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The influence of temperature and body size on food consumption in prairie lizards (Sceloporus consobrinus)

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The influence of temperature and body size on food consumption in prairie lizards (*Sceloporus consobrinus*)

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Abstract

Understanding the effect of temperature on physiological and digestive processes, such as voluntary consumption rate, is critical for assessing the impact of climate change. Food consumption is required for lizard survival and reproduction and its rate is dependent on temperature. For ectotherms, as temperatures increase, the amount of food consumed to meet the energy requirements related to survival and reproduction must also increase. Information on the amount of food voluntarily consumed may aid in determining if lizards can meet energy requirements. Such information could also aid in predicting survival of lizard populations, through construction of predictive climate change models. In this study, I investigated the effect of body temperature on voluntary consumption for the prairie lizard, *Sceloporus consobrinus*. I also determined the effects of body mass, body size (snout-vent length), and total length (TL) on consumption rates. In the laboratory, I conducted feeding trials over a range of temperatures (23.0°C, 28.0°C, 30.0°C, 33.0°C, and 36.0°C) and body sizes measuring the amount of food consumed by each individual lizard. I found that consumption per lizard was highly dependent on temperature, and that between body temperatures 23.0°C - 36.0°C, consumption increased with subsequent increases in temperature. No relationship was found between body mass, body size (SVL), or total length (TL) on consumption rate. I concluded that body temperature significantly influences voluntary consumption rates of *Sceloporus consobrinus*. Through effects on body temperature, climate change will influence critical physiological functions such as feeding rates. These effects have important implications for growth, reproduction, and survival of lizard populations in novel climates.

Introduction

Anthropogenic climate change has been proven to account for ecosystem changes at various scales (Rosenzweig et al. 2008). Evidence suggests that climate change affects species in many ways, such as distributional changes (Parmesan 2007), phenological shifts (Easterling et al. 2000), and altered rates of physiological processes (Bozinovic and Pörtner 2015). A key concern of climate change is the continuing increase of global temperatures (Jackson et al. 2017), with a 0.5℃ overall increase in global temperatures over the past century (Jones and Wigley 1990), as well as changes in daily temperature cycles (Easterling et al. 1997). Ectotherms are especially susceptible to climate change because their physiological functions are dependent on temperature (Deutsch et al. 2008). Ectotherms make up a significant portion of terrestrial and aquatic biodiversity (Wilson 1992; Atkinson and Sibly 1997). Therefore, increased knowledge of ectotherms' responses to climate change is helpful for assessing the overall impacts of climate change on ecosystems.

As climate change progresses, the importance of studying organisms' response to temperature change increases. The ability to thermoregulate behaviorally in response to temperature change is a crucial characteristic of many ectotherms. As temperatures increase, there are fewer opportunities in the environment for lizards to regulate body temperature behaviorally (Huey 1974). Reduced ability to thermoregulate, caused by decreasing availability of a thermally suitable habitat, can influence ectotherm body temperature and subsequent rates of temperature-dependent physiological processes (Avery et al. 1982; Sinervo and Adolph 1994). One specific group of ectotherms of concern are lizards, which have been predicted to decline due to climate change (Sinervo et al. 2010). Life history traits of lizards are dependent on their thermal ecology (Beaupre et al. 1993a,b; Angilletta 2001), potentially making them more susceptible to climate change. Warmer temperatures along with low precipitation can result in decreased reproductive output in lizards (Wang et al. 2016), which could ultimately lead to a decline in the population. To better understand how temperature affects fitness, reproduction, and physiological functions in lizards, it is important to consider the effects of body temperature on food consumption. To a certain extent, an increase in body temperature can increase voluntary feeding (Van Damme 1991; Brewster 2019) and metabolic rate (Beaupre et al. 1993a) of lizards. Changes in temperature and subsequently consumption rate have been found to affect digestion in lizards (Beaupre et al. 1993b). Temperature constraints on activity time and resource availability could dramatically affect the energy available for lizards to harvest food and the ability to process the food already harvested, which could limit an individual's daily energy assimilation (Congdon 1989). Thermal constraints on feeding rates and thus energy assimilation could limit the available energy for growth and reproduction of organisms. Consumption data from this research can be used to determine the metabolizable energy intake (MEI), which is the quantity of energy that can be allocated to maintenance, growth, and reproduction (Angilletta 2001). Metabolizable energy intake (MEI) can be used to estimate energy assimilation, an important source of life history variation in ectotherms (Angilletta 2001). Such interactions among temperature, consumption, digestion and energy assimilation may be important in biological systems where thermal constraints or other external factors may decrease food consumption while increasing energetic demands.

The survival of lizard populations is partially dependent on food availability and consumption. Changes in food availability can affect individual foraging success (Dunham 1978), as well as lizard persistence by altering body mass and the energy available for reproduction (Waldschmidt et al. 1985). Many lizards, such as those in the genus *Sceloporus*, are insectivores, having a diet consisting of invertebrates such as ants, beetles, moths, grasshoppers, crickets, etc. (Johnson 1966). Invertebrates typically respond to climate change more quickly than vertebrates (Johnson and Jones 2017) and the plants they consume (Berggren et al. 2009), which could result in a decline in lizard prey items. However, higher temperatures could cause insects to increase, as warm-adapted insects have high population growth rates (Frazier et al. 2006). As temperature increases, the energy required for growth, reproduction, and supporting metabolic processes increases in *Sceloporus* lizards (Angilletta 2001; Beaupre et al. 1993). An increase in available prey items may make it easier for lizards to meet energetic demands to perform such processes, however, potential declines in prey items may be problematic.

To be able to execute many biological and physiological functions necessary for survival, lizards must obtain energy from food consumption. Body size can influence the metabolic rate of *Sceloporus* lizards (Beaupre et al. 1993a), with lizards of larger body masses having higher metabolic rates than lizards of smaller size (Toledo et al. 2008). Increased temperature could increase lizard growth rate (Sinervo and Adolph 1989), while also resulting in higher metabolisms (Roe et al. 2005), causing a need for increased consumption to meet energy requirements. Previous studies have indicated that consumption is strongly influenced by body mass and temperature, finding consumption positively correlated with body mass in *Sceloporus undulatus* (Angilletta 2001). Lizards with larger body size should have larger gut capacities, resulting in the ability to consume more food in one meal. Data on the interaction of voluntary consumption, temperature, and body size are important when predicting how climate change will influence *Sceloporus* with regards to available energy for physiological processes, persistence, and reproduction. Additionally, quantifying lizard gut capacity through the relationship of body size and voluntary consumption is useful for predictive modeling tools. While we can hypothesize that the relationship found in previous studies of increasing consumption with increasing temperature and body size (Angilletta 2001) holds true in most *Sceloporus* species, there are no empirical data to support this hypothesis for less studied prairie lizards (*Sceloporus consobrinus*) in northwest Arkansas.

Study Objectives

The purpose of this study was to examine the interactions of temperature and body size on voluntary food consumption in *S. consobrinus*. I hypothesized that warmer temperatures would result in a significant increase in consumption rate in *S. consobrinus* when compared to cooler temperatures, because this trend is observed in related species. Additionally, the increase in metabolism with increasing temperature can result in a need for a larger food intake. I also hypothesized that increased body mass and body size (snout-vent length) would result in an increased consumption rate in *S. consobrinus* because of the positive relationship of body size and metabolism increasing energetic demands and larger body size results in larger gut size. There are often limitations in knowledge and the ability to perform research with species of concern. *Sceloporus consobrinus* provides a great opportunity to study organismal responses to climate changes because lizards in the genus *Sceloporus* have been widely studied by many herpetologists and thermal biologists. *Sceloporus consobrinus* are relatively abundant, not difficult to capture, and prove to tolerate the laboratory environment well. Therefore, *S. consobrinus* is a good model organism that can be used to broadly represent the responses of similar lizards to climate change predictions.

Methods and Materials

Study Organism

Prairie lizards (*S. consobrinus*) range throughout the central United States, located in Texas, New Mexico, South Dakota, Louisiana, Arkansas, Missouri, and Illinois (Leaché 2009). *Sceloporus consobrinus* are small (~26-70mm snout-vent length), diurnal lizards (Litmer 2020, unpublished data). Lizards were collected in Northwest Arkansas in spring 2021. Fifty adult lizards were captured with a lizard loop (a fishing pole with a loop on the end) or by hand. The lizards were held individually in 10-gallon tanks filled with a few inches of sand and provided a heat lamp while maintained in the lab. The lizards were fed crickets (*Acheta domestica*) three times a week, given water *ad libitum*, and the tanks were misted with water three times a week.

Temperature trials

The observed daytime body temperatures for *S. consobrinus* range between 22.9℃-36.0℃ in Arkansas, and the mean body temperature is 31.5℃ (Litmer 2020, unpublished data). To observe the influence of temperature on food consumption, lizards were randomly assigned to one of five constant temperature treatments: 23.0℃, 28.0℃, 30.0℃, 33.0℃, and 36.0℃, spanning the range of field-active body temperatures. In each temperature trial, nine lizards were used, with sex represented as equally as possible. An environmental chamber was used to manipulate temperature. In the environmental chamber, lizards were held in small, plastic containers (34.6 cm x 21 cm x 12.4 cm) and provided with a hide box and water bowl. Before beginning each trial, lizards were acclimated to their specific temperature treatment for 5 days and fasted for the last 3 days of acclimation to ensure the gut was empty prior to trials. Prior to the acclimation period, a clear ruler was used to measure (to the nearest mm) snout-vent length (SVL) and total length (TL) and a Pesola spring scale was used to measure mass to the nearest 0.1 g for each lizard.

During the trials, lizards were fed Fluker's crickets. To ensure that the crickets would pack tightly into the gut of the lizard, allowing gut capacity to be fully measured, the crickets' hind legs were removed. The crickets to be consumed by each lizard were weighed to the nearest 0.1 mg. Lizards were fed crickets *ad libitum* in each trial until feeding was refused. The last remaining cricket was left in the container with the lizard for two hours to ensure there was sufficient time for the lizard to consume it without an excess of time where digestion could begin, causing the gut to empty and resulting in consumption. Crickets not consumed were removed and the trial was considered complete. The total mass of crickets consumed was used to indicate voluntary feeding at each temperature treatment. Since lizards cannot consume more than their gut can hold, I assumed that the maximum mass of crickets they were able to consume at the temperature found to maximize voluntary feeding was an indication of maximum gut capacity.

We used a Shapiro-Wilk normality test to determine if the consumption results were normally distributed. The consumption data violated assumptions of normality, so nonparametric tests were used. A Kruskal-Wallis test and post-hoc Dunn's test were performed with R statistical software (R Core Team 2020) to test if and where significant differences were present in consumption among the temperature treatments. Generalized linear models were used comparing lizard initial snout-vent length (SVL) to consumption, initial body mass to consumption, and initial total length (TL) to consumption. A value of $p<0.05$ was used to determine significance. Using these methods and analyses, the effects of body temperature, body mass, body size (SVL), and total length (TL) on food consumption of *Sceloporus consobrinus* was determined.

Results

The average grams consumed at each temperature treatment were recorded and analyzed. Lizards consumed an average wet mass of 0.18 (±0.07 g) at 23.0℃, 0.32 (± 0.06 g) at 28.0℃, 0.46 (± 0.10 g) at 30.0℃, 0.49 (± 0.08 g) at 33.0℃, and 0.62 (± 0.12 g) at 36.0℃ (Table 1). We found a general trend that voluntary consumption increases as body temperature increases for *S. consobrinus* (Fig. 1). The Kruskal Wallis test (χ^2 =11.253, df=4, p=0.0239) indicated that there were differences in consumption among the temperature treatments. A pairwise post-hoc Dunn's test indicated there was a significant difference in consumption between 23.0℃ and 30.0℃ (p=0.0204), 23.0℃ and 33.0℃ (p=0.0070), 23.0℃ and 36.0℃ (p=0.0010), and 28.0℃ and

36.0°C ($p=0.0409$). No other temperature treatments had significant differences. The temperature found to maximize voluntary feeding rates was at 36.0°C, indicating that maximum gut capacity for *S. consobrinus* is closest to 0.62 (± 0.12 g) consumed, with regards to treatments within the current study. Linear regression analysis using R software indicated that body mass, body size (SVL), and total length (TL) had no significant effect on voluntary consumption ($p > 0.1$).

Discussion

The goal of this study was to assess the influence of temperature and body size on voluntary consumption in *S. consobrinus*. I found that an increase in body temperature does result in a significant increase in voluntary consumption, which is consistent with the hypothesis and previous reports for other species of lizards (Angilletta 2001; Brewster et al. 2020; Cox et al. 2008; Waldschmidt et al.1986; Van Damme et al. 1991). The results that there are no significant differences in consumption between 30.0°C and 33.0°C are contrary to previous research done on *Sceloporus*, which found that lizards ate significantly more at 33.0°C (Angilletta, 2001). One possible explanation for consumption not differing significantly in temperature treatments 30.0°C, 33.0°C, and 36.0° in this study is that *S. consobrinus* experience all three temperatures when active. Therefore, the ability to maximize feeding at all three temperatures could be advantageous. The typical average daytime body temperature ranges from 31.5°C – 36.0°C for *Sceloporus consobrinus* (Bangs 2016; preliminary field data Litmer 2020), which is when lizards are actively foraging. Under natural conditions, lizards are typically active over a large range of body temperatures (Porter and Tracy 1983), and the various temperature ranges experienced by the different lizards may affect feeding at the temperatures used in the studies. Previous research found that the increase in food intake with higher temperatures corresponds with an increase in feeding attempts, decreased gut-throughput time, and increased ability to capture and handle prey (Van Damme et al. 1991). It is possible that lower consumption rates observed at 23.0°C and 28.0°C are due to limitations on locomotor performance. However, it is more likely due to these being the temperatures typically experienced at night, when lizards are not actively foraging for food. Other research suggests that higher temperatures result in shorter passage times, which correlates with an increase in voluntary consumption over longer time frames (Angilletta 2001). As we have demonstrated in this study, low body temperatures restrict the amount of food eaten. Lizards in food-rich environments must also reach favorable body temperatures to take advantage of the high food availability. The trend of observed voluntary consumption increasing with increasing temperature for *Sceloporus* may be important when considering changes in thermal restrictions or other external factors. Consumption data from this research can be used to determine if the amount of energy ingested can account for the increase in metabolic rates at higher temperatures, and the amount of energy that can be allocated to activity, growth, and reproduction. The increase in feeding rates observed at warmer temperatures suggests that as lizard body temperatures increase with climate change, they may need to consume a greater amount of food for survival.

Contrary to previous work with other *Sceloporus* lizards (Parker and Pianka 1973; Angilletta 2001), my results indicate that SVL, TL, and mass do not correlate with consumption rate. The differences in results may be due to the research performed in previous studies being on a different species of *Sceloporus*. The difference in results also may have been due to the limited range of body sizes available in the current study. It is possible that if lizards of smaller size were included in the current study, that results may have been different. A greater representation of different body sizes in the treatments may have given different results for *S. consobrinus* and may be necessary for a more accurate understanding of the effect of body size on voluntary consumption. Because no statistical interaction was found between SVL, body mass, or total length on voluntary consumption, it can be assumed that temperature is the driving component that determines the feeding rates of *S. consobrinus*.

Results were analyzed maintaining the assumption that the temperature found to maximize voluntary feeding is an indication of maximum gut capacity. Similar to previous research, we found that consumption rate is highest at 36.0°C and thus, is the closest estimate of maximum gut capacity for *S. consobrinus* within the current study. These results may be due to the average mass and SVL of the lizards at this temperature treatment being slightly larger than at any of the other treatments, although the results of this study did not find a correlation of body size and consumption. However, it is possible that *S. consobrinus* may consume greater amounts at even warmer temperatures than those considered. Research performed by Harwood 1979 found that for lizards *S. occidentalis, C. tigris,* and *G. multicarinatus*, consumption increased with increasing temperature until body temperatures reached the upper lethal limit.

Conclusions

The results of this study indicate that voluntary consumption is influenced by temperature in *S. consobrinus*. Due to the increase in voluntary feeding observed among temperature treatments, I suggest that additional research be done at higher temperatures to determine the temperature that results in a decrease in voluntary feeding. This study has provided data that had not yet been obtained for *S. consobrinus* and will be important in the understanding of how temperature effects feeding for this species as well as other *Sceloporus* species. Results from this study have important implications in *Sceloporus consobrinus* conservation. Knowledge on how this species responds to different temperatures will help construct a mechanistic individual-based model (IBM) which will provide further knowledge on how the feeding activity of *Sceloporus consobrinus* is affected by temperature (Beaupre 2002; Deangelis et al. 1991). The results suggest that as climate change continues and lizard body temperatures rise, there is a need for greater food availability to compensate for the increase in consumption rates. If prey availability decreases for *S. consobrinus* while temperatures increase, it could result in the inability to consume enough food to meet daily energetic demands. The inability to consume enough food to meet daily energetic demands coupled with warmer temperatures could potentially result in a decline in survival and abundance for *S. consobrinus* over time. Higher temperatures result in a faster growth rate (Sinervo and Adolph 1989), which increases energy requirements necessary for survival, and the increase in consumption rate could help lizards meet these energy requirements. This study provides the critical data necessary to determine the changes in energy required to perform biological and physiological functions necessary for survival that result from an increase in food consumption at warmer temperatures.

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Appendix

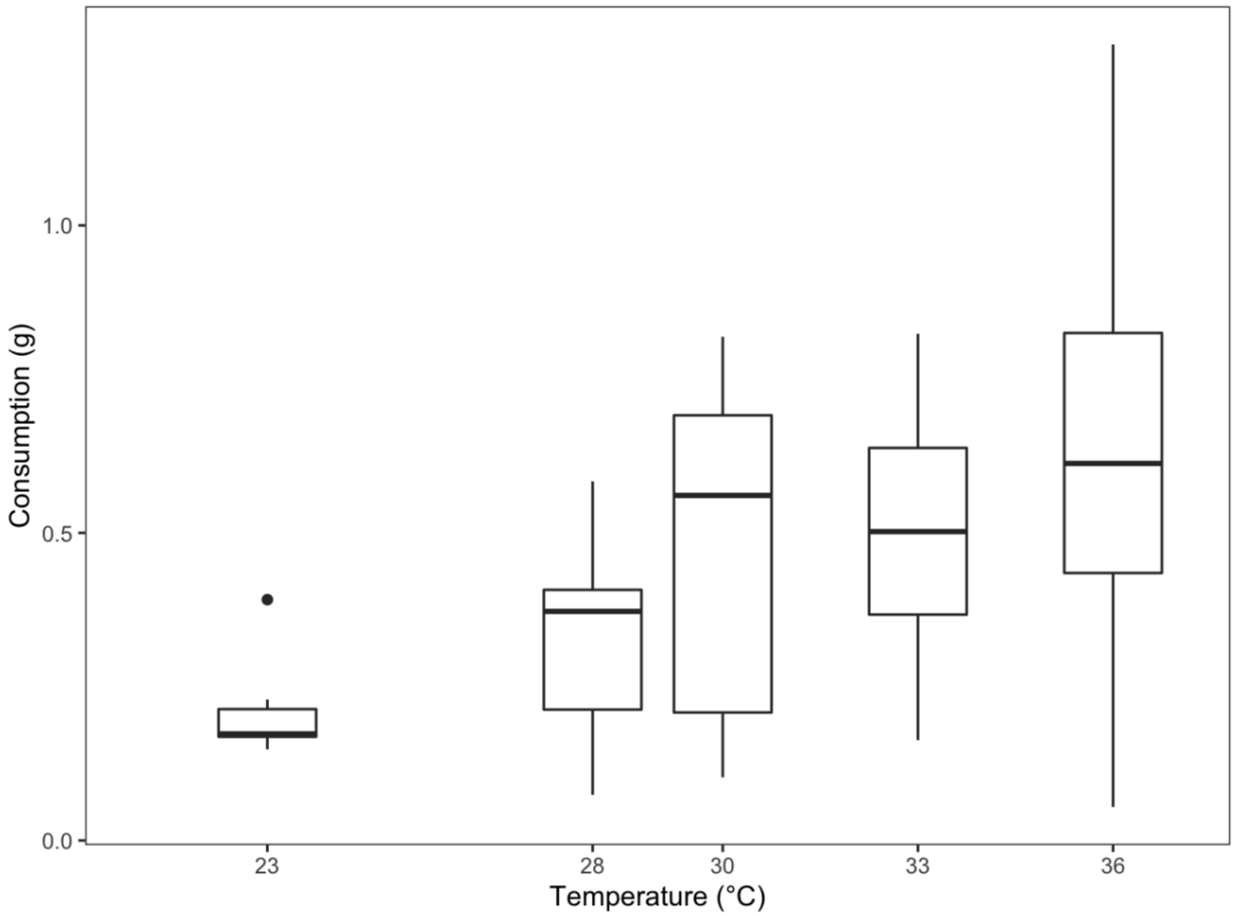

Figure 1: Average grams consumed as a function of body temperature for temperatures 23.0℃, 28.0℃, 30.0℃, 33.0℃, and 36.0℃. Average grams consumed increased linearly with temperature for *Sceloporus consobrinus* lizards, when fed *ad libitum*.

Table 1: Total number of lizards, average masses, average snout-vent lengths (SVL), average total lengths (TL), average consumption, and standard deviations at five constant temperature treatments.

Treatment (℃)	n	Mass (g)	SVL (mm)	TL (mm)	Consumption (g)
23℃	9	6.5 ± 0.7	59.1 ± 2.5	130.7 ± 6.5	0.18 ± 0.07
28℃	9	6.4 ± 1.0	57.3 ± 2.8	121.7 ± 8.9	0.32 ± 0.06
30℃	9	6.0 ± 1.0	60.0 ± 2.3	143.6 ± 5.0	0.46 ± 0.10
33℃	9	6.2 ± 0.9	57.8 ± 2.8	115.7 ± 6.5	0.49 ± 0.08
36℃	9	8.7 ± 0.9	63.1 ± 2.2	144.0 ± 6.5	0.62 ± 0.12