with food consumption for *Sceloporus undulatus* (NJ and SC) compared to *Sceloporus consobrinus* (AR), at 36°C.

# **Cycling Temperature Treatments Affect Estimates of Digestive Performance in an Ectotherm**

## **3.1 Abstract**

In nature, many organisms experience a range of body temperatures over the course of a day or season. Many studies interested in the influence of temperature on performance extrapolate data collected under stable temperature treatments to predict function in a cycling environment. However, additional factors, including temperature order and timing, may influence rates of physiological processes. The current study quantified food consumption, digestive passage time, metabolizable energy intake (MEI), and assimilated energy (AE) across three stable temperature treatments (30°C, 33°C, 36°C) and two temperature cycles. Cycles rotated through 30°C, 33°C, 36°C daily, with equal durations of time at each temperature. Cycle one consisted of warm days and cool nights and cycle two was the reverse of cycle one. For analyses, results at stable temperatures were compiled into a single dataset and compared to cycles. If stable temperatures accurately represent cycling regimes, then performance averages from stable treatments should compare favorably to performance under cycling treatments. Physiological parameters responded differently to temperature treatments. Consumption, MEI and AE were similar between stable trials and cycle one (warm days). Passage time was quicker in cycle one than predicted by stable treatments. The relationship between consumption and MEI and AE differed among treatments, with slower increases in MEI and AE with consumption at cooler daytime temperatures. Physiological data collection requires careful consideration of potential effects of cycling versus stable temperature treatments. The results of the current study suggest that stable temperature treatments may not adequately predict performance in cycling regimes, and particular consideration should be paid to order of temperatures within a cycle.



### 3.2 Introduction

In nature, organisms usually experience a range of environmental temperatures over the course of a day or season. Ectotherms in particular are susceptible to fluctuations in body temperature and subsequently need to maintain adequate function in a variable thermal regime. As a result, behavioral and physiological mechanisms are implemented to work towards maintaining a preferred body temperature. However, thermoregulation can be imprecise, and more challenging at different parts of the season or day (Huey and Pianka 1977; Ortega and Pérez-Mellado 2016). Understanding how organismal performance varies in response to daily temperature cycles, and temperature order and duration within a cycle, compared to stable temperatures may be a critical advancement in thermal biology and ecology and in making predictions for novel environments.

There are multiple ways in which researchers attempt to understand the relationship between performance and temperature. One common method includes collecting data on processes of interest (ex. growth rate, tadpole or embryonic development, digestive passage time, metabolic rate, etc.) at a relevant range of stable temperatures (e.g., Sanger et al. 2018, Plasman et al. 2019). From there, data from each temperature are integrated and a curve is fit to create a time-temperature weighted relationship (or to generate a thermal performance curve; TPC) (Huey and Stevenson 1979; Niehaus et al. 2012). The TPC is then used to predict organism function in a fluctuating (or cycling) environment (e.g. Hertz et al. 1983; Pinch and Claussen 2003; Telemeco 2014). Researchers also use TPCs to hypothesize how organisms evolve in response to environmental conditions over space, time, and taxa (Huey 1982; Gvoždík and Damme 2008; Malusare et al. 2022). However, stable temperatures do not mimic what an organism experiences in nature. Quantifying performance under stable temperatures usually

results in researchers finding a threshold where activity ceases, or begins to decline after reaching an optimum, due to chronic exposure to thermal extremes (Huey 1975; Kaufmann and Bennett 1989).

In nature, organisms may experience extreme temperatures for short periods during the day or season, which may not have the same effect on an organism as chronic exposure in lab trials. Thermal performance curves assume function is solely based on body temperature. Therefore, TPCs fail to consider variation with respect to acute temperature fluctuations or the duration and patterns of daily body temperatures experienced. Additionally, order of temperatures in a cycle could play a role in performance for some processes. Predictions of animal performance in natural systems may be misdirected if temperature pattern, timing, and duration of exposure influence processes. Additionally, evolution of thermal tolerance and performance is likely not a result of chronic stable temperature exposure, but due to cumulative function across daily and seasonal ranges. As a result of heavy reliance on TPCs, there is currently a knowledge gap regarding the influence of daily thermal cycling on physiology and evolution of thermal performance, as well as understanding whether performance is dependent on the pattern of temperatures experienced.

Alternative to measuring thermal performance in a lab, researchers also study processes in the field. Studying organismal body temperature and function at field-relevant temperatures can be done in a variety of ways, including taking body temperatures ( $T_b$ ) throughout the day and season with data loggers (Kerr et al. 2004), taking cloacal (or internal) temperature with a thermometer upon capture (Congdon et al. 1979), or through temperature-sensitive radio telemetry (Lefcourt and Adams 1996; Nordberg and Schwarzkopf 2019). Typically patterns in body temperature are understood in reference to environmental thermal distributions as measured

by operative temperature models (Bakken et al. 1985; Logan et al. 2015). In conjunction with recording field temperatures, processes can be measured in active organisms, such as metabolism through doubly labeled water, activity, growth rate, and reproductive behaviors (Kingsbury 1995; Warner and Andrews 2002; Kerr and Bull 2004). Researchers can draw conclusions on performance in a natural setting, which may not be replicable in the lab. However, field studies have limitations, including inability to directly assess the influence of specific biotic and abiotic changes of interest and lack of control over factors not considered in the study (ex. humidity, rainfall, predation, etc.). Therefore, direct causation cannot always be inferred from a field study, and estimates of future temperature scenarios from field data can be hard to predict.

It is evident that assessments are needed to identify whether differences occur in physiological data collected under cycling and stable temperature treatments. Effective methodology is a crucial component to collecting and interpreting realistic data. To draw conclusions about performance and evolution in relation to temperature, it is imperative to ensure that methods consider relevant factors influencing how organisms experience temperature in nature. It is often assumed that lab methods represent natural conditions; if untrue, resulting interpretations are likely incorrect. Therefore, examining whether factors such as temperature cycling, pattern, and timing alter performance is imperative to informing methodology in thermal biology.

It is possible that processes respond differently to cycling temperatures (Dong et al. 2006; Ragland and Kingsolver 2008). Processes occurring during the day, or processes that do occur continuously throughout the course of the day and night, may be more comparable to stable treatments. For example, sprint speed and food consumption are relatively instantaneous where animals engage in such processes at certain points and body temperatures throughout the day.

Therefore, if temperature is a primary driver determining rates of such processes, it is possible that organismal body temperature as the process occurs is the main factor to consider. In comparison, digestion can continuously occur throughout the day and night, where overall performance could vary in response to the history and pattern of body temperatures. If processes are initiated early in the day and warm body temperatures are sustained for long periods, temperature cycles could promote quick rates. However, if continuous processes are initiated late in the day before retreat, when body temperatures may decrease, daily temperature cycles may reduce rates. Therefore, timing of the process and temperature pattern could play critical roles, and influence processes differently.

Concerns of how temperature influences organisms have become of greater importance due to climate change. Climate change is expected to alter daily temperature ranges (Easterling et al. 1997), not just mean temperature. Lab experiments may be critical for understanding how temperature shifts drive change in organisms because they allow researchers to identify direct causality. When modeling temperature effects, useful predictions require empirical data under realistic scenarios that organisms experience in nature. However, many studies to date, especially with regards to adult reptiles, rely on stable temperature treatments making it difficult to interpret results in relation to realistic temperature regimes (e.g. Beaupre et al. 1993; Angilletta 2001b; Isaac and Gregory 2007; Racic et al. 2020).

Attempts to extrapolate data from stable treatments to predict outcomes in cycling regimes have proven difficult. For example, Niehaus et al. (2012) measured metamorphic performance in striped marsh frogs (*Limnodynastes peronii*) at various stable and cycling scenarios. Measurements at stable temperatures were used to generate a temperature dependent reaction rate to predict results in the daily cycling treatment. At most stages individuals

developed quicker than predicted using the stable temperature trials (Niehaus et al. 2012). Whereas some studies indicate data differs when collected under stable and cycling temperatures (Bestgen and Williams 1994; Radmacher and Strohm 2011), there is a lack of research on differences in physiological data. For example, experiments comparing stable and cycling temperature treatments have found differences in development, growth, and maturation (Meeuwig et al. 2004; Dhillon and Fox 2007; Kern et al. 2015; Kingsolver et al. 2015; Coulter et al. 2015), egg development (Li et al. 2013), morphology (Du and Ji 2006; Patterson and Blouin-Demers 2008), reproductive output (Podrabsky et al. 2008; Žák and Reichard 2020), thermal tolerances (Arias et al. 2011), and genetics (Podrabsky and Somero 2004). However, physiological parameters, especially those relating to energy acquisition and allocation, are critical to making mechanistic predictions about individual and population level processes (Dunham et al. 1989; Kearney 2012). Comparisons of physiological performance at stable and daily cycling regimes, as well as at different patterns of temperature exposure, are needed. Such information would provide meaningful data for informing methods of future physiological studies and making predictions with bioenergetic models. Comparing temperature patterns could provide additional information on circadian cycles and whether body temperature profiles alter physiological performance.

The objective of this study was to make comparisons among physiological data collected under stable temperature treatments and two daily temperature cycles. Prairie lizards (*Sceloporus consorbinus*) are used as a model organism for the current study, as the genus *Sceloporus* are often used in thermal biology and climate change models (e.g. Buckley 2008, Sinervo et al. 2010), with known sensitivity to temperature change (Beaupre et al. 1993; Angilletta 2001). Physiological parameters assessed were rate of food consumption, digestive passage time,

metabolizable energy intake (MEI), and assimilated energy (AE). Such parameters were chosen because they directly relate to energy acquisition and assimilation, which influences total energy budgets. Energy budgets are important because they limit allocation to growth, reproduction, storage, and maintenance, which in turn affects individual fitness and population-level processes (Congdon et al. 1982; Dunham et al. 1989; Porter et al. 1994).

To make comparisons, performance was assessed at three stable temperature treatments and two temperature cycles. Both cycles spanned the range of stable temperature treatments but had different patterns. The first cycle (hereafter “cycle 1”) represented warm days and cool nights, where the second cycle (hereafter “cycle 2”) represented cool days and warm nights. If stable treatments mimic daily cycles and temperature pattern is influential, then the average physiological rate estimated when pooling stable temperature data should compare favorably to both cycles. I hypothesized that food consumption, MEI, and AE would be higher, and passage time would be lower in cycle 1 than predicted by stable trials. My rationale is that lizards will experience warm days promoting rapid digestion and high rates of consumption prior to reaching cooler nighttime temperatures. Meanwhile, the average from stable treatments is most likely going to be moderate in comparison because of averaging rates of processes at high and low temperatures. I also hypothesized that food consumption, MEI, and AE would be lower, and passage time would be higher in cycle 2 than predicted by stable temperatures, due to cold days. I also predict that temperature is the primary factor driving rates of the physiological processes addressed, and temperature pattern is influential.

### **3.3 Methods**

#### *3.3.1 Field Collection*

Male and female adult *S. consobrinus* were collected in northwest Arkansas from 2020 – 2022. Upon capture, lizard body temperature was measured using a thermocouple inserted in the cloaca to inform lab treatments. Lizards were immediately brought to the University of Arkansas and individually housed in 10-gallon tanks with a natural sand substrate, a heat lamp and hide box, water provided ad-libitum, fed a diet of crickets, and supplemented with vitamin D every two weeks.

### *3.3.2 Temperature Treatments*

Lizards were randomly assigned to one of five temperature treatments, stable 30°C (n = 14), stable 33°C (n = 12), stable 36°C (n = 11), cycle 1 (n = 12), or cycle 2 (n = 15), with males and females as evenly divided as possible. The temperature treatments were selected based on body temperature profiles in the field. The amount of time spent at each temperature during cycling trials was identical for a 24-hour period. One full daily cycle totaled 6 hours and 40 minutes at each temperature, with a one-hour transition period for the environmental chamber to reach the next set point (Figure 1). The first cycling temperature treatment (referred to as cycle 1) consisted of a nighttime temperature of 30°C and a daytime temperature of 36°C, with a sunrise and sunset temperature of 33°C during the transition between the low and high temperatures. To compare performance under different patterns of temperature cycles, and the timing of temperature experienced, the second cycling temperature treatment (referred to as cycle 2) consisted of a nighttime temperature of 36°C and a daytime temperature of 30°C, with a sunrise and sunset temperature of 33°C during the transition between the low and high temperatures. By flipping the timing of warm and cool temperatures, it can be determined if day versus night activity varies irrespective of temperature. Specifically, if factors associated with daytime and nighttime activity influence digestive physiology, it could be predicted that cycle 2

would closely match the stable 30°C treatment. In contrast, if temperature is primary factor influencing digestive physiology in the current study, processes may differ between the stable 30°C treatment and cycle 2. If so, rates of performance in cycle 1 should be similar to the stable 36°C trial, and cycle 2 should be similar to the stable 30°C trial.

### *3.3.3 Physiological Data Collection*

For lab trials, lizards were housed in plastic containers (41.9 cm x 33 cm x 16.8 cm) lined with butcher paper, a hide box, and water provided ad libitum. Prior to beginning trials lizards were acclimated to their respective temperature treatment for 5 days. At the beginning of the acclimation period lizards were fed one meal to allow for digestion at the treatment temperature, and then fasted to ensure the gut was clear. Temperature was maintained using an environmental chamber ( $\pm 0.5^\circ\text{C}$ ). During trials lizards were fed Fluker's 2- and 3-week-old crickets ad-libitum every morning. The uneaten crickets were removed after ~3 hours. Lizards were also provided water ad-libitum and a hide-box. Crickets were weighed to the nearest 0.1 mg. Digestive passage time represents the time it takes to pass food from consumption to excretion. Metabolizable energy intake is a measure of the maximum potential energy to be allocated to growth, maintenance, storage, and reproduction, and is calculated using the formula:

$$\text{MEI} = \text{C} - \text{F} - \text{U}$$

where C is energy consumed, F is energy lost as feces, and U is energy lost as uric acid, measured in kilojoules. Assimilated energy represents digestible energy, and is calculated using the formula:

$$\text{AE} = \text{C} - \text{F}$$

To begin trials, a single cricket was injected with a marker, made from UV-fluorescent powder mixed with water (Beaupre et al. 1993). The fluorescent powder associates with feces and does



not influence the edibility of crickets, so lizards consumed the mark voluntarily. Trials began when lizards ate the first mark, and time of feeding was noted. Lizard tanks were then monitored every 2 – 4 hours during the day for feces until the fluorescent powder was identified, indicating passage time (amount of time from mark consumption to first appearance in feces). After the first mark was excreted, typically 10 or more days were allotted to feed lizards and collect feces and urates for adequate measurement of consumption and bomb calorimetry. Afterwards, a second marker was fed, and tanks were monitored again every 2 – 4 hours. Once the second marker appeared in feces, the trial was considered complete.

During trials all feces and urates were collected, separated, frozen, and freeze dried. To quantify energy ingested (consumption rate), a wet mass was taken for 10 crickets, which were then freeze dried, and re-weighed. The relationship between wet and dry cricket mass allowed for conversion of wet cricket mass consumed to be converted to dry cricket mass consumed. Using a Parr Semimicro Calorimeter, the energy density of crickets was determined, which was used to convert dry cricket mass consumed to kilojoules consumed for each lizard. To determine fecal and urate production (kJ), excrement samples collected during the trials were pooled for individual lizards, weighed, homogenized, and analyzed using a Parr Semimicro Calorimeter. Metabolizable energy intake and AE could then be calculated.

#### *3.3.4 Statistical Analyses*

ANCOVAs were run to determine the effect of temperature treatment on food consumption (kJ), digestive passage time, MEI (kJ) and AE (kJ). In addition to comparing each trial, all data from stable treatments were pooled into a single dataset, averaged, and included as a treatment in all analyses. By pooling data from stable treatments for comparison to cycles, it could be determined if the cycles represented results extrapolated from stable treatment. For all

analyses trial length was included as a covariate and an interaction term of trial length\*treatment was included to test for heterogeneous slopes. When assessing food consumption, snout-vent length (SVL) was also included as a covariate and an interaction term of SVL\*treatment to test for heterogeneous slopes. For MEI and AE, food consumption was included as a covariate and an interaction term of food consumption\*treatment was included to test for heterogeneity of slopes. Post-hoc analyses were made by comparing adjusted means and 95% confidence intervals generated from adjusted means (*Day and Quinn 1989*). Significance among treatments was determined based on non-overlapping confidence intervals with adjusted treatment means, assuming the probability of a type 1 error is 0.05. The residuals of analyses were examined to determine if the assumptions of parametric statistics were met.

### **3.4 Results**

The analyses of residuals indicated slight variation from normality in some instances, however, all followed a hump-shape distribution and were deemed suitable for the robust procedures of ANCOVA (Blair 1981). The average body temperature of *S. consobrinus* in the field was 32.4°C and ranged from 22.9° – 36.7°C. Therefore, the temperature treatments implemented were within the range of active body temperatures. Food consumption significantly differed among treatments (ANCOVA  $p < 0.001$ ,  $F = 12.438$ , Figure 2A), with no effect of lizard SVL (covariate). Trial length had a positive influence on food consumption (covariate,  $p = 0.008$ ,  $F = 7.328$ ). In the stable 36°C treatment, food consumption was significantly higher than all other treatments. There were no differences in consumption among the stable 33°C treatment, cycle 1 (warm days and cool nights), and the average of all stable treatments combined. Food consumption in the stable 30°C treatment and cycle 2 (warm nights and cool days) were similar but significantly lower than all other treatments. Passage time significantly differed among

treatments (ANCOVA  $p < 0.001$ ,  $F = 7.219$ , Figure 2B), and there was no influence of trial length (covariate) and no interaction between trial length and treatment. Passage time was slowest in the stable 30°C treatment. The stable 33°C trial did not differ from the stable 36°C, cycle 1, cycle 2, and the average of all stable treatments. However, passage time in cycle 2 was significantly slower than the stable 36°C and pooled stable treatments. Passage time was quickest on average in the stable 36°C and cycle 1, which did not differ from each other.

When comparing MEI among all trials, there was a significant interaction between treatment and food consumed (ANCOVA  $p < 0.001$ ,  $F = 5.747$ ), preventing further combined analyses of all treatments. However, it was found that the slopes for stable 33°C, 36°C, the pooled average, and cycle 1 were homogenous (Figure 3), and the slopes for stable 30°C and cycle 2 while different from the others, were homogenous (Figure 4). Therefore, the data for the stable 33°C, 36°C, the pooled average, and cycle 1 were compared, and the data for stable 30°C and cycle 2 were compared, respectively. When comparing the stable 33°C, 36°C, the pooled average, and cycle 1, there was a significant difference in MEI among treatments (ANCOVA  $p < 0.001$ ,  $F = 694.704$ , Figure 2C), a positive effect of food consumption (covariate,  $p < 0.001$ ,  $F = 5169.673$ ), and no interaction between food consumed and treatment. There was no influence of trial length (covariate) on MEI and no interaction between trial length and treatment on MEI. Metabolizable energy intake was highest in the stable 36°C treatment and did not differ among the other trials considered. When comparing the stable 30°C and cycle 2, 30°C had significantly higher MEI than cycle 2 (ANCOVA  $p < 0.001$ ,  $F = 52.670$ , Figure 2D). There was also a positive effect of food consumed on MEI (covariate,  $p < 0.001$ ,  $F = 1,009.099$ ) for both treatments, no interaction between food consumed and treatment, and no influence of trial length (covariate) or interaction between trial length and treatment on MEI.

Assimilated energy also had a significant interaction between food consumption and treatment (ANCOVA  $p < 0.001$ ,  $F = 5.11$ ). Again, the slopes of the stable 33°C, 36°C, the pooled average, and cycle 1 were found to be homogenous (Figure 6) and the slopes for the stable 30°C and cycle 2 were homogenous (Figure 7), but different from the other treatments. Therefore, the stable 33°C, 36°C, the pooled average, and cycle 1 were compared (Figure 2), and the data for stable 30°C and cycle 2 were compared (Figure 5), respectively. When comparing the stable 33°C, 36°C, the pooled average, and cycle 1 there was a significant difference in AE among treatments (ANCOVA  $p < 0.001$ ,  $F = 3,311.488$ , Figure 2E), a positive effect of food consumption (covariate,  $p < 0.001$ ,  $F = 25,765.516$ ), and no interaction between food consumed and treatment. There was no effect of trial length (covariate) and no interaction between trial length and treatment on AE. Assimilated energy followed the same pattern as MEI, with highest AE in the stable 36°C trial, and no difference between the stable 33°C, cycle 1, and the pooled average. When comparing stable 30°C and cycle 2, 30°C had significantly higher AE than cycle 2 (ANCOVA  $p < 0.001$ ,  $F = 209.341$ , Figure 2F). There was also a positive effect of food consumed on AE (covariate,  $p < 0.001$ ,  $F = 4663.399$ ), no interaction between food consumed and treatment, and no effect of trial length or interaction between trial length treatment on AE.

### **3.5 Discussion**

Physiological data can differ when collected under stable and cycling temperature treatments, and variation is process dependent. Stable temperature treatments followed predicted and established patterns (e.g. Beaupre et al. 1993; Alexander et al. 2001; McConnachie and Alexander 2004) of decreasing passage time while increasing food consumption, MEI, and AE with warming temperatures. Such trends in thermal sensitivity when comparing stable temperatures is expected, although *S. consobrinus* appears to be more efficient at warmer

temperatures under stable scenarios than other *Sceloporus* lizards (Dutton et al. 1975; Beaupre et al. 1993; Angilletta 2001). For the purposes of comparing stable treatments to cycling regimes, data from stable treatments were compared independently and when pooled into a single dataset. The pooled dataset closely represented the stable 33°C treatment, except for passage time, which indicated on average slower passage than the 33°C trial. The similarity in the stable 33°C trial and pooled average is likely a result of the high and low rates at stable 36°C and 30°C treatments averaging and being comparable to the stable 33°C trial.

A common assumption made in thermal biology is that rates of processes at stable temperatures accurately represent rates in daily cycling regimes, with no regard to temperature pattern (Sinclair et al. 2016). If true, the average rate of processes from the pooled stable treatments should not have differed from the cycles in the current study. However, not all processes responded similarly to temperature cycling, and unique similarities and differences were found based on temperature pattern. Specifically, in cycle 1 food consumption, MEI, and AE were comparable to the pooled average from stable trials. Therefore, extrapolation of such variables from stable treatments to cycling regimes may be possible. However, this may only be the case when the cycling regime has equal durations of time spent at each temperature and specific regard is given to temperature pattern. Cycle 1 followed a regime where food consumption was most likely occurring near the average temperature from the stable treatments (33°C). As a result, MEI and AE followed the same pattern because they are heavily influenced by food consumption.

In contrast, digestive passage time in cycle 1 was the same as that in the stable 36°C trial. Cycle 1 maintained lizards at 36°C during peak daytime hours. Therefore, the results suggest that the majority of passage occurred during the day. Stable temperature treatments indicate that *S.*

*consobrinus* is highly efficient at 36°C. In the current trials, lizards were fed in the morning, when experiencing temperatures from 33°C (sunrise) to 36°C (daytime) for cycle 1. One possible explanation of the observed trend is that lizards were consuming food when their body temperature was transitioning from 33°C to 36°C, and therefore consumption rates were closest to the 33°C and the pooled average. However, after consumption, digestive passage began, which would have been when lizards were transitioning to, or already at, 36°C. Due to the efficiency at 36°C, lizards may have been able to pass a significant portion of their food prior to reaching the sunset temperature (33°C) or nighttime temperature (30°C).

It was expected to find that passage time and food consumption follow similar patterns as food cannot be consumed if the gut is full. When comparing stable temperature treatments, passage time decreases, and consumption increases proportionally with temperature. However, in cycle 1 passage time and food consumption do not follow the same patterns. The current study measured time to the first appearance of the mark in feces, not time to the last appearance. One explanation for the discrepancy of passage time and food consumption is that while lizards were able to excrete feces at a quick rate at a stable 36°C, it may have taken longer to fully excrete the item in cycle 1. Longer times to full excretion could be due to the cooler nighttime temperatures imposing a constraint, which may not be reflected in time to the first appearance of the mark. If more food remained in the gut when lizards ate in the morning during cycle 1 compared to the stable 36°C trial, it could have constrained consumption to lower rates.

In addition to cycling regimes, order of temperature within a cycle may play a crucial role in rates of physiological processes over the course of a day. Cycle 2 was designed to reverse the temperature pattern of cycle 1. It was found that temperature pattern and timing play a role in digestion, because rates quantified at each cycle differed. When comparing cycle 2 to the stable

30°C trial, passage time was slower in cycle 2, but MEI and AE were higher, when lizards were at a stable 30°C. However, food consumption was comparable between cycle 2 and the stable 30°C trial. In cycle 2 lizards were fed when body temperatures were undergoing the transition to the cooler temperature, 30°C. Therefore, body temperature at time of consumption is more likely to have caused the similarity between cycle 2 and the stable 30°C trial than temperature pattern. Passage time showed the greatest difference when comparing cycle 2 and the stable 30°C trial, being quicker under a cycling regime likely due to time spent at warmer temperatures within the cycle. The inefficiency of *S. consobrinus* at 30°C resulted in passage occurring all day and into sunset (33°C) during cycle 2, resulting in a quicker passage time than if experiencing 30°C consistently. The differences in passage between cycle 2 and 30°C support the idea that in cycle 1 lizards were so efficient at 36°C that they did not spend time digesting at night. Similar differences among temperature cycles have also been observed in growth and developmental rates (Kern et al. 2015; Kingsolver et al. 2015; Verheyen and Stoks 2018; Vajedsameil et al. 2020) and thermal tolerance and survival (Bozinovic et al. 2016).

Due to the heterogeneity of slopes, cycle 1 and 2 could not be directly compared. Utilization plots indicated that MEI and AE increased more rapidly with consumption in the stable 33°C, 36°C, cycle 1, and in the pooled average than in the stable 30°C and cycle 2. Therefore, it appears that under cooler daytime temperatures the relationship between consumption, AE, and MEI differs from that under warm daytime temperatures. Physiological parameters quantified also tended to be more efficient in cycle 1 based on steeper slopes relating consumption and MEI or AE. Such findings indicate that temperature pattern plays a critical role in rates of digestive processes and that the relationships among variables are not static across temperature regimes for stable and cycling treatments.

Food consumption is an important component for predicting energy budgets (e.g. Kitchell and Windell 1972; Hudson et al. 2021). It was found that food consumption is the most important determinant of MEI. One approach to ad-libitum feeding in lab studies on lizards is to offer food all at once (e.g. Christian 1985; Levy et al. 2017), and after a certain amount of time, remove what is uneaten. The method of offering food at a single time was implemented in the current study, and therefore lizards primarily ate at a single point in the temperature cycle (typically sunrise or early in the daytime temperature cycle). As a result, food consumption reflected the body temperature at which lizards were offered food and may not have been influenced by the cycle itself. The cycles used here had a single daytime temperature. In nature, lizards experience a range of body temperatures throughout the day (Light et al. 1966; Bauwens et al. 1999). It is possible that animals do not just consume food in the morning or all at once, and instead eat throughout the day. However, few data are available on feeding frequency of lizards in nature. If consumption does occur throughout the day, natural fluctuations in body temperature may alter rates of food consumption based on the body temperature when food is encountered, with potential effects for resulting energy budgets. However, when estimating the influence of temperature cycles on brown trout (*Salmo trutta*), food was also offered at one temperature within the cycle and variation was still observed (Flodmark et al. 2004). A better approach to informing lab methods may be to first estimate frequency of feeding in the field to be replicated in lab trials. By doing so, researchers could better understand how cycling regimes and temperature influence consumption.

In contrast to food consumption, digestive passage time was not restricted to a single temperature within the cycle, as it is a continuous process that occurs until completion. Therefore, the influence of the temperature cycling was apparent on passage time. While



consumption can be influenced by passage time, it appears that in cycling regimes passage was never slow enough to restrict consumption. Different patterns may be observed if lizards experience even colder temperatures, when digestion and consumption begin to halt (Alexander et al. 2001). However, the temperature ranges implemented are within realistic body temperatures *S. consobrinus* experiences in nature throughout parts of the season. Although, lizards likely experience nighttime body temperatures colder than 30°C. The results suggest that for processes occurring continuously throughout the day, stable temperature treatments do not accurately predict cycles. Even more so, the underlying relationships, such as the slopes between consumption and MEI and AE differ in cold treatments, complicating the ability of researchers to extrapolate data. Additionally, other physiological variables assessed may have only been adequately predicted in cycle 1 by stable treatments because they occurred at a single point in the cycle, which may not represent realistic scenarios.

Cycle 1 results suggest it may be reasonable to predict certain physiological processes in a cycling regime based on stable temperature data. However, making such extrapolations should be done with great caution, as passage did not follow the predicted trend, and the order of temperatures altered results. Additionally, mechanisms underlying the differences identified are not fully understood. The consistency of temperatures in cycle 1 and the stable treatments, and the equal duration of time spent at each temperature within the cycle, are likely the reason for comparable findings in consumption, MEI, and AE. If lizards experienced different durations at each temperature within a cycle a different approach would be required where weights are applied based on hours at each temperature. The order of temperatures in a cycle play an important role in organismal performance. The temperature when food is consumed is a critical factor because it influences individual appetite and satiation. Consequently, temperatures

experienced when consuming food have cascading effects on other digestive processes, as MEI and AE are heavily influenced by consumption, and passage does not begin until food is consumed. Therefore, when considering temperature cycles, is important to assess at which temperatures and time of day organisms are eating.

The influence of temperature on organismal performance has long been an area of interest (Porter and Gates 1969). Recently, focus has increased on temperature effects due to climate change. Performance under daily temperature cycles is of particular concern because they more accurately represent nature, and daily cycles are beginning to shift (Morash et al. 2018). Evidence from multiple fields of study indicates that stable temperature treatments do not always accurately represent responses to daily temperature cycles. The current study contributes to these findings by indicating that physiology can also differ based on stable and cycling temperatures, and temperature order. Lizards were used here as a model organism, but the findings may be applicable to other ectothermic taxa. There is currently little information on how temperature cycles influence digestion and energy budgets. However, bioenergetics offer important insight to variation in life history, survival, reproduction, and population dynamics (Dunham et al. 1989). Future studies should aim to increase understanding of how temperature patterns and cycles influence digestion and energy budgets. Additionally, studies examining how realistic feeding scenarios affect responses of digestive parameters due to temperature profiles are needed. In conclusion, extrapolating rates of physiological processes from stable temperatures to daily cycles may provide inaccurate results, especially under variable temperature patterns. The best approach to understanding how daily cycles influence organisms may be to estimate body temperature profiles in nature to inform lab treatments. Directly collecting data under cycles of interest and aiming to represent patterns and behaviors used by

organisms in the field will offer the most accurate estimate of performance. Such estimates will be invaluable to understanding how climate influences organisms, making accurate predictions for future scenarios, and understating the influence of temperature of performance and evolution of thermal tolerances.

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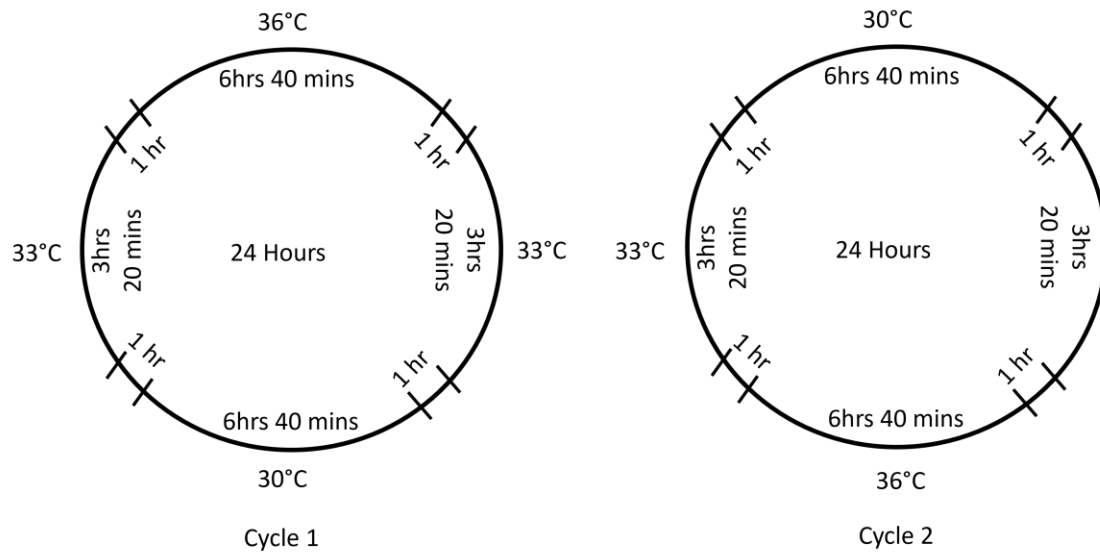
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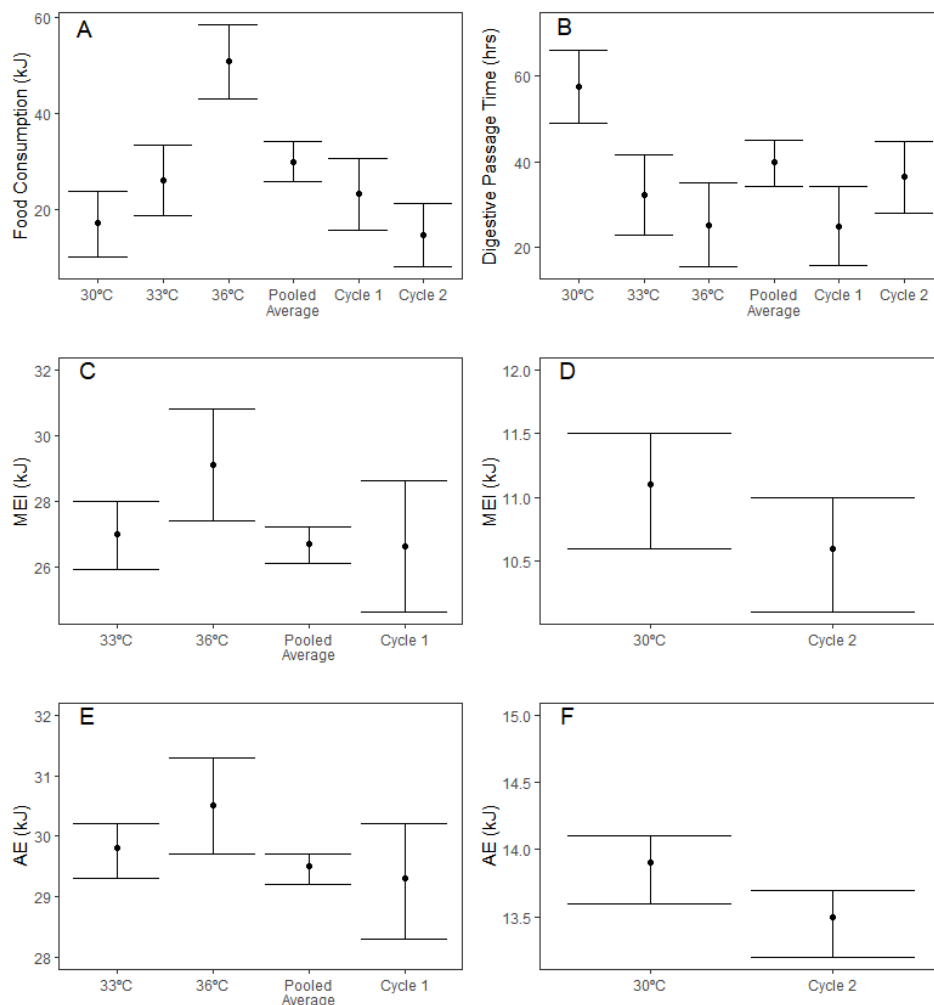
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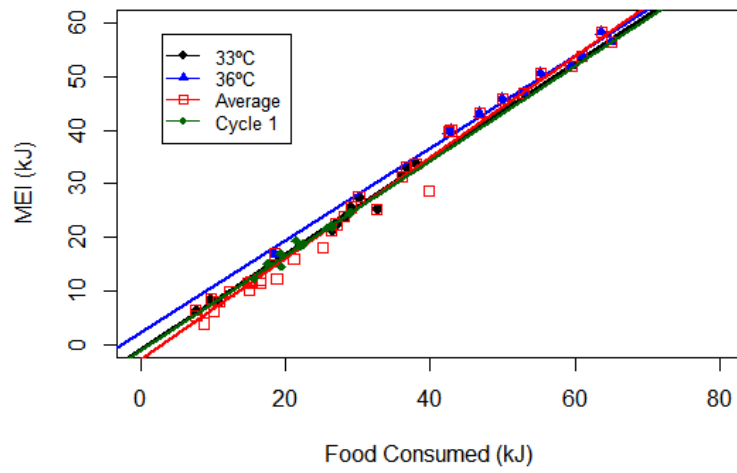
### 3.8 Figures



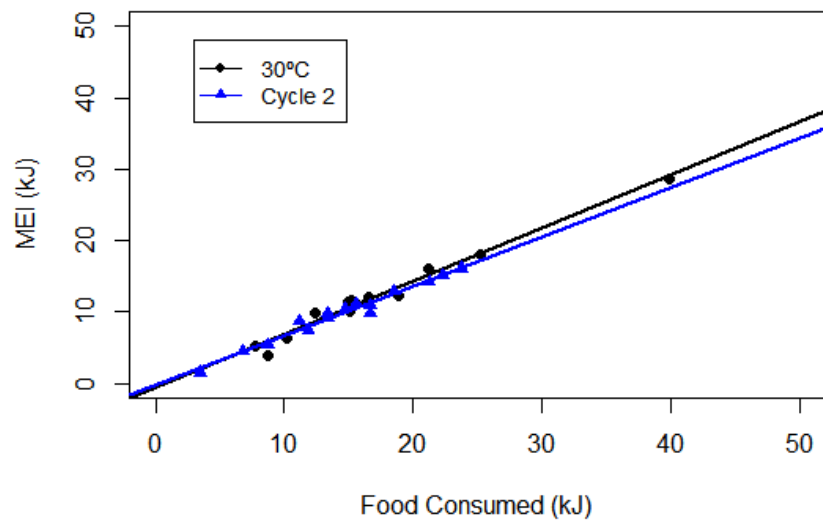
**Figure 1.** Within a 24-hour period the temperature cycled through 30°C, 33°C, and 36°C for cycles 1 and 2, with equal duration spent at each temperature. A one-hour period was allotted for transition between temperatures. Cycle 1 represented warm days and cool nights, while cycle 2 represented cool days and warm nights.



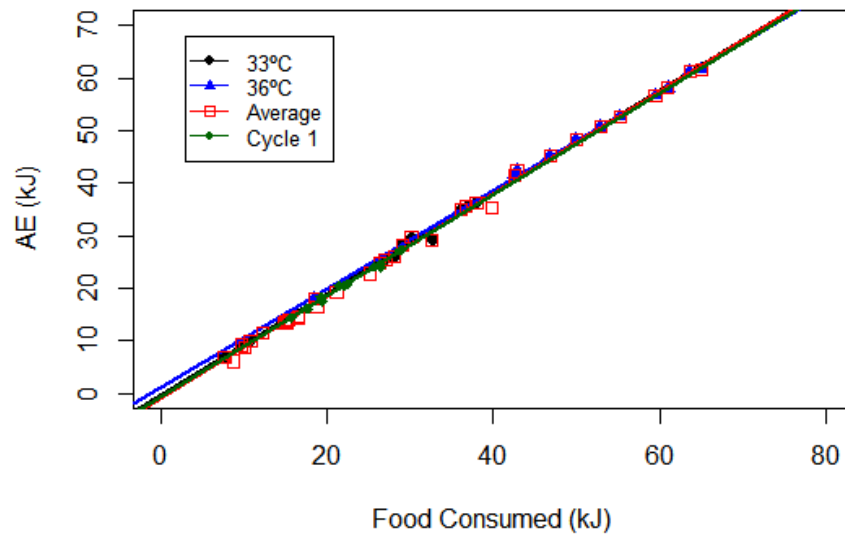
**Figure 2.** Food consumption increased and passage time decreased with warming temperatures among stable temperature treatments. Food consumption, metabolizable energy intake (MEI), and assimilated energy (AE) showed similar patterns between the pooled average of stable treatments and cycle 1. Digestive passage time did not compare to the average of stable treatments. Results were compared among stable 33°C, 36°C, the pooled average of stable treatments, and cycle 1, and between stable 30°C and cycle 2 for MEI and AE, respectively, based on homogenous slopes. The plot depicts means adjusted for food consumption and error bars representing 95% confidence intervals calculated from adjusted means, for all treatments and the pooled average.



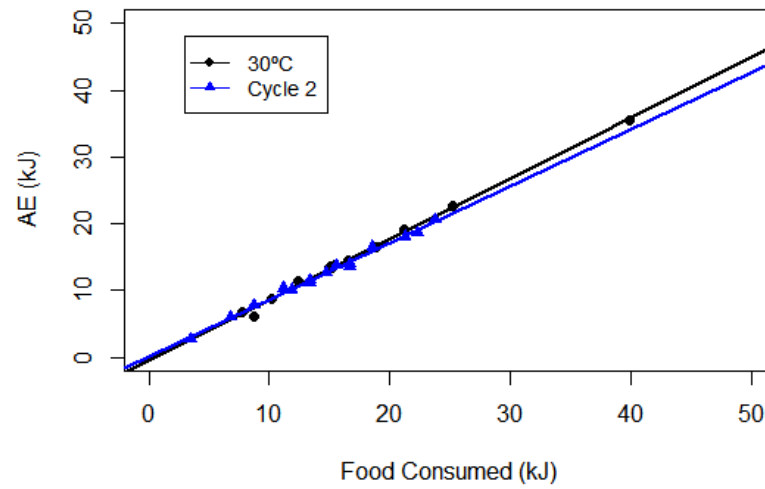
**Figure 3.** The utilization plot indicates that metabolizable energy intake increased with food consumption for the stable 33°C, 36°C, the pooled average, and cycle 1.



**Figure 4.** The utilization plot indicates that metabolizable energy intake increased with food consumption for the stable 30°C and cycle 2.



**Figure 5.** The utilization plot indicates that assimilated energy increased with food consumption for the stable 33°C, 36°C, the pooled average, and cycle 1.



**Figure 6.** The utilization plot indicates that assimilated energy increased with food consumption for the stable 30°C and cycle 2.

## **Warming nighttime temperatures and prey availability interact to influence digestive physiology in an ectotherm**

### **4.1 Abstract**

Abiotic and biotic attributes can interact to influence organism function, life history, and persistence. Temperature and food availability are primary drivers of individual and population characteristics, especially for ectotherms. Many ectotherms thermoregulate daily but face challenges at night due to homogenization of the thermal landscape, which is often not considered in climate change studies. Temperature warming can increase energetic demands, which may be amplified or mitigated based on the ability to consume more prey. The current study examined the interactions between warming nighttime temperatures and altered prey availability as they affect food consumption, digestive passage time, metabolizable energy intake, assimilated energy, and fecal and urate production in a model organism, prairie lizards (*Sceloporus consobrinus*). Three experimental temperature treatments (current conditions, +2°C nighttime increase, and +4°C nighttime increase) and three levels of prey availability (low, moderate, and high) were used to examine multiple scenarios. Nighttime warming and prey availability were interdependent and varied based on the magnitude of change. Under a 2°C nighttime increase, lizards were efficient and maintained or increased energy budgets, compared to current conditions. In contrast, under a 4°C nighttime increase, energy budgets only increased under moderate prey, and were lower than current conditions when prey were high, but equivalent when prey were low. Thermal performance can change solely due to nighttime temperatures, and can be antagonistic or additive, depending on prey availability. Future studies should focus on changes in daily temperature cycles and the interaction with co-occurring biotic changes to understand factors influencing organism function.

## 4.2 Introduction

While understanding the interaction between organisms and climate is not a new topic in science (Porter and Gates 1969; Parmesan 2006), it has become of increasing focus in response to anthropogenic climate change (Williams et al. 2009; Heino et al. 2009). Physiology, which can be influenced by the environment for ectotherms (Ohlberger 2013; Sokolova 2021), plays an important role in determining individual fitness and life history (Congdon et al. 1982; Dunham et al. 1989). Therefore, studies examining interactions among inter-dependent physiological processes and external factors are critical for understanding the influence of climate on organisms (Urban et al. 2016). Environmental changes can induce biotic change (Andr  n et al. 1985; Haile 2020), such as altered prey abundance, predation, and disease, which could have interactive effects on organisms (Coors and De Meester 2008). Consideration of how co-occurring abiotic and biotic changes can influence physiology may be beneficial for enhancing theory on drivers of population change and informing climate change studies and predictions (Davis et al. 1998; Beaupre 2002; Poloczanska et al. 2008; Williams and Middleton 2008; Huey and Kingsolver 2019).

Persistence and life history are known to vary in response to energetic trade-offs, induced by both the abiotic and biotic environment (Dunham et al. 1989). Environmental attributes can pose constraints on behaviors that would otherwise be favorable, if all else were equal. For example, temperature restrictions can prevent organisms from being active, reducing foraging time or mate search behavior (Chong and Lee 2009; Oyugi et al. 2012; Pilakouta and Baillet 2022). Reductions in rainfall or humidity can also reduce activity in the interest of preventing dehydration, at the expense of engaging in other beneficial tasks (Berger et al. 2014; Pintor et al. 2016). If such abiotic changes occur in tandem with biotic changes, such as altered prey



availability, effects could interact to have beneficial or negative consequences (Gilman et al. 2010; Vucic-Pestic et al. 2011; Dell et al. 2014). However, studies examining singular environmental attributes in the lab, or in field studies, lack the ability to mechanistically understand how changes in multiple parameters can interact to influence individuals.

For many animals, temperature and food are primary drivers of performance and fitness. Various studies have examined the influence of temperature change on prey acquisition and consumption, with particular focus on population and community ecology (e.g. Post and Peterson 2008; Brodie et al. 2012; Dell et al. 2014). With respect to ectotherms, temperature can strongly influence behavior, duration of activity, and rates of physiological processes (Grant and Dunham 1988; Gunderson and Leal 2015; McMunn and Pepi 2022). Warmer temperatures have been found to increase rates of food consumption and prey attacks and decrease handling time in ectotherms (Persson 1986; Hewitt and Duncan 2001; Niu et al. 2003; Haubrock et al. 2020). Increases in food consumption have been predicted, and documented, to have cascading effects on communities through changes in abundance and behavior at different trophic levels (Rodríguez-Castañeda 2013; Veselý et al. 2019; Durant et al. 2019). While it is known that functional relationships and physiological processes can vary in response to temperature, less attention has been paid to the influence of interacting effects of temperature and food on individuals.

Populations are a common focus for predicting and quantifying the influence of environmental change on systems (e.g. Warren et al. 2001; Sattertwate 2009; Liang et al. 2021). However, populations are composed of individuals, and ecological processes observed within populations are a result of multiple mechanisms acting at the individual level (Dunham and Beaupre 1998). Therefore, understanding mechanisms governing individual responses to

environmental change can provide insight into population characteristics and observed phenomenon. While individual changes in physiology and behavior within a single trophic level, due to abiotic conditions, can have cascading effects, it is likely that environmentally induced trophic changes influence individual processes as well. If the environment imposes constraints on prey availability (e.g. behavioral changes, abundance, movement, etc.) predators may experience bottom-up effects. Reduced prey could pose constraints on individual processes, especially when combined with altered thermal regimes.

Energy available for allocation to growth, storage, maintenance, and reproduction is primarily dictated by the amount of food animals can consume (Congdon et al. 1982). However, the nature of temperature-dependent food consumption is curvilinear, where organisms consume more food at warmer temperatures, before experiencing a thermal optimum, after which performance declines (Huey 1982; Beaupre et al. 1993b; Angilletta 2001b). Warmer body temperatures can increase metabolic rate (Beaupre et al. 1993a; Angilletta 2001a; Hölker 2003), while decreasing digestive passage time (time to pass a single food item from consumption to excretion) (Waldschmidt et al. 1986; Plasman et al. 2019). Subsequently, higher metabolic rates, if the magnitude is great enough, can result in the need for greater food consumption to meet energetic demands. Additionally, if animals forage when there is room in the gut and the environment is favorable, decreased passage time could result in increased frequency of foraging and food consumption. Therefore, if warming temperatures are paired with decreased food availability, ectotherms could experience critical declines in energy budgets (Beaupre 1995), as energetic costs associated with maintenance and food acquisition could increase without sufficient prey. Such changes in individual energy budgets with temperature could have subsequent effects on populations. Even when ectotherms maintain current body temperatures,

prey decreases could result in lower energy budgets, potentially altering reproduction, life history, and persistence.

When considering compounding effects of temperature and prey availability, a variety of scenarios are possible. Researchers often study the effects of changing daily body temperatures, or temperatures exceeding critical thermal limits (Deutsch et al. 2008). However, many ectotherms actively regulate body temperature during the day through behavioral and physiological mechanisms, as the sun and habitat structures can provide thermal heterogeneity (Huey and Slatkin 1976; Ouedraogo et al. 2003). Additionally, ectotherms are known to sustain activity during the day across a range of temperatures (Mautz and Case 1974; Grant and Dunham 1988; Gunderson and Leal 2016). At night, the thermal landscape becomes more homogenous, and many ectotherms cease activity and find retreats. When activity ceases at night, it is likely that an ectotherms' body temperature reaches equilibrium with the surrounding habitat (Porter and Gates 1969). Therefore, if environmental temperatures change, nighttime temperature may have a greater influence than daily temperatures or extremes on ectotherms. Additionally, some studies indicate that nighttime temperatures are warming more rapidly than daytime temperatures due to climate change (Vose et al. 2005; Davy et al. 2017).

Lizards have been the focus of studies of thermal biology and life history for decades (e.g. Porter and Gates 1969; Huey and Slatkin 1976; Beaupre et al. 1993b; Sears 2005; Hao et al. 2021). Lizards in the genus *Sceloporus* are particularly useful for studying the influence of environmental attributes, including nighttime temperature, on ectotherms because they have a known sensitivity to temperature, are diurnal, and widely distributed with variable life history (Tinkle and Ballinger 1972; Beaupre et al. 1993b; Niewiarowski 1995; Angilletta 2001b; Buckley 2008). *Sceloporus* lizards are insectivorous, which is comparable to many other

organisms, including other reptiles, amphibians, birds, mammals, and invertebrates. Predictions for insect response to climate change vary. Increases are predicted to occur in instances where warmer temperatures result in earlier emergence and development, less overwintering mortality, and where insects live below their thermal optimum (Whittaker and Tribe 1998; Bale et al. 2002; Deutsch et al. 2008; Adamo and Lovett 2011). Alternatively, insect metabolism is highly sensitive to temperature change, which may result in rapid responses to climate change compared to their food sources (Berggren et al. 2009; Jamieson et al. 2012). Therefore, the synchrony of plants and insects may be disrupted influencing survival and fitness of insects emerging before their host plants. Additionally, reduced snowfall could make invertebrates overwintering in leaf litter experience higher mortality due to loss of snow insulation and water, resulting in freezing and desiccation (Bale 1991; Lombardero et al. 2000). Therefore, it is possible that insectivorous organisms, including *Sceloporus* lizards, may experience an increase or decrease in prey.

The objectives of the current study were to quantify the effects of warming nighttime temperatures and variable prey availability on digestive physiology, in prairie lizards (*Sceloporus consobrinus*). Specifically, rates of food consumption, digestive passage time, metabolizable energy intake (MEI), assimilated energy (AE), fecal production, and urate production were measured under multiple scenarios of nighttime warming and prey availability. Temperature treatments were designed to examine current temperature regimes and two scenarios forecasted by the Intergovernmental Panel on Climate Change (IPCC). Prey availability treatments represented low, moderate, and high prey, based on quantified food consumption rates for *S. consobrinus*. The physiological variables of interest were selected because they directly influence energy budgets and likely vary in response to prey and temperature. Analyses were run to consider the influence of prey availability on physiology under each temperature scenario, and

to consider the influence of each nighttime temperature increase on physiology. I hypothesized that lizards would increase consumption, MEI, AE, fecal production, and urate production with warming nighttime temperatures, while passage time would decrease, as ectotherm physiology often has higher rates at warmer temperatures. I also hypothesized that lizards would proportionally increase food consumption and energy budgets in relation to prey availability.

## **4.3 Methods**

### *4.3.1 Field Temperature Measurements*

To inform lab treatments of current body temperature profiles of *S. consobrinus*, field data were collected. To determine daytime body temperatures ( $T_b$ ) of active lizards, measurements were made in 2020 and 2021 by inserting a fine wire thermocouple into the cloaca of active lizards captured within two minutes of being located. To inform lab trials, daytime  $T_b$  was averaged across all measurements taken. To determine nighttime retreat temperature, 45 iButton temperature loggers were placed in lizard retreats (primarily rock crevices) at field sites in 2021 for three consecutive nights in March, April, May, June, July, and August. To inform lab trials of nighttime body temperature, all nighttime retreat temperatures were averaged. It was assumed that at night, lizard body temperature reflected retreat temperature (Porter and Gates 1969).

### *4.3.2 Study Organism*

Adult *Sceloporus consobrinus* were captured by hand or with a lizard loop in northwest Arkansas from 2021 – 2022. Data collected on lizards included snout-vent length (SVL) using a clear ruler, mass using a Pesola spring scale, and sex via presence (male) or absence (female) of post-anal scales. Lizards were immediately brought to the University of Arkansas and individually housed in 10-gallon tanks with a natural sand substrate, a heat lamp, and a hide box,

with water provided ad-libitum. Lizards were fed a diet of crickets, were misted with water every other day, and supplemented with vitamin D every two weeks.

#### *4.3.3 Nighttime Warming and Food Availability Treatments*

Three temperature treatments were implemented, one representing current conditions, and two scenarios reflecting climate change forecasts. The IPCC created a goal of maintaining a 2°C or less global temperature increase to reduce catastrophic (IPCC 2019). However, to achieve this goal global policy would have had to quickly shift emissions at the time of the suggestion (New et al. 2011). Instead, it is predicted that the world is on a trajectory to a global mean increase of 3 – 5°C increase, or at least exceeding +2°C temporarily before dropping again, upon future reductions in emissions (Knutti et al. 2015; Dunlop and Spratt 2018). Based on current predictions of likely scenarios for global temperature increases, two trials were implemented to reflect climate predictions, one consisting of a 2°C nighttime temperature increase, and another consisting of a 4°C nighttime temperature increase. Daytime body temperatures in every trial reflected the average body temperature of active lizards under current conditions. Therefore, the three temperature treatments all had a daytime temperature of 32.4°C (based on field data), and treatment 1 (current conditions) had a nighttime temperature of 20.4°C (based on field data), treatment two (+2°C) had a nighttime temperature of 22.4°C, and treatment three (+4°C) had a nighttime temperature of 24.4°C.

Three prey availability treatments were implemented within each temperature treatment. To determine prey availability treatments, a preliminary lab study was conducted at 33°C (temperature maintained with an environmental chamber,  $\pm 1.0^\circ\text{C}$ ) to determine the amount of food a lizard would voluntarily eat when at the daytime body temperature. For the preliminary study, lizards ( $n = 9$ ) were placed in plastic containers (41.9 cm x 33 cm x 16.8 cm) with a hide

box and water bowl and acclimated for 5 days to 33°C. Lizards were fasted for the last 3 days of acclimation to ensure the gut was empty. To quantify voluntary consumption rate, lizards were offered Fluker's 2- and 3-week-old crickets weighed to the nearest 0.1 mg, until feeding ceased. Once lizards stopped eating, the final cricket was left in the tank for two hours before removal to ensure satiation. Based on the results of the voluntary food consumption rates at 33°C, for the current study the high prey availability treatment lizards were offered  $0.45 \pm 0.025$  grams wet mass daily, the moderate prey availability treatment lizards were offered  $0.3 \pm 0.025$  grams wet mass daily, and the low prey availability treatment lizards were offered  $0.15 \pm 0.025$  grams wet mass daily. The high prey availability treatment was slightly lower than the observed maximum consumption, because the preliminary trial was based on fasted animals, whereas in the actual prey availability treatments lizards would be fed daily. Additionally, the average body temperature in the preliminary trial was slightly higher than that in the actual nighttime warming treatments. The low prey availability treatment was determined by rounding the lowest observed consumption in the preliminary trial. The low value was selected knowing that lizards would be offered food daily and with the objective of preventing starvation or decreased body condition. The moderate prey availability treatment was selected to be in the middle of the high and low treatments. Lizards were randomly assigned to treatments, with males and females as evenly divided as possible to randomize the effect of sex. Treatments consisted of: 1) current conditions (32.4°C day, 20.4°C night) with high (n = 11), moderate (n = 11), and low (n = 8) food availability, +2°C conditions (32.4°C day, 22.4°C night) with high (n = 10), moderate (n = 11), and low (n = 8) food availability, and +4°C conditions (34.4°C day, 22.4°C night) with high (n = 10), moderate (n = 9), and low (n = 10) food availability.

#### *4.3.4 Feeding Trials*

During lab trials, lizards were housed in plastic tanks (41.9 cm x 33 cm x 16.8 cm) lined with butcher paper, a hide box, and water provided ad-libitum. Lizards were acclimated to their respective temperature treatments 5 days prior to the onset of trials. At the beginning of the acclimation period lizards were fed a single meal to allow for digestion, and then fasted for 3 days to ensure the gut was empty. Temperature was maintained using a walk-in environmental chamber ( $\pm 0.5^{\circ}\text{C}$ ). During trials lizards were fed Fluker's 2- and 3-week-old crickets, weighed to the nearest 0.1 mg every morning, and allotted ~2 hours for consumption. Any uneaten food remaining after this time was removed and reweighed.

To begin lab trials, a single cricket was injected with a mark consisting of a UV-fluorescent powder mixed with water. The fluorescent powder associates with feces (Beaupre et al. 1993b), and does not influence edibility of the cricket, so consumption is voluntary. The time lizards consumed the first mark was noted, and then tanks were monitored every 2 – 4 hours for feces. After the first mark was excreted, typically 10+ days were allotted to feeding lizards and collecting feces and urates, to adequately measure consumption and collect samples for calorimetry. Following this period, a second marked food item was fed to lizards, and tanks were monitored again every 2 – 4 hours until the first appearance of the mark in feces. Trials were considered complete at the first appearance of the second marked food item in feces. Feces and urates were collected, and consumption measured, during trials in between the first appearance of the first mark and the first appearance of the second mark. All feces and urates were separated, frozen, and freeze dried.

#### *4.3.5 Data Collection*

To determine food consumption (kJ), a wet mass for 20 crickets was taken. Crickets were then freeze dried, and reweighed, to determine the percent water. The percentage of water in



crickets was used to convert wet mass consumed by lizards into dry mass consumed. The energy density of crickets was then determined by homogenizing the 20 freeze dried crickets, which were analyzed in triplicate using bomb calorimetry (Parr Semimicro Calorimeter). The results were averaged and used to convert dry mass consumed into kilojoules. Digestive passage time is a measurement of the time it takes to pass a food item from consumption to excretion. Passage time was calculated as the time from consumption of the marked cricket to the first appearance of the mark in feces.

Fecal samples collected throughout the trial were pooled for each individual lizard, respectively. Feces were then homogenized, weighed, and analyzed via bomb calorimetry to determine the energy density. The energy density of feces was averaged across individuals, and a single value was used to determine fecal production. The same methods used to determine fecal production were used to determine urate production. Urate samples collected throughout a trial were pooled for each individual lizard, homogenized, weighed, and analyzed via bomb calorimetry to determine the energy density. The energy density of urates was averaged across individuals, and a single value was used to determine urate production.

Metabolizable energy intake measures the maximum potential energy to be allocated towards growth, maintenance, storage, and reproduction, and is calculated using the formula:

$$MEI = C - F - U$$

where C is energy consumed (kJ), F is energy lost as feces (kJ), and U is energy lost as uric acid (kJ). Assimilated energy represents digestible energy, and is calculated using the formula:

$$AE = C - F$$

#### *4.3.6 Statistical Analyses*

##### Influence of Nighttime Temperature

To determine how digestive physiology varied due to nighttime temperature in each prey scenario, analyses were run within each prey availability treatment, among temperatures. ANCOVAs were applied within each prey treatment to determine the effect of nighttime warming on food consumption with lizard SVL and trial length as covariates along with interaction terms (SVL\*temperature treatment and trial length \*treatment treatment) to test for heterogeneity of slopes. ANCOVAs were run within each prey availability treatment to determine the effect of nighttime warming on passage time, fecal production, urate production, MEI, and AE with covariates of trial length along with interaction terms (trial length\*temperature treatment) to test for heterogeneity of slopes. Post-hoc Tukey HSD tests were run on means adjusted for the covariate for each significant ANCOVA to determine which temperature treatments differed. The probability of a type 1 error was assumed to be 0.05 for all analyses. Food consumption is likely to influence fecal production, urate production, MEI, and AE. However, consumption was not included as a covariate because the current study was focused on how varying food consumption influences physiology and energy budgets, and therefore analyses were performed without adjusting for consumption. The residuals from all analyses were assessed to meet the assumptions of parametric statistics with the probability of committing a type 1 error equal to 0.05. All analyses were run in R (version 4.1.3) (R Core Team 2022).

#### Influence of Prey Availability

To determine how digestive physiology varied in response to prey availability within each temperature treatment, analyses were run within each temperature treatment comparing prey availability scenarios. ANCOVAs were applied within each temperature treatment to determine the effect of prey availability on food consumption with lizard SVL and trial length as

covariates along with interaction terms (SVL\*temperature treatment and trial length \*treatment treatment) to test for heterogeneity of slopes. ANCOVAs were applied within each temperature treatment to determine the effect of prey availability on passage time, fecal production, urate production, MEI, and AE with covariate of trial length along with interaction term (trial length\*temperature treatment) to test for heterogeneity of slopes. Post-hoc Tukey HSD tests were run on means adjusted for the covariate for each significant ANCOVA to determine which prey availability treatments differed. The probability of a type 1 error was assumed to be 0.05 for all analyses. The residuals from all analyses were assessed to meet the assumptions of parametric statistics with the probability of committing a type 1 error equal to 0.05. All analyses were run in R (version 4.1.3) (R Core Team 2022).

## **4.4 Results**

### *4.4.1 Preliminary Food Consumption Trial*

Fasted lizards, on average, consumed  $0.49 \pm 0.2$  grams of crickets at 33°C, which informed the high prey availability treatment. The minimum consumed by lizards in the preliminary study was 0.16 grams wet mass, which was used to inform the low prey availability treatment.

### *4.4.2 Statistical Analyses*

While some residuals deviated slightly from normality, all followed a hump-shaped distribution and were deemed suitable for the robust procedures of ANCOVA (Blair 1981). The prey availability treatments were successful in achieving a distribution of consumption for all temperature treatments, ranging in consumption from 2.95 – 30.34 kJ ( $\bar{x}$  = 12.64 kJ) for the current condition treatment, 5.13 – 26.84 kJ ( $\bar{x}$  = 16.52 kJ) for the +2°C treatment, and 3.36 – 26.40 kJ ( $\bar{x}$  = 12.46 kJ) for the +4°C treatment. For high food availability treatments, lizards

rarely consumed all food offered, and regularly ate until satiation. Trial length had no influence on any analyses conducted and was therefore removed.

### Influence of Nighttime Temperature

#### Food Consumption

The energy density of crickets was  $23.2 \pm 0.28$  kJ/gram. In the low prey availability treatment, consumption significantly differed among temperature treatments (ANCOVA  $p = 0.0011$ ,  $F = 9.969$ , Figure 1A). Food consumption was significantly higher in the +2°C treatment than current conditions (Tukey HSD  $p < 0.001$ ) and the +4°C treatment (Tukey HSD  $p = 0.014$ ), while the current condition trial and +4°C trial did not differ. There was a significant effect of lizard SVL, where food consumption decreased as SVL increased (covariate,  $p = 0.0215$ ,  $F = 6.280$ , Figure 2). There was no interaction between SVL and temperature treatment. Under moderate and high prey availability, there was no effect of lizard SVL on food consumption (covariate) and no interaction between SVL and temperature trial, and therefore ANOVAs were run without an SVL covariate. In contrast to the low prey conditions, when lizards experienced moderate and high prey availability, nighttime temperature did not significantly influence food consumption.

#### Digestive Passage Time

In the low prey availability treatment, passage time significantly differed (ANCOVA  $p = 0.0167$ ,  $F = 4.954$ , Figure 1B), with the current condition treatment significantly slower than the +4°C treatment (Tukey HSD  $p = 0.0133$ ). Under moderate and high prey availability digestive passage time was not influenced by nighttime temperature.

#### Fecal Production

Under low prey availability, fecal production significantly differed among temperature treatments (ANCOVA,  $p < 0.001$ ,  $F = 11.0$ , Figure 1E), with significantly lower production in the current condition treatment than the +2°C (Tukey HSD  $p > 0.001$ ) and +4°C (Tukey HSD  $p = 0.0035$ ) treatments. Under moderate and high prey availability there was no significant difference in fecal production among temperature treatments

#### Urate Production

Under low prey availability, urate production significantly differed among temperature treatments (ANCOVA  $p < 0.001$ ,  $F = 15.15$ , Figure 1F), with lower urate production in the current condition treatment than the +2°C (Tukey HSD  $p < 0.001$ ) and +4°C (Tukey HSD  $p < 0.001$ ) treatments. In the moderate prey availability treatment, urate production significantly differed (ANCOVA  $p = 0.0067$ ,  $F = 6.068$ , Figure 1E), with the current condition treatment being lower than the +2°C treatment (Tukey HSD  $p = 0.006$ ). Under high prey availability there was no effect of temperature treatment on urate production.

#### Metabolizable Energy Intake

In the low prey availability treatment, metabolizable energy intake significantly differed among temperature treatments (ANCOVA  $p < 0.001$ ,  $F = 6.962$ , Figure 1C), with the +2°C treatment significantly higher than current conditions (Tukey HSD  $p = 0.005$ ) and the +4°C treatment (Tukey HSD  $p = 0.0142$ ), and no difference between the current condition trial and the +4°C trial. Under moderate and high prey availability, metabolizable energy intake did not significantly differ among temperature treatments.

#### Assimilated Energy

Following the same pattern as MEI, AE significantly differed with warming nighttime temperatures under low prey availability (ANCOVA  $p < 0.001$ ,  $F = 8.036$ , Figure 1D), with AE

significantly higher in the +2°C treatment than the current condition treatment (Tukey HSD  $p = 0.0021$ ) and the +4°C treatment (Tukey HSD  $p = 0.0193$ ). Assimilated energy did not differ among temperature treatments under moderate and high prey availability.

### Influence of Prey Availability

#### Food Consumption

For all temperature trials, there was no effect of lizard SVL (covariate) and no interaction between prey availability and SVL, so ANOVAs were run in place of ANCOVAs. Significant differences in food consumption among prey availability treatments were detected for all temperature trials. For the current condition treatment, food consumption significantly differed among the low, moderate, and high prey treatments (ANCOVA  $p < 0.001$ ,  $F = 35.76$ , Figure 1A), with food consumption significantly high in the ‘high’ prey availability treatment compared to the moderate (Tukey HSD  $p < 0.001$ ) and low (Tukey HSD  $p < 0.001$ ). In the +2°C nighttime increase trial, food consumption significantly differed (ANCOVA  $p = 0.0482$ ,  $F = 3.342$ , Figure 1A), with higher consumption in the high prey availability treatment than in the low treatment (Tukey HSD  $p = 0.0385$ ). The high and moderate, and moderate and low, prey availability treatments were not significantly different under +2°C nighttime warming. In the +4°C trial, food consumption also significantly differed (ANCOVA  $p = 0.0096$ ,  $F = 5.589$ , Figure 1A), being higher in the high (Tukey HSD  $p = 0.0256$ ) and moderate (Tukey HSD  $p = 0.0169$ ) prey availability treatments in comparison to the low treatment.

#### Digestive Passage Time

Digestive passage time only differed among prey availability treatments in the current condition trial (ANCOVA  $p < 0.001$ ,  $F = 11.77$ , Figure 1B). Passage time was significantly

slower in the low prey treatment than the moderate (Tukey HSD  $p < 0.001$ ) and high (Tukey HSD  $p = 0.001$ ) treatments.

#### Fecal Production

In the current condition trial, fecal production significantly differed (ANCOVA  $p < 0.001$ ,  $F = 35.46$ , Figure 1E), with the high prey availability treatment having higher production than the low (Tukey HSD  $p < 0.001$ ) and moderate (Tukey HSD  $p < 0.001$ ) prey treatments. In the +2°C and +4°C treatments, the ANCOVA did not detect differences in fecal production among prey availability treatments.

#### Urate Production

In the current condition trial, urate production significantly differed (ANCOVA  $p < 0.001$ ,  $F = 25.23$ , Figure 1F), with the high prey treatment significantly higher than the low (Tukey HSD  $p < 0.001$ ) and moderate (Tukey HSD  $p < 0.001$ ) treatments. Urate production did not differ by prey availability in the +2°C and +4°C treatments.

#### Metabolizable Energy Intake

Prey availability significantly influenced MEI in all temperature trials. In the current condition trial, MEI significantly differed (ANCOVA  $p < 0.001$ ,  $F = 33.47$ , Figure 1C), with the high prey availability treatment significantly higher than the low (Tukey HSD  $p < 0.001$ ) and moderate (Tukey HSD  $p < 0.001$ ) treatments. In the +2°C trial, MEI significantly differed (ANCOVA  $p = 0.0455$ ,  $F = 3.505$ , Figure 1C), being significantly higher in the high prey availability treatment than the low (Tukey HSD  $p = 0.0385$ ), with the moderate prey availability not differing from other prey availability treatments. In the +4°C trial, MEI significantly differed (ANCOVA  $p < 0.001$ ,  $F = 547.2$ , Figure 1C), being lower in the low prey availability treatment than the moderate (Tukey HSD  $p = 0.0073$ ) and high (Tukey HSD  $p = 0.01884$ ).

### Assimilated Energy

In the current condition trial, AE significantly differed (ANCOVA  $p < 0.001$ ,  $F = 34.41$ , Figure 1D), with the high prey availability treatment significantly higher than the low (Tukey HSD  $p < 0.001$ ) and moderate (Tukey HSD  $p < 0.001$ ) treatments. In the +2°C trial, AE was significantly higher in the high prey availability treatment than the low (ANCOVA  $p = 0.0494$ ,  $F = 3.4$ , Tukey HSD  $p = 0.0415$ , Figure 1D). The +4°C trial significantly differed in AE (ANCOVA  $p = 0.008$ ,  $F = 5.72$ , Figure 1D), with the low prey availability treatment significantly lower than the moderate (Tukey HSD  $p = 0.0165$ ) and high (Tukey HSD  $p = 0.0223$ ) treatments

### **4.5 Discussion**

Warming nighttime temperatures and prey availability interacted to influence digestive physiology and energy budgets in *Sceloporus consobrinus*. Many studies emphasize the singular effects of temperature change, or prey availability, on organisms (e.g. Yang et al. 2005; Barton et al. 2019; Thorl et al. 2021). However, the current study exemplifies how the two factors can have additive and antagonistic effects. Climate change studies often focus on daytime temperatures or thermal extremes (Speights 2017), but animals who behaviorally thermoregulate during the day may experience the most drastic changes in body temperature at night. Therefore, the effect of increasing nighttime temperatures altering energy budgets may be of great concern. The results presented here suggest that a 2°C increase in nighttime temperature could maintain, or increase, rates of food consumption and subsequent MEI and AE, proportionally with prey availability. However, a 4°C increase in nighttime temperature has varying effects, depending on prey availability. Therefore, changes in nighttime temperature interact with prey availability differently, and have variable effects on digestive physiology.



Under a +4°C nighttime temperature regime, lizards may have experienced physiological and processing constraints which prevented greater food consumption. Instead of continuously increasing consumption with prey, lizards had a large increase in food consumption between the low and moderate treatments before leveling off, reaching maximum consumption under moderate prey availability conditions in the +4°C trial. In comparison, lizards in the current condition treatment consistently increased food consumption based on prey availability, with the largest increase between moderate and high prey availability. Therefore, when prey availability was high and temperatures increased by +4°C, lizards had relatively smaller energy budgets than when prey was high, and temperatures represented current conditions. When prey availability was low or moderate and nighttime temperatures increased by 4°C, energy budgets either remained relatively the same or increased in comparison to current conditions.

In contrast to current conditions and +4°C trials, lizards in the +2°C treatment had the highest rates of food consumption, MEI, and AE in low and moderate prey availability scenarios, and had comparable values as current conditions in the high prey availability scenario. Food consumption played a primary role in dictating MEI and AE. Lizards in the +2°C trial had the highest rates of food consumption in low prey availability treatments. From there, lizards greatly increased food consumption under moderate prey availability, which was sustained under high prey availability. The initially high rates of consumption and subsequent increase among lizards in the +2°C trial allowed for higher, or comparable, MEI and AE in comparison to other temperature treatments, regardless of prey availability. Therefore, if nighttime temperatures warm by +2°C, lizards may benefit by having higher energy budgets under low and moderate prey availability conditions or experience no change with comparable energy budgets under high prey availability conditions.

Many thermal performance curves are based on measurements at stable temperatures (Huey and Stevenson 1979; Pinch and Claussen 2003; Telemeco 2014). However, the variable rates in digestive physiology observed among daily temperature cycles suggest that warming nighttime temperatures alone can influence performance and generate unique performance curves. In the current study, the optimum for consumption within the daily cycle was closest to the +2°C nighttime treatment. Therefore, when nighttime temperatures were low lizards could increase consumption with prey availability because initial consumption rates were low, and they had not reached maximal performance. When nighttime temperatures warmed by 2°C, lizards tended to have higher consumption rates when prey was limiting, while still increasing consumption with prey availability. Thereafter, when nighttime temperatures increased by 4°C, consumption began to decline and the overall range of consumption was narrower. It is possible that lizards under 4°C had reached a maximal ability to process food items, and were restricted in comparison to other temperatures. However, future studies are needed to identify if lizards are physically capable of consuming more food under the 4°C increase.

The difference occurring at a +4°C became most pronounced when prey was low, as lizards in current conditions were comparable to those in the +4°C treatment, with the +2°C treatment having significantly higher food consumption. The changes in consumption due to nighttime temperatures and prey availability indicate that thermal performance curves can vary in response to temperature changes experienced for portions of the day. Therefore, daily temperature cycles are important to understanding performance in nature. Despite the ability of *S. consobrinus* to survive and function at the nighttime temperatures implemented and experiencing daily body temperatures here comparable to those in nature, food consumption began to differ as nighttime temperatures exceeded the +2°C increase. Performance curves of

*Sceloporus* lizards constructed from stable temperature treatments indicate that performance increases from 20°C to 24°C (and warmer) (Angilletta et al. 2002). Additionally, a study manipulating food and temperature in *S. graciosus* found performance to improve from 20°C to 24°C, when only considering stable temperatures throughout the day (Waldschmidt et al. 1985). However, the current study found that performance can decrease across these temperatures when lizards experience a daily cycle, and the changes occur at night. Such differences exemplify how thermal performance curves generated from stable treatments may not be representative of natural cycles and do not accurately predict performance in realistic conditions. Additionally, the variation in performance found here indicates that thermal performance curves may interact with the biotic environment.

The interactions of prey availability and warming nighttime temperature on digestion were most pronounced when lizards had low food availability. Differences occurred among temperature treatments at low food availability for all processes measured. Metabolizable energy intake and AE were lowest under low prey availability, due to the considerably lower food consumption at all temperature treatments. Such effects became less prominent as prey increased and overall, MEI and AE increased. Digestive passage only differed among temperature trials in the low food availability treatment, where passage time decreased with warming nighttime temperatures. Additionally, passage time only differed due to consumption in the current condition treatment, with slowest passage times under low prey availability. Digestive processes are suspected to experience diminishing returns (Levy et al. 2017). However, if animals are continuously refilling the gut when room is available, the digestive system is always engaged and, in part, operating at relatively high efficiency. It is possible that under low prey availability, food is completely digested prior to consumption of the next meal, resulting in a more prominent

effect of diminishing returns. In the low prey availability treatment, lizards consumed the lowest amount in the current condition trial. Therefore, the influence of warming temperatures and consumption on passage time was more apparent under low consumption. The change in passage time may be due to lizards experiencing a decreased efficiency of digestive processes more frequently, and slower digestion, when food is low. Retention of food items may increase under low food conditions, possibly maximizing absorption, resulting in a slower passage time under low prey conditions. The findings here are similar to a previous study, indicating that passage time is slower when lizards are fed restricted diets (Waldschmidt et al. 1986). Explicit studies would need to be conducted to determine why passage time may have a greater change under low food consumption.

Nighttime temperatures have been found to influence other organismal processes and differ among taxa. In side-blotched lizards (*Uta stansburiana*) warming nighttime temperatures increased reproductive output, decreased the duration of the reproductive cycle, and increased hatchling mass (Clarke and Zani 2012). However, in common lizards (*Zootoca vivipara*), warming nighttime temperatures decreased reproductive output and success (Brusch IV et al. 2022). Warming nighttime temperature also increased ectoparasitic infestation and altered allocation of resources towards structural growth instead of mass in common lizards (Rutschmann et al. 2021). In English grain aphids (*Sitobion avenae*), warming nighttime temperatures on warm days reduced survival and adult performance, and was predicted to have detrimental effects on the intrinsic rate of population growth (Zhao et al. 2014). In other insects, warming nighttime temperatures are predicted to increase rates of development and allow insects to live closer to their thermal optimum (Speights et al. 2017). However, additional constraints may exist for insects, such as light availability and circadian rhythm. Therefore, the findings of

the current study in conjunction with others indicate that that warming nighttime temperatures may increase ectotherm performance in some instances, but not always.

Previous research has examined food consumption in relation to daily temperature and activity. It was predicted that longer activity at warm body temperatures for lizards may not directly influence food consumption but quicken digestion (Levy et al. 2017). However, when considering nighttime temperatures in the current study, it was found that even if animals consume food until satiation during the day, nighttime temperature can influence digestion and restrict daytime consumption. When only considering stable temperatures, studies indicate that digestive performance follows a standard performance curve and increases with temperature until hitting an optimum (Angilletta 2001; Ojanguren et al. 2001; Angilletta 2002), and the peak is higher if prey availability increases (Waldschmidt et al. 1985; Jonsson et al. 2001). Other studies using daily temperature regimes have found similar results. Specifically, findings at stable temperatures repeatedly indicate performance under reduced prey interacts with temperature change in the same way as performance under high prey, just with reduced efficiency (e.g. Vidal et al. 2002; Mc Donnell et al. 2014; Allan et al. 2022). However, when using cycles in the current study, performance did not always increase proportional to prey availability. Some studies in natural systems have found similar interactions as the current study between temperature and prey on performance. For example, in whitespotted congers (*Conger myriaster*) individual growth rate was more sensitive to temperature when prey availability was low (Mu et al. 2022). White crappie (*Pomoxis annularis*) in reservoirs fed below physiological capacity despite high prey availability at moderate temperatures, but increased consumption when temperatures warmed in ways which were unreproducible under stable temperatures in the

lab (Michaletz et al. 2012). Therefore, including temperature cycles in lab studies may better exemplify complex interactions in nature.

Evidence suggests that nighttime temperatures may be increasing more quickly than daytime temperatures (Vose et al. 2005; Davy et al. 2017). However, many studies examining the influence of temperature and climate change on organisms fail to specifically consider nighttime changes of thermoregulating animals (e.g. Paaijmans et al. 2013; Verberk et al. 2016; Pontes-da-Silva et al. 2018). Meanwhile, many ectotherms face greater challenges with thermoregulating at night, due to the homogeneity of the thermal landscape. Little information exists on how changes in nighttime temperatures could influence organisms, especially with regards to energy budgets. Energy budgets provide important information on resources available for allocation to growth, reproduction, storage, and maintenance, with implications for individual fitness and life history (Congdon et al. 1982). Such factors then have the potential to influence population-level processes and can be beneficial for predictive modeling (Dunham et al. 1989; Beaupre 2002; Kearney 2012). Additionally, temperature changes may interact with the biotic environment, with compounding effects on organisms.

The current study used lizards as a model organism. However, the patterns identified may be applicable to other ectotherms. In particular, the additive and antagonistic effects of increasing nighttime temperature and altering prey abundance may be prevalent among other taxa. The current study indicated that the abiotic and biotic environment can interact to influence bioenergetics, and such interactions can differ based on specific temperatures and prey scenarios. Energy budgets changed in unexpected ways. Current conditions and +4°C nighttime temperature increase can result in similar energy budgets under low prey availability but differ under moderate and high prey availability. Additionally, a thermal optimum for nighttime

temperature may exist and differ from the daily thermal optimum, influencing physiological processes. Such findings not only have implications for climate change and understanding how organisms interact with their environment, but for population-level processes. Prey availability can change in response to factors aside from climate change, including intraspecific and interspecific competition (Anderson 2001). The findings here could be expanded upon by considering how population ecology varies in response to both environmental and internal processes.

Based on the interactions among food consumption, prey availability, and nighttime temperatures, it is likely that if temperatures increased by more than 4°C, *S. consobrinus* would continue to have lower energy budgets due to changes in food consumption. However, increases of 2°C could be beneficial under low and moderate prey. More studies are needed across a range of taxa and disciplines to understand how predicted changes in the abiotic and biotic environment interact to influence organisms. The current study is limited by assuming that animals will behaviorally thermoregulate to their average body temperature daily. However, it is possible that daily variation in thermoregulation is important, or animals will face difficulties in the future with daily thermoregulation. Additionally, only three prey availability scenarios were examined. It is possible that prey could vary in different ways than considered here, which could result in different outcomes. Therefore, future studies should aim to consider more prey conditions and temperature scenarios where nighttime temperatures change, interactions with other critical factors, and incorporate more taxonomic groups.

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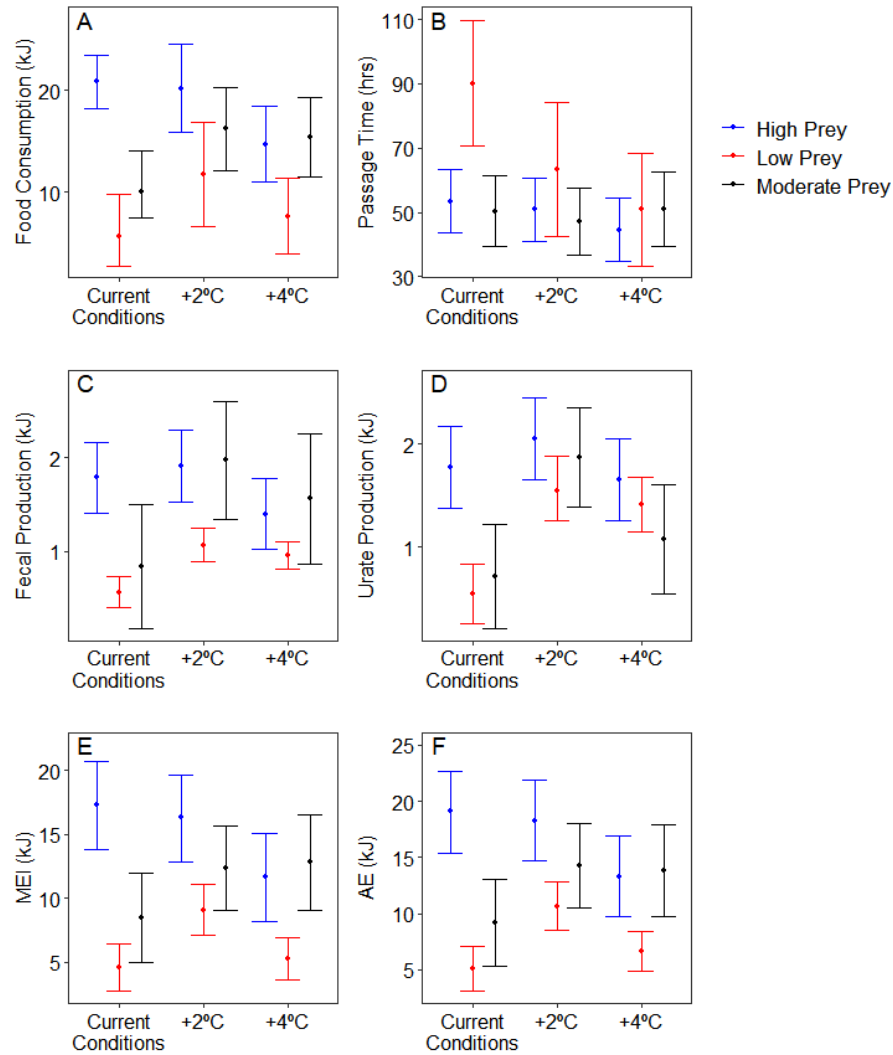
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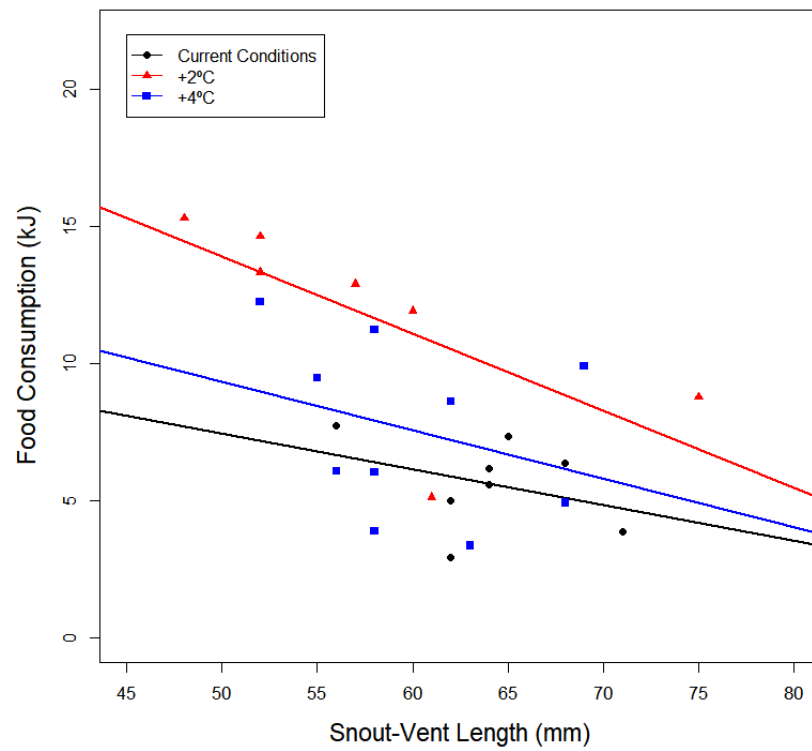
#### **4.8 Figures**





**Figure 1.** Digestive physiology was influenced by nighttime temperature and prey availability.

The 2°C nighttime temperature increase consistently had comparable or more efficient digestive physiology as other temperature trials at all levels of prey availability. Under current conditions, prey availability had a positive effect on digestion, whereas in the 4°C temperature nighttime increase trial performance was maximized under moderate prey availability. The plot for food consumption depicts means adjusted for lizard snout-vent length, and all other plots depict true means. Error bars represent 95% confidence intervals.



**Figure 2.** Food consumption declined with lizard snout-vent length under low prey availability conditions

## **Nighttime warming and altered prey availability influence predicted reproductive output and population growth rate in a modeled ectotherm**

### **5.1 Abstract**

Abiotic and biotic factors can induce changes in individual level processes, which in turn affect populations. With regards to climate change, warming temperatures may be most influential at night for ectotherms who thermoregulate during the day, which is not typically considered in current models. Warming nighttime temperatures could impose energetic tradeoffs, potentially mediated by food consumption. However, prey availability may change in tandem with temperature, resulting in additive effects on reproduction and survival, and population growth. The objectives of the current study were to examine the effects of warming nighttime temperatures and altered prey availability on projected reproductive output and population growth rates using a model organism (prairie lizards: *Sceloporus consobrinus*). Three temperature regimes (current conditions, +2°C, and +4°C) and three prey availability scenarios (high, moderate, and low) were modeled. Clutch sizes were predicted based on metabolizable energy intake and used to inform Leslie matrices, in conjunction with published age-specific survival rates. Populations were projected over ten years. Clutch size changed with warming and prey, which was reflected in population growth rates. Populations grew with high prey under current conditions and 2°C warming but always declined at 4°C warming. Therefore, lizards may not be able to compensate for nighttime warming depending on the magnitude of increase, assuming no plasticity or evolutionary responses. Population growth rate can be influenced by changes in individual energy budgets, and how combined changes in the abiotic and biotic environment have additive effects. Future studies should examine additional factors predicted to change in the future and examine effects of nighttime warming on additional taxa.

## 5.2 Introduction

The environment interacts with biophysical and physiological properties to influence individuals and population dynamics. Populations are composed of individuals, and the individual has been considered the fundamental unit of ecology (Dunham and Beaupre 1998). Therefore, variation in individual behavior and function plays a major role in determining characteristics of populations (Dunham and Beaupre 1998; Plard et al. 2019). However, many studies focus on either individuals or populations respectively, with few approaches examining how individual-level mechanisms influence life history traits, and their contribution to population-level changes. Additionally, many climate change studies at the individual-level do not consider mechanisms involving both abiotic and biotic changes. There is currently a need to identify mechanistically how environmental and biotic changes interact to alter individual performance, and subsequently influence populations. Additionally, data connecting mechanisms on both the individual and population scale will provide clarity as to how and why changes occur in complex systems.

Evidence already suggests that anthropogenic climate change influences species distributions, abundances, and phenology (Strum et al. 2001; Perry et al. 2005; Parmesan 2007). While we are often aware of generalized patterns that occur in nature, and therefore what could potentially result as climate changes, the direct mechanisms mediating phenomena are not always thoroughly understood or even assessed (Lomnicki 1999). One reason for lack of knowledge on mechanisms is that many modeling procedures predicting organismal responses focus on correlative broad scale patterns as opposed to fine scale individual processes (Hannah et al. 2014; Urban et al. 2016). While correlative models can be useful in some contexts (Lomnicki 1999; Buckley et al. 2010), they are limited in their predictive ability. Correlative models are

unable to predict outcomes under novel circumstances (Urban et al. 2016), especially if variables have nonlinear relationships. Mechanistic modeling has increased in popularity over time, but many ecological models concerned with temperature still rely upon thermal performance curves (TPCs) constructed from stable temperature treatments (e.g. Deutsche et al. 2008; Huey et al. 2012; Sinervo et al. 2010; Kingsolver et al. 2013; Vasseur et al. 2014; Huey and Kingsolver 2019). However, TPCs are limited in applicability to predicting performance under realistic cycling temperature regimes (Niehaus et al. 2012). Additionally, TPCs have been found to change due to biotic conditions, such as altered prey availability (Vidal et al. 2002; Donnell et al. 2014; Allan et al. 2022), making combined changes of temperature and biotic conditions hard to predict based on TPCs solely focused on performance across a range of stable temperatures.

Alternatively, some approaches to predicting effects of climate change emphasize temperature-induced restrictions on activity time and make extrapolations of potential effects at the population or species level (e.g. Sinervo et al. 2010; Huang et al. 2020). However, such studies also lack information on resource acquisition, energy allocation, or specific life history traits, which may be key to counteracting the effect of reduced daily activity. Including bioenergetic data has been shown to be important for model predictions (Kearney 2013). Many climate studies draw conclusions based on changes in bioenergetics without making direct measurements. For example, Ivey et al. (2020) assessed available activity time in blunt-nosed leopard lizards (*Gambelia sila*) and predicted population extirpation and potential species extinction. The basis for predictions made by Ivey et al. (2020) were primarily rooted in the suggestion that temperatures will not allow lizards to be active long enough to forage and meet energetic demands, despite lack of data on lizard energetics and resource use. Sinervo et al. 2010 predicted that over the next 70 years 20% of lizard species will be extinct, primarily due to

activity restrictions caused by warming. However, when the model was reconstructed by Kearney (2013) to consider life history and bioenergetics, results concluded that drastic restrictions in activity time were unlikely among most species considered by Sinervo et al. 2010. Additionally, the reconstructed model found that life history and bioenergetic factors play a considerable role in species responses to climate change (Kearney 2013). Such studies lacking a mechanistic basis may have high potential for error, as shown by Kearney (2013). Inaccuracy may be especially concerning when modeling broad taxonomic levels or distributions, as such models often assume all organisms considered will respond similarly without testing the assumption.

Cycling temperature regimes are of significance in thermal biology because they more accurately represent natural conditions experienced by organisms than stable temperatures (Litmer 2023). Nighttime temperatures have been documented to increase quicker than daytime temperatures (Vose et al. 2005; Davy et al. 2017). Additionally, thermoregulating animals (many ectotherms) may be able to sustain body temperatures during the day when active but face greater challenges at night when the thermal landscape becomes more homogenous (Huey and Slatkin 1976). Therefore, daytime body temperatures may not be as susceptible to change as nighttime body temperatures. In addition to temperature, food consumption is a primary factor influencing fitness and the life history of organisms. Energy budgets are heavily dictated by food consumption, which in turn influences allocation to growth, storage, reproduction, and maintenance (Congdon et al. 1982). For many ectotherms, temperature can induce changes in food consumption and digestive physiology, where rates of consumption and digestion typically increase with temperature until an optimum is reached, followed by a decline in performance (e.g. Jonsson et al. 2001; Niu et al. 2003). Warming temperatures can also increase energetic

demands (i.e. metabolic rate), if the magnitude of warming is great enough (Johansen et al. 2015). Warming temperatures, even if only experienced at night, have the potential to alter digestive physiology and energy budgets of ectotherms (Dunham et al. 1989; Grant and Dunham 1990; Brewster et al. 2021), and in turn alter population vital rates. Additionally, prey availability may interact with temperature and digestive physiology in antagonistic or additive ways to influence energy budgets (Beaupre 2002).

It is possible that predator-prey dynamics could change with a warming climate, including altered behavior and changes in abundance (Schmitz and Barton 2014; Laws 2017). If prey availability is high, it may be possible that warming body temperatures could increase energy budgets via higher rates of food consumption for organisms currently operating below their thermal optimum. However, if prey availability is low, warming temperatures could result in higher energetic demands which organisms are unable to compensate for with food consumption. Additionally, some temperature warming may have beneficial effects (placing organisms near their optimum), but too much warming could have negative effects (resulting in a decline in performance). The combined influences of warming body temperature, even if just at night, and prey availability on individual energy budgets could alter allocation to growth and reproduction. If growth and reproduction change, population vital rates and overall population growth may also change (Dunham et al. 1989).

Lizards have been a study organism in thermal biology for decades (e.g. Porter and Gates 1969, Tinkle and Ballinger 1972, Huey 1982, Grant and Dunham 1990) and have been the focus of prominent climate change models and studies (e.g. Kearney and Porter 2004; Sinervo et al. 2010; Huey et al. 2012; Kearney 2013). Lizards are ideal model organisms for examining the effects of temperature and prey availability on individuals and populations. More specifically,

lizards in the genus *Sceloporus* have known sensitivity to temperature, including digestion and energy budgets (Beaupre et al. 1993; Andrews et al. 2000; Angilletta 2001a). Population vital rates, life history, and seasonal activity have also been documented for multiple populations of *Sceloporus* lizards (Tinkle and Ballinger 1972; Adolph and Porter 1993; Haenel and John-Alder 2002; Mosbey 2021). *Sceloporus* lizards are insectivorous and considering climate change insect populations have been predicted to decline (Berggren et al. 2009; Jamieson et al. 2012) or increase abundances (Deutsch et al. 2008; Adamo and Lovett 2011), depending on the circumstance. Therefore, *Sceloporus* lizards offer an ideal opportunity to model the effects of individual-level processes on population dynamics with regards to temperature and prey availability. A model integrating individual- and population-level mechanisms will not only provide predictions of future scenarios with regards to climate change but also inform theory on how temperature and prey availability interact to influence organisms.

The current study's objectives were twofold: 1) examine the influence of warming nighttime temperatures and prey availability on reproductive output, and 2) model the influence of variable reproductive output (due to nighttime warming and prey availability) on population growth rates over a ten-year span, for a population of *Sceloporus* lizards. Three temperature scenarios were considered: one scenario representing current conditions, and two representing potential increases in nighttime temperatures due to climate change (+2°C and +4°C nighttime warming). Three prey availability scenarios were also implemented, a low, moderate, and high scenario. Bioenergetic data were acquired from a previous lab study quantifying energetics under all modeling scenarios of nighttime warming and prey availability. Nine simulations of a bioenergetic model were run to evaluate clutch sizes for first year and adult female lizards, representing all combinations of nighttime temperature and prey availability. The results of the



bioenergetic models were used to inform Leslie Matrix models to project population growth rates for all nine simulations. Sensitivity analyses were run for each simulation to look at sensitivity of population growth rates to survival of each age class and reproductive output. Age-specific survival rates used in the Leslie matrices were obtained from published literature and assumed to be invariant. It was predicted that reproductive output would be influenced by both nighttime warming and prey availability. Specifically, based on the bioenergetic lab trials, it was hypothesized that a 2°C nighttime warming paired with high prey availability would increase reproductive output and population growth rates. In contrast, it was hypothesized that a 4°C nighttime warming may pose constraints on energy budgets and have lower reproductive output and population growth rates, especially under low prey availability.

### **5.3 Methods**

#### *5.3.1 Study Organism*

Simulations were focused on prairie lizards (*Sceloporus consobrinus*), because data have been previously collected on the influence of warming nighttime temperatures and prey availability on individual energy budgets, as well as age-specific survival. *Sceloporus consobrinus* reach sexual maturity in their second active season at ~49 mm snout-vent length (SVL) (Mosbey 2021). Lizards typically become active in March and the first clutches are laid by the end of May, with the second clutches laid by mid-July (Lenard and Gifford 2019). In their first reproductive season, *S. consobrinus* females typically only lay one clutch near the end of the reproductive season. For females in their first reproductive season, energy is allocated towards growth in the beginning of the season until reaching a sexually mature size. By their third active season (second reproductive season), females can lay two clutches per season and are typically an average SVL of 63 mm (Mosbey 2021).

### 5.3.2 Nighttime Warming and Prey Availability Scenarios

Three nighttime temperature scenarios were considered, where each scenario had the same daytime body temperature ( $T_b$ ) of 32.4°C but differing nighttime body temperatures. The daytime  $T_b$  and current nighttime  $T_b$  was determined in a previous study (Chapter 4) based on active *S. consobrinus* lizards in Arkansas and retreat temperatures at night. The three nighttime warming temperature scenarios were: current conditions (nighttime  $T_b$ : 20.4°C), 2°C nighttime temperature increase (nighttime  $T_b$ : 22.4°C) and a 4°C nighttime temperature increase (nighttime  $T_b$ : 24.4°C). The +2°C temperature increase scenario was informed by predictions made by the Intergovernmental Panel on Climate Change (IPCC), who initiated a goal of a +2°C or less global temperature increase (IPCC 2019). However, emissions would have needed to dramatically decline to achieve the IPCC goal (New et al. 2011). Instead, others predict that Earth will likely experience a global increase of 3 – 6°C, at least temporarily (Knutti et al. 2015; Dunlop and Spratt 2018). More extreme predictions were used to inform the +4°C temperature scenario. Three prey availability scenarios were modeled. Prey availability was also based on a previous study (Chapter 4) which quantified voluntary consumption and digestive physiology under three prey availability treatments. The prey availability treatments were low (lizards offered  $0.15 \pm 0.025$  grams daily) moderate (lizards offered  $0.3 \pm 0.025$  grams daily), and high (lizards offered  $0.45 \pm 0.025$  grams daily), based on voluntary feeding rates of lizards at 33°C. A simulation was constructed for all possible combinations of nighttime temperatures and prey availability, resulting in nine simulations.

### 5.3.3 General Model Structure

To examine the effects of nighttime warming and prey availability on individual reproductive output a bioenergetic model was created calculating clutch sizes. The clutch sizes

from the bioenergetic model were then used to inform Leslie matrices, which were projected over a ten-year span. The bioenergetic model generated daily energy budgets (energy available for allocation to growth, storage, maintenance, and reproduction; Congdon 1989) for female lizards beginning at seasonal emergence through oviposition of the last clutch within a season. Females were separated into two age classes: year one females and adult females. Year one females represented lizards in their second year of life, who emerge at a sexually immature size and therefore allocate energy to growth early in the season (Tinkle and Ballinger 1972). Year one females reach sexual maturity in time to lay a single clutch at the end of the reproductive season. Adult females represent lizards in their third year or of life (or older) that emerge at a sexual mature size and lay two clutches per season (Mosbey 2021).

Energy budgets were specific to the conditions of each simulation and based on daily metabolizable energy intake (MEI) quantified in a previous study (Chapter 4) and are described in detail below. After generating daily energy budgets, lizards incurred energetic costs (kJ). Daily maintenance costs were represented by daily metabolic rate during activity and resting metabolic rate at night (in kilojoules) and subtracted from daily energy budgets. Energy remaining after accounting for maintenance, could then be allocated towards growth (and storage) and/or reproduction. Year one females incurred the cost of growth at the beginning of the active season until reaching sexual maturity. The cost of growth, represented by energy (kJ) needed to generate tissue and the metabolic cost of growth (kJ) was subtracted from the remaining daily energy budget. Any remaining energy after maintenance and growth was then allocated to generating eggs for year one females. Adult females emerge at sexual maturity and do not incur a cost of growth. Therefore, any energy remaining after accounting for maintenance costs was allocated towards generating eggs. Adult females laid two clutches per year, and

therefore after ovipositing clutch one, energy budgets were calculated again, based on the number of days before ovipositing for the second time. The energy budget for clutch two used the same protocol as clutch one. Clutch sizes were determined for all combinations of nighttime warming (current, +2°C, and +4°C) and prey availability (low, moderate, and high).

Clutch sizes calculated in the bioenergetic model were used to inform age-specific reproduction in stage-based Leslie matrix models (described below). Leslie matrices were constructed for all nine combinations of nighttime warming and prey availability, using published age-specific survival rates (Tinkle and Ballinger 1972). Leslie matrices were projected over the course of ten years. Projections examined how population growth rates changed in response to effects of varied clutch sizes due to warming nighttime temperatures and prey availability. Sensitivity analyses were then used to determine if population growth rate changed in sensitivity due to simulation conditions. All analyses were ran using R (*version 4.1.3*) (*R Core Team 2022*).

#### *5.3.4 Influence of Nighttime Warming and Prey Availability on Clutch Size*

A bioenergetic model was constructed to predict clutch sizes for reproductive females. In *S. consobrinus*, there are two groups of reproductive females: females in the second year of life (referred to as first year reproductive females hereafter) laying one clutch, and asymptotic females in the third year of life, or older, laying two clutches per season (Mosbey 2021). For each simulation, clutch sizes were simulated for both, the second-year females and third year or older females. For the third year and older female lizards, independent predictions were made for each clutch within a season. All bioenergetic simulations were run for 50 female lizards.

#### Initial Energy Budget Model

For each simulation all lizards were active for 8 hours a day, which is comparable to observed summer activity (when reproduction occurs) for *Sceloporus* lizards (Angilletta 2001a).

Metabolizable energy intake (MEI), which is calculated as:

$$\text{MEI} = \text{C} - \text{F} - \text{U}$$

where C represents food consumption (kJ), F represents fecal production (kJ), and U represents urate production (U), was used to determine energy budgets in each simulation. Metabolizable energy intake was quantified in a previous study (Chapter 4) under each nighttime warming and prey availability scenario, which was used to inform simulations. An index of daily MEI was calculated by dividing total MEI per lab trial in Chapter 4 by the number of days in the trial. Average daily MEI was calculated for each nighttime temperature scenario (current, +2°C, and +4°C) at each prey availability treatment (low, moderate, and high), resulting in a unique estimation of daily MEI for all nine simulations. Fifty values of daily MEI (one per female in the model) were generated using a normal distribution, bounded by 0.25 standard deviations (SD). The 0.25 SD was selected because it maintained energy budgets within the bounds of those observed in lab trials and mimicked natural variation. Daily MEI was considered for days in the active season between emergence and oviposition, which was specific to each reproductive class (outlined below). Emergence through oviposition was considered in the model because it represents a relevant time frame for lizards to acquire and allocate energy prior to and during reproduction. The time frame remained constant among simulations.

To account for daily metabolic costs lizards incurred between emergence and oviposition, resting metabolic rate (RMR) was determined using the RMR formula quantified by Angilletta (2001b) for *S. undulatus* for all simulations. Available RMR data for *S. consobrinus* use mass-specific measurements (Hughes et al. 1982) and were therefore unable to be applied to the

current model. However, *S. undulatus* and *S. consobrinus* appear to have a similar allometric relationship between metabolism and temperature (Hughes et al. 1982; Angilletta 2001b). The formulas to calculate metabolic cost per hour in joules, derived from Angilletta (2001b), were:

$$\text{Photophase: } 2 * (0.4 * \text{Temperature} + 0.9 * (\log(\text{mass})) - .91)$$

$$\text{Scotophase: } (0.3 * \text{Temperature} + 0.9 * (\log(\text{mass})) - .64)$$

The metabolic rate for lizards in each simulation was dependent on  $T_b$  and body mass. Daytime, active metabolic rate was represented using a metabolic scope of two, which has been documented for *Sceloporus* (Christian et al. 1997), and a  $T_b$  of 32.4°C. Resting metabolic rate at night was based on the respective body temperature for each simulation (20.4°C, 22.4°C, or 24.4°C). Hourly metabolic rates were used to calculate the metabolic cost during the day (8 hours) and night (16 hours). To determine energy available to allocate towards egg development, daily metabolic cost was subtracted from daily MEI, to produce a value representing net available energy (NAE) for allocation per day. The NAE per day was then multiplied by the number of days a lizard would be active before oviposition for each clutch using the formula:

$$\text{NAE} = [(\text{Daily MEI} - (\text{Scotophase RMR} * \text{hours inactive}) - ((\text{Photophase RMR} * 2) * \text{hours active})) * \# \text{ of days before oviposition}]$$

The number of eggs in a clutch was determined using an energy density per egg of 3.1589 kJ (Derickson 1976). The total NAE available per clutch was divided by the energy density of an egg to calculate clutch size. Clutch sizes were rounded down to the nearest whole number and averaged among simulated females to inform population models. Lizards were not allowed to reproduce if it would put them in a negative energy balance, and clutch sizes were constrained by body size, dependent on the body size of the reproductive class (described below).

#### First Year Reproductive Females

For first year females, lizard SVL for 50 females at the beginning of the season was generated using a normal distribution with a mean of 40.0 mm and a standard deviation of 0.25 (range: 39.4 – 40.8). Mass was generated following a normal distribution with a mean of 2.4 grams and a standard deviation of 0.25 (range: 1.8 – 3.2 grams). A standard deviation (SD) of 0.25 was used to allow variation in lizard body size, without exceeding realistic bounds generated without constraining SD. Initial SVL was calculated assuming lizards needed to reach a minimum size of maturity at 49 mm (Mosbey 2021) before mid-July to lay a clutch in their first season and using published growth rates for *S. consobrinus* in the field (Niewiarowski and Roosenberg 1993; Nebraska population - formerly *S. undulatus*). Initial mass was calculated based on the relationship between SVL and mass of *S. consobrinus*, determined by data on wild-caught lizards (Figure 1).

First year reproductive females incurred a cost of growth at the beginning of the season. The cost of growth was determined by first determining the dry mass of the lizard. Lizards were considered 28.325% dry mass (Jones et al. 1987). Next, dry mass to be developed by lizards was calculated based on the difference in initial dry mass and dry mass at minimum size for reproduction. Grams of dry mass to be developed were then multiplied by 23.33 kJ/g to determine energy needed for growth to reach sexual maturity (Jones et al. 1987). Metabolic cost of growth was also included as 8.63 kJ/gram of dry mass developed (Peterson et al. 1999). Therefore, the total cost of growth was represented with the formulas:

$$\text{Dry Mass Grown (DM)} = (\text{Reproductive mass} - \text{initial mass}) * 0.28325$$

$$\text{Cost of Growth} = \text{DM} * 23.33 \text{ kJ/g} + \text{DM} * 8.63 \text{ kJ/g}$$

First year reproductive females do not oviposit until the end of the reproductive season and were therefore allotted 136 days (March – mid-July) to accrue and allocate energy. Clutch

size was constrained to 10 eggs, based on the maximum clutch size observed by a 60 mm lizard (Mosbey 2021).

#### Adult Females

For asymptotic females, body mass was generated following a normal distribution with a mean of 7.2 grams. A standard deviation was not applied for asymptotic female mass, because the generated distribution did not exceed realistic bounds (range: 6.6 – 7.8 grams). The average mass for asymptotic adults was calculated based on the relationship between SVL and mass of *S. consobrinus*, determined by data on wild-caught lizards (Figure 1), assuming an average SVL of ~63 for reproductive adults (Mosbey 2021).

Asymptotic females did not incur a cost of growth and laid two clutches per reproductive season. Clutch size was constrained to 15 eggs based on the largest clutches observed in *S. consobrinus* (Mosbey 2021). For the first clutch, lizards were allotted 92 days (March – May) to accrue and allocate energy, as oviposition is from the end of May to early June (Mosbey 2021). If lizards had remaining energy (kJ) after oviposition (and clutch size was constrained to 15 eggs via body constraints, not energetic constraints), it was allocated to costs associated with the second part of the reproductive season (maintenance costs or egg development). For the second clutch, lizards were allotted 44 days (June – mid-July) to accrue and allocate energy to oviposit by July (Robinson and Gifford 2015).

#### *5.3.5 Leslie Matrix Population Projections - Based on Nighttime Temperature and Prey Availability*

Life tables were constructed for all nine simulations (Table 1), using age-specific reproduction projections from the bioenergetic models and age-specific survival rates based on prairie lizards in Colorado (Tinkle and Ballinger 1972; formerly *S. undulatus*), as there are no



published survival data for adult lizards in Arkansas (where bioenergetic data are available). Population growth rates were projected over ten years for female *S. consobrinus* using stage-based, pre-breeding, Leslie matrices (Table 2). Stages included were hatchlings, first year reproductive females, two-year reproductive females, and three-year reproductive females. Two- and three-year reproductive females had the same reproductive output and were considered the adult females. Age-specific reproduction was based on average clutch size predictions from the bioenergetic model for year one reproductive females and asymptotic females. Life tables only considered female eggs (and subsequent hatchlings), assuming an even sex ratio, which has been reported for young age classes of *Sceloporus* lizards (Ballinger 1973; Tinkle 1976). When there was an odd number of eggs, sex ratios favored females (Ballinger 1973; Tinkle 1976). All populations began with an initial size of 50 female lizards. The stable age distribution for each scenario was used to inform the number of lizards in each age class for year one of all simulations. Population projections were made for all combinations of warming nighttime temperatures (current conditions, +2°C and +4°C) and prey availability (low, moderate, and high) resulting in nine simulations.

#### 5.3.6 Sensitivity Analyses

Sensitivity analyses were performed for each simulation to determine if population growth rate varied in relation to survivorship and reproduction of different age classes, based on nighttime warming and prey availability. Survival and reproduction were selected for sensitivity analyses because they are directly considered in the Leslie matrices, and reproduction was the primary factor considered in the bioenergetic models. Age-specific survival rate was varied for 50 values ranging from zero to one, for each age class. Age-specific reproduction was also varied from zero to ten (using discrete whole numbers) for year one reproductive females and from zero

to 15 (using discrete whole numbers) for two- and three- year females. Sensitivity was compared based on the slope relating population growth rate to age-specific survival or age-specific reproduction of each age class.

## **5.4 Results**

### *5.4.1 Influence of Nighttime Warming and Prey Availability on Clutch Size*

Nighttime warming and prey availability interacted to influence lizard clutch size for both reproductive age classes (Figure 2).

#### First Year Reproductive Females

Under the current climate scenario (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 20.4^\circ\text{C}$ ), prey availability had a strong influence on clutch size, especially when prey was low (Figure 2A). When prey availability was high, and temperatures represented current conditions, the primary constraint on clutch size was body size, and all lizards were able to produce the maximum clutch size possible (10 eggs, largest reported for a 60 mm SVL *S. consobrinus*, Mosbey 2021). When prey availability was moderate, and temperatures represented current conditions, clutch sizes only slightly decreased. However, when prey availability was low under current conditions clutch sizes dramatically declined.

Under the  $2^\circ\text{C}$  nighttime warming scenario (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 22.4^\circ\text{C}$ ), prey availability continued to influence clutch size, although not as dramatically as under current temperature conditions (Figure 2A). When prey availability was high, and temperatures represented  $+2^\circ\text{C}$  nighttime warming, the primary constraint on clutch size was still body size, and all lizards were able to produce the maximum clutch sizes possible. When prey availability was moderate, clutches only decreased by one egg on average. When prey availability was low,

and there was a 2°C nighttime increase, clutches still declined but were larger than under low prey and current conditions.

Under the 4°C nighttime warming scenario (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 24.4^\circ\text{C}$ ), prey availability continued to influence clutch size (Figure 2A). When prey availability was high, and temperatures represented +4°C nighttime warming, the primary constraint on clutch size was no longer body size, but energetic constraints, and lizards produced clutches slightly smaller than other high prey scenarios. When prey availability was moderate, lizards maintained the same clutch sizes on average as high prey conditions, under a 4°C nighttime increase. When prey availability was low, clutches dramatically declined under a 4°C increase in nighttime temperature and were comparable to current conditions with low prey.

#### Adult Females

##### **Clutch One –**

Similar to first year reproductive females, prey availability had a strong influence on the size of the first clutches laid by asymptotic females, especially when prey was low (Figure 2B). When prey availability was high, and temperatures represented current conditions (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 20.4^\circ\text{C}$ ), the primary constraint on the first clutch was body size, and all lizards were able to produce the largest clutch sizes deemed physically possible in the model (15 eggs, Mosbey 2021). Clutch sizes declined proportionally with decreasing prey availability (Figure 2B). Many lizards under low prey conditions and current temperatures were unable to produce clutches. Under 2°C warming, the size of the first clutch laid varied with prey availability (Figure 2B). When prey availability was high, and temperatures represented +2°C nighttime warming (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 22.4^\circ\text{C}$ ), lizards produced large first clutches. Clutches decreased with prey availability, with the biggest decrease between moderate

and low prey conditions (Figure 2B). Under 4°C warming, the size of the first clutch laid also varied with prey availability, but differently than current conditions and +2°C nighttime warming. Moderate prey conditions had higher clutch sizes than high prey conditions, although of comparable sizes (Figure 2B). However, under low prey availability and a +4°C, clutch sizes were low and comparable to low prey and current condition lizards.

### **Clutch Two –**

The size of the second clutch laid by asymptotic adults varied in a similar way as the size of the first clutch, with temperature and prey but second clutches were smaller (Figure 2C). When prey availability was high, and temperatures represented current conditions (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 20.4^\circ\text{C}$ ), lizards produced large second clutches, comparable to their first clutch (Figure 2C). When prey availability was moderate, second clutches were less than half the size of those produced under high prey conditions. When prey availability was low, and temperatures represented current conditions, lizards could not produce a second clutch. Under a 2°C temperature increase, the size of the second clutch also followed a similar pattern as clutch one, although again, at overall smaller sizes (Figure 2C). When prey availability was high, and temperatures represented +2°C nighttime warming (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 22.4^\circ\text{C}$ ), lizards produced smaller second clutches than those in current conditions. While the size of the second clutch decreased with prey, changes were not as strong as those found under current conditions (Figure 2C). Under a 4°C temperature increase, the second clutch continued to vary with nighttime warming and prey availability (Figure 2C). When prey availability was high, and temperatures represented 4°C nighttime warming (daytime  $T_b = 32.4^\circ\text{C}$ , nighttime  $T_b = 24.4^\circ\text{C}$ ), lizards produced slightly larger, although comparable, second clutches as other temperature regimes. Similar to the first adult clutches, when prey availability was moderate, and there was a

4°C increase, lizards produced slightly larger clutches than under high prey conditions (Figure 2C). However, when prey availability was low, lizards were unable to produce a second clutch. with a 4°C increase in nighttime temperature,

#### *5.4.2 Leslie Matrix Population Projections - Based on Nighttime Temperature and Prey Availability*

When prey availability was high, and temperatures represented current conditions, the lizard population increased over the course of ten years ( $\lambda = 1.09$ , Figure 3A). In scenarios where lizards experienced current temperatures, but prey was moderate ( $\lambda = 0.84$ ) or low ( $\lambda = 0.38$ ), populations declined (Figure 3A). The final population size ( $N_0 = 50$ ) at year ten under current temperatures was 123 lizards when prey was high and 10 when prey was moderate. The low prey availability scenario under current temperatures experienced extinction by year five.

Similar to current conditions, when prey availability was high, and temperatures represented +2°C nighttime warming, populations increased over the course of ten years ( $\lambda = 1.04$ , Figure 3B), although at a slower rate than current conditions. Under the +2°C nighttime warming scenarios, when prey was moderate ( $\lambda = 0.94$ ) or low ( $\lambda = 0.74$ ), populations declined (Figure 3B). However, population declines under low and moderate prey availability were not as rapid under a +2°C temperature regime compared to the current temperature regime. The final population size ( $N_0 = 50$ ) at year ten under 2°C nighttime warming was 73 lizards when prey was high, 28 when prey was moderate, and three when prey was low.

Under the 4°C nighttime warming regime, lizard populations always declined, regardless of prey availability. Populations declined quickest under low prey, and similarly under high and moderate prey (high prey:  $\lambda = 0.94$ , moderate prey:  $\lambda = 0.97$ , low prey:  $\lambda = 0.32$ , Figure 3C). The final population size ( $N_0 = 50$ ) at year ten under 4°C nighttime warming was 28 lizards when

prey were high, and 37 when prey were moderate. The low prey availability scenario under the 4°C nighttime warming regime experienced extinction by year five, similar to the projection under current temperatures and low prey.

#### *5.4.3 Sensitivity Analyses*

Overall, population growth rate ( $\lambda$ ) was always most sensitive to age-specific survival of hatchling lizards, regardless of nighttime warming and prey availability.

##### Age-Specific Survival

Regarding age-specific survival, population growth rate ( $\lambda$ ) was most sensitive to the hatchling age class under high (current conditions:  $m = 5.3209$  Figure 4A, +2°C:  $m = 5.3465$  Figure 5A, +4°C:  $m = 5.2059$  Figure 6A), moderate (current conditions:  $m = 4.1892$  Figure 4B, +2°C:  $m = 5.2059$  Figure 5B, +4°C:  $m = 5.241$  Figure 6B), and low prey conditions (current conditions:  $m = 1.099$  Figure 4C, +2°C:  $m = 4.1218$  Figure 5C, +4°C:  $m = 1.1316$  Figure 6C) across all temperatures. However, under low prey conditions population growth rate increased at a quicker rate with hatchling survivorship under the +2°C conditions. Under high (current conditions:  $m = 1.027$  Figure 4A, +2°C:  $m = 0.9526$  Figure 5A, +4°C:  $m = 0.7833$  Figure 6A) and moderate (current conditions:  $m = 0.7594$  Figure 4A, +2°C:  $m = 0.7833$  Figure 5A, +4°C:  $m = 0.8289$  Figure 6A) prey availability, population growth rate was secondly sensitive to age-specific survival of year one females at all temperatures. Third, for current temperature and +2°C scenarios with high prey, population growth rate was sensitive to age-specific survival of year two females (current conditions:  $m = 0.2234$  Figure 4A, +2°C:  $m = 0.2145$  Figure 5A) followed by year three females (current conditions:  $m = 0.1919$  Figure 4A, +2°C:  $m = 0.2022$  Figure 5A). However, the +4°C scenario with high prey was the opposite of the other temperature regimes, being thirdly sensitive to year three females ( $m = 0.2297$ ) followed by year two females ( $m =$

0.1914) (Figure 6A). Under moderate prey all temperature regimes were thirdly sensitive to survival of year three reproductive females (current conditions:  $m = 0.2869$  Figure 4B,  $+2^{\circ}\text{C}$ :  $m = 0.2297$  Figure 5B,  $+4^{\circ}\text{C}$ :  $m = 0.2217$  Figure 6B) followed by survival of year two females under high and moderate (current conditions:  $m = 0.2004$ ,  $+2^{\circ}\text{C}$ :  $m = 0.1914$ ,  $+4^{\circ}\text{C}$ :  $m = 0.1980$ ).

Under low prey conditions, the current condition and  $+4^{\circ}\text{C}$  simulations had similar sensitivity to age specific survival, which differed from high and moderate prey. Specifically, current ( $m = 0.7361$  Figure 4C) and  $+4^{\circ}\text{C}$  conditions ( $m = 0.7361$  Figure 6C) were secondly sensitive to survival of year three females, followed by year one females (current conditions:  $m = 0.3100$  Figure 4C,  $+4^{\circ}\text{C}$ :  $m = 0.3100$  Figure 6C), and then year two females (current conditions:  $m = 0.1496$  Figure 4C,  $+4^{\circ}\text{C}$ :  $m = 0.1496$  Figure 6C). In contrast, under low prey and a  $+2^{\circ}\text{C}$  nighttime increase, sensitivity to survivorship under low prey was more comparable to high and moderate conditions. Under a  $2^{\circ}\text{C}$  increase and low prey, populations were secondly sensitive to survival of year one females ( $m = 0.5933$ ) followed by year three females ( $m = 0.3359$ ), and then year two females ( $m = 0.1726$ ) (Figure 5C). However, population growth rates were always lowest under low prey availability.

#### Age-Specific Reproduction

Regarding age-specific reproduction, population growth rates were most sensitive to year one reproductive females under all temperatures under high (current conditions:  $m = 0.0674$  Figure 7A,  $+2^{\circ}\text{C}$ :  $m = 0.0683$  Figure 8A,  $+4^{\circ}\text{C}$ :  $m = 0.0707$  Figure 9A), moderate (current conditions:  $m = 0.0716$  Figure 7B,  $+2^{\circ}\text{C}$ :  $m = 0.0707$  Figure 8B,  $+4^{\circ}\text{C}$ :  $m = 0.0700$  Figure 9B), and low (current conditions:  $m = 0.0883$  Figure 7C,  $+2^{\circ}\text{C}$ :  $m = 0.0752$  Figure 8C,  $+4^{\circ}\text{C}$ :  $m = 0.0883$  Figure 9C) prey scenarios (Figures 7 – 9). Next, population growth rate was most sensitive to changes in year two female reproductive output at high (current conditions:  $m =$

0.0194 Figure 7A, +2°C:  $m = 0.0201$  Figure 8A, +4°C:  $m = 0.0217$  Figure 9A) moderate (current conditions:  $m = 0.0223$  Figure 7B, +2°C:  $m = 0.0217$  Figure 8B, +4°C:  $m = 0.0212$  Figure 9B) and low (current conditions:  $m = 0.0302$  Figure 7C, +2°C:  $m = 0.0243$  Figure 8C, +4°C:  $m = 0.0302$  Figure 9C) prey availability. Populations were least sensitive age-specific reproduction of year three female reproductive output at high (current conditions:  $m = 0.0061$  Figure 7A, +2°C:  $m = 0.0067$  Figure 8A, +4°C:  $m = 0.0216$  Figure 9A), moderate (current conditions:  $m = 0.0094$  Figure 7B, +2°C:  $m = 0.0081$  Figure 8B, +4°C:  $m = 0.0077$  Figure 9B), and low (current conditions:  $m = 0.0213$  Figure 7C, +2°C:  $m = 0.0115$  Figure 8C, +4°C:  $m = 0.0213$  Figure 9C) prey availability. Population growth rate under all temperature scenarios followed a similar pattern of sensitivity to age-specific reproduction based on prey availability, where populations growth rate was always lower with low prey, yet high (Figures 7A, 8A, and 9A) and moderate prey (Figures 7B, 8B, and 9B) scenarios were comparable. Low prey availability treatments had a higher sensitivity to year three adult reproductive output than other treatments (Figures 7C, 8C, and 9C).

## 5.5 Discussion

Effects of the abiotic and biotic environment on individuals can influence population dynamics. Climate change may pose challenges for many organisms with regards to regulating body temperature, which could have effects on performance and fitness. However, climate effects could be mediated by changes in physiological processes and behavior, including increased rates of food consumption to counter-act higher energetic demands associated with warming temperatures. The findings of the current study indicate that warming nighttime temperatures and changes in prey availability interact to influence individual reproductive output, and subsequent rates of population growth. As nighttime temperatures warmed, clutch



sizes tended to decline, which was then reflected in population growth rates. At the highest level of nighttime warming (4°C) considered, populations always declined regardless of prey availability, and individuals were not able to compensate for higher energetic demands associated with warming temperatures. While populations always experienced declines at low and moderate prey, declines occurred at a slower rate when nighttime temperatures were 2°C above current conditions because clutches were larger. However, at 4°C nighttime warming, population declines at low and moderate prey were comparable to those under current thermal conditions, as were clutch sizes. Overall, the bioenergetic and population models exemplified how warming nighttime temperatures paired with changes in prey availability alter energy budgets, with subsequent effects on reproductive output. Changes in reproductive output, even if reduced by just a few eggs per clutch, had consequential effects on populations and resulted in declines, and in some instances extinction, in less than ten years.

Currently, many climate change models focus on the effects of changes in daily temperatures or thermal extremes (e.g. Sinervo et al. 2010; Kingsolver et al. 2013; Crowell et al. 2021). Such studies fail to account for the ability of animals to behaviorally thermoregulate during the day, which may still be achievable for some organisms under climate warming circumstances. Predictions for ectotherms focused on daily changes in body temperature suggest that energy budgets decline proportionally with reductions in food consumption, with lower performance when prey are low (Huey and Kingsolver 2019). However, the current study indicated that if just nighttime body temperatures increase, energy budgets and subsequent reproduction do not always change proportionally with prey and temperature. Specifically, in the 2°C nighttime warming scenarios, lizards compensated with higher energy budgets and reproductive output in low and moderate prey scenarios, but not in the high prey scenario,

compared to current temperatures. Compensation in low and moderate prey at 2°C warming was still not enough to prevent population declines. Additionally, under a 4°C nighttime warming high and moderate prey treatments had comparable clutch sizes for year one females and clutch two for asymptotic females. Standard thermal performance curves (based on stable temperatures) for *Sceloporus* lizards suggest that performance increases at all nighttime temperatures implemented (Angilletta et al. 2002). If the model constructed in the current study followed the assumptions of Huey and Kingsolver (2019) and standard thermal performance curves, population growth rates likely would have consistently increased with temperature at high prey availability and proportionally decreased with prey at each temperature. Therefore, consideration of the potential for daily thermoregulation and data based on voluntary feeding rates at the temperature cycles of interest likely resulted in different outcomes than otherwise found using traditional approaches.

Climate change forecasts based on stable or daily temperature changes vary based on geographic distribution and taxa. When assessing stable, daily temperature changes and prey availability, findings indicated that clutch size is primarily influenced by prey, not temperature, in pond frogs (*Pelophylax nigromaculatus*) (Gao et al. 2015). However, in coral reef damselfish (*Acanthochromis polyacanthus*), stable, daily warming temperatures induced behavioral changes reducing reproduction despite food availability (Donelson et al. 2010). Contrastingly, in mosquitofish (*Gambusia affinis*), somatic and gonadal growth increased with both warming daily temperatures and food availability (Vondracek et al. 1988). Therefore, daily temperature studies indicate that organisms respond differently to changing temperature and prey availability. However, the magnitude of changes should be carefully considered, as taxa may vary in sensitivity. Currently, data are lacking across taxonomic groups on how combined changes in

nighttime warming and prey availability alter performance representing a knowledge gap. Information across taxonomic groups and distributions on the influence of nighttime warming are needed to determine variability and enhance climate predictions.

The current study found that when nighttime temperatures warm and daytime temperatures remain the same, clutch sizes vary based on prey availability and reproductive age class. For year one reproductive females, when prey was high clutch size did not change with a 2°C increase, and only declined by one egg under a 4°C increase. Adult females experienced continual declines in clutch size with nighttime temperature warming despite high prey availability, due to higher metabolic costs. For both age classes, moderate prey resulted in an increase in clutch size, although by a very low amount, with temperature increases. Under low prey availability, all clutches were largest under a 2°C temperature increase, with the greatest variation in clutch size by temperature in year one females. The variation in clutch size due to age class, prey availability, and temperature suggest that it is important to consider relevant factors besides temperature when predicting future scenarios. Additionally, age classes could respond differently to environmental change due to varying allocation in energy, as year one females incurred a cost of growth but lower maintenance costs due to smaller body size. Additionally, year one females delay reproduction to the end of the season, compared to females emerging already sexually mature, who can reproduce earlier in the season. Larger, older, females had higher maintenance costs and allocated energy between two clutches. Therefore, year one reproductive females under high and moderate prey had smaller changes in clutch size than adult females.

Population predictions based on thermal performance curves and daily warming indicate that population growth rates could change regionally with warming (Deutsch et al. 2008).

Population and species distribution models corroborate such findings, predicting that distribution changes will vary in response to climate change based on location (Herrando-Pérez et al. 2018; Lourenço-de-Moraes et al. 2019). Many population-level climate models do not consider effects of altered prey availability or specific nighttime warming on local persistence. Predator-prey models are commonly used to understand changes in abundance due to prey consumption under different environmental conditions (e.g. McCauley and Murdoch 1990; DeLong and Lyon 2020). Warming temperatures could strengthen the effect of predators on prey populations in the short term, resulting in increased predator and/or prey extinction risk long-term (Rall et al. 2010; Dagaard et al. 2018). Additionally, slight temperature warming has been found to increase the effect of predators on prey, while high degrees of warming reduce the effect of predators (under stable temperatures) (Wasserman et al. 2016). Few predator-prey models consider changes in prey with regards to combined abiotic conditions and the mechanisms occurring at the individual level. Population growth rates for lizards in the current study closely followed predictions for clutch size. Findings indicated that decreased reproductive output by even a few eggs per clutch could cause populations to transition from growing to declining. Therefore, the mechanisms acting on individual energy acquisition and allocation due to temperature heavily dictated the ability for populations to persist under warming nighttime temperatures. Even if prey availability were to remain high, annual reproduction (for all age classes combined) was predicted to decrease by 13 eggs with nighttime warming, with the greatest effect on the oldest age classes. However, it should be noted that the specific model outcomes here may only be applicable to *S. consobrinus*. Although, a major takeaway applicable to future research is how the consideration of individual energetics provided critical information for understanding how temperature and prey interacted with organisms to alter population growth rates over time.

Little information exists on how specific changes in nighttime temperature can influence individuals and populations. Research suggests that nighttime warming could be beneficial or detrimental, depending on the degree of warming and taxon of interest. Side-blotched lizards (*Uta stansburiana*) increase reproductive success (Clarke and Zani 2012), while common lizards (*Zootoca vivipara*) decrease reproductive success (Brusch IV et al. 2022), as nighttime temperatures warm. Studies on insects have also found differing results, where warming nighttime temperatures may reduce survival for some (Zhao et al. 2014) but allow others to live closer their thermal optimum (Speights et al. 2017). However, such findings have yet to be modeled with regards to how changes in individual performance will affect populations (Speights et al. 2017). Moreso, while statistical approaches may deem differences in performance nonsignificant, population models allow for data to be placed into biological context. The original dataset modeled here (Chapter 4) used ANCOVAs to test for differences and found individual energy budgets (MEI) to be statistically similar among nighttime temperature scenarios when prey was high and moderate. However, the bioenergetic and population models revealed that MEI was different enough among temperatures and high and moderate prey to result in different clutch sizes and population trajectories. Therefore, considering individual processes in the context of fitness and population growth can provide additional details of biological variation that may not be captured with traditional statistical approaches. Such information deemed from models can provide operative uses for managing and conserving systems.

A common consideration among climate change models is the possibility of thermally imposed activity restrictions in the future (Sinervo et al. 2010; Leal and Gunderson 2015; Cosendey et al. 2022). If daily temperatures warm, thermoregulating animals may seek refuge to

prevent exposure to high temperatures. Many studies assume that reduction in activity throughout the day will reduce foraging time and food consumption. However, data are lacking on how drastic activity restrictions must be to constrain food consumption (Chapter 1). By quantifying effects of reduced prey availability and food consumption, the current study indirectly addressed the concern of lower food consumption due to restrictions in daily activity. However, as pointed out, food consumption may decline for reasons other than daily activity, such as prey declines, prey behavior, and physiological or functional constraints on food consumption. Future studies should directly examine how quickly organisms obtain food, and if predicted thermal restrictions in activity would alter rates of food consumption and energy budgets. Understanding activity time necessary to maintain adequate food consumption, and other influential factors, would provide insight to the implications of activity time models for understanding energy budgets.

The current study assumed that thermoregulating organisms maintain precision under future climate warming. However, it is possible that for some species daily body temperatures may change despite thermoregulatory efforts. If animals increase time in retreats during the day, they could experience an overall decrease in body temperature (Grant and Dunham 1990; Martín and López 1999). Decreasing body temperature has been found to reduce food consumption (Angilletta 2001a; Hewitt and Duncan 2001), which could lower energy budgets. Alternatively, poikilotherms may remain active under future climate scenarios but experience warm body temperatures more frequently. Warmer daily body temperatures could allow for greater rates of food consumption (Yee and Murray 2004; Zhang et al. 2018) allowing for compensation of warming nighttime temperatures. However, currently there is no data available specifically

evaluating scenarios of warming nighttime temperatures in conjunction with various scenarios of daytime temperatures.

The sensitivity of populations to age-specific survival and age-specific reproduction varied in response to prey availability, and slightly in response to nighttime warming. Populations were always most sensitive to changes in age-specific survival of hatchlings. Hatchling survival plays a major role in dictating the number of year one reproductive females. Year one females are important to population growth because they have the least dramatic change in clutch size due to temperature and prey. Additionally, the hatchling age class typically has the highest rates of mortality. Therefore, if survivorship increases for hatchlings, more individuals survive to older ages, where survivorship is already comparatively high. Under low prey in current conditions and a 4°C nighttime increase, populations became more sensitive to age-specific survival of year three female adults than other scenarios, likely due to high rate of population decline in the simulation. Additionally, population growth rates in sensitivity analyses consistently declined with prey availability. More specifically, under low prey in current conditions and a 4°C nighttime increase, sensitivity analyses indicated that populations only experienced growth when survivorship was above 0.45 for hatchlings and 1.0 for year three adults in current conditions, and above 0.7 for female hatchlings and 1.0 for year three adults in the 4°C temperature increase.

Population growth had fewer differences among prey availability and temperature with regards to sensitivity of age-specific reproduction. Regarding reproductive output, all scenarios were most sensitive to year one reproductive females. However, sensitivity to age-specific survival of hatchlings was comparably greater, as this influences the number of individuals reproducing as year one adults. Similar to age-specific survival, as prey declined population

growth became more sensitive to age-specific fertility of year three females. Population growth rates in response to age-specific reproduction increased with prey availability, and under low prey populations only grew when year one reproductive females had high age-specific reproduction. The sensitivity analyses indicate that prey and temperature interact to determine which age classes contribute most to population growth. Additionally, populations had the potential to experience growth under low prey but would require high age-specific survival of hatchlings and year three females, or high age-specific reproduction of year one females. The variation in sensitivity based on abiotic and biotic conditions indicated that population-management may need to focus on different age classes and vital rates depending on environmental conditions.

Understanding how individual processes mediate population dynamics are important for understanding phenomenological patterns associated with climate change (Helmuth et al. 2005). Digestive processes in ectotherms can be more sensitive than other physiological processes to temperature (Huey 1982; Gunderson and Leal 2015). The thermal sensitivity of digestive processes (including food consumption) and their influence on energy budgets makes assessment and modeling of individual digestion necessary for climate change studies (Leal and Gunderson 2015). Bioenergetic studies provide the ability to mechanistically quantify how biotic and abiotic factors alter reproduction and survival, which is scalable to population dynamics (Dunham et al. 1989; Dunham and Overall 1994). However, few studies on terrestrial organisms make direct, mechanistic, consideration of digestive and bioenergetic processes on population dynamics.

Phenomenological models are informative for understanding what patterns may emerge under certain circumstances, however, such knowledge is limited in use without understanding underlying mechanisms (Dunham and Beaupre 1998). Specifically, prairie lizard populations



may experience declines under current thermal regimes if prey availability declines. Prairie lizards may also decline if nighttime temperatures warm by 2°C in tandem with prey declines, or if nighttime temperatures warm by 4°C regardless of prey. Prairie lizards were used here as a model organism, due to their sensitivity to temperature, diurnal activity patterns, and comparable insect prey source to many other organisms. The specific predictions may not be transferable to other systems as thermal responses vary locally. Additionally, the current study assumed no evolution or plasticity over the predicted time frame. However, the implications of altered nighttime warming and prey availability on bioenergetics and population growth are likely to apply to other groups of ectotherms and should be examined further. The current study was able to examine combined effects of abiotic and biotic changes on individuals to understand why changes may occur among populations due to climate change. Future studies should aim to predict the effects of warming nighttime temperatures on other taxonomic groups across a geographic range, as variation is predicted to occur based on geographic location and population. Additional considerations of other factors likely to change in the future, such as habitat structure, rainfall and humidity, or changes among additional trophic levels, should be made in conjunction with temperature change. Examining more potential temperature cycles, including changing nighttime temperatures and various possible changes in daytime temperatures, is needed to understand how various organisms may be affected by climate change.

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## 5.8 Tables

**Table 1.** Life tables were created for *Sceloporus consobrinus* under three nighttime warming conditions (daily  $T_b = 32.4^\circ\text{C}$ ) and three prey availability conditions. Conditions included current temperatures (nighttime  $T_b = 20.4^\circ\text{C}$ ),  $2^\circ\text{C}$  warming (nighttime  $T_b = 22.4^\circ\text{C}$ ) and  $4^\circ\text{C}$  warming

(nighttime  $T_b = 24.4^\circ\text{C}$ ), and high, moderate, and low prey availability. Age-specific fecundity ( $m_x$ ) was based on bioenergetic model predictions and age-specific survival ( $p_x$ ) data were acquired from Tinkle and Ballinger (1972).

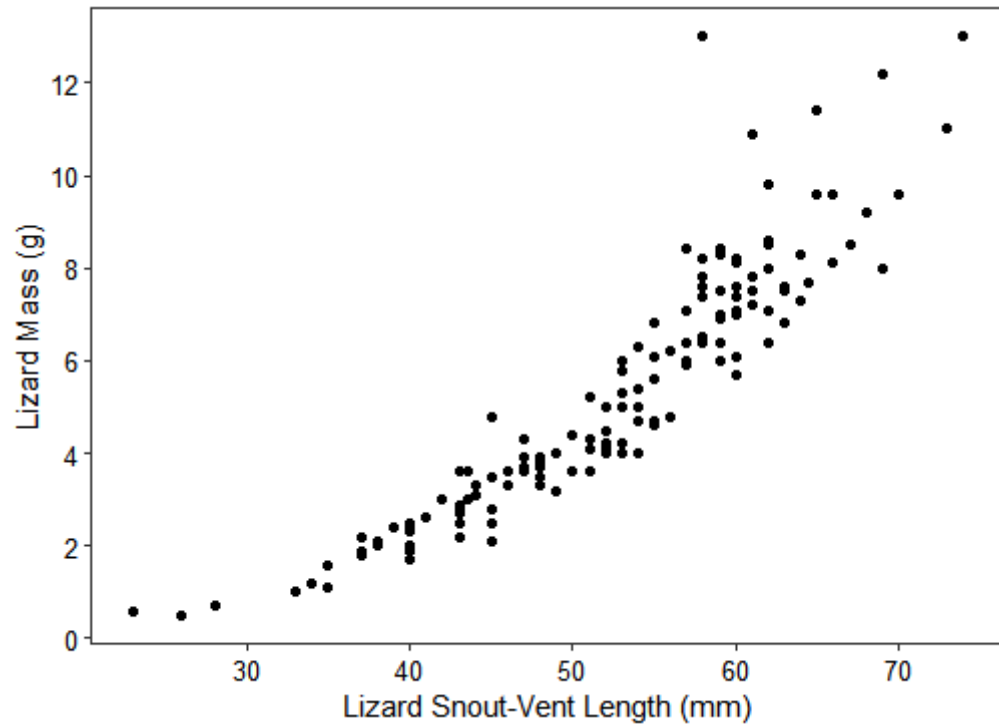
High Prey Availability			Moderate Prey Availability		Low Prey Availability	
Current Temperatures						
Stage	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>
Hatchling	0	0.14	0	0.14	0	0.14
YR1 Adult	5	0.27	4	0.27	1	0.27
YR2 Adult	15	0.33	8	0.33	1	0.33
YR3 Adult	15	0.05	8	0.05	1	0.05
2°C Nighttime Temperature Increase						
	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>
Hatchling	0	0.14	0	0.14	0	0.14
YR1 Adult	5	0.27	5	0.27	4	0.27
YR2 Adult	13	0.33	9	0.33	5	0.33
YR3 Adult	13	0.05	9	0.05	5	0.05
4°C Nighttime Temperature Increase						
Stage	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>	m <sub>x</sub>	p <sub>x</sub>
Hatchling	0	0.14	0	0.14	0	0.14
YR1 Adult	5	0.27	5	0.27	1	0.27
YR2 Adult	9	0.33	10	0.33	1	0.33
YR3 Adult	9	0.05	10	0.05	1	0.05

**Table 2.** Pre-breeding, stage-based Leslie matrices were created for *Sceloporus consobrinus* under three nighttime warming conditions (daily  $T_b = 32.4^\circ\text{C}$ ) and three prey availability conditions. Conditions included current temperatures (nighttime  $T_b = 20.4^\circ\text{C}$ ), 2°C warming (nighttime  $T_b = 22.4^\circ\text{C}$ ) and 4°C warming (nighttime  $T_b = 24.4^\circ\text{C}$ ), and high, moderate, and low

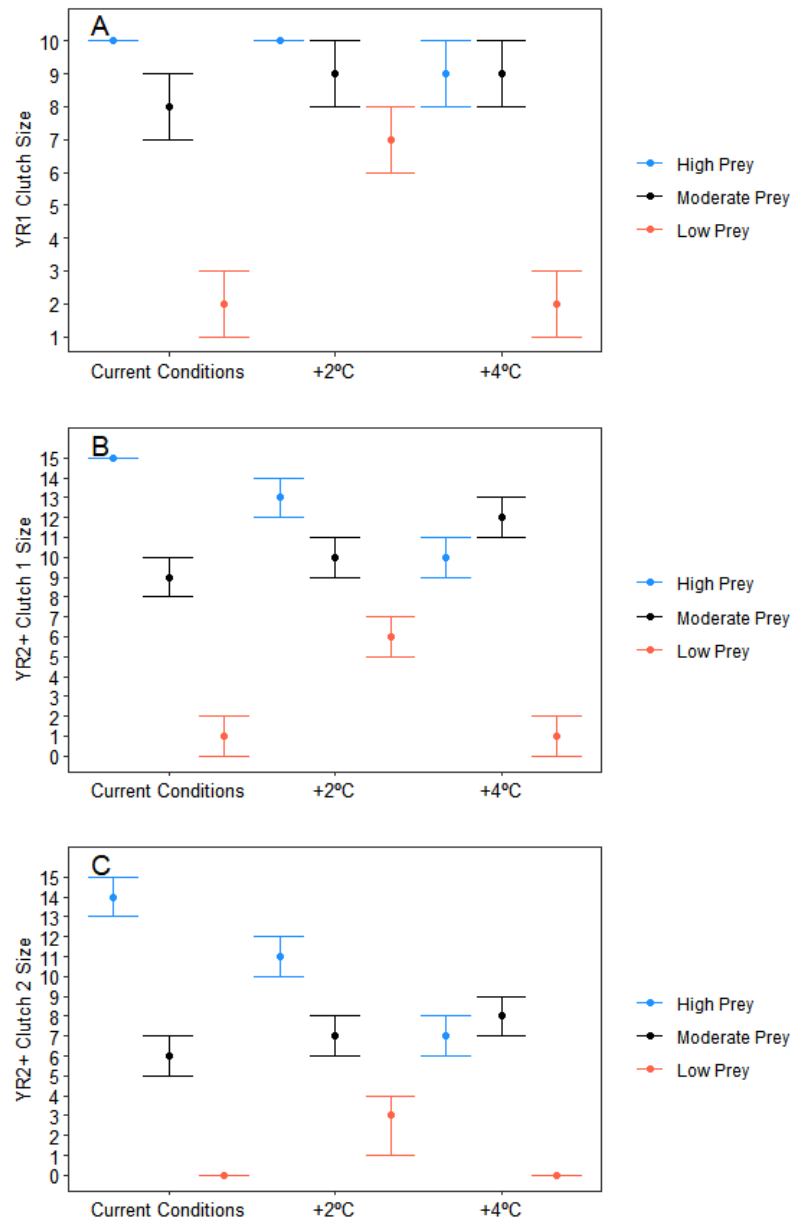
prey availability. Leslie matrices were based on predicted age-specific fecundity from bioenergetic models and age-specific survival data acquired from Tinkle and Ballinger (1972).

High Prey Availability			Moderate Prey Availability			Low Prey Availability		
Current Temperatures								
0.55	1.65	1.65	0.44	0.88	0.88	0.11	0.11	0.11
0.27	0	0	0.27	0	0	0.27	0	0
0	0.33	0.05	0	0.33	0.05	0	0.33	0.05
2°C Nighttime Temperature Increase								
0.55	1.43	1.43	0.55	0.99	0.99	0.44	0.55	0.55
0.27	0	0	0.27	0	0	0.27	0	0
0	0.33	0.05	0	0.33	0.05	0	0.33	0.05
4°C Nighttime Temperature Increase								
0.55	0.99	0.99	0.55	1.10	1.10	0.11	0.11	0.11
0.27	0	0	0.27	0	0	0.27	0	0
00	0.33	0.05	0	0.33	0.05	0	0.33	0.05

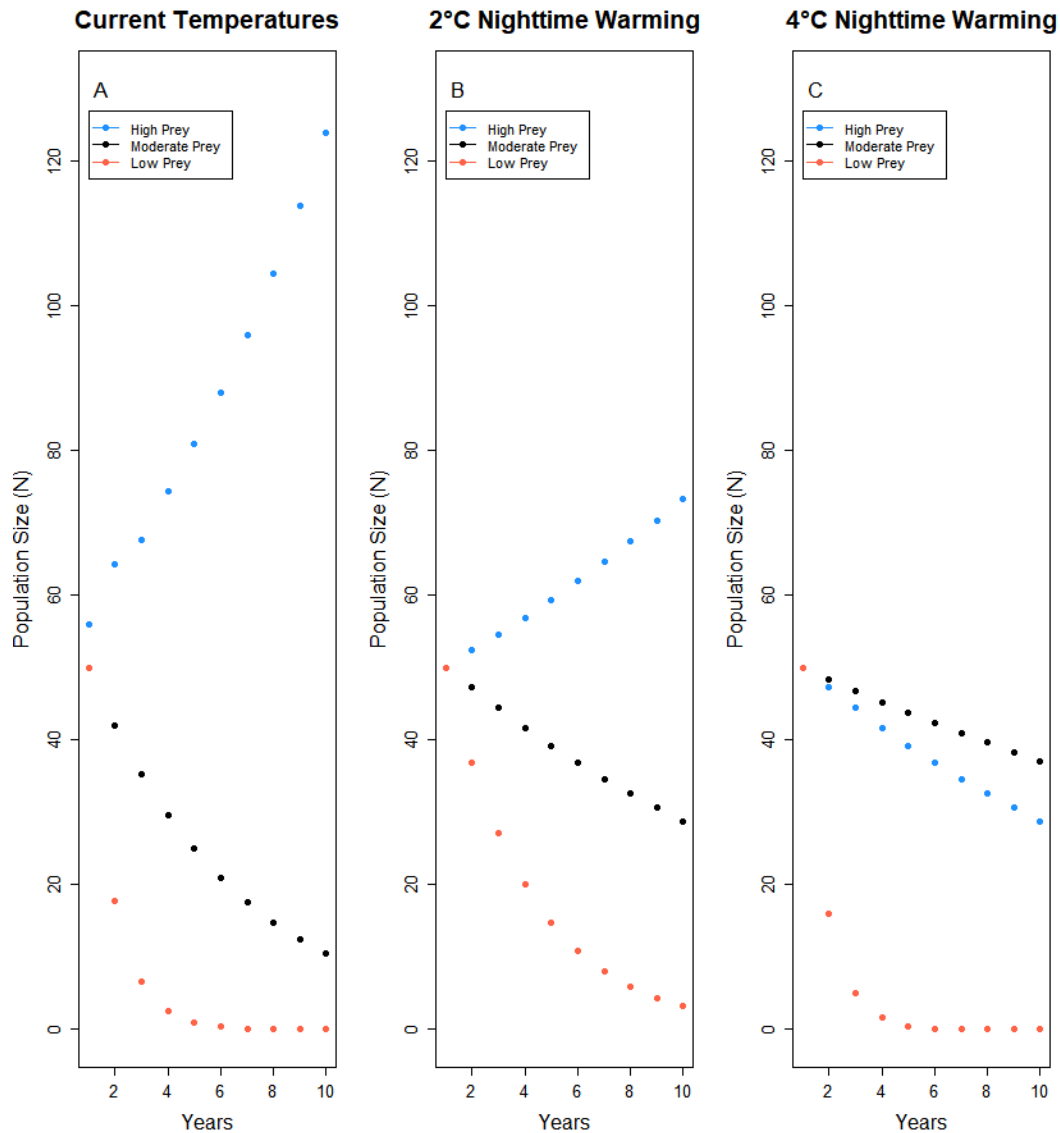
## 5.9 Figures



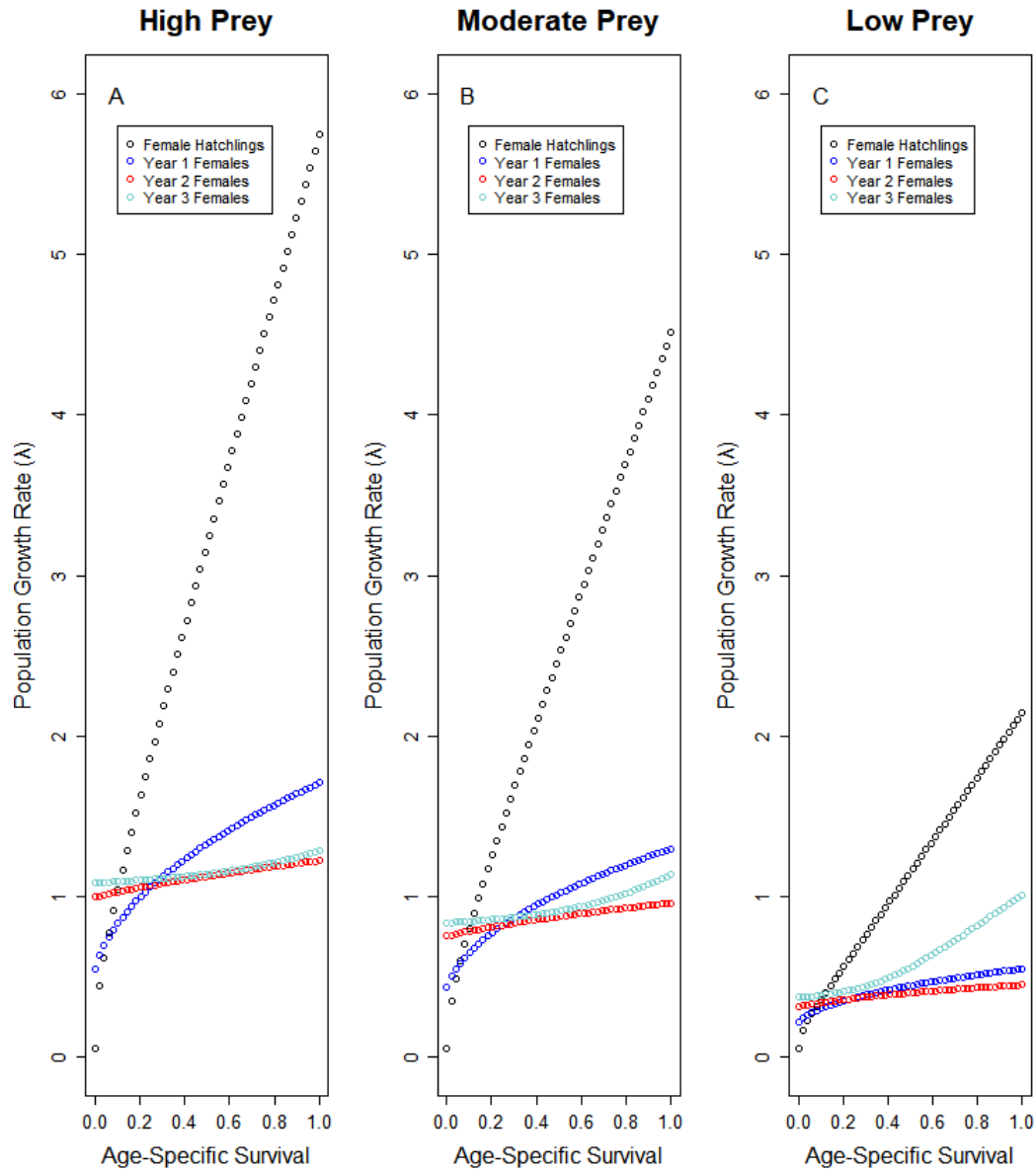
**Figure 1.** The relationship of lizard mass to lizard snout-vent length (SVL) was quantified for *Sceloporus consobrinus* in Arkansas, based on wild-caught lizards. The mass-SVL relationship was used to inform bioenergetic models.



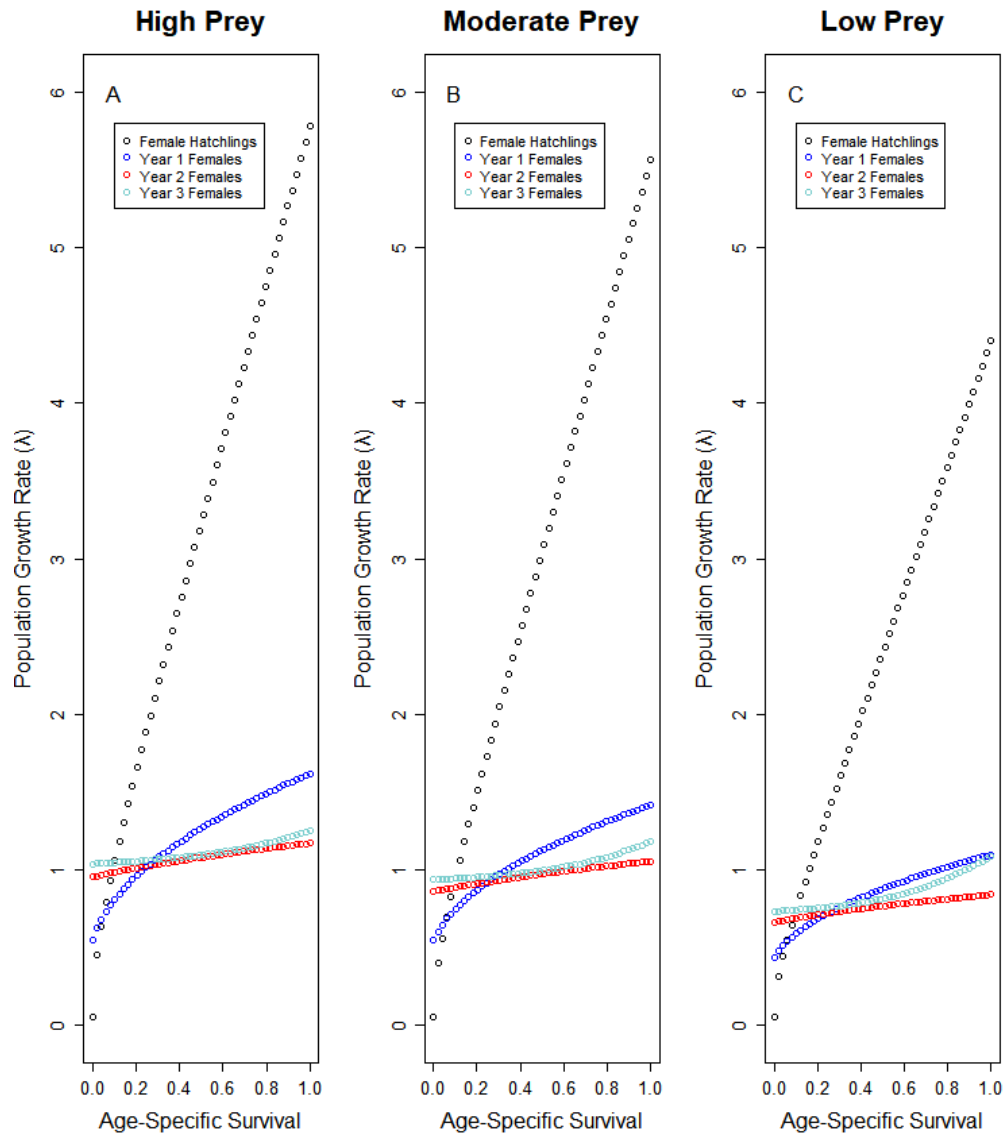
**Figure 2.** Predicted clutch sizes for *Sceloporus consobrinus* varied in response to warming nighttime temperatures and prey availability. Clutch sizes were always lowest under low prey availability but interacted with temperature under moderate and high prey availability. The figures show clutch sizes for year one reproductive females (A) and year two or older (asymptotic) females (B, C). Year two or older females produce two clutches per year.



**Figure 3.** Leslie matrix projections indicated that populations of prairie lizards (*Sceloporus consobrinus*) experience growth under current temperatures and a 2°C nighttime warming, when prey availability is high. When prey availability is moderate and low under current temperatures and a 2°C nighttime warming, populations decline. Populations always decline when nighttime temperatures warm by 4°C.



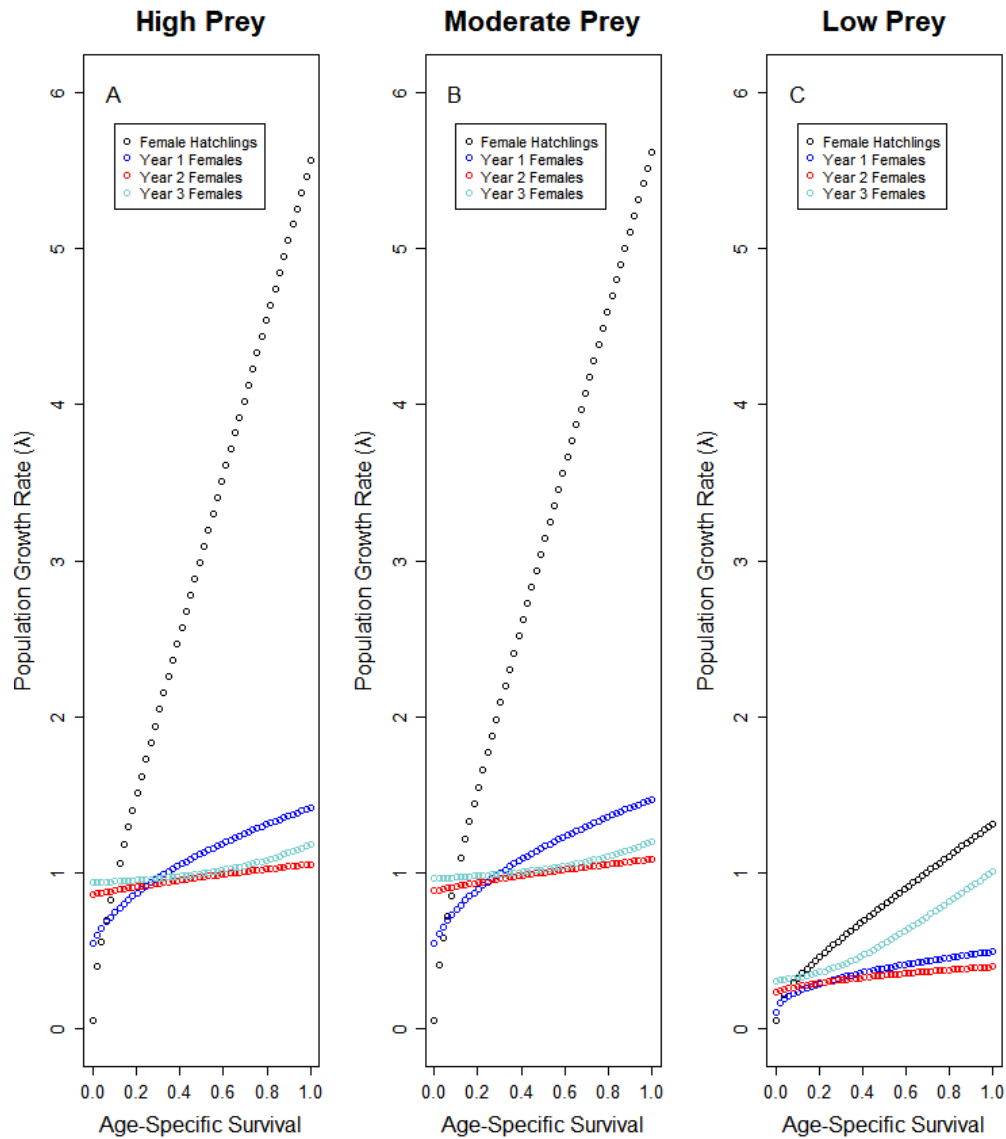
**Figure 4.** Under current temperatures, the population growth rate for *Sceloporus consobrinus* is most sensitive to changes in age-specific survival of hatchlings. Under high and moderate prey, population growth rates are also sensitive to age-specific survival of year one reproductive females, with low sensitivity to year two and year three female survival. Under low prey, population growth is comparably sensitive to age-specific survival of year three females.



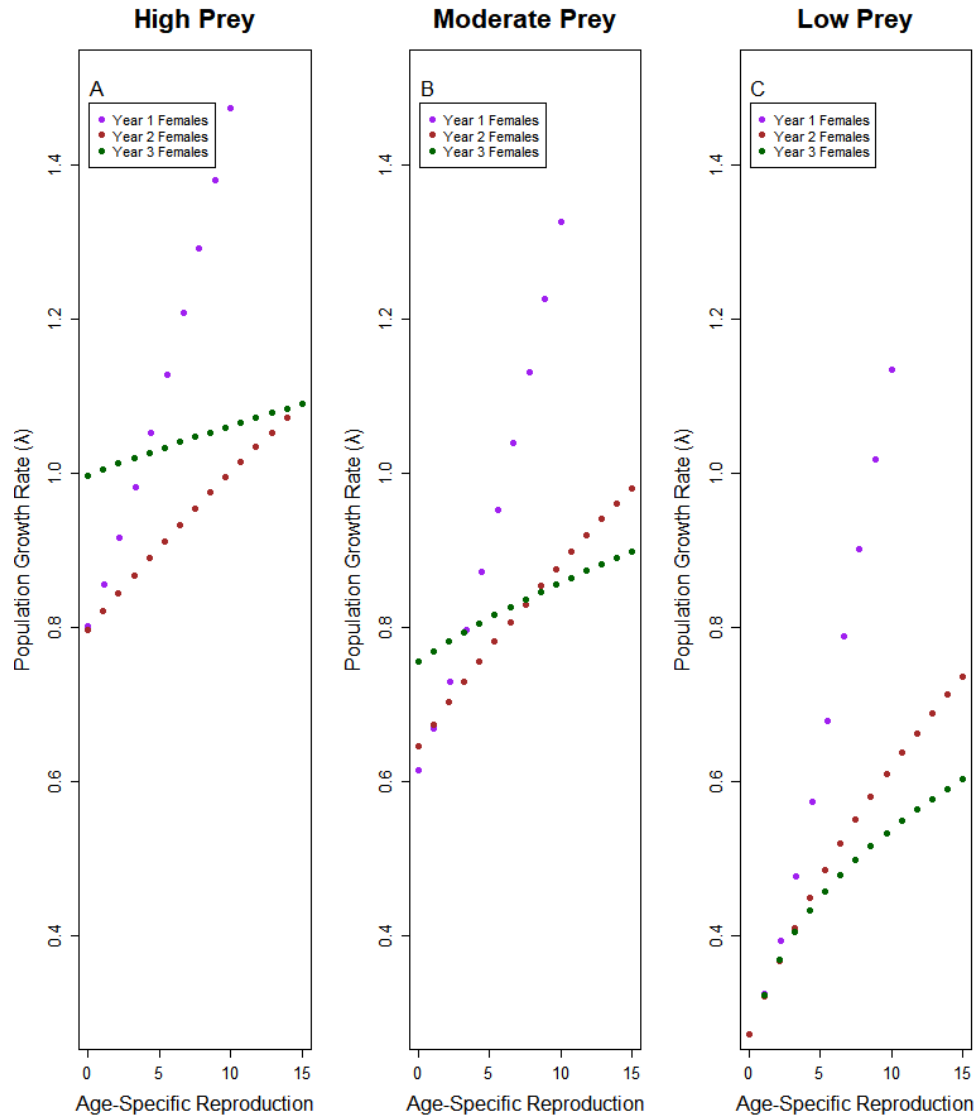
**Figure 5.** Under a 2°C nighttime temperature increase, population growth rate for *Sceloporus consobrinus* is most sensitive to changes in age-specific survival of hatchling females.

Population growth rates are also sensitive to age-specific survival of year one reproductive females, with low sensitivity to year two and year three female survival.

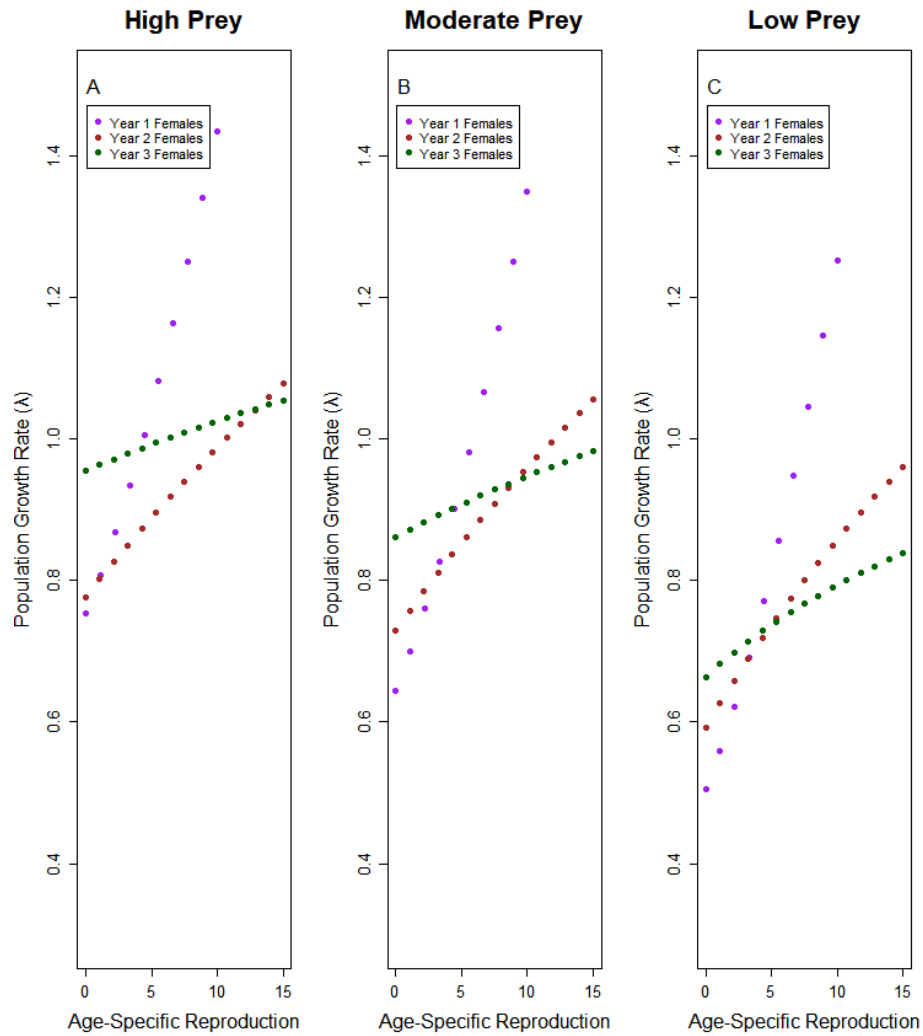




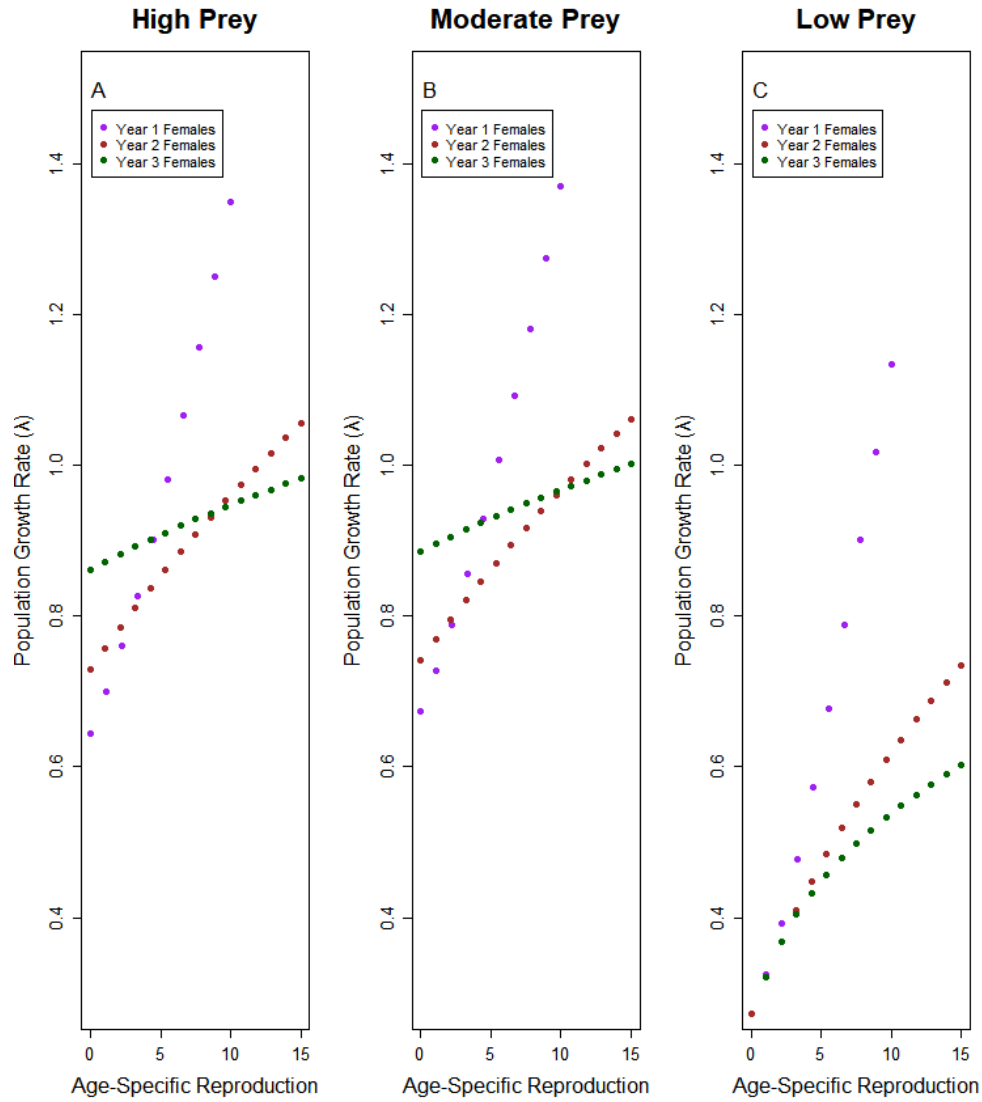
**Figure 6.** Under a 4°C nighttime temperature increase, population growth rate for *Sceloporus consobrinus* is most sensitive to changes in age-specific survival of hatchling females. Under high and moderate prey, population growth rates are also sensitive to age-specific survival of year one reproductive females, with low sensitivity to year two and year three female survival. Under low prey, population growth is comparably sensitive to age-specific survival of year three females.



**Figure 7.** Under current temperatures, with regards to age-specific reproduction population growth rate for *Sceloporus consobrinus* is most sensitive to year one females, followed by year two females, and year three females. As prey availability declines, population growth rate becomes increasingly influenced by age three reproductive females' age-specific reproduction.



**Figure 8.** Under a 2°C nighttime temperature increase, with regards to age-specific reproduction population growth rate for *Sceloporus consobrinus* is most sensitive to year one females, followed by year two females, and year three females. Under low prey availability, population growth rate is more sensitive to age three reproductive females’ age-specific reproduction than other prey scenarios.



**Figure 9.** Under a 4°C nighttime temperature increase, with regards to age-specific reproduction population growth rate for *Sceloporus consobrinus* is most sensitive to year one females, followed by year two females, and year three females. Under low prey availability, population growth rate is more sensitive to age three reproductive females’ age-specific reproduction than other prey scenarios.

## **Dissertation Conclusions**

Temperature changes can influence ectotherms in various ways, with subsequent effects on populations (Dunham et al. 1989). Even closely related organisms can vary in thermal sensitivity (Beaupre et al. 1993, Angilletta 2001), although commonly overlooked by many modeling approaches (e.g. Sinervo et al. 2010; Buckley 2010). A common approach in thermal biology is quantifying performance under stable temperatures, for extrapolation to daily cycles. However, some evidence suggests that traits vary when responding to stable temperatures versus daily temperature cycles (Meeuwig et al. 2004; Podrabsky and Somero 2004; Dhillon and Fox 2007; Kern et al. 2015; Kingsolver et al. 2015; Coulter et al. 2015). As temperatures warm with regards to climate change, understanding realistic scenarios for making projections has become increasingly important. For many ectotherms, it is possible that nighttime warming poses a greater risk than daily warming, due to homogenization of the thermal landscape at night. However, specific nighttime warming is not commonly addressed. Additionally, factors aside from temperature could change in tandem with the climate, including prey availability. Both temperature and prey can influence individual energy budgets, with subsequent effects on fitness.

In Chapter 1, I conducted meta-analyses to determine patterns in direct and indirect effects of climate change on food consumption, daily activity, and growth rates in lizards. Few studies were identified on the processes of interest, despite the abundance of climate models surrounding lizard activity and persistence. However, the findings indicated that warming temperatures increase rates of food consumption but decrease growth rates. Meanwhile, increasing food consumption alone increases growth rates. The results of Chapter 1 exemplify the need for more empirical studies to inform climate models, in addition to mechanistic explanations for identified patterns. The primary factor considered in lizard climate models is

restrictions in daily activity (Cosendey et al. 2022). However, few studies exist examining daily restrictions and the resulting influence on energy budgets and fitness. Therefore, a knowledge gap was identified through the meta-analyses, which should be explored in future studies.

In Chapter 2, I quantified the thermal sensitivity of digestion in prairie lizards (*Sceloporus consobrinus*) in Arkansas. Prairie lizards have a unique life history for *Sceloporus* lizards by maturing relatively quickly with regards to season length and having moderate reproductive output comparatively. Therefore, prairie lizards offer an interesting study system for understanding variation in life history and underlying physiological processes. In addition to examining thermal sensitivity of digestion in prairie lizards, I made direct comparisons to the closely related species *S. undulatus*, in South Carolina and New Jersey. The comparisons allowed me to test a common assumption that closely related species and populations do not drastically vary in thermal sensitivity. Chapter 2 found that *S. consobrinus* continues to increase efficiency in digestion with temperature, whereas *S. undulatus* peaks and either plateaus or declines in performance. Such differences suggest that research should consider population variation when making projections regarding thermal sensitivity, as distinct differences may be prevalent.

In Chapter 3, I made direct comparisons of digestive data collected under stable and daily cycling temperature treatments using *S. consobrinus* as a model organism. The results found that processes differed in response to temperature treatments, with digestive passage time having the greatest differences. Additionally, I compared data between two different patterns of daily temperature cycles. Results drastically varied based on temperature pattern, indicating that not only do stable temperatures inaccurately represent daily cycles, but temperature pattern is also influential. Chapter 3 has direct implications for future studies in thermal biology. Methods

should aim to include daily cycles, if realistic conditions are of interest, as stable treatments may provide inaccurate results if extrapolated to a cycling regime. Caution should be taken when informing lab trials of temperature treatments, and quantifying function in response to temperature.

In Chapter 4, I quantified the effects of warming nighttime temperatures and altered prey availability on digestive physiology and energy budgets in *S. consobrinus*. The results indicated that warming nighttime temperatures interact with prey availability in multiple ways. When nighttime temperatures warmed by 2°C, lizards increased or maintained rates of food consumption, while a 4°C increase had variable effects. Specifically, under low prey and a 4°C increase, lizards had similar energy budgets as current conditions and low prey. However, under a 2°C increase and low prey, energy budgets were higher. The findings here show that temperature changes can interact with biotic factors in nonlinear ways and may be dependent on the magnitude of change. Additionally, nighttime warming alone can affect performance, which can be amplified by prey availability. Nighttime warming is concerning with regards to climate change, as many ectotherms can behaviorally thermoregulate during the day, with increased challenges at night (Huey and Slatkin 1976). More studies examining different taxonomic groups and warming scenarios are needed to understand nuances regarding how temperature influences organismal performance.

In Chapter 5, I projected Chapter 4 data on the effects of warming nighttime temperatures and altered prey availability, calculating reproductive output, and the subsequent effects on population growth rates over ten years in *S. consobrinus*. The model projected decreases in clutch sizes in response to warming nighttime temperatures in high prey availability simulations. However, under moderate and low prey availability, a 2°C increase in nighttime temperatures

resulted in slower declines over time in comparison to current conditions and a 4°C increase in nighttime temperatures. In 4°C nighttime temperature warming simulations, populations declined regardless of prey, due to higher energetic costs resulting in lower reproductive output. The models also indicated that older adult females experience greater declines in reproductive output due to warming temperatures and reduced prey than younger age females. The difference in warming effects on reproductive age classes was a result of higher maintenance costs at high temperatures for females with larger body sizes. The projections from Chapter 5 indicate how individual processes can be influenced by interdependent abiotic and biotic conditions, resulting in decreases in reproductive output. As a result of individual mechanisms, population growth rates varied among simulations, and switched from increasing, to declining or extinction, within a ten-year span or less.

The collective findings from my dissertation identify knowledge gaps for mechanistically understanding how climate change may affect organisms in the future, while expanding upon current approaches and projections. Temperature plays a critical role in ectotherm function and fitness. However, temperature can also interact with the biotic environment, with interdependent effects on organisms. The results found here elucidate the importance of testing assumptions of current modeling approaches and methodologies, while considering factors in addition to temperature which may alter performance and fitness over time. Local acclimation and genetic differentiation can result in differing thermal sensitivity among even closely related organisms. Energetics and digestive physiology provide a direct way to mechanistically assess the temperature effects on organism function and fitness, with implications for population predictions. Future work should aim to consider additional taxonomic groups for assessing local variation in thermal sensitivity and effects of nighttime warming and prey availability on



bioenergetics. Additional abiotic and biotic factors should be integrated into studies of thermal biology to determine combined effects of environmental change. There is also a prominent knowledge gap to be explored regarding how temperature-induced activity restrictions influence bioenergetics.

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