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Thermal sensitivity of digestion in *Sceloporus consobrinus*, with comments on geographic variation

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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. Even closely related taxa may differ in the thermal sensitivity of performance, which in turn influences 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 *Sceloporus* lizards, to compare closely related, but geographically distinct, populations. *Sceloporus* lizards are 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 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 understanding variation in physiological traits across the range of *Sceloporus* lizards.

1. Introduction

Predictive models are a useful tool for understanding how and why biological systems change over time (Mouquet et al., 2015). Threats of climate change and habitat alterations are continuing to increase (Tabor et al., 2018; IPCC 2022). 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 can vary in response to environmental attributes (e.g. Niewiarowski and Roosenburg, 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.

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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 created to determine and predict how organisms' function at various temperatures (Huey and Slatkin 1976). The exact shape and magnitude of TPCs 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., 1993a, Angilletta, 2001a; 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. 2008; Kearney et al., 2010, Berriozabal-Islas et al., 2018). 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 Tracy, 1983; 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, 2014). Multiple climate change models predict *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 differ among *Sceloporus* lizards (e.g. Tinkle and Ballinger 1972, Beaupre et al., 1993b; Angilletta, 2001a). Two populations with differing thermal sensitivities are *S. undulatus* residing in South Carolina and in New Jersey (Angilletta, 2001a). South Carolina lizards mature quickly, have high reproductive rates, small body sizes, and high mortality (Tinkle and Ballinger 1972). In comparison, New Jersey fence lizards have delayed maturation, low reproductive rates, relatively large body sizes, and reduced mortality (Haenel and John-Alder 2002). One additional population of *Sceloporus* lizards of interest, and comparatively understudied, are prairie lizards (*S. consobrinus)*. Prairie lizards have a unique life history with relatively quick maturation in relation to their active season length (Adolph and Porter 1996) and moderate reproductive output and survival (Tinkle and Ballinger 1972, Mosbey, 2019). Additionally, *S. consobrinus* were historically diagnosed as being *S. undulatus*, or a subspecies of *S. undulatus*, but are now distinct (Leaché et al., 2016). Therefore, it is likely that variation in temperature sensitivity influences the life history of *S. consobrinus*. However, bioenergetic data have yet to be collected for *S. consobrinus*.

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 NJ and SC 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 compared were food consumption rate, digestive passage time, fecal and urate production, metabolizable energy intake (MEI), and assimilated energy (AE). Analyses were conducted to compare digestive processes among temperatures for *S. consobrinus*, and to compare digestive process among populations within each temperature. We hypothesized that *S. consobrinus* would 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. Methods

2.1. *Study animals*

Surveys were conducted in the spring and summer of 2020 and 2021 in northwest Arkansas for adult *S. consobrinus*, by searching viable habitat. In order to prevent overharvesting animals from a single site, lizards were collected from sites within an 8-mile radius. Sites were selected based on comparable habitat within forested parks, composed of primarily of hardwood trees and a rocky understory, where lizards likely experienced a similar abiotic and biotic environment. Forty-seven adult lizards (29 females and 18 males, snout-vent length >48 mm) were captured by hand or loop (consisting of a fishing pole with a loop on the end) and marked 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 2 min 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. All lizards captured were brought to the lab at the University of Arkansas in a cloth bag for use in lab trials. 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 37.85 L tanks with a natural sand substrate, heat lamps, a hide box, and were misted with water three times a week. Lizards were offered crickets for voluntary consumption three times a week, supplemented with vitamin D every two weeks, and provided water ad-libitum. While the original study by Angilletta (2001b) does not clarify the season lizards were captured for lab experiments, field body temperatures were taken in the spring and summer, comparable to the current study.

2. *Influence of temperature on digestion in Sceloporus consobrinus*

To make direct comparisons of *S. consobrinus* in Arkansas and *S. undulatus* in SC and NJ, 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), or 36 °C (n = 11). Temperatures were maintained using an environmental chamber (± 0.5 °C). During trials, lizards were maintained in plastic tanks (41.9 cm × 33 cm x 16.8 cm) lined with butcher paper, with a hide box, and provided water ad-libitum.

Feeding trials were conducted using Fluker's (Port Allen, LA) 2- and 3-week-old crickets (*Acheta domestica*) and began after lizards had been acclimatized for five days and had processed a meal, followed by a 3-day fasting period to clear the gut. At the onset of feeding trials, a single cricket was injected with ~0.02 mL of a slurry containing water mixed with an ingestible, UV-fluorescent powder, which associates with feces

(Beaupre et al., 1993b). The marked cricket was offered to lizards, which they voluntarily consumed, and the time of consumption was recorded. Lizards were offered food directly in their tanks for voluntary consumption. Lizards were then monitored every 2–4 h for marked feces to estimate digestive passage time (Beaupre et al., 1993b). After the first mark was expelled, ~10+ days were allotted to quantify food consumption in grams (later converted to kilojoules, described below) 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 ad libitum every day, weighed to the nearest 0.1 mg. 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. 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). There were no outliers within the datasets to manage statistically.

2.4. *Sceloporus consobrinus* data analysis

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). To determine digestive passage time, the time from consumption of the marked cricket to the first appearance of the mark in feces was calculated.

Respective fecal and urate samples from each individual lizard were homogenized and analyzed via bomb calorimetry to determine fecal and urate production. Energy densities for feces and urates, respectively, were averaged among lizards within each treatment and used to kJ excreted. 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:

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

where C is energy consumed (kJ), F is fecal production (kJ), and U is urate production (kJ). Assimilated energy represents digestible energy and was calculated using the formula:

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

When comparing food consumption, a covariate of lizard mass was included and an interaction term (mass*temperature). When comparing fecal production, urate production, MEI, and AE, a covariate of food consumption was included with an interaction term (food consumption*temperature).

2.5. 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 (2001a). In brief, Angilletta (2001a) 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 were determined via bomb calorimetry. Metabolizable energy intake and AE were calculated using the aforementioned formulas. When comparing food consumption, a covariate of lizard mass was included and an interaction term (mass*population). When comparing fecal production, urate production, MEI, and AE, a covariate of food consumption was included with an interaction term (food consumption*population). Maximum seasonal energy budgets were calculated for all three populations at 33 °C, as this is near the average field body temperature reported for all three populations (Angilletta, 2001a; Bangs 2016), using the same approach as Angilletta (2001a), with the following formula:

Seasonal Energy Budget (kJ) = (Max MEI (kJ) / Trial Length (days)) / (hours of activity/ 24)

where the maximum MEI found in lab trials was converted to daily MEI. Hours of seasonal activity for each population was acquired from Adolph and Porter (1996) as 2000 h for AR, 2632 h for SC, and 1864 h for NJ. In conducing comparisons to previous literature there were inherent limitations on sample size and proximity in time of data collection.

3. Results

3.1. 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 to 36.7 °C, with an average body temperature of 32.5 °C (Table 1), supporting the relevance of temperature treatments.

The energy density of crickets was 20.5 ± 1.4 kJ/g 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, Fig. 1A). Lizard mass (covariate) had no effect on food consumption and there was no interaction of mass and temperature. Passage time significantly decreased with warming temperatures (ANCOVA $p < 0.001$, F = 18.410, Fig. 1B), but did not significantly differ between 30 °C and 33 °C.

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

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 (2001a).

Species	Location	Average Body Temperature (°C)
Sceloporus consobrinus	Arkansas	32.5 ± 2.0
Sceloporus undulatus	New Jersey	34.0 ± 0.3
Sceloporus undulatus	South Carolina	33.1 ± 0.4

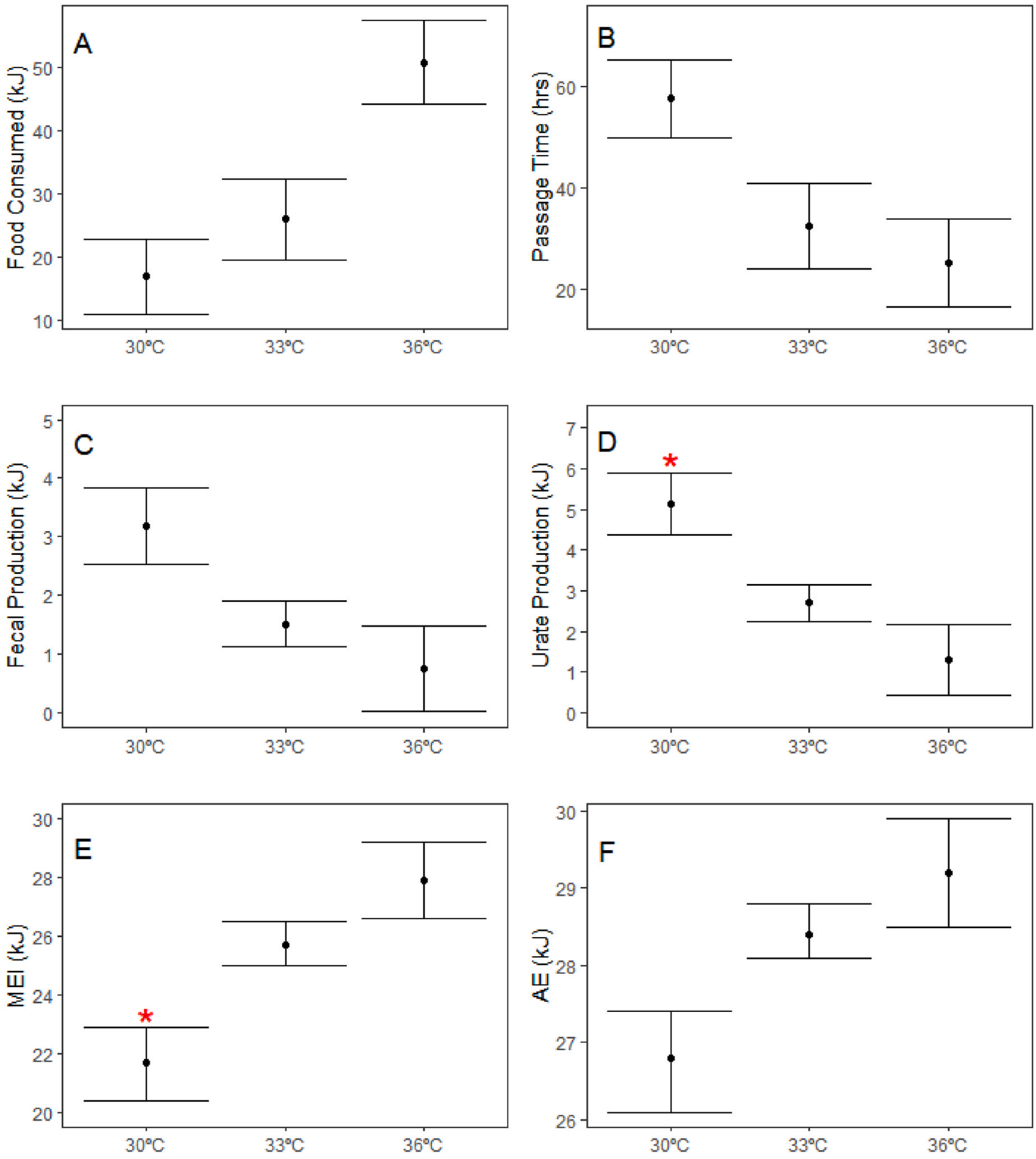

Fig. 1. When assessing the influence of temperature on digestive physiology in *Sceloporus consobrinus*, passage time decreased while everything else increased as temperatures warmed. At 30 °C, MEI and urate production did not have homogeneous covariate slopes with other temperatures, as indicated by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

between temperature and food consumption. Urate production had a significant interaction between temperature and food consumption (ANCOVA $p < 0.001$, F = 5.098, Fig. 2B) due to 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, Fig. 2C), with no interaction between food consumption and temperature.

There was a significant interaction between temperature and food consumption on MEI (ANCOVA $p = 0.0159$, F = 4.747, Fig. 2D), 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 = 2068.701, Fig. 1E), and MEI significantly increased with food consumption (covariate, $p < 0.001$, F = 1505.273, Fig. 4). There was no interaction between food consumption and temperature treatment between the 33 °C and 36 °C trials on MEI. Assimilated energy significantly increased with warming temperatures (ANCOVA $p < 0.001$, F = 9551.954, Fig. 1F), with all temperatures significantly different. Assimilated energy also significantly increased with food consumption (covariate, $p < 0.001$, F = 9080.281, Fig. 2), with no significant interaction between consumption and temperature.

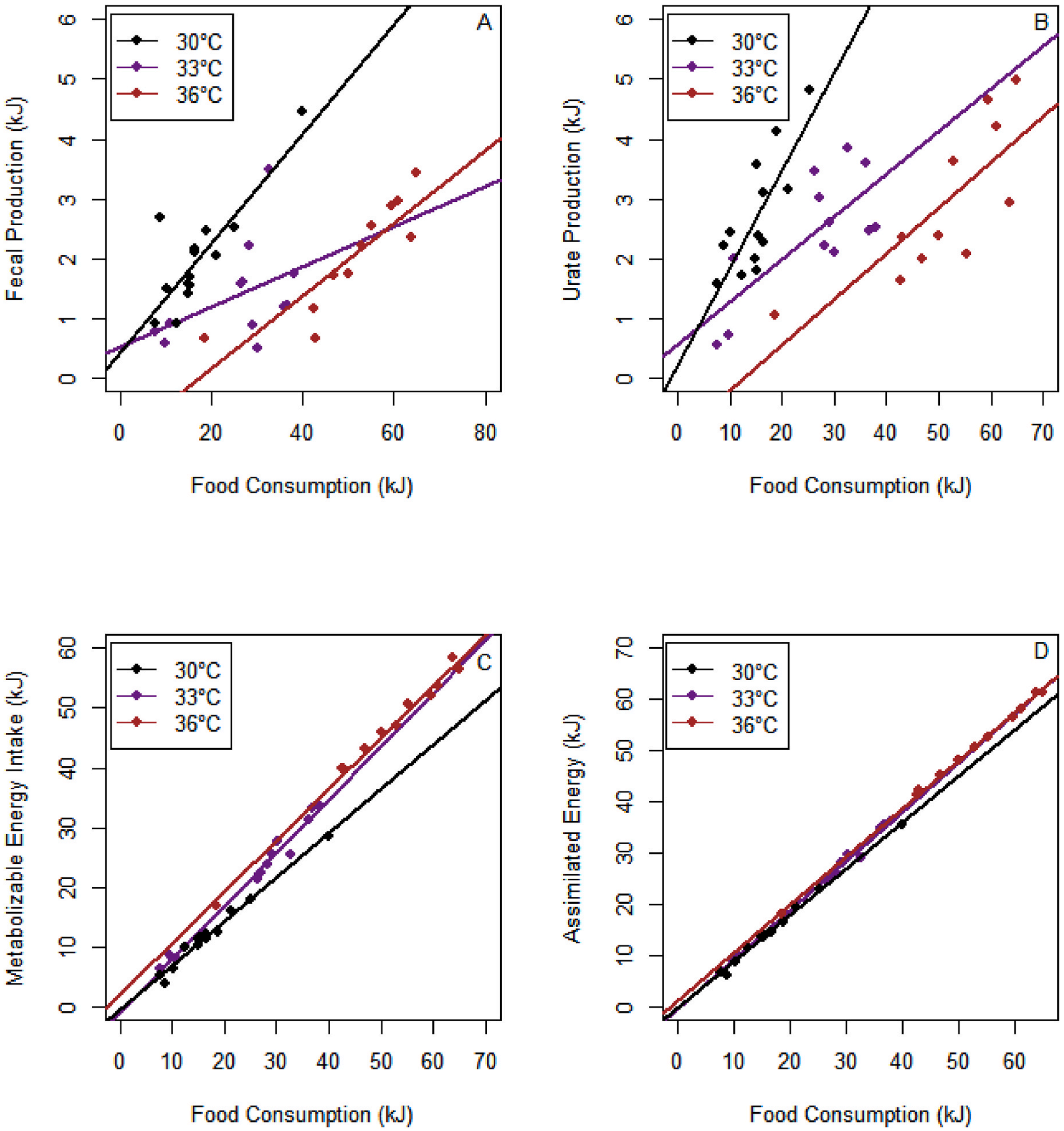

Fig. 2. The graphs indicate interactive effects of covariates with physiological variables in *Sceloporus consobrinus* in Arkansas based on temperature. Specifically, fecal production increased with food consumption (A), urate production increased at a quicker rate in relation to food consumption at 30 °C than 33 °C and 36 °C (B), metabolizable energy intake increased at a slower rate in relation to food consumption at 30 °C than 33 °C and 36 °C (C), and assimilated energy increased with food consumption at at all temperatures (D).

3.2. *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 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 $p = 0.0115$, $F = 5.537$, Table 2, Fig. 3A) lizards from AR consumed significantly less food than NJ and SC lizards, with no effect of weight and no interaction between mass and population. At 36 °C, there was a significant interaction between lizard mass and population (ANCVOA $p = 0.003$, $F = 7.812$, Fig. 4A) due to little change in food consumption in relation to lizard mass for AR lizards. In contrast, NJ and SC had a positive relationship between food consumption and mass. 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). Passage time estimates did not significantly differ among populations at any temperature (Table 2, Fig. 3B). There was an influence of mass on passage time at 36 °C (mass*temperature interaction: $p = 0.0279$, $F = 5.777$, Table 2, Fig. 4B), 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 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 $p < 0.001$, $F = 17.345$, Table 2, Fig. 3C), with AR lizards excreting the least, followed by SC and then NJ. Additionally, food consumption had a positive, significant, influence on fecal production (covariate, $p < 0.001$, $F = 26.321$), with no interaction between

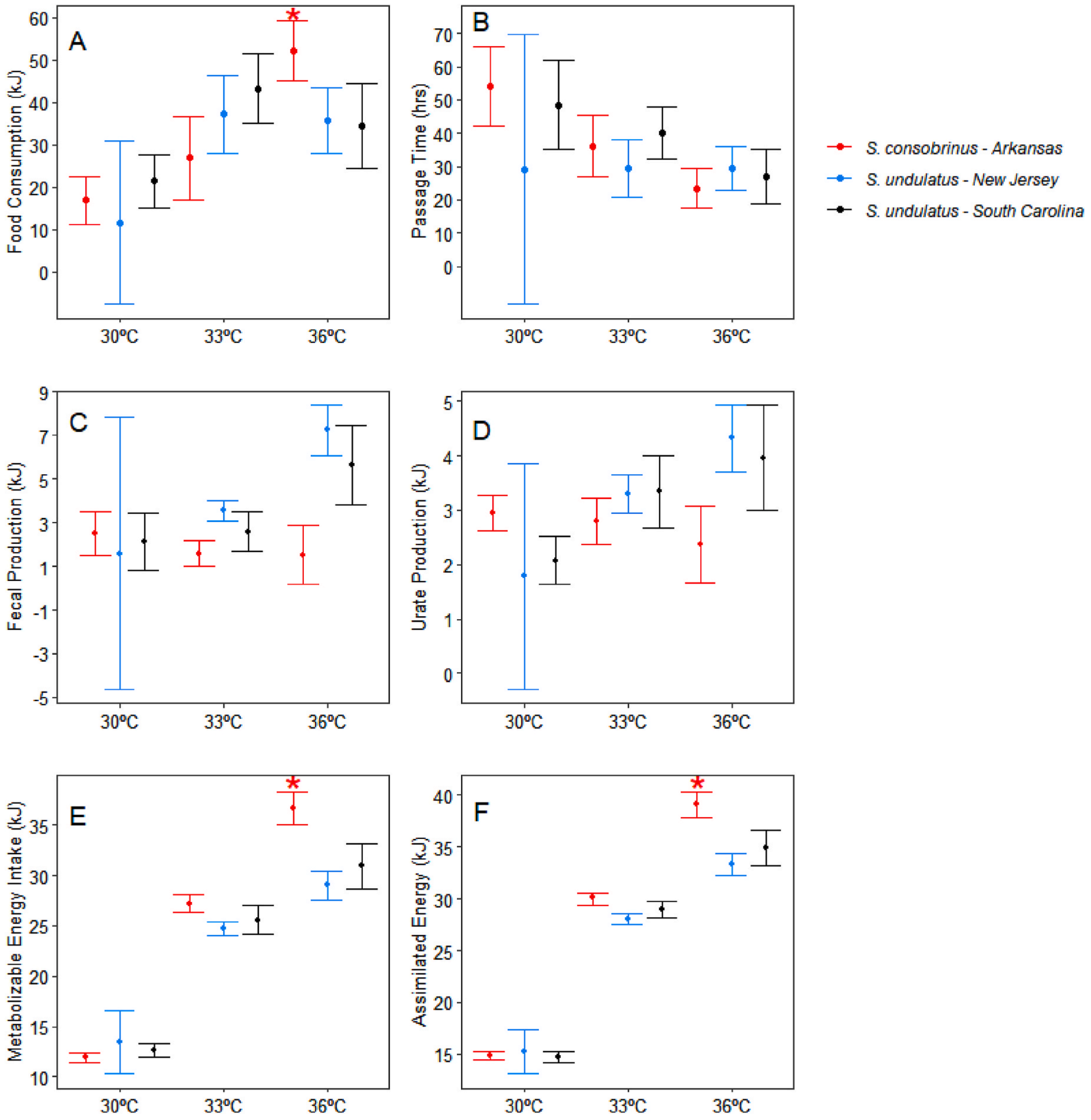

Fig. 3. Prairie lizards (*Sceloporus consobrinus*) decreased passage time while increasing food consumption, MEI and AE, with no change in urate and fecal production, as temperatures increased. *Sceloporus undulatus* in NJ and SC followed the same trend as *S. consobrinus*, except for reducing food consumption 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.

population and food consumption. At 36 °C, AR lizards produced significantly less feces than SC and NJ (ANCOVA $p < 0.001$, F = 11.769, Table 2, Fig. 3C). 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 significantly differed among populations at 30 °C (ANCVOA $p < 0.001$, F = 12.614, Table 2, Fig. 3D) and 3 °C (ANCOVA $p < 0.001$, F = 20.538, Table 2, Fig. 3D), 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 AR had significantly greater urate production than SC. At 33 °C, AR lizards had significantly lower urate production than NJ, with SC not differing from AR or NJ.

Metabolizable energy intake significantly differed among populations at 30 °C (ANCOVA: 30 °C: $p < 0.001$, F = 90.812, Table 2, Fig. 3E) and 3 °C (ANCOVA $p < 0.001$, F = 264.034, Table 2, Fig. 3E), 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, AR lizards had significantly higher MEI than SC and NJ. Metabolizable energy increased with food consumption at 30 °C (covariate, $p < 0.001$, F = 1172.267) and 33 °C (covariate, $p < 0.001$, F = 1776.879) 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, Table 2, Fig. 4C) due to an increase in MEI with food consumption occurring more rapidly for 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 was significantly different among populations at 30 °C (ANCOVA $p < 0.0001$, F = 281.330, Table 2, Fig. 3F) and 3 °C (ANCOVA $p < 0.001$, F = 803.350, Table 2, Fig. 3F). Assimilated energy significantly increased with food consumption for all populations at 30 °C (covariate, $p < 0.001$, F = 4133.7, Fig. 4D) and 33 °C (covariate, $p < 0.001$, F = 5205.604, Fig. 3), with no interaction between food

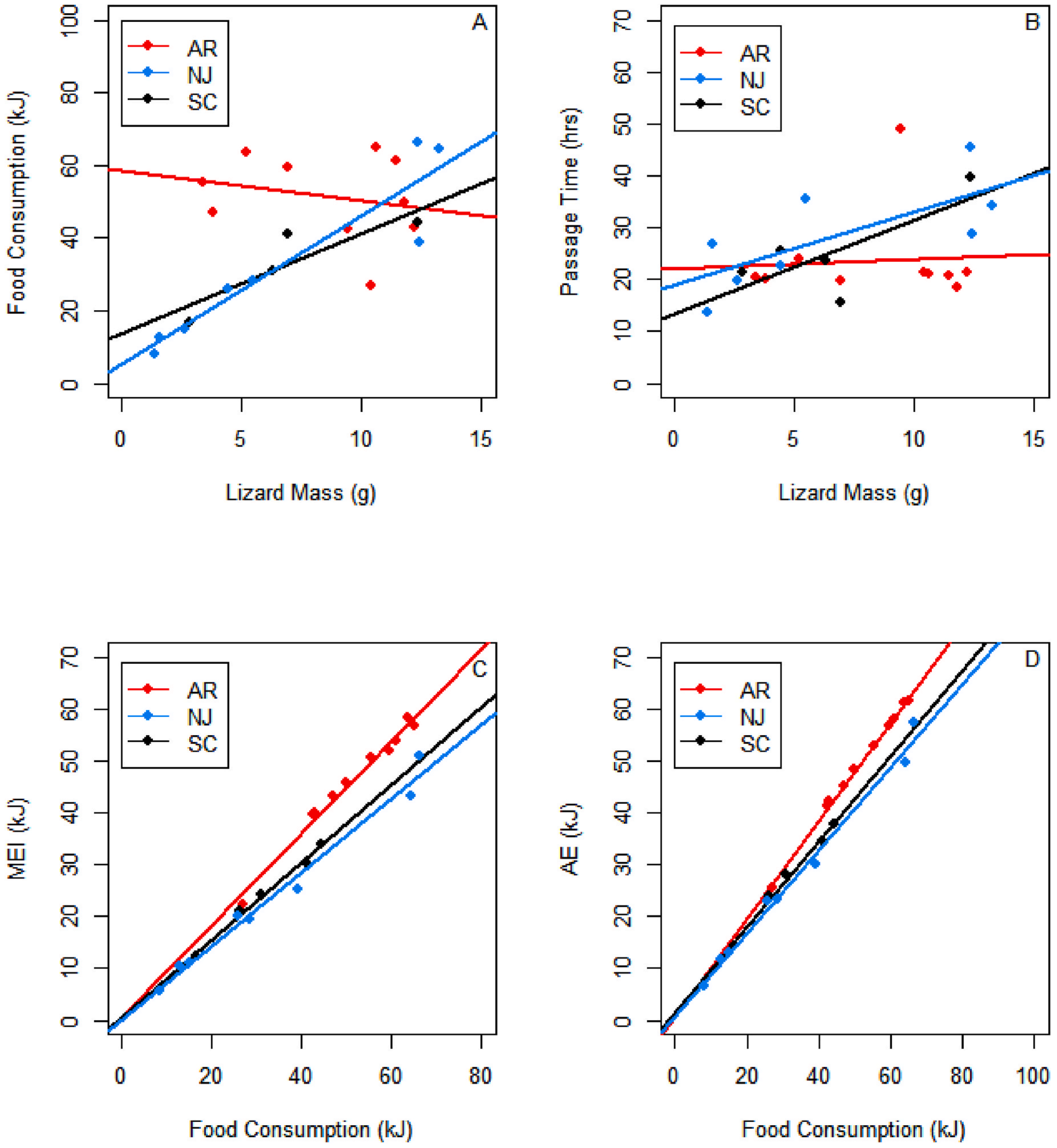

Fig. 4. The graphs indicate interactive effects of lizard population and temperature for *Sceloporus consibrinus* (AR) and *Sceloporus undulatus* (NJ and SC) at 36 °C. Specifically, food consumption (A) and passage time (B) increased with lizard mass for *S. undulatus* but not *S. consobrinus*. Additionally, metabolizable energy intake (MEI; C) and assimilated energy (AE; D) increased slower with food consumption for *S. undulatus* compared to *S. consobrinus*.

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, Table 2, Fig. 4D). Again, AR lizards increased AE more rapidly with food consumption in comparison to NJ and SC.

The maximum seasonal energy budgets were 140.83 kJ for AR, 507.76 kJ, and 264.10 kJ for NJ.

4. Discussion

Temperature can play a critical role in regulation performance, which may vary among even closely related organisms. The current study found a significant influence of temperature on digestive physiology in *Sceloporus consobrinus* lizards in Arkansas. Even more, the study highlighted the potential for variation in temperature-dependent digestive physiology among two species spanning three populations of *Sceloporus* lizards. For *S. consobrinus*, performance consistently increased in efficiency and rate as lizards warmed from 30 to 36 °C. Perhaps most notably, *S. consobrinus* increased digestive efficiency at 36 °C; a rare finding of temperature-dependent digestion efficiency in lizards (Wehrle and German, 2023). When comparing populations of *Sceloporus* among AR, SC, and NJ, 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, SC and NJ lizards did not exhibit an increase in digestive efficiency with temperature, like AR lizards. Digestive physiology and resulting energy budgets are important considerations for

Table 2
The table indicates results of ANCOVA analyses comparing (A) physiological performance at 30 °C, 33 °C, 36 °C for *Sceloporus consobrinus* lizards in Arkansas, and (B) physiological performance among *S. consobrinus* in Arkansas, and *S. undulatus* in South Carolina and New Jersey at 30 °C, 33 °C, 36 °C. Asterisks and "NA" indicate analyses with interactive effects with covariates at 36 °C, resulting in comparison of just 30 °C and 33 °C.

Source	df	*P*	*F*
A. **Arkansas *Sceloporus consobrinus* Temperature Effects**			
Food Consumption	2,31	<0.001	29.278
Digestive Passage Time	2,34	<0.001	18.410
Fecal Production	2,31	0.0254	4.146
*Urate Production**	1,19	0.158	2.165
*MEI**	1,19	<0.001	2068.701
AE	2,31	<0.001	9551.954
B. **Population Comparisons**			
Food Consumption			
30	2,18	0.199	1.770
33	2,30	0.0115	5.537
36	2,17	0.003	7.812
Digestive Passage Time			
30	2,18	0.187	1.845
33	2,30	0.148	2.034
36	2,17	0.511	0.699
Fecal Production			
30	2,18	0.446	0.844
33	2,30	<0.001	17.345
36	2,17	<0.001	11.769
Urate Production			
30	2,18	<0.001	12.614
33	2,30	<0.001	20.538
36	2,17	0.107	2.552
Metabolizable Energy Intake			
30	2,18	<0.001	90.812
33	2,30	<0.001	264.034
36	NA	NA	NA
Assimilated Energy			
30	2,18	<0.001	281.330
33	2,30	<0.001	803.305
36	NA	NA	NA

understanding life history, persistence, and fitness (Grant and Dunham 1990; Brewster et al., 2021). Therefore, the results of the current study provide further evidence for temperature-dependent digestion and energetics, particularly in *Sceloporus* lizards. The study highlights possible variability among populations in response to temperature change, which could be useful for understanding climate effects in the future. Additionally, findings indicated that various functions associated with food acquisition and digestion respond differently, and nonlinearly, with respect to temperature, within a single population. However, it is important to note that this study is limited in population-level comparisons as the data were acquired from a previously published source with low sample sizes.

The population of *S. consobrinus* in northwest Arkansas exhibited a strong association in between digestive performance and temperature, for all variables measured. The increase in digestive efficiency at 36 °C represents a unique finding in the ability of lizards to uptake more energy from a food item based on temperature. The use of ANCOVA analyses here allowed for the interaction between temperature and food consumption on MEI to be identified, in comparison to historical methods of analyzing digestive data with ratios (Raubenheimer 1995; Beaupre and Dunham 1995). Further comparisons of AR lizards were made to NJ and SC populations of *S. undulatus* lizards. One reasoning for comparing AR to NJ and SC lizards, is that data are often derived from single species or select populations, such as *S. undulatus* in NJ and SC, and used to understand the thermal performance of an entire distribution or genera (Buckley et al., 2010; Sinervo et al., 2010). Therefore, we were interested in doing a comparison among populations while filling a data gap in thermal performance of *S. consobrinus*. We found that 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, quickest passage times, and lowest energy lost in excretion 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, comparatively. 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*.

Extraction of data from the literature, as done here for population comparisons, includes limitations. Data available on thermal sensitivity of digestion for *S. undulatus* stem from a paper published in 2001 (Angilletta), 22 years prior to the current study. As a result, it is possible that local acclimation or selection have shifted thermal performance of *Sceloporus* lizards across this time period. Comparisons among populations with data collected within a more comparable time frame would be ideal for drawing conclusions. However, it is important to note that many modeling procedures projecting the influence of temperature on performance extrapolate data from historical datasets (Walker et al., 2015, Piantoni et al., 2016), like the one used here. Thus, the inclusion and comparison among previously collected data in the current study further makes the point that critical variation in performance, behavior, and thermal responses, not only among space but time, may be not be adequately considered in projections. However, the incorporation of physiological mechanism does provide a critical component for model implications and clarity, which correlational models lack (Peterson et al., 2018; Briscoe et al., 2019). Therefore, use of mechanistic approaches which incorporate such physiological responses to temperature may be more informative (e.g. Buckley et al., 2015, Kearney et al., 2021). Additional limitations here in making population comparisons are the low sample sizes used by the initial dataset for NJ and SC lizards and potential error associated with replication methods.

In comparison to the populations studied here, digestive processes quantified in *S. merriami* differ where processes measured were least efficient at 34 °C, when compared to 31 °C and 36 °C (Beaupre et al., 1993b; Beaupre and Dunham 1995). *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, endurance, and metabolism in some *Sceloporus* plateau at warm temperatures (Crowley, 1987; Angilletta et al., 2002). 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 a higher metabolism and quicker sprint speed incur costs at increased rates. 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. An additional explanation for variation in thermal traits could be microbiota, which have been found to alter thermal tolerance, performance, and fitness (Fontaine et al., 2022). However, such data are unavailable for many species, including those studied here, making it difficult to draw conclusions on additional variables may influence thermal sensitivity.

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, 1983). Life history theory predicts that growth rate and body size have important consequences (Sears and Angilletta 2004). The AR lizards studied here maintain body temperatures ~33 °C in the field on average throughout spring and summer (Bangs 2016, Table 1), yielding a seasonal energy budget of 140.83 kJ. However, if temperatures warm, this value may increase based on the higher performance values associated with warming temperatures for *S. consobrinus*. Seasonal energy budgets are predicted to be. 507.76 kJ for SC and 264.10 kJ for NJ, comparatively higher than S. consobrinus likely due to being larger lizards who consume more food. However, *S. undulatus* lizards did not exhibit an increased thermal performance with warming temperatures above 33 °C. If this relationship of performance with temperature still exists in current populations, energy budgets may remain the same or decline with warming temperatures. However, it is important to consider individual variation which may exist with regards to thermal performance, energy acquisition, and energy allocation, which could influence overall energy budgets and fitness, and affect long term population responses to environmental change. The seasonal energy budgets calculated here attempted to follow the protocol described by Angilletta (2001b), however, we were 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* have been characterized by high growth rates, high reproductive output, relatively small body sizes, and quick maturation (Tinkle and Ballinger 1972) while the NJ population have been characterized by slow growth rates, larger body size, delayed maturation, and low reproductive output (Haenel and John-Alder 2002; Mosbey 2019). The AR population of S. *consobrinus* have been characterized by high growth rates, moderate reproductive output, moderate body size, and quick maturation (Mosbey 2019). New Jersey lizards are least likely to experience hot temperatures, and potentially incur lower costs seasonally, potentially explaining lower thermal sensitivity. Warmer temperatures and higher reproductive output of South Carolina lizards (Adolph and Porter, 1996; Angilletta 2001b) could contribute to increased thermal sensitivity as a mechanism to increase reproductive output in a warm environment. However, the current study did not examine evolutionary or genetic factors, which should be quantified to test proposed hypotheses associated with selection for thermal performance based on population-specific environmental temperatures.

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 and Tracy, 1983) who have relatively high growth rates despite short active seasons and lower energy budgets than NJ and SC lizards. Therefore, it appears *S. consobrinus* may allocate a greater proportion of energy to growth maturing 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 highly 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 effectively. Therefore, the current study contributes to our understanding of *Sceloporus* lizard physiology and performance, which could be considered in conjunction with life history.

The findings of the current study exemplify how temperature can play a prominent role in regulating performance of important physiological processes. Even more, such responses may vary among organisms. However, more studies are needed where data are collected among populations within a comparable time frame to determine current differences in thermal performance. 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, temporally or spatially, could result in inaccurate or inapplicable model predictions (Kearney, 2013). Considering 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. The findings here also indicate that thermal sensitivity of ectotherms is nonlinear, and therefore challenging to extrapolate. The overall TPC shape and temperature optimizing performance can be variable. *Sceloporus consobrinus* have increased digestive efficiency in digestive physiology at warm temperatures, which is not commonly identified. 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.

5. Conclusions

In conclusion, variation in performance due to temperature is an important consideration, and may play a role in determining population success in light of climate change. 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. 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.

Authorship statement

All authors conceptualized ideas, designed the methodology, provided resources, conducted formal analyses and visualization, worked on acquiring funding, project administration, and reviewed and edited the manuscript. Allison R. Litmer conducted the investigations, curated data, conducted software programming for analyses, and wrote the original draft of the manuscript. Steven J. Beaupre supervised the research.

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CRediT authorship contribution statement

Allison R. Litmer: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Steven J. Beaupre:** Writing – review &

editing, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

None.

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